

Chapter 9

Biogeography, Ecology, and Vulnerability of Chemosynthetic Ecosystems in the Deep Sea

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9.1 Life Based on Energy of the Deep

9.1.1 A spectacular discovery

This chapter is based upon research and findings relating to the Census of Marine Life ChEss project, which addresses the biogeography of deep-water chemosynthetically driven ecosystems (www.noc.soton.ac.uk/chess). This project has been motivated largely by scientific questions concerning

phylogeographic relationships among different chemosynthetic habitats, evidence of conduits and barriers to gene flow among those habitats, and environmental factors that control diversity and distribution of chemosynthetically driven fauna. Investigations of chemosynthetic environments in the deep sea span just three decades, owing to their relatively recent discovery. Despite the excitement of many discoveries in the deep ocean since the early nineteenth century, nothing could have prepared the scientific community for the discovery made in the late 1970s, which would challenge some fundamental principles of our understanding of life on Earth. Deep hot water venting was observed for the first time in 1977 on the Galápagos Rift, in the eastern Pacific. To the astonishment of the deep-sea explorers of the time, a prolific community of bizarre

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animals were seen to be living in close proximity to these vents (Corliss *et al.* 1979). Giant tubeworms and huge white clams were among the inhabitants, forming oases of life in the otherwise apparently uninhabited deep seafloor (Figs. 9.1A, B, and C). Most of the creatures first observed on vents were totally new to science, and it was a complete mystery as to what these animals were using for an energy source in the absence of sunlight and in the presence of toxic levels of hydrogen sulfide and heavy metals.

9.1.2 Chemosynthetic ecosystems: where energy from the deep seabed is the source of life

Until the discovery of hydrothermal vents, benthic deep-sea ecosystems were assumed to be entirely heterotrophic, completely dependent on the input of sedimented organic matter produced in the euphotic surface layers from photosynthesis (Gage 2003) and, in the absence of sunlight, completely devoid of any *in situ* primary productivity. The deep sea is, in general, a food-poor environment with low secondary productivity and biomass. In 1890, Sergei Nikolaevich Vinogradskii proposed a novel life process called chemosynthesis, which showed that some microbes have the ability to live solely on inorganic chemicals. Almost 90 years later the discovery of hydrothermal vents provided stunning new insight into the extent to which microbial primary productivity by chemosynthesis can maintain biomass-rich metazoan communities with complex trophic structure in an otherwise food-poor deep sea (Jannasch & Mottl 1985). Hydrothermal vents are found on mid-ocean ridges and in back arc basins where deep-water volcanic chains form new ocean floor (reviewed by Van Dover 2000; Tunnicliffe *et al.* 2003). The super-heated fluid (up to 407°C) emanating from vents is charged with metals and sulfur. Microbes in these habitats obtain energy from the oxidation of hydrogen, hydrogen sulfide, or methane from the vent fluid. The microbes can be found either suspended in the water column or forming mats on different substrata, populating seafloor sediments and ocean crust, or living in symbiosis with several major animal taxa (Dubilier *et al.* 2008; Petersen & Dubilier 2009). By microbial mediation, the rich source of chemical energy supplied from the deep ocean interior through vents allows the development of densely populated

ecosystems, where abundances and biomass of fauna are much greater than on the surrounding deep-sea floor.

Eight years after the discovery of hydrothermal vent communities, the first cold seep communities were described in the Gulf of Mexico (Paull *et al.* 1984). Cold seeps occur in both passive and active (subduction) margins. Seep habitats are characterized by upward flux of cold fluids enriched in methane and often also other hydrocarbons, as well as a high concentration of sulfide in the sediments (Sibuet & Olu 1998; Levin 2005). The first observations of seep communities showed a fauna and trophic ecology similar to that of hydrothermal vents at higher taxonomical levels (Figs. 9.1D and E), but with dissimilarities in terms of species and community structure.

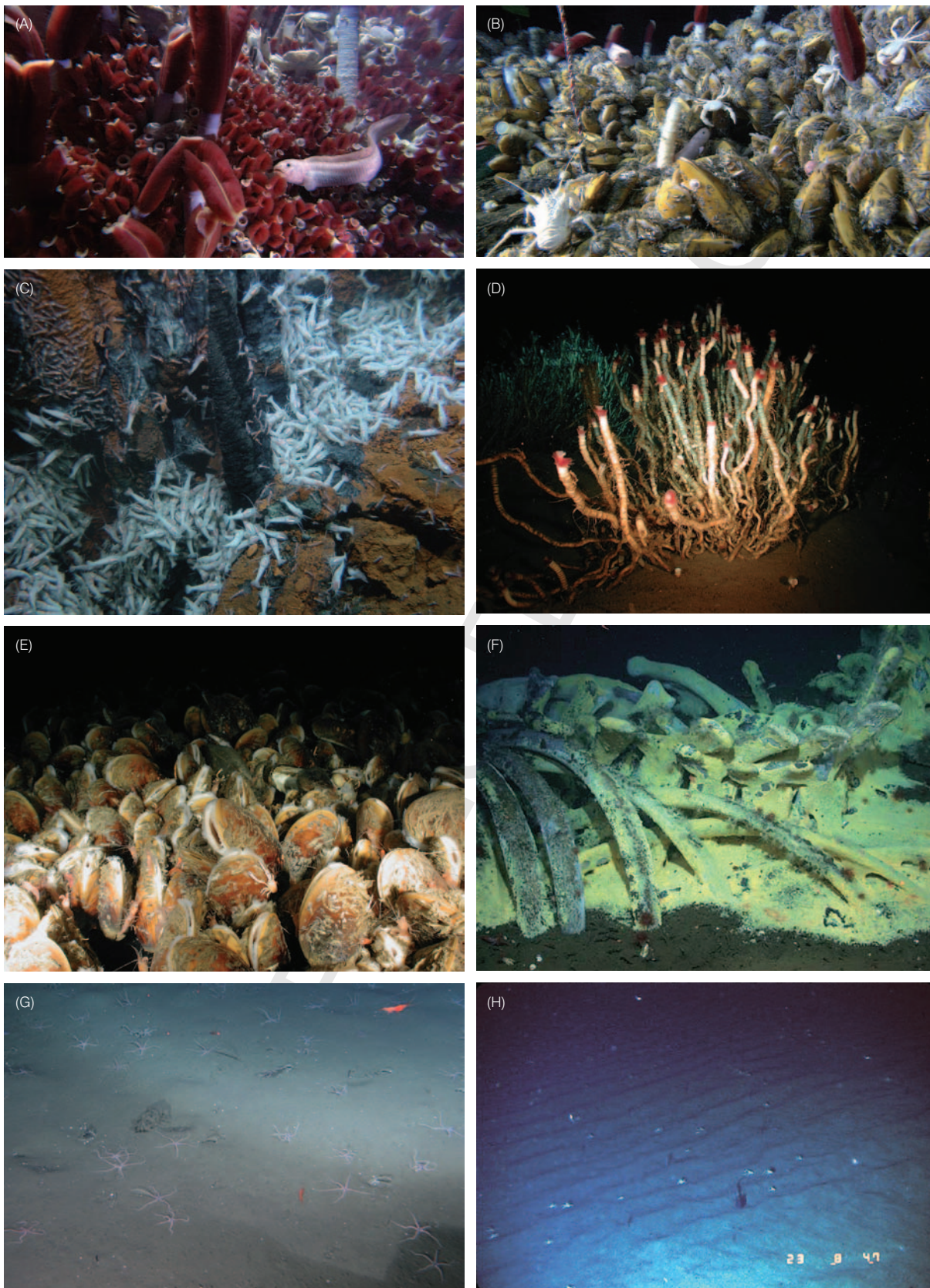
The energetic input to chemosynthetic ecosystems in the deep sea can also derive from photosynthesis as in the case of large organic falls to the seafloor, including kelp, wood, large fish, or whales. After a serendipitous discovery of a whale fall in 1989, the first links between vents, seeps, and the reducing ecosystems at large organic falls were made (Smith & Baco 2003). Bones of whales consist of up to 60% lipids that, when degraded by microbes, produce reduced chemical compounds similar to those emanating from vents and seeps (Fig. 9.1F) (Treude *et al.* 2009). Another deep-water reducing environment is created where oxygen minimum zones (OMZs, with oxygen concentrations below 0.5 ml l⁻¹ or 22 μM) intercept continental margins, occurring mainly beneath regions of intensive upwelling (Helly & Levin 2004) (Figs. 9.1G and H). Only in the second half of the twentieth century was it understood that OMZs support extensive autotrophic bacterial mats (Gallardo 1963, 1977; Sanders 1969; Fossing *et al.* 1995; Gallardo & Espinoza 2007) and, in some instances, fauna with a trophic ecology similar to that of vents and seeps (reviewed in Levin 2003).

9.1.3 Adaptations to an “extreme” environment

Steep gradients of temperature and chemistry combined with a high disturbance regime, caused by waxing and waning of fluid flow and other processes during the life cycle of a hydrothermal vent, result in low diversity communities with only a few mega- and macrofauna species dominating any given habitat (Van Dover & Trask 2001; Turnipseed

Fig. 9.1

Hydrothermal vent (A, B, and C), cold seep (D and E), whale fall (F), and OMZ communities (G and H). (A) Zoarcid fish over a *Riftia pachyptila* tubeworm community in EPR vents; (B) *Bathymodiolus* mussel community in EPR vents (© Stephen Low Productions, Woods Hole Oceanographic Institution, E. Kristof, the National Geographic Society, and R. A. Lutz, Rutgers University). (C) Dense aggregations of the MAR vent shrimp *Rimicaris exoculata* (© Missao Sehama, 2002 (funded by FCT, PDCTM 1999/MAR/15281), photographs made by VICTOR6000/IFREMER). (D) *Lamellibrachia* tubeworms from the Gulf of Mexico cold seeps (© Charles Fisher, Penn State University). (E) *Bathymodiolus* mussel bed by a brine pool in the Gulf of Mexico cold seeps (© Stéphane Hourdez, Penn State University/Station Biologique de Roscoff). (F) Skeleton of a whale fall covered by bacteria (© Craig Smith, University of Hawaii). (G) Ophiuroids on an OMZ in the Indian margin (© Hiroshi Kitazato, JAMSTEC, and NIOO). (H) Galatheid crabs on an OMZ on the upper slopes of Volcano 7, off Acapulco, Mexico (© Lisa Levin, Scripps Institution of Oceanography).



et al. 2003; Dreyer *et al.* 2005). The proportion of extremely rare species (fewer than five individuals in pooled samples containing tens of thousands of individuals from the same vent habitat) is typically high, in the order of 50% of the entire species list for a given quantitative sampling effort (C.L. Van Dover, unpublished observation).

Deep-water chemosynthetic habitats have also been shown to have a high degree of species endemism in each habitat: 70% in vents (Tunnicliffe *et al.* 1998; Desbruyères *et al.* 2006a), about 40% in seeps both for mega epifauna (Bergquist *et al.* 2005; Cordes *et al.* 2006) and macro infauna (Levin *et al.* 2009a). In OMZs, the percentage of endemism is relatively low (Levin *et al.* 2009a), but has yet to be quantified. Some of the most conspicuous of the endemic species of reduced environments have developed unusual physiological adaptations for the extreme environments in which they live. These include symbiotic relationships with bacteria, organ and body modifications, and reproductive and novel adaptations for tolerating thermal and chemical fluctuations of great magnitude. Because chemosynthetic habitats are naturally fragmented and ephemeral habitats, successful species must also be specially adapted for dispersal to and colonization of isolated “chemosynthetic islands” in the deep sea (Bergquist *et al.* 2003; Neubert *et al.* 2006; Vrijenhoek 2009a).

9.1.4 Chemosynthetic islands: a biogeographic puzzle with missing pieces

Since their discovery just over 30 years ago, more than 700 species from vents (Desbruyères *et al.* 2006a) and 600 species from seeps have now been described and are listed on *ChEssBase* (Ramirez-Llodra *et al.* 2004; www.noc.soton.ac.uk/chess/database/db_home.php). This rate of discovery is equivalent to one new species described every two weeks, sustained over approximately one-quarter of the past century (Lutz 2000; Van Dover *et al.* 2002). Furthermore, geomicrobiologists have explored microbial diversity of chemosynthetic ecosystems, revealing a plethora of interesting and novel metabolisms, but also signature compositions for the different types of reduced habitat, and symbiotic organism (Jørgensen & Boetius 2007; Dubilier *et al.* 2008).

Although several hundred hydrothermal vent and cold seep sites have now been located worldwide (see ChEss web-pages), only approximately 100 have been studied so far with respect to their faunal and microbial composition, and even for their ecosystem function. Nevertheless, through such investigations, scientists soon noticed the differences and in some cases similarities among the animal communities from different vent and seep sites. For example, why is the giant tubeworm *Riftia pachyptila* only found at Pacific vents whereas shrimp species in the genus *Rimicaris* are only found at Atlantic and Indian Ocean vents? Why is the mussel

genus *Bathymodiolus* generally widespread at vents and seeps but largely absent from seeps and vents in the north-eastern Pacific Ocean? In 2002, at the onset of the ChEss project, biological investigations of known vent sites provided enough data to describe six biogeographic provinces for vent species (Van Dover *et al.* 2002) and identified several gaps that needed to be closed to complete the “biogeographical puzzle of seafloor life” (Shank 2004) (Fig. 9.2). In contrast, cold seep and whale fall communities appear to share many of the key taxa across all oceans. The ChEss project developed a major exploratory program to address and explain global patterns of biogeography in deep-water chemosynthetic ecosystems and the factors shaping them.

9.2 Finding New Pieces of the Puzzle (2002–2010)

9.2.1 Technological developments for exploration

One of the most significant advances in deep-sea investigations of chemosynthetic ecosystems, developed and implemented as a new international state of the art technique within the lifetime of the ChEss project, has been the use of deep-sea autonomous underwater vehicles (AUVs) to trace seafloor hydrothermal systems to their source or to map cold seep systems in the necessary resolution to quantify the distribution of chemosynthetic habitats. This approach (Baker *et al.* 1995; Baker & German 2004; Yoerger *et al.* 2007) was sufficient for geological investigations of global-scale heat-flux and chemical discharge to the oceans. However, the ChEss hypotheses concerning global-scale biogeography required more precise location of hydrothermal venting and hydrocarbon seepage on the seafloor; ideally with preliminary characterization of not only the vent and seep site itself but also a first-order characterization of the dominant species present.

So far, the method has been applied on seven separate hydrothermal vent cruises, from 2002 to 2009, throughout the Southern hemisphere, the least explored part of the global deep ocean. These expeditions have located 16 different new sites on the Galápagos Rift (Shank *et al.* 2003), in the Lau Basin (southwest Pacific; German *et al.* 2008a), the Mid-Atlantic Ridge (MAR) (South Atlantic; German *et al.* 2008b; Melchert *et al.* 2008; Haase *et al.* 2009), the southwest Indian Ridge (Southern Indian Ocean; C. Tao, personal communication), the East Pacific Rise (southeast Pacific; C. Tao, personal communication), and the Chile margin (C. German, unpublished observation). For cold seep mapping, a major success was the combined AUV and remotely operated vehicle (ROV) deployment in the Nile Deep Sea Fan, leading to the description of several new types of hydrocarbon seep in depths between 1,000 and 3,500 m

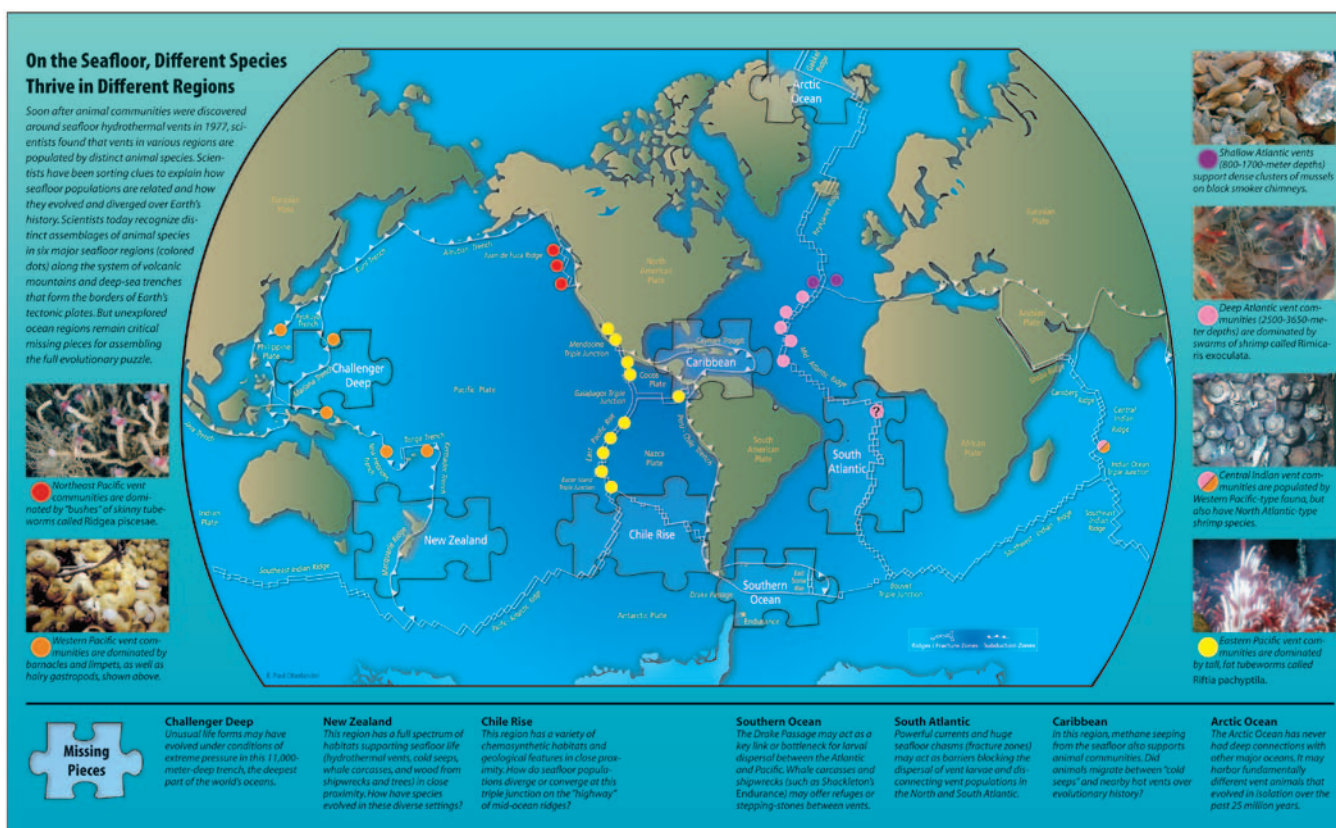


Fig. 9.2

Global map showing the mid-ocean ridge system, the recognized hydrothermal vent biogeographic provinces (colored dots) and the unexplored regions that are critical missing pieces of the full evolutionary puzzle. From Shank 2004.

(Foucher *et al.* 2009; technical details described in Dupré *et al.* (2009)).

The way the AUV technique works for the exploration of vents is described in detail by German *et al.* (2008a). Perhaps most surprising to us, and of widest long-term significance, is that, when flying close to the seafloor, the techniques have not only been sufficiently sensitive to locate high-temperature "black-smoker" venting, but also sites of much more subtle lower-temperature diffuse flow (Shank *et al.* 2003). Building on these successes, future investigations will be reliant upon the new generation of exploratory vehicles such as a new hybrid AUV–ROV vehicle (Bowen *et al.* 2009), which has already been applied in ChEss studies (see below) as a technological precursor to future under-ice investigations (Jakuba *et al.* 2008; German *et al.* 2009).

9.2.2 Finding new species

In the past decade, we have seen a significant increase in molecular tools for studies to understand species evolution, metapopulations, and gene flow in chemosynthetic regions (Shank & Halanych 2007; Johnson *et al.* 2008; Plouviez

et al. 2009; Vrijenhoek 2009b). New high-resolution and high-throughput methods will result in the first insight into the structure and biogeography of microbial communities of chemosynthetic ecosystems in the Census International Census of Marine Microbes (ICoMM) project (see Chapter 12). However, a major concern today for marine biodiversity analysis is the paucity of taxonomists using morphological methods, and in particular taxonomists specializing in deep-sea species. Both morphological and molecular taxonomy are essential to develop fundamental knowledge and sustainable management of our marine resources. In an effort to raise the profile of taxonomy once more, ChEss set up an annual program of Training Awards for New Investigators (TAWNI). These awards have been made to a total of 10 scientists from around the globe to develop further their taxonomic skills relating to chemosynthetic organisms (www.noc.soton.ac.uk/chess/science/sci_tawni.php). As a result, they have collectively achieved impressive outputs where many meio-, macro-, and megafauna species have been described and new records identified from different sites (Table 9.1). These descriptions have been added to the approximately 200 species that have been described and published from vents, seeps, and whale falls

Table 9.1

Species new to science described or identified by TAWNI awardees during the ChEss project.

Group	Family	Species	Location	References	TAWNI
Anomura	Kiwaidae	<i>Kiwa</i> sp. nov.	Costa Rica seeps	Thurber <i>et al.</i> in preparation	Andrew Thurber
Polychaete	Spionidae	Gen. & sp. nov.	New Zealand seeps	Thurber <i>et al.</i> in preparation	Andrew Thurber
Polychaete	Ampharetidae	Gen. & sp. nov.	New Zealand seeps	Thurber <i>et al.</i> in preparation	Andrew Thurber
Polychaete	Ampharetidae	Gen. & sp. nov.	New Zealand seeps	Thurber <i>et al.</i> in preparation	Andrew Thurber
Harpacticoid copepod	Tegastidae	<i>Smacigastes barti</i>	9° 50' N EPR vents	Gollner <i>et al.</i> 2008	Sabine Gollner
Nematoda	Monhysteridae	<i>Thalassomonhystera fisheri</i> n. sp.	9° 50' N EPR vents	Zekely <i>et al.</i> 2006	Julia Zekely
Nematoda	Monhysteridae	<i>Halomonhystera hickeyi</i> n. sp.	9° 50' N EPR vents	Zekely <i>et al.</i> 2006	Julia Zekely
Nematoda	Monhysteridae	<i>Thalassomonhystera vandoverae</i> n. sp.	Mid-Atlantic Ridge vents	Zekely <i>et al.</i> 2006	Julia Zekely
Nematoda		<i>Anticoma</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Chromadorita</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Daptonema</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Daptonema</i> sp. 2	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Euchromadora</i> sp.	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Eurystomina</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Halomonhystera hickeyi</i>	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Halomonhystera</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Leptolaimus</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Metoncholaimus</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Microlaimus</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Molgolaimus</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Paracantonchus</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Paralinhomoeus</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Rhabdocoma</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Nematoda		<i>Prooncholaimus</i> sp. 1	9° 50' N EPR vents		Julia Zekely
Actiniaria		<i>Amphianthus</i> sp. nov.	Lau Basin vents		Kevin Zelnio
Actiniaria		<i>Anthosactis</i> sp. nov.	Lau Basin vents		Kevin Zelnio
Actiniaria		<i>Bathydactylus</i> sp. nov.	Lau Basin vents		Kevin Zelnio
Actiniaria		<i>Chondrophellia</i> sp. nov.	Lau Basin vents		Kevin Zelnio

Group	Family	Species	Location	References	TAWNI
Actiniaria		<i>Sagartiogeton</i> sp. nov.	Lau Basin vents		Kevin Zelnio
Actiniaria		Gen. et sp. nov.?	Lau Basin vents		Kevin Zelnio
Zoanthid		Sp. nov.?	Lau Basin vents		Kevin Zelnio
Frenulate polychaete	Siboglinidae	<i>Bobmarleya gadensis</i> gen. et sp. nov.	Gulf of Cadiz mud volcanoes	Hilário & Cunha 2008	Ana Hilário
Frenulate polychaete	Siboglinidae	<i>Spirobrachia tripeira</i> sp. nov.	Gulf of Cadiz mud volcanoes	Hilário & Cunha 2008	Ana Hilário
Frenulate polychaete	Siboglinidae	<i>Lamellisabella denticulata</i> (new record in Gulf of Cadiz)	Gulf of Cadiz mud volcanoes	Hilário & Cunha 2008	Ana Hilário
Frenulate polychaete	Siboglinidae	<i>Lamellisabella</i> sp. nov.	Gulf of Cadiz mud volcanoes	Hilário <i>et al.</i> in prep	Ana Hilário
Frenulate polychaete	Siboglinidae	<i>Polybrachia</i> sp. nov.	Gulf of Cadiz mud volcanoes	Hilário <i>et al.</i> in prep	Ana Hilário
Frenulate polychaete	Siboglinidae	<i>Polybrachia</i> sp. nov.	Gulf of Cadiz mud volcanoes	Hilário <i>et al.</i> in prep	Ana Hilário
Frenulate polychaete	Siboglinidae	<i>Siboglinum poseidoni</i> (new record in Gulf of Cadiz)	Gulf of Cadiz mud volcanoes	Hilário <i>et al.</i> submitted	Ana Hilário



Fig. 9.3

The yeti crab, *Kiwa hirsuta*, from the Easter Island microplate hydrothermal vents. © Ifremer/A. Fifis.

since the onset of the ChEss project in 2002. One of the most extraordinary animals that has consequently received much media attention was discovered on southeast Pacific vents in 2005: the yeti crab *Kiwa hirsuta* (Fig. 9.3). This is not only a species new to science, but also represents a new genus and new family (Macpherson *et al.* 2005). Recently, a close relative of the vent yeti crab was discovered from Costa Rican cold seeps and is being described

with the aid of a TAWNI grant (A. Thurber, personal communication).

9.2.3 Global biogeography patterns in deep-water chemosynthetic ecosystems

Addressing global biogeographic patterns for species from all deep-water chemosynthetic ecosystems and the phylogenetic links among habitats needed a coordinated international effort, with shared human and infrastructure resources, that no single nation could attempt alone. In 2002, ChEss outlined a field program for the strategic exploration and investigation of chemosynthetic ecosystems in key areas that would provide essential information to close some of the main gaps in our knowledge (Tyler *et al.* 2003). The ChEss field program was motivated by three scientific questions. (1) What are the taxonomic relationships among different chemosynthetic habitats? (2) What are the conduits and barriers to gene flow among those habitats? (3) What are the environmental factors that control diversity and distribution of chemosynthetically driven fauna? To address these questions at the global scale, four key geographic areas were selected for exploration and investigation: the Atlantic Equatorial Belt (AEB), the New Zealand Region (RENEWZ), the Polar Regions (Arctic and

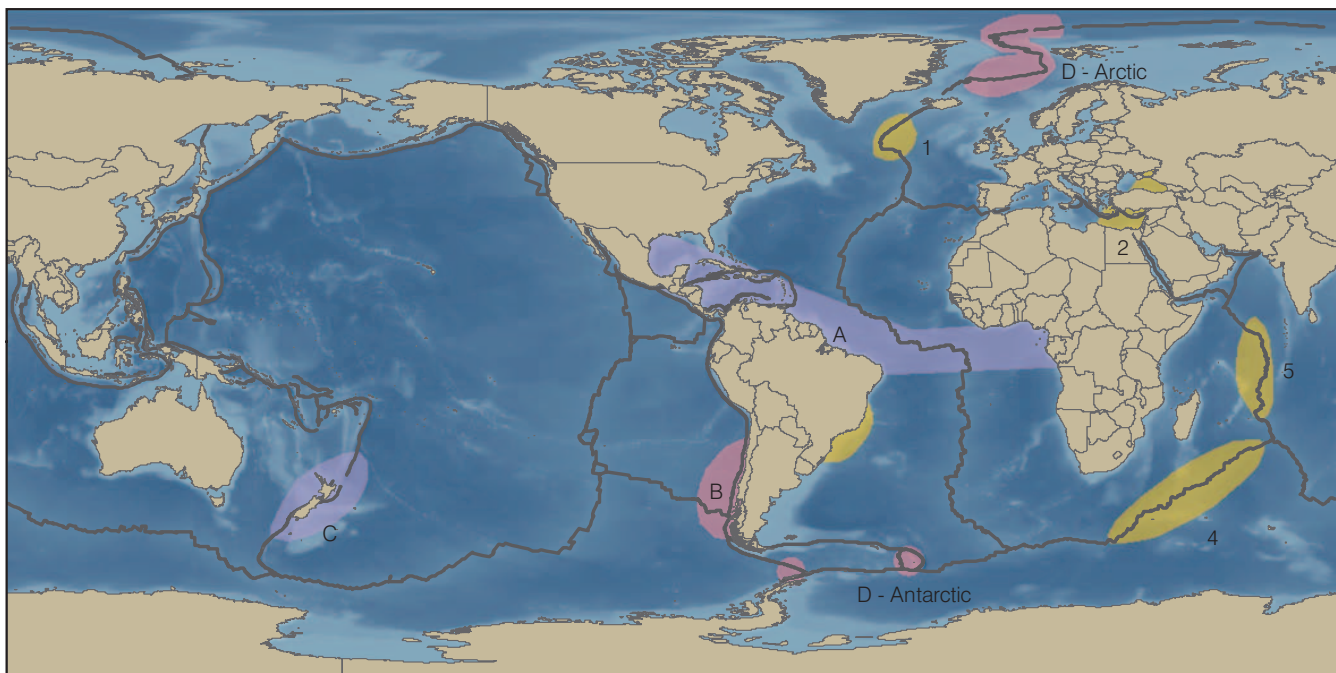


Fig. 9.4

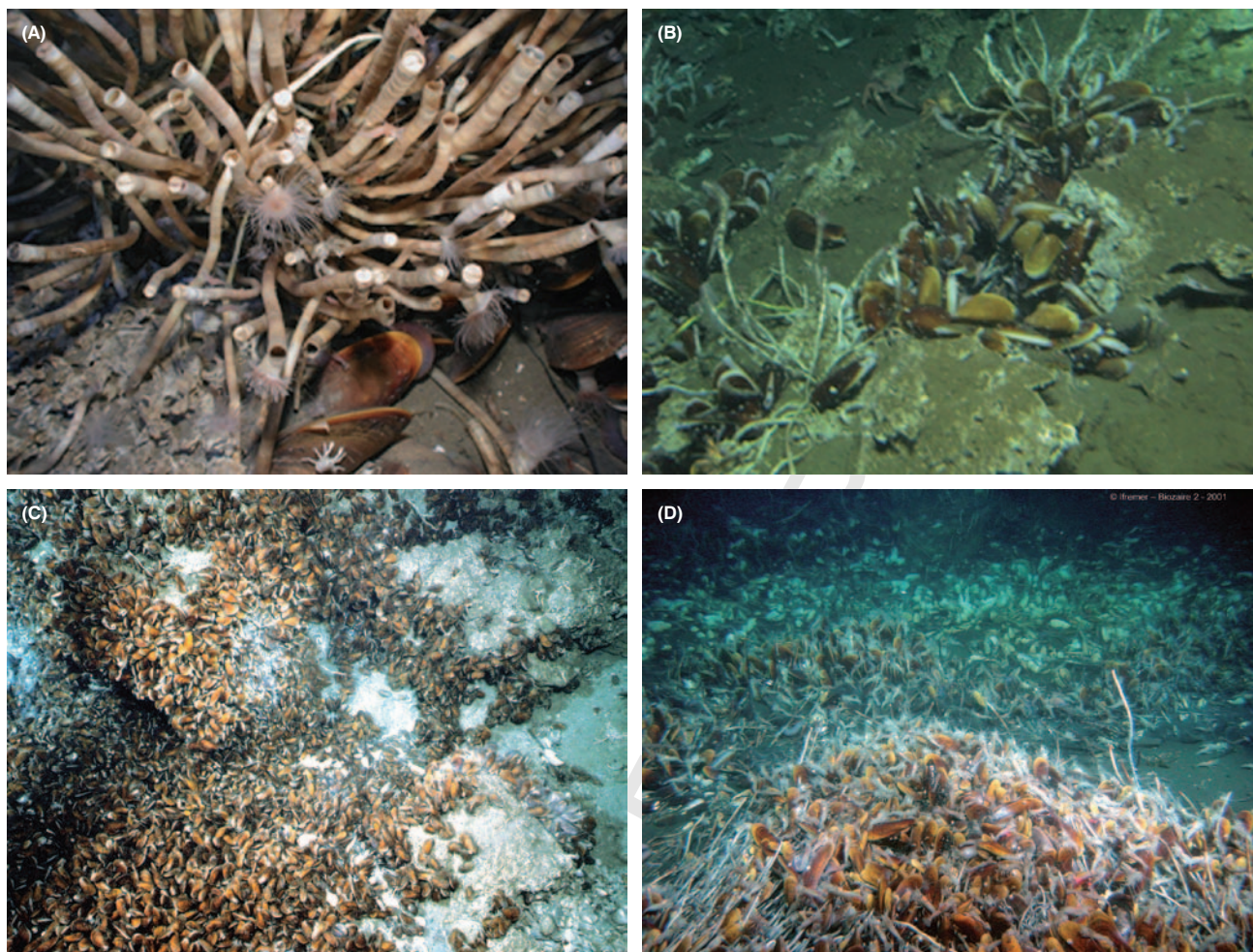
ChEss field program study sites. Light blue and pink areas are key priority regions: **(A)** Equatorial Atlantic Belt region; **(B)** Southeast Pacific region; **(C)** New Zealand region; **(D)** Polar regions. Yellow areas are important for ChEss-related activities: 1, northern MAR between the Iceland and Azores hot-spots; 2, Eastern Mediterranean; 3, Brazilian continental margin; 4, southwest Indian Ridge; 5, Central Indian Ridge.

Antarctic), and the southeast Pacific off Chile region (INSPIRE) (Fig. 9.4). Below, we describe the issues addressed and main findings in each area.

9.2.3.1 The Atlantic Equatorial Belt: barriers and conduits for gene flow

The AEB is a large region expanding from Costa Rica to the West Coast of Africa that encloses numerous seep (for example Costa Rica, Gulf of Mexico, Blake Ridge, Gulf of Guinea) and vent (e.g., northern MAR (NMAR), southern MAR (SMAR), Cayman Rise) habitats. This region is particularly significant for investigating connectivity among populations and species' maintenance across large geographic areas. Potential gene flow across the Atlantic (west to east) is subject to the effects of deep-water currents (Northeast Atlantic deep water), equatorial jets, and topographic barriers such as the MAR. When considering a north–south direction, gene flow along the MAR may be affected by mid-ocean ridge offsets such as the Romanche and Chain fracture zones. These fracture zones are significant topographic features 60 million years old, 4 km high and 935 km ridge offset, which cross the equatorial MAR prominently, affecting both the linearity of the ridge system and large-scale ocean circulation in this region. North Atlantic Deep Water flows south along the East coasts of

North and South America as far as the Equator before being deflected east, crossing the MAR through conduits created by these major fracture zones (Speer *et al.* 2003). Circulation within these fracture zones is turbulent and may provide an important dispersal pathway for species from west to east across the Atlantic (Van Dover *et al.* 2002), for example between the Gulf of Mexico and the Gulf of Guinea. The cold seeps in the Pacific Costa Rican margin were included in this study to address questions of isolation between the Pacific and the Atlantic faunas after the closure of the Isthmus of Panama 5 million years ago. The fauna from methane seeps on the Costa Rica margin, just now being explored, are yielding surprising affinities, which suggests that this site operates as a crossroads. Some animals appear related to the seep faunas in the Gulf of Mexico and off West Africa, whereas others show phylogenetic affinities with nearby vents at 9°N on the East Pacific Rise and with more distant vents at Juan de Fuca Ridge and the Galápagos (L. Levin, unpublished observations). Furthermore, recent investigations have shown (C. German, C.L. Van Dover & J. Copley, unpublished observation) there is active venting in the ultra-slow Cayman spreading ridge in the Caribbean at depths of 5,000 m (CAYTROUGH 1979), and investigations are underway to determine, how the animals colonizing these vents are related to vent and seep faunas on either side of the Isthmus of Panama. The first

**Fig. 9.5**

Cold seep communities from different Atlantic Equatorial Belt areas. **(A)** Gulf of Mexico; **(B)** Costa Rica; **(C)** Barbados Prism; **(D)** Congo margin. © Erik Cordes, Temple University (photographs A and B); © Ifremer (photographs C and D courtesy of Karine Olu).

plumes were located in November 2009 at depths below 4,500 m, suggestive of active venting, and these plumes were further explored by ChEss scientists in 2010 who located the source of active venting at 5,000 m – the deepest known vent ever found. Exploration on the MAR has also led to the discovery of the hottest vents (407°C) (Kochinsky 2006; Kochinsky *et al.* 2008), as well as another deep vent (4,100 m), named Ashadze (Ondreas *et al.* 2007; Fouquet *et al.* 2008).

In the AEB, the connections across the Atlantic have been relatively clearly defined. The seeps of the African margin contain a fauna with very close affinities to the seep communities in the Gulf of Mexico (Cordes *et al.* 2007; Olu-Le Roy *et al.* 2007; Warén & Bouchet 2009) and the seep communities on the Blake Ridge and Barbados accretionary wedge (Fig. 9.5). The communities are dominated by vestimentiferan tubeworms and bathymodioline mussels and the common seep-associated families of galatheid crabs

and alvinocarid shrimp. The bathymodioline species complexes on both sides of the Atlantic sort out among the same species groupings within the genus *Bathymodiolus*, with *B. heckeriae* from the Gulf of Mexico and Blake Ridge and *Bathymodiolus* sp. 1 from the African Margin in one grouping, and *B. childressi* from the Gulf of Mexico and *Bathymodiolus* sp. 2 from Africa in another group (Cordes *et al.* 2007). However, our understanding of the biogeographic puzzle beyond this is less clear and requires further investigation (E. Cordes, unpublished observation).

The discovery of vent sites on the southern MAR (Haase *et al.* 2007, 2009; German *et al.* 2008b) and the morphological similarity of their fauna to that of NMAR vents, suggest that the Chain and Romanche fracture zones are less of an impediment to larval dispersal than previously hypothesized (Shank 2006; Haase *et al.* 2007). Further support for unhindered dispersal of vent fauna along the MAR comes from molecular analyses of the two dominant

invertebrates of MAR vents, *Rimicaris* shrimp and *Bathymodiolus* mussels. These studies showed recent gene flow across the equatorial zone for these key host species and their symbionts (Petersen & Dübiller 2009; Petersen *et al.* 2010). In addition to finding known species, new species, including the shrimp *Opaepele susanna* (Komai *et al.* 2007), have been described, and now more than 17 (morpho-) species have been identified from the SMAR. Many of these have been genetically compared with taxonomically similar fauna on the NMAR and reveal significant genetic divergence among species considered “the same” in both regions (T. Shank, unpublished observation).

9.2.3.2 New Zealand region: phylogenetic links among habitats

The New Zealand region hosts a wide variety of chemosynthetic ecosystems, all in close geographic proximity. During the ChEss/COMARGE New Zealand field program (RENEWZ), more than 10 new seep sites were discovered off the New Zealand North Island (Baco-Taylor *et al.* 2009). One of these sites (Builder’s Pencil) covers 135,000 m², making it one of the largest known seep sites in the world. These initial and ongoing research activities aim at locating the sites, describing their environmental characteristics, investigating their fauna, and determining potential phylogeographic relationships among species from vents, seeps, and whale falls found in close proximity to one another.

In the New Zealand region, sampling and description of chemosynthetic communities is in its infancy. Baco-Taylor *et al.* (2009) have now provided an initial characterization of cold seep faunal communities of the New Zealand region. Preliminary biological results indicate that, although at higher taxonomic levels (family and above) faunal composition of vent and seep assemblages in the New Zealand region is similar to that of other regions, at the species level, several taxa are apparently endemic to the region. Bathymodiolin mussels and an eolepadid barnacle dominate (in number and biomass) at vent sites on the seamounts of the Kermadec volcanic arc. Genetic analysis of mussels from chemosynthetic habitats by Jones *et al.* (2006) revealed the New Zealand vent mussel *Gigantidas gladius* to be closely related to species from New Zealand and Atlantic cold seeps.

New Zealand vents are often characterized by the barnacle *Vulcanolepus osheai* (Buckeridge 2000), found at very high densities which is different from those found farther north in the Pacific, and is most similar to an undescribed species found on the Pacific–Antarctic Ridge (Southward & Jones 2003). The most abundant motile species at Kermadec vent sites are caridean shrimp, including two species of endemic alvinocarids (*Alvinocaris niwa*, *A. alexander*), and one hippolytid (*Lebbeus wera*) (Webber 2004; Ah Yong 2009), as well as two species of alvinocarid found else-

where in the western Pacific (*A. longirostris*, *Nautilocaris saintlaurentae*; Ah Yong 2009).

Only two species of low abundance and sparsely distributed vestimentiferan worms have been sampled so far from Kermadec vent sites (Miura & Kojima 2006). Of these species, *Lamellibrachia juni* has been found elsewhere in the western Pacific, whereas the other species, *Oasisia fujikurai*, is closely related to *O. alvinae* from the eastern Pacific (Kojima *et al.* 2006). Other species of macro- and megafauna found associated with Kermadec vent sites (Glover *et al.* 2004; Anderson 2006; Schnabel & Bruce 2006; McLay 2007; Munroe & Hashimoto 2008; Buckeridge 2009) suggest that levels of species endemism in the New Zealand region are relatively high, although some species are either closely related to species, or are found, elsewhere in the wider Pacific region. Community-level analysis (an update of the analysis of Desbruyères *et al.* (2006b)) suggests that although the New Zealand region does apparently contain a vent community with a distinct composition, there is a degree of similarity with communities from elsewhere in the western Pacific (A. Rowden, unpublished observation).

In total, the analysis of samples either compiled or collected as part of the ChEss/COMARGE project provide some support for the hypothesis that the region may represent a new biogeographic province for both seep and vent fauna. However, there is clearly a need for further sampling.

9.2.3.3 Exploring remote polar regions

The Polar Regions have received an increasing interest in the first decade of the twenty-first century, facilitated by new AUV technologies being developed to work in these remote areas of difficult access caused by ice coverage (Shank 2004; Jakuba *et al.* 2008). The exploration of the Arctic Ocean revealed, in 2003, evidence for abundant hydrothermal activity on the Gakkel Ridge (Edmonds *et al.* 2003). The Gakkel Ridge is an ultra-slow spreading ridge, which lies beneath permanent ice cover within the bathymetrically isolated Arctic Basin. The deep Arctic water is isolated from deep-water in the Atlantic by sills between Greenland and Iceland and between Iceland and Norway. This has important implications for the evolution and ecology of the deep-water Arctic vent fauna. In July/August 2007, the AGAVE (Arctic Gakkel Vent Exploration) project investigated the Gakkel Ridge using AUVs and a video-guided benthic sampling system (Camper). Investigations suggested “recent” and explosive volcanic activity (Sohn *et al.* 2008). Extensive fields and pockets of yellow microbial mats dominated the landscape. Microbial samples revealed highly diverse chemolithotrophic microbial communities fueled by iron, hydrogen, or methane (E. Helmke, personal communication). Macrofauna associated with these mats included shrimp, gastropods, and amphipods with hexactinellid sponges peripherally attached to “older lavas”. These communities may be sustained by weak fluid discharge from cracks in the young volcanic surfaces (T. Shank, unpublished observation).

So far, the northernmost vent sites that have been investigated by ROV are at 71°N on the Mohs Ridge (Schander *et al.* 2009). The shallow (500–750 m) sites located there support extensive mats of sulfur-oxidizing bacteria. However, of the 180 species described from two fields explored, the only taxon that is potentially symbiont-bearing is a small gastropod, *Rissoa* cf. *griegi*, also known from seeps and wood falls in the North Atlantic. Arctic cold seeps have also been investigated at the Haakon Mosby Mud Volcano (HMMV) on the Barents Sea slope (72°N) at 1,280 m depth (Niemann *et al.* 2006; Vanreusel *et al.* 2009). This site has large extensions of bacterial mats and is dominated by siboglinid tubeworms (Lösekann *et al.* 2008), with many small bivalves of the family Thyasiridae living among them. In terms of macrofauna, the HMMV is dominated by polychaetes, with higher abundances and diversity at the siboglinid fields compared to the bacterial mats. The meiofauna is dominated by benthic copepods in the active centre, whereas the nematode *Halomonhystera disjuncta* dominates in the bacterial mats (Van Gaever *et al.* 2006). The other Nordic margin cold seeps of the Storegga and Nyegga systems are also characterized by a high abundance of potentially endemic siboglinid tubeworms in association with methane seepage, as well as the occurrence of diverse mats of giant sulfide-oxidizing bacteria, attracting large numbers of meio- and macrofauna (Vanreusel *et al.* 2009).

In the Southern Ocean, vent exploration in the East Scotia Arc and seep investigations on the Weddell Sea have addressed the role of the Circumpolar Current in dispersal of deep-water fauna as a conduit between the Pacific and the Atlantic, or as a barrier between these two oceans and the Southern Ocean. The ChEsSo (ChEss in the Southern Ocean) project explored the East Scotia Ridge in 2009 and 2010, providing further detail to the vent plume data described by German *et al.* (2000). A follow-up cruise is planned for 2011 to investigate further and locate the vent source and any potential vent fauna.

On the continental margin of the Antarctic Peninsula in the Weddell Sea, cold seep communities were discovered in 800 m water beneath what was the Larsen B ice shelf. The site was once covered by extensive areas of bacterial mat and beds of live vesicomyid clams (Domack *et al.* 2005), but hydrocarbon seepage appeared extinct only a few years later (Niemann *et al.* 2009). The discovery of vesicomyid clams is evidence that the hydrographic boundary between the southern Atlantic and Pacific Oceans with Southern Ocean is not a biogeographic barrier, at least for this taxon, though it remains to be determined if the Weddell Sea vesicomyid has been sufficiently isolated to be genetically distinct from any other vesicomyid species. An international team has recently returned to the Larsen B seep sites to determine the phylogeographic alliance of the Weddell Sea clams with other vesicomyids from the Atlantic and Pacific Basins.

9.2.3.4 Southeast Pacific off Chile: a unique place on Earth

The southeast Pacific region off Chile is of high interest for deep-water chemosynthetic studies, especially for the study of inter-habitat connectivity through migration and colonization. Only here can we expect to find every known form of deep-sea chemosynthetic ecosystem in very close proximity to one another. A key reason for this unique juxtaposition of chemosynthetic habitats is the underpinning plate-tectonic setting. The Chile Rise is one of only two modern sites where an active ridge crest is being swallowed by a subduction zone and the only site where such subduction is taking place beneath a continental margin (Cande *et al.* 1987; Bangs & Cande 1997). Consequently, one would expect to find hydrothermal vent sites along the East Chile Rise, cold seeps associated with subduction along the Peru–Chile trench at the intersection with the Chile Rise, and an oxygen minimum zone that abuts and extends south along the Peru and Chile margins (Helly & Levin 2004). Along with these geologic/oceanographic occurrences, significant whale feeding grounds and migration routes occur on the southwest American margin (Hucke-Gaete *et al.* 2004), and there is strong potential for wood-fall from the forests of southern Chile as the Andes slope steeply into the ocean south off approximately 45°S (V. Gallardo, personal communication). To what extent will the same chemosynthetic organisms be able to take advantage of the chemical energy available at all of these diverse sites? Alternatively, will each type of chemosynthetic system host divergent fauna based on additional factors (for example depth, longevity of chemically reducing conditions, extremes of temperature, and/or fluid compositions)? Some seep sites are already known further north along the margin (Sellanes *et al.* 2004) and first evidence for hydrothermal activity on the medium-fast spreading Chile Rise was suggested by metalliferous input to sediments in this region (Marienfeld & Marching 1992). Systematic exploration at the very intersection of the ridge-crest and adjacent margin has recently been conducted during a joint ChEss–COMARGE cruise (February–March 2010) and sources of venting were recorded, along with evidence of at least one cold seep site relatively close by, thereby confirming expectations of the scientists on board (A. Thurber, personal communication).

The Peru–Chile margin and subduction zone contain hydrate deposits and seep sites venting methane-rich fluids (Brown *et al.* 1996; Grevemeyer *et al.* 2003; Sellanes *et al.* 2004). Until recently these habitats had only been sampled remotely by trawl. A recent expedition provided the first Chile seep images and quantitative samples using a video-guided multicorer (A. Thurber, personal communication). Based on trawl collections, seeps of the Chilean Margin appear to have evolved in relative isolation from other chemosynthetic communities. There are at least eight species of symbiotic bivalves, including vesicomyids,

thyasirids, solemyids, and lucinids, and at least one species of the tubeworm *Lamellibrachia* (Sellanes *et al.* 2008). The bivalve species do not appear to have close affinities to the chemosynthetic fauna of other seeps, in particular the seeps off the coast of Peru (Olu *et al.* 1996) or New Zealand (Baco-Taylor *et al.* 2009). The general composition of the community, including a high diversity of vesicomids (four species) is similar to that of other seep sites of the eastern Pacific. Further taxonomic resolution of this key fauna along with a complete analysis of the Costa Rica fauna will help to refine further the location of this biogeographic puzzle piece.

9.2.4 Larval ecology: shaping faunal distribution under ecological timescales

The biological communities that inhabit chemosynthetic environments face several challenges that arise from the peculiarities of the habitat. Firstly, relatively few species are specifically adapted to the physical and chemical characteristics of these habitats. Secondly, these habitats are generally ephemeral at decadal scales (with the notable exception of seeps and OMZs) either because they are geologically unstable (vents) or because they are short lived (large organic falls). Thirdly, these habitats are patchy and can be separated by hundreds to thousands of kilometers of habitat unsuitable for the organisms that are adapted to chemosynthetic conditions. An additional challenge is that most of the organisms that inhabit chemosynthetic environments are either sessile (being attached to a substratum) or show limited mobility in their adult life; they rely solely on planktonic propagules, mainly larvae (Mills *et al.* 2009) (Fig. 9.6) to maintain existing populations and to colonize newly opened areas (e.g., after an eruption at a vent or when a whale lands on the ocean floor). Given the patchy distribution and ephemeral nature of their habitat, adaptations during larval life can have pronounced implications for the success of these species. Yet, our knowledge of the larval ecology of these species, and of deep-sea species in general, remains extremely limited (reviewed in Young 2003; Mills *et al.* 2009).

Most of our current understanding of larval ecology is based on species that inhabit hydrothermal vents, and information from other chemosynthetic habitats is sorely lacking. Larval populations are being increasingly sampled to assess their abundance and distribution relative to the hydrothermal vent where they most likely originated. In general, larvae are found in greater abundance near the ocean floor than near the plume at hundreds of meters above the bottom, suggesting that they may be dispersing along the ocean floor, taking advantage of the along-axis currents there. Although these types of study were initiated in the 1990s (e.g., Kim *et al.* 1994; Kim & Mullineaux 1998),

they accelerated in the 2000s. However, they have only focused at a handful of sites on the Juan de Fuca Ridge (Metaxas 2004), the East Pacific Rise (Mullineaux *et al.* 2005; Adams & Mullineaux 2008), and the Mid-Atlantic Ridge (Khripounoff *et al.* 2001; 2008). Similar studies were initiated in the 2000s and are ongoing at vents in Lau Basin and volcanically active seamounts on arcs in the southern (Kermadec) and western (Mariana) Pacific. These studies suggested that hydrodynamics can provide a mechanism of both larval retention to re-seed existing populations, as well as along-axis transport and dispersal to colonize newly opened areas within hundreds of kilometers. Larval abundance in cold seeps has been measured for two species in the Gulf of Mexico (Van Gaest 2006; Arellano 2008), indicating that, unlike most species at vents (except some crustaceans), larval migration from the seep of origin to surface waters likely occurs.

Larval colonization is better understood and has received more attention than larval dispersal. Since 2002, studies have focused on vents, seeps, whale and wood falls (see, for example, Mullineaux *et al.* 2003; Govenar *et al.* 2004; Pradillon *et al.* 2005; Levin *et al.* 2006; Braby *et al.* 2007; Kelly *et al.* 2007; Fujiwara *et al.* 2007; Tyler *et al.* 2007; Arellano 2008). In all habitats, larvae of different species settle and colonize areas in a particular sequence that appears to be related to chemical and biological cues of the environment. We now know that colonization and succession at vents can be quite rapid and communities can recover from catastrophic disturbances within 2–5 years (Shank *et al.* 1998). It appears that the spatial and temporal patterns of colonists are primarily related to the physicochemical environment and secondarily to biological interactions. However, the evidence on the latter is still scant, and both experimental manipulations and numerical modeling are being used increasingly to address this gap (Neubert *et al.* 2006; Shea *et al.* 2008; N. Kelly, personal communication).

The largest gap in our understanding of larval life is the factors that affect larval growth and development in all chemosynthetic environments. The main challenge is larval rearing for species that inhabit deep-water environments with very particular chemical and physical characteristics. Only a few studies have succeeded in rearing larvae of only a handful of species from vents (Marsh *et al.* 2001; Pradillon *et al.* 2001), seeps (Young *et al.* 1996; Van Gaest 2006; Arellano & Young 2009), and whale falls (Rouse *et al.* 2009), but none were successful in following larvae through to the end of that life stage. Larval rearing *in situ* has been attempted and has been partly successful (Marsh *et al.* 2001; Pradillon *et al.* 2001; Brooke & Young 2009).

A key unknown aspect of the question of larval development is the duration of the larval stage, the period that larvae spend in the water column, and thus their potential dispersal distance. Some specific exceptions include

**Fig. 9.6**

Photographs of vent larvae and juveniles collected from the 9°50'N EPR vent field. **(A)** larva of the gastropod genus *Lepetodrilus*; **(B)** juvenile of a polynoid polychaete; **(C)** megalopa larval stage of decapod crustacean *Bythograea thermydron*; **(D)** larva of the bivalve *Bathymodiolus thermophilus*. © Stace Beaulieu (photographs A, B, and D) and Susan Mills (photograph C), Woods Hole Oceanographic Institution.

experiments to estimate dispersal time in the vent tube-worm *Riftia pachyptila* (Marsh *et al.* 2001), the whale-fall polychaete *Osedax* (Rouse *et al.* 2009), the vent gastropod *Bathynnerita* (Van Gaest 2006), and the mussel *Bathymodiolus* (Arellano & Young 2009). Other major gaps in knowledge include larval growth rates in relation to temperature, pressure, and food availability; the cues that induce them to stop swimming and settle onto a suitable habitat (or

avoid an unsuitable one); and the role of larval behavior in vertical positioning while in the water column or near bottom. Increased knowledge of larval connectivity and colonization processes will add conceptual understanding of reducing ecosystems as metapopulations (Leibold *et al.* 2004; Neubert *et al.* 2006) and their response or resilience in the face of natural and anthropogenic disturbance (Levin *et al.* 2009b).

9.3 Limits to Knowledge

9.3.1 Understanding remote and dynamic ecosystems

Discovery of deep-water chemosynthetically driven communities is relatively recent. Thus the investigation of these habitats has a very strong exploration component. Biologically, the unknowns exceed the knowns. How many species are there? What is their distribution and why? How do species reproduce, disperse, and colonize new sites? What are the evolutionary history and phylogenetic relationships of species from different chemosynthetic habitats? The remoteness and abrupt topography of deep-water chemosynthetic ecosystems make observation, sampling, and experimentation difficult in these habitats. There is a strong need for international collaboration and sharing of resources, which has been accomplished through projects such as the Census, contributing greatly to our knowledge of chemosynthetically driven ecosystems. The ongoing learning process allows identifying gaps and provides a driver for science to transform the unknowns into knowns (Gomory 1995; Marchetti 1998).

Chemosynthetic research depends on our capacity to sample, observe, and experiment at great depths in “extreme” physicochemical conditions. Therefore research in chemosynthetic ecosystems closely follows technological developments. For example, the use of submersibles and ROVs made possible direct observation and *in situ* precise sampling of the ecosystem. AUVs are useful for investigation of regions that are not accessible from the surface (i.e. oceans under ice) and in revolutionizing the efficiency of deep-sea hydrothermal exploration (German *et al.* 2008a; Sohn *et al.* 2008). Deep-towed sidescan sonar instruments can produce detailed acoustic images of the deep seafloor. Submersible-mounted multibeam bathymetry can achieve centimeter-scale resolution maps of the sea floor. High-resolution, high-definition cameras are being used to produce photo-mosaics of remote habitats, providing a comprehensive overview of the habitat and allowing for first interpretations of the relationships between habitat and fauna. New types of biogeochemical sensor module and incubation instrument allow quantification of the transport of energy and the benthic community activities *in situ* (Boetius & Wenzhöfer 2009). Technology is also advancing rapidly in laboratory techniques, for example molecular biology, which has aided our understanding of processes that, until recently, were hidden from our senses. However, are there limits to knowledge? This question can be considered in terms of different timescales. At the ecological timescale, one of the major limits to knowledge is imposed by society

itself. The first barrier is one of economics and human resources.

In the case of the discrete and dynamic deep-water chemosynthetic ecosystems, some aspects might be unknown and unknowable at any given time. German & Lin (2004) have estimated that, for fast- and intermediate-spreading ridges, there should be a volcanic eruption approximately every 50 years for any given 100km of ridge section. Slow-spreading ridges may exhibit much greater irregularity (German & Lin 2004). It would take the equivalent of one 1- to 2-year expedition to explore all of the southern MAR from north to south. Taking into account the episodic volcanic activity of mid-ocean ridges, we would expect three or four major new eruptions to have occurred over the time it would take to explore the whole 7,000km of the MAR. By that reckoning (approximately one new vent area on the MAR each year), our current rate of discovery (nine sites on the northern MAR since 1986) is not even keeping pace with the rate of new production. Here, the limit to knowledge is a consequence of the dynamic characteristics of mid-ocean ridges. Cold seeps at passive margins are more stable ecosystems than vents (Sibuet & Olu 1998), but those on active margins (e.g., Chile, Costa Rica) are subject periodically to some of the most violently destructive forces on Earth. We can study these systems in their current “dormant” state and investigate their geophysics and geochemistry interactions and associated fauna. However, the episodicity of the great earthquakes (an approximate 100-year cycle predicted for the magnitude 9.5 great earthquake) may render the responses to such events impossible to observe and the extent to which the associated organisms are impacted by – or even anticipate – major tectonic events unknowable. Similar issues apply to stochastic, discrete, and ephemeral “habitats” such as whale falls and large organic falls. The life cycle of vents on fast-spreading ridges (i.e. East Pacific Rise) or cold seeps on active margins is equivalent, in time, to the construction of a cathedral in the Middle Ages (approximately 100 years), whereas on slower-spreading ridges they can extend to more than 10,000 years (Cave *et al.* 2002), longer than the oldest known European prehistoric constructs such as Stonehenge in the southern United Kingdom. These are unknowables for ChEss.

Furthermore, the fauna from deep-water vents, seeps, and whale falls is often new to science. Although the diversity of megafauna is low and the new species are described at a pace that keeps with discovery, this is not the case for the more diverse meiofauna, where up to 90% of the species collected can be new to science. The inability to keep up the rate of taxonomic identification is increasingly affected by the continuous decrease in taxonomic expertise among the new generations of marine biologists.

9.3.2 Technology: pushing backwards the limits to knowledge

Despite the best possible combinations of sensors and technologies, a limit to progress will remain related to accessing the appropriate sections of the global ocean using suitable research ships. As we develop AUV-based approaches we can improve the rates of exploration and discovery. Because AUVs are decoupled from ships' positions and motions (unlike ROVs) and do not put human lives in harm's way at the bottom of the ocean (unlike manned submersibles), we will be able to expand our systematic exploration surveys to higher and higher latitudes. Furthermore, a new generation of AUVs is now under construction that will have ranges in excess of 1,000 km and could ultimately span entire ocean basins. At this level, and with artificially intelligent control systems, we can imagine a day when long-range AUVs will be able to conduct first pass investigations along entire sections of the global ridge crest, interrogating, processing, and interpreting their data underway, to allow second pass mapping and, potentially, even photographic surveys of the seafloor. Although such approaches may seem like so much science fiction, preliminary algorithms to interpret hydrothermal field data on-the-fly have already been trialed (for example on the MAR) and a first long-range mid-ocean ridge ship-free AUV cruise has already reached the planning stage.

9.4 Human Footprints in Deep-Water Chemosynthetic Ecosystems

Deep-sea ecosystems support one of the highest biodiversities of the Planet as well as important natural and mineral resources. In the last decades, the depletion of resources in the upper layers of the oceans together with technological development has fueled the increasing interest of industry to explore and exploit deep-sea resources. Industries such as mining, hydrocarbon extraction, and fishing are working at great depths (below 1,000 m), and some of these activities affect chemosynthetic ecosystems. We briefly discuss below only anthropogenic impacts that have been addressed by ChEss scientists (i.e. mining, hydrocarbon extraction, and trawling), but other impacts such as litter accumulation or climate change are also important.

9.4.1 Major known impacts

Probably the most important industry potentially affecting chemosynthetically driven habitats and their fauna is mining

for precious metals on seafloor massive sulfide deposits (SMS) from vents. SMS contain significant quantities of commercially valuable metals, such as gold, silver, copper, and zinc (Baker & German 2009). Although at a very early stage of exploration, the SMS industry is already extremely active, with two major companies (Nautilus Minerals and Neptune Minerals) developing plans for exploitation in national waters of Papua New Guinea and New Zealand. ChEss scientists have participated in the environmental impact assessment conducted by Nautilus Minerals, who have produced an environmental impact statement for mining activities in Papua New Guinea, and considerable baseline research has been done (Levin *et al.* 2009b; Erickson *et al.* 2009; see EIS at www.cares.nautilusminerals.com/Downloads.aspx). Although it seems highly likely that economically viable extraction of sulfides from the deep-sea floor may begin within the next decade, the true nature of mining impact on the ecosystem is still mostly unknown. There are several potential environmental effects of mining that are of concern to some stakeholders. These include direct physical damage to the sea bed at the operation site and the surrounding area; potential extinction of isolated populations; production of sediment plumes and deposition of sediment, which will affect marine life by smothering or inhibiting filter feeders; alteration of fluid-flow paths at a vent, on which the benthic, often sessile, vent fauna rely; noise pollution; wastewater disposal; and equipment failure which may result in leakage (ISA 2004; Van Dover 2007). ChEss has been instrumental in instigating key collaborations including all stakeholders, conducting baseline research, participating in workshops and discussion fora, and contributing to the "Code for Environmental Management of Marine Mining" (IMMS 2009) and the International Seabed Authority's guidelines for environmental baselines and monitoring programs (International Seabed Authority 2004; Van Dover 2007), which both serve to monitor and mitigate the potential effects of deep-sea mining.

Another important extractive industry is oil and gas exploitation. Seep communities often coincide with large subsurface hydrocarbon reservoirs and the outcropping of gas hydrates. Thus they may also be susceptible to damage from oil and methane exploration and extraction activities in the future. One of the most intensive areas of deep-water oil industry activity is in the Gulf of Mexico, leased and monitored by the US Minerals Management Service. Collaborations between scientists and the Minerals Management Service in the Gulf of Mexico are well established (Fisher *et al.* 2007; Roberts *et al.* 2007), and exploration for new sources of hydrocarbons often coincides with the discovery of new biological communities. As new high-density biological communities are discovered, the Minerals Management Service establishes "mitigation areas" to prevent oil industry activity from impacting these sensitive

areas. ChEss has also established strong collaborations with Fondation Total to promote science in chemosynthetic ecosystems.

Finally, ChEss scientists have been involved in issues related to deep-water trawling that affect chemosynthetic sites. Recent exploration of the eastern margin of New Zealand provided not only the first descriptions of seep communities in the region but evidence that seep sites have been subjected to bottom fishing (Baco-Taylor *et al.* 2009), with visible accumulations of coral or vesicomid shell debris, lost trawl gear, or trawl marks in seep adjacent sediments. Similarly, signs of trawling have been found on the California margin at 500 m depth (Levin *et al.* 2006) and on the Chilean margin, where the commercially fished Patagonian toothfish is closely associated with seeps (Sellanes *et al.* 2008).

9.4.2 Marine protected areas

As vent sites have become the focus of intensive, long-term investigation, both governmental and non-governmental organizations have been discussing the need to introduce appropriate measures that combine preservation of habitat with scientific interests, tourism, and, potentially, mining (Mullineaux *et al.* 1998; Dando & Juniper 2000; Santos *et al.* 2003). The ChEss project has been an active participant in the planning of biogeographically representative networks of sites of interest for conservation and continued scientific research. ChEss scientists have contributed also to the Convention of Biological Diversity effort, to produce scientific criteria and guidance for the identification of ecologically or biologically significant marine areas and the designation of representative networks of marine protected areas (MPAs) (Convention on Biological Diversity 2009). So far, ecological reserves and/or MPAs have been proposed at the Mid-Atlantic Ridge and the East Pacific Rise, and have already been established on the Juan de Fuca Ridge (<http://www.dfo-mpo.gc.ca/oceans/marineareas-zonesmarines/mpa-zpm/pacific-pacifique/factsheets-feuillets/endeavour-eng.htm>). At the MAR, three sites – Lucky Strike, Menez Gwen, and Rainbow – were proposed to be included on the network of MPAs of The Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) maritime region V (the wider Atlantic). In the New Zealand region, some hydrothermal vent sites are currently protected from bottom trawling by a Benthic Protected Area. Although licenses that have been issued for exploratory mineral mining overlap with this area, it is expected that collaborations among stakeholders will instigate new prospects for conservation. The scientific community has recognized also the potential impact of continuous research activities at certain sites. This led to the “Statement of Responsible Research Practices at Hydrothermal Vents”, developed by InterRidge with the collaboration of ChEss scientists (Devey *et al.* 2007). Following on those steps, the OSPAR convention

also proceeded with the design of a Code of Conduct for Research on Hydrothermal Vents, which included the usefulness of MPAs (OSPAR draft background report 2009).

9.5 Conclusions

Under the ChEss project, the scientific community has expanded our knowledge beyond the vent biogeographic regions recognized in the early twenty-first century (Van Dover *et al.* 2002). New technologies have been developed, making available the necessary tools to explore and investigate remote habitats of difficult access in a very efficient way, resulting in the discovery of new sites in all oceans on Earth. The number of species described from vents, seeps, whale falls, and OMZs is constantly growing, providing essential data to understand global biodiversity and phylogenetic links among habitats to refine existing biogeographic provinces and define new ones.

Indeed, Bachraty *et al.* (2009) have recently addressed the biogeographic relationships among deep-sea vent faunas at a global scale using statistical analysis of comprehensive vent data. They delineate six major hydrothermal provinces and identify possible dispersal pathways. Furthermore, detailed ecological investigations (for example trophic structure, reproduction, larval ecology) of known sites have resulted in a better understanding of ecosystem functioning and the role played by the environment in shaping deep-water chemosynthetic communities. Table 9.2 summarizes some of the key contributions the ChEss project participants have made toward a better global understanding of the distribution of chemosynthetic environments, the species that inhabit them, and some underlying ecological processes. Nevertheless, there are important geographic gaps in the global chemosynthetic biogeographic puzzle that remain to be explored and gaps to knowledge that remained unanswered in 2010. The momentum created by the Census and ChEss initiatives has promoted major international collaborations and strengthened existing ones. This synergy between laboratories around the globe, sharing expertise and resources in joint research projects, will continue beyond 2010 as one of the main legacies of ChEss. The scientific results obtained are crucial for the development of conservation and management options in an ecosystem that is already affected by human activities.

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Table 9.2

Summary of key discoveries, new technological developments and conclusions from the ChEss project.

Key Discovery/Insight/Tools	References
Hottest known hydrothermal vent discovered on MAR (407°C).	Kochinsky 2006; Kochinsky <i>et al.</i> 2008
Deep vent (Ashadze) discovered at 4,100m on MAR. Fauna here is strikingly different from that of other Atlantic sites.	Ondreas <i>et al.</i> 2007; Fouquet <i>et al.</i> 2008
Deepest known vent discovered at 5,000m on Cayman Rise in 2010.	German, Copley, Connelly, Tyler, unpublished observation
First vent sites discovered south of the equator on the southern Mid-Atlantic Ridge (SMAR).	Haase <i>et al.</i> 2007; German <i>et al.</i> 2008b
New species discovered from SMAR vents.	Komai <i>et al.</i> 2007
Morphological similarity of fauna from SMAR and NMAR suggestive of unhindered larval dispersal.	Shank 2006; Haase <i>et al.</i> 2007; Petersen, personal communication; van der Heijden, personal communication
Faunal affinities discovered between seep species across Atlantic Equatorial Belt. Communities dominated by vestimentiferan tubeworms, bathymodioline mussels, and the common seep-associated families of galatheid crabs and alvinocarid shrimps.	Cordes <i>et al.</i> 2007; Olu-Le Roy <i>et al.</i> 2007; Warén & Bouchet 2009
More than 10 new seep sites discovered off of the New Zealand North Island including one of largest cold seeps known covering about 135,000m ² (approximately 33 acres) (Builder's Pencil).	Baco <i>et al.</i> 2009
Initial characterization of cold seep faunal communities of the New Zealand region.	Baco <i>et al.</i> 2009
Species of macro- and megafauna found associated with Kermadec vent sites suggest that levels of species endemism in the New Zealand region are relatively high.	Glover <i>et al.</i> 2004; Anderson 2006; Schnabel & Bruce 2006; McLay 2007; Munroe & Hashimoto 2008; Buckeridge 2009
Overall, the analysis of samples either compiled or collected as part of the ChEss project, provide some support for the hypothesis that the New Zealand region may represent a new biogeographic province for both seep and vent fauna.	Rowden, unpublished observation
Abundant hydrothermal activity revealed on Gakkel Ridge, Arctic Ocean, bathymetrically isolated from Atlantic Ocean. Yellow microbial mats supporting shrimps and amphipods discovered.	Edmonds <i>et al.</i> 2003; Sohn <i>et al.</i> 2008; Helmke, personal communication; Shank, unpublished observation
The northernmost vent sites investigated by ROV discovered at 71°N on the Mohs Ridge.	Schander <i>et al.</i> 2009
Arctic cold seeps investigated at the Haakon Mosby Mud Volcano on the Barents Sea slope (72°N) at 1280m depth revealed large extensions of bacterial mats, siboglinid tubeworms, small bivalves, polychaetes, benthic copepods, and nematodes.	Niemann <i>et al.</i> 2006; Van Gaever <i>et al.</i> 2006; Lösekann <i>et al.</i> 2008; Vanreusel <i>et al.</i> 2009
ChEss has begun to explore the Southern Ocean for chemosynthetic communities during the ChEsSo programme in 2009 and 2010. Investigations to continue in 2011.	Tyler, unpublished observation; Connelly, personal communication
Initial studies of vesicomid clams from Weddell Sea cold seeps suggest that the hydrographic boundary between the southern Atlantic and Pacific Oceans with Southern Ocean is not a biogeographic barrier at least for this taxon. Further work is planned for 2010.	Domack <i>et al.</i> 2005; Niemann <i>et al.</i> 2009; Van Dover, unpublished observation
Based on trawl collections, seeps of the Chilean Margin appear to have evolved in relative isolation from other chemosynthetic communities. There are at least eight species of symbiotic bivalves including vesicomids, thyasirids, solemyids, and lucinids, four seep gastropods, and at least one species of the tubeworm <i>Lamellibrachia</i> .	Sellanes <i>et al.</i> 2008; Waren, personal observation
Studies of vent larval abundance suggest that hydrodynamics can provide a mechanism of both larval retention to re-seed existing populations, as well as along-axis transport and dispersal to colonize newly opened areas within hundreds of kilometers. In cold seeps, larval migration likely occurs from the seep of origin to surface waters. Some estimates of larval dispersal times have been made.	Metaxas 2004; Mullineaux <i>et al.</i> 2005; Van Gaest 2006; Adams & Mullineaux 2008; Arellano 2008; Khripounoff <i>et al.</i> 2008; Arellano & Young 2009; Rouse <i>et al.</i> 2009

Key Discovery/Insight/Tools	References
Since 2002, larval colonization studies have focused on vents, seeps, whale and wood falls. In all habitats, larvae of different species settle and colonize areas in a particular sequence that appears to be related to chemical and biological cues of the environment.	Mullineaux <i>et al.</i> 2003; Govenar <i>et al.</i> 2004; Pradillon <i>et al.</i> 2005; Levin <i>et al.</i> 2006; Neubert <i>et al.</i> , 2006; Braby <i>et al.</i> 2007; ; Fujiwara <i>et al.</i> 2007; Kelly <i>et al.</i> 2007; Tyler <i>et al.</i> 2007; Arellano 2008; Shea <i>et al.</i> 2008; Kelly, personal communication
Development and implementation of AUV and AUV–ROV hybrid technology for vent and seep exploration and investigation (including under-ice investigations).	Baker <i>et al.</i> 1995; Baker & German 2004; Shank 2004; Yoerger <i>et al.</i> 2007; German <i>et al.</i> 2008a; German <i>et al.</i> 2008b; Jakuba <i>et al.</i> 2008; Melchert <i>et al.</i> 2008; Dupre <i>et al.</i> 2009; Foucher <i>et al.</i> 2009; German <i>et al.</i> 2009; Haase <i>et al.</i> 2009
Significant increase in molecular tools for studies to understand species evolution, metapopulations, and gene flow in chemosynthetic regions.	Shank & Halanych 2007; Johnson <i>et al.</i> 2008; Plouviez <i>et al.</i> 2009; Vrijenhoek 2009b
New types of biogeochemical sensor module and incubation instrument to quantify the transport of energy and the benthic community activities <i>in situ</i> .	Boetius & Wenzhöfer 2009
Approximately 200 species have been described and published from vents, seeps, and whale falls since the onset of the ChEss programme in 2002.	ChEssBase: www.noc.soton.ac.uk/database
TAWNI outputs: many meio-, macro-, and megafauna species have been described and new records identified from different vent and seep sites.	Zekely <i>et al.</i> 2006; Gollner <i>et al.</i> 2008; Hilário & Cunha 2008; Hilário, personal communication; Thurber, personal communication
The much publicized yeti crab <i>Kiwa hirsuta</i> discovered on the Pacific vents represents a new species, genus, and family. A close relative of this crab has also been discovered from Costa Rican cold seeps and is being described with the aid of a TAWNI grant.	Macpherson <i>et al.</i> 2005; Thurber, personal communication
Cold seep species from Costa Rica Margin are related to those from cold seeps in the Gulf of Mexico and West Africa, and to seep species in the Pacific.	Levin & Waren, unpublished observation
Novel reproductive adaptations found in vent animals, including seasonality.	Young 2003; Hilário <i>et al.</i> 2005; Tyler <i>et al.</i> 2007; Rouse <i>et al.</i> 2009
Adaptations to hypoxia and thermal tolerance in vent and seep animals.	Hourdez & Lallier 2007
ChEss scientists have provided leadership on global hydrothermal vent conservation.	ISA 2004; Van Dover 2007; Fisher <i>et al.</i> 2007; Roberts <i>et al.</i> 2007; CBD 2009; IMMS 2009

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