

**The Exploration
of Marine Biodiversity
Scientific and Technological
Challenges**

Carlos M. Duarte (ed.)

Offprint of the Chapter

**3. DEEP-SEA ECOSYSTEMS: PRISTINE BIODIVERSITY
RESERVOIR AND TECHNOLOGICAL CHALLENGES**

by

Eva Ramírez Llodra^{1,2} and David S. M. Billett²

1 Institute of Marine Sciences (CMIMA-CSIC), Barcelona, Spain

2 National Oceanography Centre (NOC), Southampton, UK

© Fundación BBVA, 2006

www.fbbva.es

ISBN: 978-84-96515-27-7



3.1. INTRODUCTION

THE DEEP SEA is the largest ecosystem on Earth, with approximately 50% of the surface of the Earth covered by ocean more than 3,000 metres deep. It supports one of the largest reservoirs of biodiversity on the planet, but remains one of the least studied ecosystems because of its remoteness and the technological challenges for its investigation. The HMS *Challenger* Expedition (1872-1876) marked the beginning of the “heroic” age of deep-sea exploration, and our knowledge has progressed since in parallel with technological developments.

The deep-sea floor extends from around 200 m depth down the continental slope to the abyssal plains (3,000-6,000 m) and reaches the deepest part of the oceans in the Marianas Trench (11,000 m). These ecosystems are characterised by the absence of light, increasing pressure with depth and low temperature waters (with some exceptions). The deep sea contains extremely large habitats such as abyssal plains (millions km²) and mid-ocean ridges (65,000 km long). At the same time, it encloses relatively small, localised geological features such as canyons, seamounts, deep-water coral reefs, hydrothermal vents and cold seeps, which support unique microbial and animal communities.

State-of-the-art technology is essential for the study of deep-sea ecosystems, providing the necessary tools for the location, mapping and study of the different habitats and their associated fauna. These include, amongst others, high definition sea-floor mapping, manned submersibles, remote operated vehicles, autonomous underwater vehicles, deep-towed vehicles and sampling equipment, landers, hydro-acoustic instruments and isothermal and isobaric chambers as well as laboratory techniques such as new molecular tools. International collaborations for sharing of equipment, expertise and human resources are crucial in driving deep-sea investigations. The deep sea also includes important

Photo 3.1: *Anoplogaster cornuta*, deep-sea Atlantic fish. Among the world’s deepest-living fishes, the common fangtooth is usually found between 200 and 2,000 m, although it has been observed as far down as 5,000 m. Its enormous head and long teeth are morphological features shared by many fish species dwelling in the total darkness of the ocean depths.

biological and geological resources. Therefore, industries such as deep-water fishing or oil and gas exploration are rapidly moving into deep-water areas. Scientists are working together with industries, conservation agencies and decision makers to develop conservation and management options for an environment that is still one of the great unknowns of our planet.

3.2. HISTORY OF DEEP-SEA EXPLORATION: FROM FORBES' "AZOIC ZONE" TO HYDROTHERMAL VENT DISCOVERY

The roots of our understanding of deep-sea ecosystems follow the path of the great expeditions that started in the 19th century, and that developed with the refinement of navigation and sampling techniques and instruments. Between 1841 and 1842, Edward Forbes developed the "azoic theory" after observing a decrease in the number of animals when dredging at increasing depths in the Aegean Sea. The extrapolation of his results led him to believe that the oceans did not support life below 600 m. However, the expeditions of HMS *Lightning* (1868) and HMS *Porcupine* (1869 and 1870) to the NE Atlantic and Mediterranean and, especially, the circumglobal expedition of HMS *Challenger* (1872-1876) demonstrated that life was present in the oceans, from the shores to the abyssal depths (Murray and Hjort 1912). The *Challenger* Expedition is considered to be at the origin of modern oceanography.

In the mid 20th century, the *Galathea* expedition (1950-1952) gave evidence that marine life exists in even the deepest zones of the ocean floor, when the expedition recovered fauna from 10,200 m on the Philippine Trench. The baseline biological data obtained from the early expeditions, together with the development of new, more precise sampling technologies, allowed for a change in the way that deep-sea marine biological research was conducted. From the mid 1960s, descriptive biology was complemented by process-oriented and ecological biology based on rigorous scientific methods (Hessler and Sanders 1967; Grassle and Sanders 1973; Grassle 1977). When boxcorers made it possible to obtain quantitative samples of the small-bodied fraction of the deep-sea fauna, it was found that the deep-sea sediments sustain a very high biodiversity, far beyond the "azoic sea-floor" predicted by Forbes (Hessler and Sanders 1967). The development of deep-water photographic instruments, and later of deep-water submersibles, allowed deep-sea fauna to be observed and studied in its own habitat, for the first time ever, providing crucial information that was traditionally missed in remote/blind sampling.

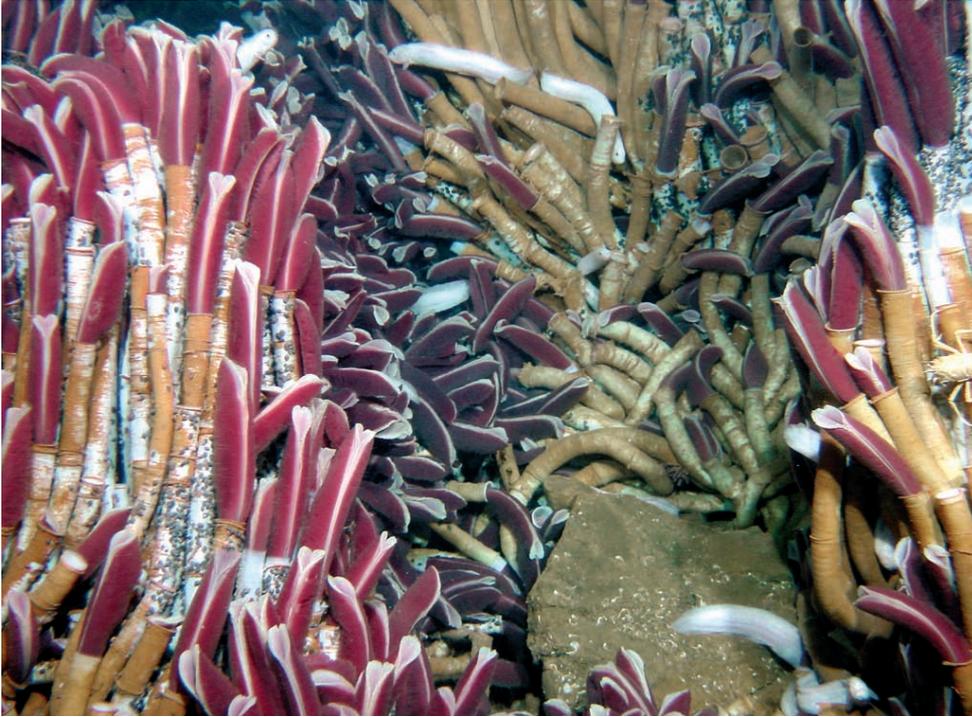


Photo 3.2: The giant tubeworm *Riftia pachyptila* from the East Pacific Rise hydrothermal vents

Less than 30 years ago, one of the most exciting discoveries of our times was made. In 1977, hydrothermal vents were discovered in the Galapagos Rift in the Pacific, as the result of geothermal studies investigating the balance of thermal flux on Earth (Lonsdale 1977; Corliss et al. 1979). But what the pilots and scientist in the U.S. research submersible *Alvin* were not expecting to find was the extraordinary landscape of black smokers colonised by dense populations of exotic and unknown animals, such as the giant tubeworm *Riftia pachyptila* (photo 3.2).

What was even more striking was the finding that these ecosystems are sustained by primary production of chemoautotrophic bacteria that use inorganic reduced chemicals from the Earth's interior to synthesize organic matter (see section 3.3.2). These new habitats where life thrives independent of solar energy are known as chemosynthetic ecosystems. Today we know that other reducing habitats such as cold seeps, whale falls or oxygen minimum zones also develop chemically-driven communities with similar species and physiology to the vent animals (see section 3.3.2).

3.3. DEEP-SEA ECOSYSTEMS: ENVIRONMENTAL CHARACTERISTICS AND BIODIVERSITY

The oceans cover 70% of the Earth's surface or the equivalent of the surface of two Mars and two Moons together. But we still know more about the geography and characteristics of our Moon or Mars than about our Oceans! Furthermore, 50% of the Earth is covered by oceans more than 3,000 m deep, with a mean depth of around 3,800 m. The deep sea is, therefore, the largest ecosystem in our planet as well as one of the least studied. It comprises a variety of habitats from the shelf break to the deepest parts of the ocean floor found in trenches, each with specific physical and geochemical characteristics that support one of the highest biodiversities on the planet. In relation to the energy that supports marine ecosystems, deep-sea habitats can be divided into two major groups: heterotrophic and chemosynthetic habitats. In heterotrophic habitats, the faunal communities depend, ultimately, on organic matter produced at the surface by photosynthesis and are therefore dependent on solar energy. In chemosynthetic habitats, the biological communities are sustained by the energy provided by inorganic reduced chemicals such as hydrogen sulphide (H_2S) or methane (CH_4) from the Earth's interior.

3.3.1. Heterotrophic ecosystems

The vast majority of life in the deep oceans is sustained by the production of organic matter on the surface from photosynthesis. It resides in what are known as heterotrophic habitats, because there is no intrinsic primary production. In the deep-sea benthos, the heterotrophic ecosystems include continental margins from the shelf break to 3,000 m depth and abyssal plains, between 3,000 m and 6,000 m in depth. Continental margins include a variety of habitats with specific and distinct physicochemical, geological and biological characteristics that are discussed below.

3.3.1.1. SEDIMENT MARGINS

Continental margins cover 13% of the world's seafloor (Wollast 2002). These systems are the largest reservoir of sediments on Earth, with up to 90% of sediments generated by erosion on land being deposited on the margins (McCave 2002). The open margin ecosystem is greatly influenced by dynamic processes such as currents that affect and drive the transport of energy and organic

matter. In some regions, wind stress along the coast can lead to upwelling events that transfer rich deep waters to the surface, feeding the nutrient-depleted surface waters and resulting in high productivity on the shelf (Wol-last 2002). In other areas, landslides cause large-scale disturbances that can destroy whole communities in a single event.

The drivers of heterogeneity in faunal distribution, composition and abundance on continental margins vary depending on the spatial scale considered. At large scales (over 1,000 km), major physical factors such as geology, temperature, currents and water masses play the main role. At mid scales (1-100 km), the distribution of animals is mainly determined by factors such as down flux of primary production, oxygen availability (i.e., areas of oxygen minima), sediment type and catastrophic events (Gage 2002). Finally, biological interactions are the main drivers of faunal distribution at small scales. Our knowledge about the biodiversity and biogeography of fauna on continental margins is still scant. Biomass as indicated by epifauna (animals living on the sediment) decreases with depth, and in deep waters the presence of a large number of burrowing animals is shown by a variety of features such as pits and mounds. Animals on deep sediment slopes are mainly sediment feeders that use the organic matter input from the surface. In shallower waters, the number of megafaunal animals and suspension feeders increases in relation with higher water currents. Finally, when the slope approaches the shelf, the increase in grain size causes a decrease in the biota of the sediment. One of the most striking observations in open margins is the peak in biodiversity at mid slopes (Stuart, Rex and Etter 2003). The exact drivers of this general observation of biodiversity maxima are still to be determined, and are the focus of a number of research projects (see section 3.5).

3.3.1.2. CANYONS

Canyons are deep incisions on the continental margins, and are common features on European margins such as the Catalan Sea (map 3.1), the south of France or the Portuguese margin.

Canyons are hotspot ecosystems on continental margins, characterised by a high biodiversity. These geological features act as major pathways for organic carbon transportation, and fast down flux of organic matter from the land to the deep sea. Canyons contain a variety of substrata, such as hard rock walls and mobile sediments on the canyon floor, that sustain complex ecosystems

Map 3.1: Bathymetric map of a section of the Catalan Sea (Eastern Mediterranean) showing canyon systems



Source: www.icm.csic.es/geo/gma/MCB.

with a high degree of endemic species. Canyons are also important hotspots for commercial species, such as the red shrimp *Aristeus antennatus*, one of the major fisheries in the Catalan Sea (Sardà, Company and Castellón 2003). However, their irregular topography and the difficulty of sampling prevented their detailed investigation until only recently. The latest developments in deep-water imaging with towed and remote-operated vehicles and submersibles are now facilitating the exploration and investigation of the geo-physical and biological characteristics of canyons (see section 3.5).

3.3.1.3. DEEP-WATER CORALS

Investigations on continental margins during the last decade led to a surprising discovery: the presence of deep-water corals that form reefs along the NE and NW Atlantic continental margins. The NE Atlantic coral reefs are found at around 1,000 m depth and extend from Norway to Portugal (photo 3.3),

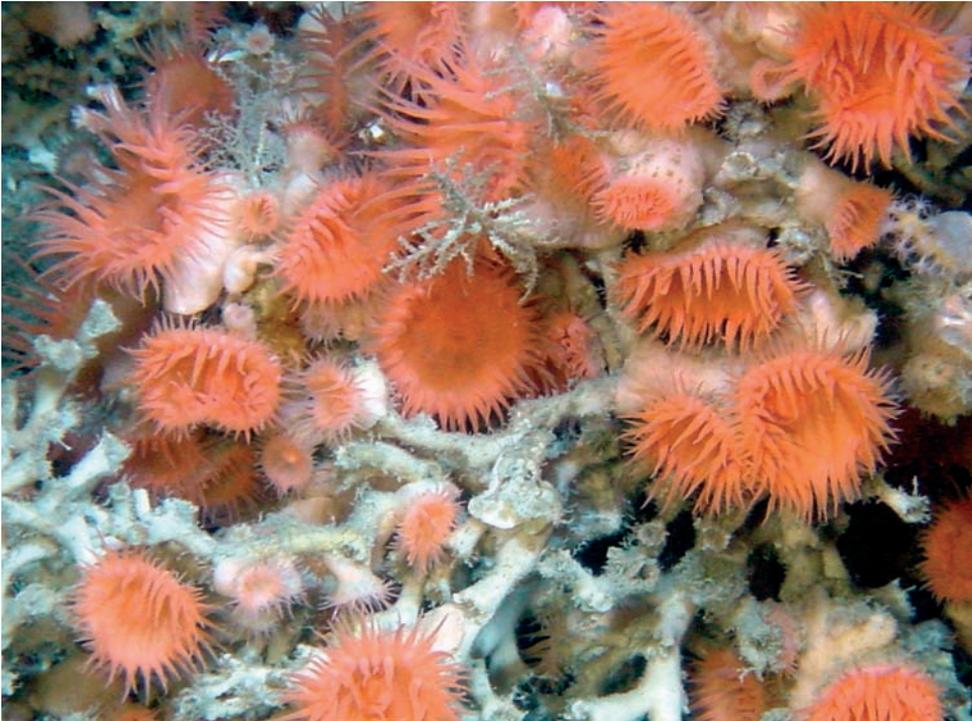


Photo 3.3: Deep-sea corals observed by French ROV *Victor 2000* at a depth of 1,650 m in the NE Atlantic

and recently similar ecosystems have been discovered in the Mediterranean. Deep-water coral species such as *Lophelia pertusa* and *Madrepora oculata* form carbonate reefs several kilometres in length and sustain a high biodiversity providing refuge, structure and nursery spots for other slope species. The reefs provide a complex three-dimensional habitat for a variety of species, including sponges, soft corals, molluscs, crustaceans and echinoderms (Freiwald 2002), as well as for commercial species. Although our knowledge on the composition and functioning of these rich communities is still low, there is already evidence of habitat damage from deep-water trawling over deep-water coral regions (see section 3.6).

3.3.1.4. SEAMOUNTS

Seamounts are undersea mountains characterised by steep slopes, the presence of hard and soft substrata, large depth ranges from abyssal to sub-littoral

depths and geographic isolation (Rogers 2004). It is estimated that around 100,000 seamounts over 1000 m in height exist around the world's oceans, and many more if we consider smaller mounts. But only around 350 of these seamounts have been sampled, and only around 100 have been studied in any detail. The particular biological features of seamounts include high productivity, large stocks of commercially valuable fishes, high biodiversity and a high degree of endemism of benthic fauna. These specific traits are driven by the particular topography and hydrography around seamounts (Forges, Koslow and Poore 2000).

As has occurred in other regions, like canyons, with difficult terrain, we still have little knowledge of the biodiversity, distribution and functioning of seamount fauna. However, seamounts have been the target of intensive fishing in recent decades (Koslow et al. 2001), which has led to potential long-term damage and biodiversity loss in an ecosystem as yet poorly understood. Today, with the help of new studies of seamounts driven by the use of new technologies such as ROVs or deep-towed cameras, management and conservation options are being put in place (see section 3.6).

3.3.1.5. ANOXIC AREAS

Mid-water oxygen minima (<0.5ml/l dissolved O₂) can intercept the continental margin, resulting in sediments with a very low oxygen concentration or Oxygen Minimum Zones (OMZs). OMZs are formed in areas of high primary production in the surface waters of the ocean and poor water circulation, where the biological degradation of the sinking organic matter results in oxygen depletion (Rogers 2000; Levin 2003). Seafloor OMZs typically occur between 200 m and 1000 m depth and are found in the eastern Pacific, NW Pacific margin, Philippines area, Bay of Bengal, Arabian Sea and SW Africa beneath the Benguela current (Rogers 2000; Levin 2003). Despite very low oxygen concentrations, protozoan and metazoan life thrive in these ecosystems. The high concentrations of organic matter sustain dense populations of sulphide-oxidising bacteria (i.e., *Beggiatoa*, *Thioploca*, *Thiomargarita*) and a low biodiversity but high density of protozoan and metazoan life. The main groups are foraminiferans, nematodes, ciliates, flagellates, polychaetes, gastropods and bivalves with specific adaptations, such as high concentrations of haemoglobins, large respiratory surfaces, small thin bodies, high concentrations of pyruvate oxydoreductases and presence of sulphide-oxidising symbionts (Levin 2003; see section 3.3.2.3 for chemosynthetic assemblages in OMZs).

3.3.1.6. ABYSSAL PLAINS

The abyssal plain ecosystem is the largest ecosystem on Earth. It lies beyond the continental slope, between 3,000 and 6,000 m depth. Abyssal plains are covered by a thick layer of fine sediment that can reach thousands of metres in thickness, resulting in the popular picture of a flat, monotonous deep-sea bed. The main characteristics of water masses at abyssal plains are: low temperature ($\sim 2^{\circ}\text{C}$ except in the Mediterranean Sea with 13°C and Red Sea with 21.5°C), salinity (35‰, except in the Mediterranean and Red Sea $>39\text{‰}$), mostly saturated waters with dissolved oxygen (5–6 ml/l), absence of light (light useful for photosynthesis does not reach below ~ 250 m depth) and high pressure (1 atmosphere every 10 m depth). This relatively uniform distribution of physical factors led to the belief that abyssal plains were very stable habitats where physical and biological processes remained unchanged over short and long time scales.

There is now evidence that physical disturbances occur at abyssal plains, causing important biological responses. For example, there are daily and annual tidal variations in the flow of cold dense water close to the seafloor. The effects of these tides on the biological communities are not well understood, but it has been suggested that they could be used by certain species for orientation or for setting internal biological cues for synchronised spawning (Tyler 1988). There are also high-energy, unpredictable events such as benthic storms or turbidity currents that have very considerable disruptive effects on the seafloor, in particular in the redistribution of sediment and consequent biological responses (Aller 1989). Another major environmental factor that greatly affects the benthic communities on abyssal plains is the seasonal deposition of phytodetritus (organic matter produced in the surface waters) following the months of high surface production (Beaulieu and Smith 1998). Because the rapid sinking of this material prevents its complete utilisation by pelagic grazers, the arrival of this organic matter to the seafloor provides the abyssal communities with a seasonal input of high-quality food resource (Ginger et al. 2001; Billett et al. 2001).

The abyssal plains support a very high biodiversity, composed mainly of macro and meiofauna. The meiofauna (size of organisms in the order of microns) is mainly dominated by nematodes and foraminifera (Gooday 1996). The macrofauna (size of organisms in the order of millimetres) is dominated by polychaetes, with small peracarid crustaceans, molluscs, nemertean, sipunculans, echiurans and enteropneusts also abundant

(Grassle and Maciolek 1992). Finally, the large megafauna (size of organisms in the order of centimetres) is made up of holothurians, asteroids, echinoids, decapod crustaceans and fish, as well as sessile fauna such as crinoids, sponges and anthozoans on hard substratum (Gage and Tyler 1991).

Even though abyssal plains have been sampled since the times of the *Challenger* expedition, only a small fraction of the vast extensions of these ecosystems has been studied to date. Latest results obtained from abyssal plain research have shown that variations in primary production in the surface waters can result in long-term changes in the composition of the plain megafauna. For example, there is evidence from the Porcupine Abyssal Plain in the NE Atlantic that an almost non-existent species of small holothurian (*Amperima rosea*) became dominant after 1996 because of its ability to rapidly exploit the nutritional resources of seasonal phytodetritus (Wigham, Tyler and Billett 2003). This indicates the strong link between the abyssal ecosystem and the surface of the biosphere, and has important consequences when considering the effect of factors such as climate change on biodiversity.

3.3.2. Chemosynthetic ecosystems

Deep-water chemosynthetic ecosystems have been known and studied for less than 30 years. The first such ecosystems to be discovered were hydrothermal vents in 1977... 8 years after Neil Armstrong and Buzz Aldrin had walked on the Moon! Then followed the discoveries of other deep-water chemically driven communities such as cold seeps, large organic falls to the deep-sea floor (i.e., whale falls or sunken wood and kelp) and areas of oxygen minimum that intersect with the margin. In chemosynthetic ecosystems, primary production is produced by chemoautotrophic microorganisms that use reduced inorganic chemicals to synthesise organic matter. These organisms are found free living, forming bacterial mats, but also in symbiosis with some of the major invertebrate groups.

3.3.2.1. HYDROTHERMAL VENTS

Hydrothermal vents were discovered in 1977 in the Galapagos Rift, in the Pacific (Lonsdale 1977; Corliss et al. 1979), and since then vents have been found in all ocean basins. Hydrothermal vents occur in mid-ocean ridges,

back-arc basins and certain active seamounts. Mid-ocean ridges are volcanic mountain chains that occur where two tectonic plates are being pulled apart. In these areas, cold seawater (2°C) penetrates through cracks in the crust. During its transition in the mantle, the fluid gets heated as it flows close to the magma chamber that feeds the ridge and is depleted of oxygen and magnesium while being charged with other metals. The superheated fluid (350°C) rises back to the surface of the seafloor, and when it mixes with the surrounding cold and oxygenated seawater, the metals precipitate, providing the aspect of dense black smoke characteristic of hydrothermal vents (photo 3.4).

Among the most striking discoveries at vents were the associated dense biological populations and the trophic structure that sustains these communities. It was unforeseen to find whole dense communities of animals living independently from solar energy by using the energy of reduced chemicals from the Earth's interior via the production of microorganisms (Karl, Wirsen and Jannash 1980; Jannasch and Mottl 1985). But it was even more astonishing to find that these microorganisms also formed symbiotic relationships with most

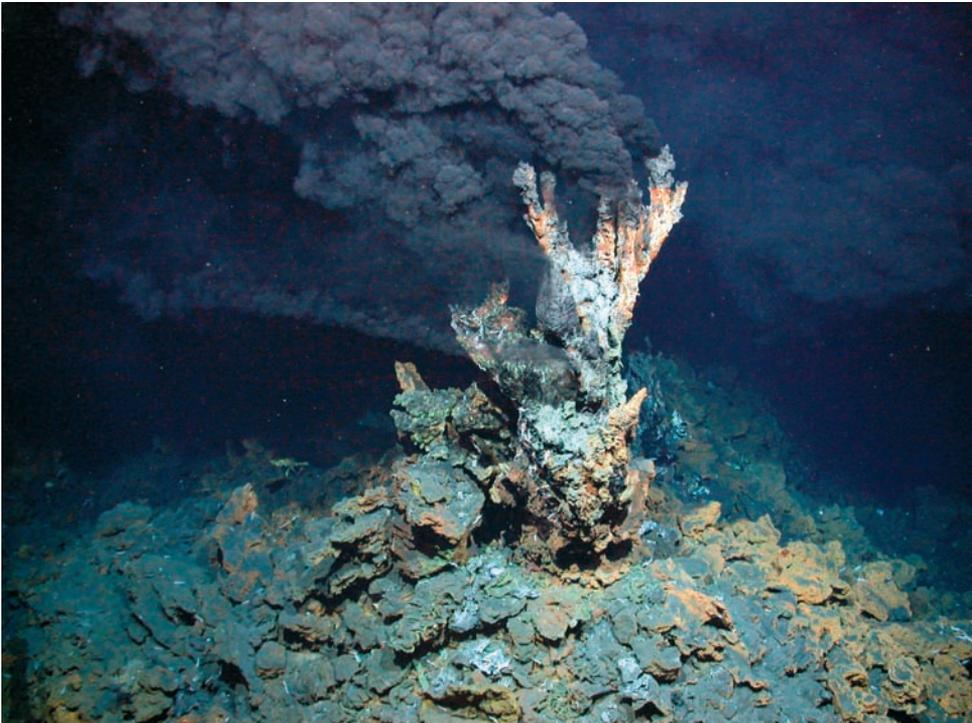


Photo 3.4: Black smoker from the Mid-Atlantic Ridge



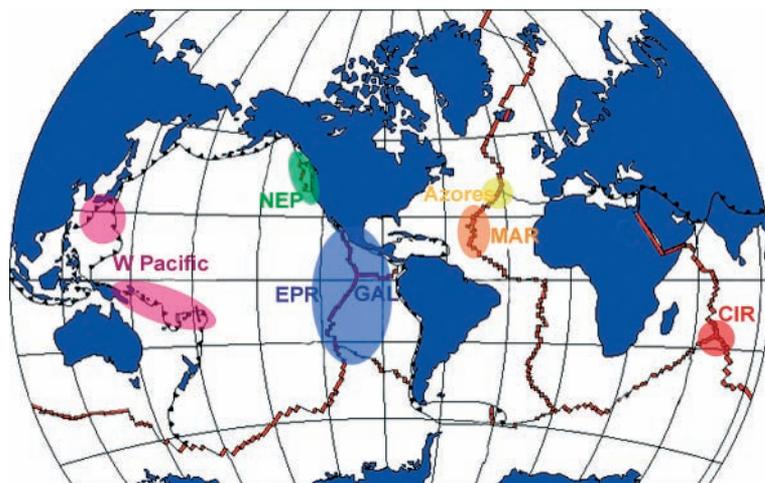
Photo 3.5 (left): Gastropods from the hydrothermal vents of the Lau Basin, in the western Pacific. **Photo 3.6 (right):** Galatheid crabs from Pacific hydrothermal vents

of the major invertebrate groups (Cavanaugh et al. 1981; Felbeck, Childress and Somero 1981), and to observe the variety of adaptations made by these invertebrates to life in hydrothermal vents. One of the most modified is probably the giant tubeworm *Riftia pachyptila* from the Pacific vents (photo 3.2). This animal does not have a mouth or digestive system, but instead has a special organ that fills most of its body, called the trophosome. The trophosome is basically a sack densely packed with chemoautotrophic bacteria. *Riftia* intakes oxygen from the surrounding water and CO_2 and H_2S from the hydrothermal fluid with its highly irrigated plume. The chemicals are sent to the trophosome via the blood vessels where the microorganisms use them to synthesise organic matter. The animal depends completely on this microbial production for its lifelong growth and reproduction. Symbiotic relationships also appear in other groups, such as clams, mussels, shrimp, crabs and polychaetes, with different degrees of dependency.

Hydrothermal vents have been called “oases” of life in the deep-sea floor because of the exuberant aspect of their dense populations of large invertebrates. However, as in other ecosystems with extreme chemicophysical environmental parameters, hydrothermal vent communities are simple systems. Biodiversity is low, but biomass is high, sustained by a constant and abundant supply of energy in the form of reduced chemicals found in the hydrothermal fluids. Since their discovery in 1977, 590 species have been described from

vents, which is the equivalent to around one new description every two weeks (Van Dover et al. 2002). Furthermore, of the almost 600 species described, approximately 400 have been identified so far as endemic to vents. The major faunal groups present are vestimentiferan tubeworms, bathymodiolid mussels, vesicomid clams, bresilid shrimp, crabs, amphipods and polychaetes (photos 3.5 and 3.6). Investigations at hydrothermal vents are still in the extensive exploration phase, with only a small fraction of the over 65,000 km of global ridge system studied to date. However, the data that has been compiled so far indicates that vent fauna form distinct biogeographical regions. In a review by Van Dover et al. (2002), six vent biogeographic regions are recognised, each with specific faunal assemblages (map 3.2). But much exploration and investigation remains to be done before we have a sound understanding of the global diversity of vent species, and the processes that shape their distribution and their functioning.

Map 3.2: The mid-ocean ridge system showing the known hydrothermal vent biogeographic provinces



Hydrothermal vent biogeographic provinces.

Azores: dominated by bathymodiolid mussels, amphipods and caridean shrimp; MAR: Northern MidAtlantic Ridge region dominated by caridean shrimp, mainly *Rimicaris exoculata*, and bathymodiolid mussels; EPR & GAL: East Pacific Rise and Galapagos Rift dominated by vestimentiferan tubeworms, bathymodiolid mussels, vesicomid clams, alvinellid polychaetes, amphipods and crabs. NEP: NE Pacific region, dominated by vestimentiferan tubeworms excluding Riftiidae, polychaetes and gastropods; W Pacific: dominated by bathymodiolid mussels, "hairy" gastropod, vesicomid clams and shrimps; and CIR: Central Indian Ridge, dominated by the shrimp *Rimicaris kairei*, mussels, scale gastropods and anemones.

Map modified from Van Dover et al. 2002.

3.3.2.2. COLD SEEPS

Cold seep communities were discovered in 1983 at approximately 500 m depth in the Western Florida Escarpment in the Gulf of Mexico (Paull et al. 1984). Cold seeps are characterised by the seepage of cold fluid with a high concentration of methane. This methane may have a biological origin, from the decomposition of organic matter by microbial activity in anoxic sediments, or a thermogenic origin, from the fast transformation of organic matter caused by high temperatures (Sibuet and Olu 1998; Levin 2005). Cold seeps also have high concentrations of H₂S in sediments, produced by the bacterial reduction of sulphates using methane. Both methane and sulphide play a major role in sustaining the highly productive cold seep communities (photo 3.7) through chemoautotrophy by free-living and symbiotic bacteria (Paull et al. 1984; Barry et al. 1997). Cold seep communities occur in both passive margins such as the Gulf of Mexico, Carolina slope, Barents Sea, Gulf of Guinea and Angola margin, and in active margins (or subduction zones), mainly in the Pacific, such as the Peru-Chile margin, as well as the Barbados Accretionary Prism and the Eastern Mediterranean among others.



Photo 3.7: A bathymodiolid mussel community in Gulf of Mexico cold seeps



Photo 3.8: Tubeworms of the genus *Lamellibrachia* from Gulf of Mexico cold seeps

As with hydrothermal vents, only a small fraction of the potential locations of cold seeps on margins has been explored to date. We only know around 35 seep sites, and only a small number of these have had their geochemistry and biology studied in any detail (Sibuet and Olu 1998; Kojima 2002; Levin 2005).

Since their discovery, around 230 species have been described from cold seeps. Cold seep habitats are more stable systems than hydrothermal vents. There is also a slow transition of physical and chemical factors between the seep habitat and the heterotrophic surrounding system, allowing for a higher biodiversity than in hydrothermal vents. The megafaunal biomass at seeps by far exceeds that of the surrounding non-chemosynthetic sediment. The major groups are bivalves (mytilids, vesicomyids, lucinids and thyasirids) and vestimentiferan tubeworms, with pogonophoran, sponges, gastropods and shrimps sometimes also abundant (Levin 2005) (photo 3.8).

3.3.2.3. OTHER REDUCING HABITATS

In 1987, Craig Smith, from the University of Hawaii, observed for the first time chemosynthetic communities on a whale skeleton (photo 3.9) that was

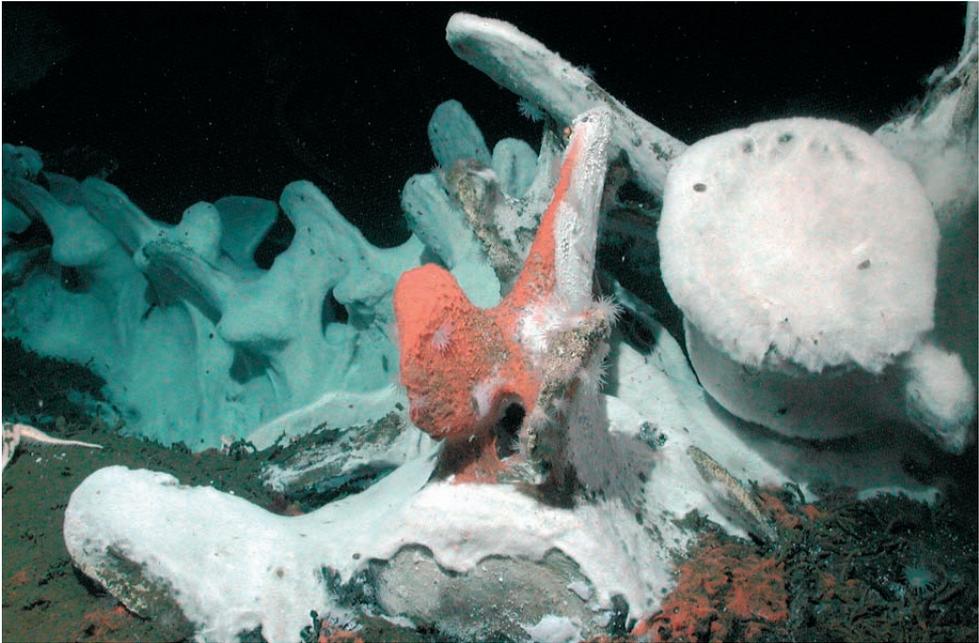


Photo 3.9: Whale skeleton colonised by bacterial mats

found by chance in the North Pacific during a dive with the submersible *Alvin* (Smith et al. 1989).

Since then, the investigation of biological assemblages on whale falls and other large organic falls to the deep-sea floor, such as sunken wood and kelp, has advanced rapidly. In the case of whale falls, there is a three-step ecological progression (Smith and Baco 2003). First, during the scavenger phase, the flesh is eaten and the skeleton left exposed. The opportunistic phase follows, when the sediment and skeleton are colonised by dense populations of opportunistic polychaetes and crustaceans. The final phase is the chemotrophic or sulphophilic phase. The bones of whales are composed 60% of lipids. The anaerobic bacterial degradation of these lipids produces sulphides that are used by chemoautotrophic microorganisms, allowing for the subsequent colonisation of chemically-driven fauna (Smith and Baco 2003).

The biodiversity of fauna colonising these isolated and ephemeral habitats is high. Since their discovery, over 400 morphological species have been described from whale falls, but most of them still remain to be identified. It has been suggested that whale falls could act as stepping stones for dispersal between chemosynthetic ecosystems (Smith et al. 1989). This is sup-

ported by the fact that the three habitats share a number of species and an even higher number of groups at higher taxonomic levels (Smith and Baco 2003).

Finally, chemosynthetic-related communities can also develop in OMZs (see section 3.3.1.5). A large number of heterotrophs in OMZs consume chemoautotrophic bacteria by grazing on bacterial mats or preying on other animals that have done so (Gallardo et al. 1995). The presence of endosymbiotic sulphur-oxidising bacteria is also widespread in foraminiferans, flagellates, ciliates, some polychaetes and some bivalves (Levin 2005). The details of the metabolic interactions between host and symbiont remain unknown, as does the extent to which chemosynthesis provides nutrients to the OMZ benthos. But ongoing and future research will no doubt extend the list of these types of relationships, and help explain the phylogenetic and evolutionary links with fauna from other deep-water chemosynthetic ecosystems.

Of all the described species from hydrothermal vents, cold seeps and whale falls, 18 are shared between vents and seeps, 11 are shared between vents and whales, 20 are shared between seeps and whales, and 7 are shared amongst the three habitats (Tunnicliffe, McArthur and McHugh 1998; Smith et al. 2003). However, these numbers will change in parallel with new discoveries and further investigation of known sites that will improve our knowledge of the diversity and distribution of species from deep-water chemosynthetic habitats and the processes driving them.

3.4. TECHNOLOGY AND DEEP-SEA EXPLORATION

Since the early oceanographic expeditions of the 19th century, the exploration and investigation of the deep sea has evolved in parallel with technological advances. The international oceanographic fleet is large and diverse, equipped with deep-tow and deep-coring cables for the use of deep seafloor sampling instruments.

Before the study of any biological community, the geophysical characteristics of the habitat need to be determined. The first step is the use of hull-mounted multi-beam swath bathymetry, a standard feature used on most modern research ships to produce bathymetric maps of the seafloor. More detailed acoustic maps can be obtained with deep-towed sidescan sonars (photo 3.10).



Photo 3.10: TOBI (Towed Ocean Bottom Instrument) is one of the UK deep sidescan sonars used to produce acoustic maps of the deep seafloor

These instruments are towed behind the ship at around 500 m above the seafloor, and produce acoustic images of the seafloor complete with detailed geophysical information, such as the presence of sediment or hard substratum, elevations and depressions. Studying the water column with instruments like CTDs that can measure conductivity, temperature and depth continuously during a vertical deployment is an important means to characterise the physical parameters of the water mass overlaying the benthic habitat under study.

In biological studies of deep-sea fauna, the most widely used equipment has traditionally included deep trawls for collecting megafauna; multicorers and megacorers to obtain quantitative samples of sediment cores with intact sediment-water interfaces used for organic chemistry, nutrient analyses and meiofauna studies; boxcorers for quantitative samples of macrofauna; sediment traps for studies of phytodetritus input to the seafloor; and current meters for the analysis of physical parameters. The study of deep-sea ecosystems moved a step forward when we acquired the capacity of visualising the habitat with photographic and video tools. Deep-towed vehicles equipped with photographic and video cameras have been very useful to describe the ecosystems *in situ*, and to provide spatial and distribution information that is lost in trawl samples. These instruments are also very efficient in habitats of difficult terrain, such as canyons, seamounts or deep-water corals, where trawling or coring is difficult or even impossible.

One of the most important technological advances for oceanography in modern times has been the development of manned submersibles, remote operated vehicles (ROVs) and autonomous underwater vehicles (AUVs). Submersibles and ROVs not only allow the direct visualisation of the seafloor and its fauna, but also provide the capability for directed and detailed sampling as well as *in situ* experimentation. These vehicles are crucial in the study of deep-water chemosynthetic ecosystems. A number of submersibles and ROVs are now available from a variety of nations (table 3.1, photo 3.11).

A number of new oceanographic vessels are being built today, such as the Spanish *B.O. Sarmiento de Balboa*, the French *N/O Pourquoi Pas?* or the British *RRS James Cook*, and all of them are being equipped with the capability to deploy and use submersibles and/or ROVs. Another area of technological development is AUV technology. AUVs allow for the investigation of areas of difficult or no accessibility, such as the seafloor under ice in the Arctic and Antarctic oceans. Recently, AUVs have been used for the exploration and location of hydrothermal vents. For example, an AUV such as ABE (WHOI, USA) can be used as the last step of a ridge section survey, providing

Table 3.1: Human-Occupied Submersibles (SUB) and Remote Operated Vehicles (ROV) currently used for research in chemosynthetic ecosystems

Name	Vehicle Type	Organisation	Country	Depth Capability
<i>Ropos</i>	ROV	CSSF	Canada	6,000 m
<i>Nautile</i>	SUB	Ifremer	France	6,000 m
<i>Robin</i>	ROV	Ifremer	France	3,000 m
<i>Victor 6000</i>	ROV	Ifremer	France	6,000 m
<i>Jago</i>	SUB	MPI Seewiesen	Germany	400 m
<i>Quest</i>	ROV	Bremen University	Germany	4,000 m
<i>Cherokee</i>	ROV	Bremen University	Germany	1,000 m
<i>Shinkai 2000</i>	SUB	JAMSTEC	Japan	2,000 m
<i>Shinkai 6500</i>	SUB	JAMSTEC	Japan	6,500 m
<i>Dolphin 3k</i>	ROV	JAMSTEC	Japan	3,300 m
<i>Aglanta</i>	ROV	Bergen University	Norway	2,000 m
<i>Argus</i>	ROV	Bergen University	Norway	2,000 m
<i>Bathysaurus</i>	ROV	Bergen University	Norway	5,000 m
<i>MIR 1 y MIR 2</i>	SUB	Shirshov Institute	Russia	6,000 m
<i>Isis</i>	ROV	NOC (Southampton)	UK	6,500 m
<i>PISCES IV y PISCES V</i>	SUB	HURL (Hawaii)	USA	2,000 m
<i>Alvin</i>	SUB	WHOI	USA	4,500 m
<i>Deepworker</i>	SUB	Nuytco Ltd (for NOAA-OE)	USA	600 m
<i>Johnson Sea Link 1</i>	SUB	HBOI	USA	900 m
<i>Hercules</i>	ROV	IFE	USA	4,000 m
<i>Jason</i>	ROV	WHOI	USA	6,000 m
<i>Tiburon</i>	ROV	MBARI	USA	4,000 m

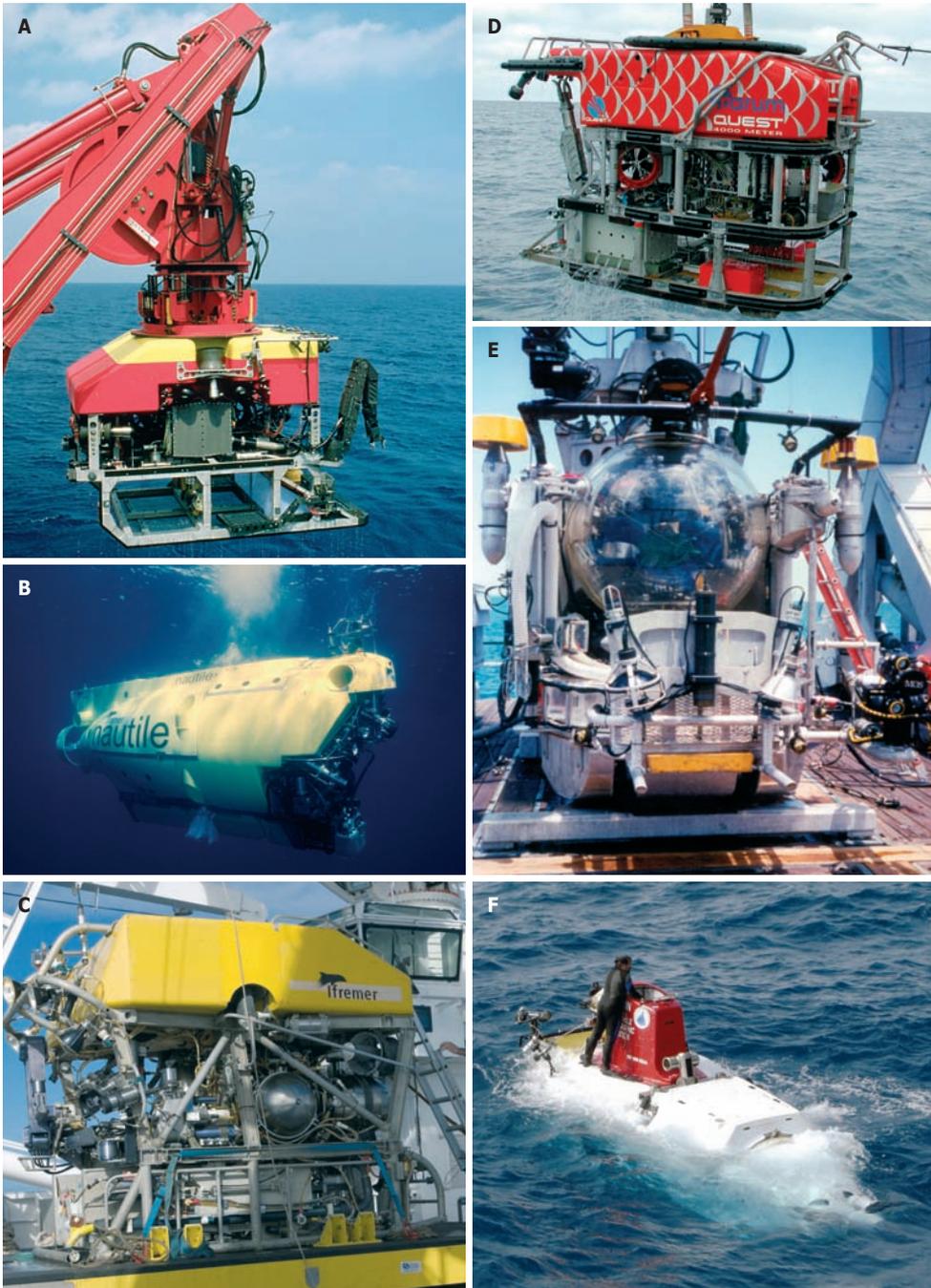


Photo 3.11: Examples of the international fleet of piloted submersibles and remote operated vehicles used for deep-sea research. A: British ROV *Isis*; B: French submersible *Nautilus*; C: French ROV *Victor*; D: German ROV *Quest*; E: North American submersible *Johnson Sea Link*; F: North American submersible *Alvin*.

the exact location and first photographic evidence of new vent sites in a single exploratory cruise (photo 3.12).

The development of new technologies is also important in laboratory and analysis methodologies. For example, marine molecular techniques have been evolving rapidly. The molecular approach provides the necessary tools to identify cryptic species and discriminate between populations and metapopulations, as well as to measure gene flow and analyse phylogenetic relationships between species of different habitats, phylogeography and evolution (Shank, Lutz and Vrijenhoek 1999). Developments in stable isotope and biomarker analyses have also been essential in the study of the trophic structure of deep-water chemosynthetic communities. For example, stable isotopes have been used to differentiate between heterotrophic and chemotrophic feeding behaviours in chemosynthetic ecosystems (Van Dover and Fry 1994). In the case of biomarkers, these analyses have been used to understand the role played by the small holothurian *Amperima rosea* in the observed long-term faunal change in the Porcupine Abyssal Plain, NE Atlantic (Wigham, Tyler and Billett 2003).

Also, the use of hyperbaric chambers is very important when working with live deep-sea animals. Pressure chambers vary in size and capabilities, from



Photo 3.12: The underwater vehicle ABE from the Woods Hole Oceanographic Institution, USA

small, single chambers made of a titanium cylinder for embryological analyses (Young et al. 1996) to large equipment such as the French IPOCAMP (Incubateur Pressurisé pour l'Observation et la Culture d'Animaux Marins Profonds) that can be taken to sea, and where large invertebrates can be exposed to varying pressures and temperatures while their responses are visualised continuously (Shillito et al. 2001). This system has been used for experimental studies of hydrothermal vent fauna. One of the major challenges for deep-water research is to find new ways to collect fauna avoiding depressurisation and changes in temperature during recovery.

3.5. MAJOR EUROPEAN DEEP-SEA RESEARCH PROGRAMMES

Our knowledge of deep-sea ecosystems is at a very early stage, where exploration plays a major role. To understand the processes that drive the different deep-sea habitats as well as the functioning of the ecosystem as a whole, deep-sea research needs to be multidisciplinary. To achieve these objectives and mobilise efficient teams, an international approach involving both small and large countries with a range of capabilities is essential both for economic and scientific reasons. The exploration and investigation of the deep sea requires the use of large platforms (i.e., research ships, observatories) and the continuous refinement of state-of-the-art technologies (i.e., deep-water vehicles, laboratory methodologies, see section 3.4). Because of its remoteness and the logistics and financial constraints related to the study of the deep sea, the investigation of its ecosystems requires the development of international and multidisciplinary programmes that allow access to large-scale facilities and expertise across national boundaries. These issues are being addressed around the world by international and multidisciplinary research collaborations. Some examples are given below.

3.5.1. CoML (www.coml.org)

The Census of Marine Life (CoML) is a growing network of scientists in over 70 nations engaged in a ten-year initiative (2000–2010) for the assessment and understanding of diversity, distribution and abundance of life in the oceans; past, present and future (O'Dor and Gallardo 2005; Yarincik and O'Dor 2005). The CoML initiative is funded by the A.P. Sloan Foundation (NYC, USA). There are 14 field projects in the CoML that cover the major marine ecosystems, from the intertidal to the abyssal plains. Four of these projects are devoted to deep-sea

research and, although international in nature, are led from European laboratories: ChEss (UK and Spain), MAR-ECO (Norway), CoMargE (France) and CeDAMar (Germany). The aim of ChEss is to study the biogeography of chemosynthetic ecosystems at the global scale. ChEss has four priority areas where field projects are being developed (see www.noc.soton.ac.uk/chess), and where international coordination and the sharing of human and infrastructure resources is essential. MAR ECO (www.mar-eco.no) is studying the pelagic and benthic non-chemosynthetic communities over the northern Mid-Atlantic Ridge. CoMargE (www.coml.org/descrip/c-margins.htm) focuses on the study of continental margins at the global scale, by comparing known data from past and ongoing projects, and developing new research. CeDAMar (www.cedamar.org) is studying life in, on and above the seafloor of abyssal plains. CeDAMar has a number of ongoing research projects in the Atlantic, Southern Ocean, Pacific and Indian Ocean. Furthermore, there are a number of other CoML projects that have direct scientific links to deep-sea research, such as the seamounts, microbes, Arctic and Antarctic projects. Finally, one of the long-term legacies of the CoML initiative will be OBIS, the Ocean Biogeographic Information System (www.iobis.org). OBIS is a web-based provider of global geo-referenced information on marine species for all data generated from CoML projects and other associated research programmes. It is a network of online databases integrated in a single portal.

3.5.2. MarBEF (www.marbef.org)

MarBEF (Marine Biodiversity and Ecosystem Functioning) is a Network of Excellence funded by the European Commission and composed of 78 European marine institutes. The aim of the MARBEF network is to integrate and disseminate knowledge and expertise on marine biodiversity, with links to researchers, industry, stakeholders and the general public. MarBEF has a deep-sea component (DEEPSETS, Deep-sea & Extreme Environments, Patterns of Species and Ecosystem Time-Series) formed by 11 European laboratories with excellence in deep-sea multidisciplinary research. Two PhD positions have been funded through DEEPSETS; one to study biodiversity and long-term change in abyssal metazoan meiofauna, and one to study biodiversity and long-term change in chemosynthetic communities. In parallel, workshops are organised on specific taxonomic groups and ecological issues, to ensure the transmission of knowledge from senior investigators to new, young scientists who will be leading research at the European level in the future.

3.5.3. HERMES (www.eu-hermes.net)

HERMES (Hotspot Ecosystem Research on the Margins of European Seas, 2005-2009) is an integrated project funded by the European Commission's Framework Six Programme and comprising 45 partners, including 9 SMEs, from 15 European countries. The project brings together expertise in biodiversity, geology, sedimentology, physical oceanography, microbiology and biogeochemistry for the study of hotspot ecosystems on continental margins. The main focus will be to determine the relationships between biodiversity and ecosystem functioning on sediment slopes in areas of land slides, deep-water corals, canyons, anoxic sediments driven by microbial communities and cold seeps.

HERMES will innovate by studying the whole European continental margin, allowing for the integration of data generated from a variety of disciplines in a range of geographical regions. This will facilitate comparison across contrasting but linked ecosystems, as well as providing the necessary data for management options across national boundaries. Research cruises, sampling and laboratory analyses will use state-of-the-art technologies and links are being established with other programmes such as ChEss and CoMargE from the Census of Marine Life.

3.6. MANAGEMENT AND CONSERVATION

The deep sea is the largest ecosystem on Earth and a reservoir of (still unknown) biodiversity. It is also one of the least studied habitats. But with the rapid development of new technologies, industries such as oil and gas exploitation, deep-water fishing or mining are rapidly entering deep-water territories. These human-based activities, as well as the use of the deep sea for dumping toxic material, are affecting a fragile ecosystem, in some cases before we even understand the diversity and functioning of faunal communities. Anthropogenic disturbance is especially important in the deep sea, because species often have long lives, with slow growth and delayed maturation, making recovery from disturbance a long process and even, in some cases, causing the extinction of a population. Some of the most endangered ecosystems are deep-water corals, seamounts and commercially fished species.

In the European Economic Zone, many areas of deep-sea fishing overlap with coral regions (Freiwald et al. 2004), and there is now evidence of important trawling damage to these ecosystems in the Atlantic. Fishing damage to deep-water coral reefs does not only lead to biodiversity loss, but also ecosystem

destruction and therefore habitat loss, affecting a large number of species. This is especially important in an ecosystem with long-lived species for the reasons stated above. In recent years, several initiatives have been developed for the protection of deep-water corals. The Convention on the Protection of the Marine Environment in the North-East Atlantic (OSPAR Convention) identified deep-water corals as one of the most vulnerable ecosystems where action is required. Also, the EC granted emergency protection to an area of cold-water coral off NW Scotland (Darwin Mounds) in 2003, and in 2004 proposed a ban on bottom trawling around areas of coral reefs in the Azores, Madeira and Canary Islands, while in 2004 Canada's Department of Fishing and Oceans (DFO) ordered the closure of a *Lophelia* area off Nova Scotia.

The hydrographic characteristics of seamounts give them a high productivity that attracts large animals, among which commercial fishes are often found. The result has been an increasing interest and exploitation of biological resources around seamounts, even before their ecosystems have been characterised and their biodiversity properly studied. This led the OSPAR Convention and the World Wide Fund for Nature (WWF) to recognise seamounts as biodiversity hotspots and a high priority for environmental management. New Zealand, Australia and Canada have taken steps towards the conservation and protection of these ecosystems, but no such protective measures are available in European waters. Deep-water fishing has also caused the near-collapse of commercial species populations in certain areas, such as orange roughy (*Hoplostethus atlanticus*) fisheries between 750 and 1,200 m depth over seamounts in New Zealand waters. These fisheries are now managed with strict catch quotas. To avoid overexploitation of commercial species as well as damage to the yet unknown deep-sea benthic habitat in the Mediterranean, the scientific community in collaboration with IUCN (World Conservation Union) and WWF obtained a legal ban on bottom trawling beyond 1,000 m and driftnet fishing, affecting all countries bordering the Mediterranean, as approved at the 29th session of the General Fisheries Commission for the Mediterranean (GFCM), held in Rome in 2005. This is known as the Principle of the Precautionary Approach, applied in this case to the protection of a rich but still unknown marine ecosystem comprising a variety of hotspot habitats such as cold seeps, deep-water corals, canyons, brine pools and seamounts.

The exploration and exploitation of hydrocarbons (e.g., gas, oil) is also moving rapidly into deeper waters. The effects of extraction platforms and exploitation processes on the surrounding ecosystems are still relatively unknown, but the

oil and gas industries have been working more closely with scientists to obtain sound data on biodiversity and ecosystem functioning for the development of efficient management practices in potentially exploitable areas.

As regards the mining of regions in international waters, the International Seabed Authority is the UN agency in charge of developing rules, regulations and procedures for the exploitation of mineral resources in the “Area” (seafloor beyond the limits of national jurisdiction), with a view to their sustainable administration. The ISA will grant countries mining rights in specified areas (e.g., for polymetallic nodules, sulphur deposits, ferromanganese crusts), while keeping a percentage of the same for conservation. The ISA is working closely with both scientists and industry to provide the international community with regulations for the management of resources and conservation of ecosystems and biodiversity in the “Area”.

REFERENCES

- ALLER, J. Y. “Quantifying sediment disturbance by bottom currents and its effect on benthic communities in a deep-sea western boundary zone”. *Deep-Sea Research* 36 (1989): 901-934.
- BARRY, J. P., R. E. KOICHEVAR, J. HASHIMOTO, Y. FUJIWARA, K. FUJIKURA, and H. G. GREENE. “Studies of the physiology of chemosynthetic fauna at cold seeps in Sagami Bay, Japan”. *JAMSTEC Journal of Deep Sea Research* 13 (1997): 417-423.
- BEAULIEU, S. E., and K. L. J. SMITH. “Phytodetritus entering the benthic boundary layer and aggregated on the sea floor in the abyssal NE Pacific: macro- and microscopic composition”. *Deep-Sea Research II* 45 (1998): 781-815.
- BILLETT, D. S. M., B. J. BETT, A. L. RICE, M. H. THURSTON, J. GALÉRON, M. SIBUET, and G. A. WOLFF. “Long-term change in the megabenthos of the Porcupine Abyssal Plain”. *Progress in Oceanography* 50 (2001): 325-348.
- CAVANAUGH, C. M., S. L. GARDINER, M. L. JONES, H. W. JANNASCH, and J. B. WATERBURY. “Prokaryotic cells in hydrothermal vent tube worm *Riftia pachyptila* Jones: possible chemoautotrophic symbionts”. *Science* 213 (1981): 340-342.
- 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, and T. H. VAN ANDEL. “Submarine thermal springs on the Galapagos Rift”. *Science* 203 (1979): 1073-1083.
- FELBECK, H., J. J. CHILDRESS, and G. N. SOMERO. “Calvin-Benson cycle and sulfide oxidation enzymes in animals from sulfide-rich habitats”. *Nature* 293 (1981): 291-293.
- FORGES, B. R. DE, J. A. KOSLOW, and G. C. B. POORE. “Diversity and endemism of the benthic seamount fauna in the southwest Pacific”. *Nature* 405 (2000): 944-947.
- FREIHALD, A. “Reef-forming cold-water corals”. In G. Wefer, D. S. M. Billett, D. Hebbeln, B. B. Jorgensen, M. Schluter and T. C. E. Van Weering. *Ocean Margin Systems. Hanse conference report*. Berlin: Springer, 2002, 365-385.
- FREIHALD, A., J. H. FOSSÅ, A. GREHAN, T. KOSLOW, and J. M. ROBERTS. *Cold-water Coral Reefs*. Cambridge, UK: UNEP-WCMC, 2004.

- GAGE, J. D. "Benthic biodiversity across and along the continental margin: patterns, ecological and historical determinants and anthropogenic threats". In G. Wefer, D. S. M. Billett, D. Hebbeln, B. B. Jorgensen, M. Schluter and T. C. E. Van Weering. *Ocean Margin Systems. Hanse conference report*. Berlin: Springer, 2002, 307-321.
- GAGE, J. D., AND P. A. TYLER. *Deep-sea biology. A natural history of organisms at the deep-sea floor*. Cambridge: Cambridge University Press, 1991.
- GALLARDO, V. A., F. D. CARRASCO, R. ROAR, and J. I. CAÑETES. "Ecological patterns in the benthic microbiota across the continental shelf off Central Chile". *Ophelia* 40 (1995): 167-188.
- GINGER, M. L., D. S. M. BILLETT, K. L. MACKENZIE, K. KIRIAKOULAKIS, R. R. NETO, D. K. BOARDMAN, V. L. C. S. SANTOS, I. M. HORSFALL, and G. A. WOLFF. "Organic matter assimilation and selective feeding by holothurians in the deep sea: some observations and comments". *Progress in Oceanography* 50 (2001): 407-421.
- GOODAY, A. J. "Epifaunal and shallow infaunal foraminiferal communities at three abyssal NE Atlantic sites subject to differing phytodetritus input regimes". *Deep-Sea Research I* 43 (1996): 1395-1421.
- GRASSLE, J. F. "Slow recolonisation of deep-sea sediment". *Nature* 26 (1977): 618-619.
- GRASSLE, J. F., and N. J. MACIOLEK. "Deep-sea richness: regional and local diversity estimates from quantitative bottom samples". *American Naturalist* 139 (1992): 313-341.
- GRASSLE, J. F., and H. L. SANDERS. "Life histories and the role of disturbance". *Deep-Sea Research* 20 (1973): 643-659.
- HESSLER, R. R., and H. L. SANDERS. "Faunal diversity in the deep sea". *Deep-Sea Research* 14 (1967): 65-78.
- JANNASCH, H. W., and M. J. MOTTL. "Geomicrobiology of deep-sea hydrothermal vents". *Science* 229 (1985): 717-725.
- KARL, D. M., C. O. WIRSEN, and H. W. JANNASCH. "Deep-sea primary production at the Galapagos hydrothermal vents". *Science* 207 (1980): 1345-1347.
- KOJIMA, S. "Deep-sea chemoautotrophy-based communities in the northwestern Pacific". *Journal of Oceanography* 58 (2002): 343-363.
- KOSLOW, J. A., K. GOLETT-HOLMES, J. K. LOWRY, T. O'HARA, G. C. B. POORE, and A. WILLIAMS. "Seamount benthic macrofauna off southern Tasmania: Community structure and impacts of trawling". *Marine Ecology Progress Series* 213 (2001): 111-125.
- LEVIN, L. A. "Oxygen minimum zone benthos: adaptation and community response to hypoxia". *Oceanography and Marine Biology: An Annual Review* 41 (2003): 1-45.
- LEVIN, L. A. "Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes". *Oceanography and Marine Biology: An Annual Review* 43 (2005): 1-46.
- LONSDALE, P. "Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers". *Deep-Sea Research* 24 (1977): 857-863.
- MCCAVE, I. N. "Sedimentary settings on continental margins – an overview". In G. Wefer, D. S. M. Billett, D. Hebbeln, B. B. Jorgensen, M. Schluter and T. C. E. Van Weering. *Ocean margin systems. Hanse conference report*. Berlin: Springer, 2002, 1-14.
- MURRAY, J., and J. HJORT. *The Depths of the Ocean*. London, 1912.
- O'DOR, R., and V. A. GALLARDO. "How to Census Marine Life: ocean realm field projects". *Scientia Marina* 69, suppl. 1 (2005): 181-199.

- PAULL, C. K., B. HECKER, R. COMMEAU, R. P. FREEMAN-LYNDE, C. NEUMAN, W. P. CORSO, S. GOLUBIC, J. E. HOOK, J. E. SIKES, and J. CURRAY. "Biological communities at the Florida Escarpment resemble hydrothermal vent taxa". *Science* 226 (1984): 965-967.
- ROGERS, A. D. "The biology of seamounts". *Advances in Marine Biology* 30 (1994): 305-350.
- ROGERS, A. D. "The role of the oceanic oxygen minima in generating biodiversity in the deep sea". *Deep-Sea Research II* 47 (2000): 119-148.
- SARDÀ, F, J. B. COMPANY, and A. CASTELLÓN. "Intraspecific aggregation structure of a shoal of a western Mediterranean (Catalan coast) deep-sea shrimp, *Aristeus antennatus* (Risso, 1816), during the reproductive period". *Journal of Shellfish Research* 22 (2003): 569-579.
- SHANK, T. M., R. A. LUTZ, and R. C. VRIJENHOEK. "Miocene radiation of deep-sea hydrothermal vent shrimp (Caridea: Bresiliidae): evidence from mitochondrial Cytochrome Oxidase subunit I". *Molecular Phylogenetics and Evolution* 13 (1999): 244-254.
- SHILLITO, B., D. JOLLIVET, P. M. SARRADIN, P. RODIER, F. LALLIER, D. DESBRUYÈRES, and F. GAILL. "Temperature resistance of *Hesiolyra bergi*, a polychaetous annelid living on deep-sea vent smoker walls". *Marine Ecology Progress Series* 216 (2001): 141-149.
- SIBUET, M., and K. OLU. "Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins". *Deep-Sea Research II* 45 (1998): 517-567.
- SMITH, C. R., H. KUKERT, R. A. WHEATCROFT, P. A. JUMARS, and J. W. DEMING. "Vent fauna on whale remains". *Nature* 341 (1989): 27-28.
- SMITH, C., and A. BACO. "The ecology of whale falls at the deep-sea floor". *Oceanography and Marine Biology Annual Review* 41 (2003): 311-354.
- STUART, C. T., M. A. REX, and R. J. ETTER. "Large-scale spatial and temporal patterns of deep-sea benthic species diversity". In P. A. Tyler, ed. *Ecosystems of the Deep Oceans. Ecosystems of the World*. Amsterdam: Elsevier, 2003, 295-311.
- TUNNICLIFFE, V., A. G. MCARTHUR, and D. MCHUGH. "A biogeographical perspective of the deep-sea hydrothermal vent fauna". *Advances in Marine Biology* 34 (1998): 353-442.
- TYLER, P. A. "Seasonality in the deep-sea". *Oceanography and Marine Biology: An Annual Review* 26 (1988): 227-258.
- VAN DOVER, C. L., and B. FRY. "Microorganisms as food resources at deep-sea hydrothermal vents". *Limnology and Oceanography* 39 (1994): 51-57.
- VAN DOVER, C. L., C. R. GERMAN, K. G. SPEER, L. M. PARSON, and R. C. VRIJENHOEK. "Evolution and biogeography of deep-sea vent and seep invertebrates". *Science* 295 (2002): 1253-1257.
- WIGHAM, B., P. A. TYLER, and D. S. M. BILLETT. "Reproductive biology of the abyssal holothurian *Amperima rosea*: an opportunistic response to variable flux of surface derived organic matter?". *Journal of the Marine Biological Association of the United Kingdom* 83 (2003): 175-188.
- WOLLAST, R. "Continental margins: Review of geochemical settings". In G. Wefer, D. S. M. Billett, D. Hebbeln, B. B. Jorgensen, M. Schluter and T. C. E. Van Weering. *Ocean Margin Systems. Hanse conference report*. Berlin: Springer, 2002, 15-31.
- YARINCIK, K., and R. O'DOR. "The Census of Marine Life: goals, scope and strategy". *Scientia Marina* 69, suppl. 1 (2005): 201-208.
- YOUNG, C. M., E. VÁZQUEZ, A. METAXAS, and P. A. TYLER. "Embryology of vestimentiferan tube worms from deep-sea methane/sulphide seeps". *Nature* 381 (1996): 514-516.

LIST OF PHOTOS AND ILLUSTRATIONS

Photo 3.1:	<i>Anoplogaster cornuta</i> , deep-sea Atlantic fish. © David Shale/naturepl.com	64
Photo 3.2:	The giant tubeworm <i>Riftia pachyptila</i> from the East Pacific Rise hydrothermal vents. © D. Desbruyères/IFREMER	67
Photo 3.3:	Deep-sea corals observed by French ROV <i>Victor 2000</i> at a depth of 1,650 m in the NE Atlantic. © K. Olu/IFREMER-Caracole	71
Photo 3.4:	Black smoker from the Mid-Atlantic Ridge. . © K. Haase/MARUM-University of Bremen	75
Photo 3.5:	Gastropods from the hydrothermal vents of the Lau Basin, in the western Pacific. © C. Fisher/PSU	76
Photo 3.6:	Galatheid crabs from Pacific hydrothermal vents. © R. Lutz	76
Photo 3.7:	A bathymodiolid mussel community in Gulf of Mexico cold seeps. © Ian MacDonald/Texas A&M-Corpus Christi Univ.	78
Photo 3.8:	Tubeworms of the genus <i>Lamellibrachia</i> from Gulf of Mexico cold seeps. © C. Fisher/PSU	79
Photo 3.9:	Whale skeleton colonised by bacterial mats. © C. Smith/University of Hawaii	80
Photo 3.10:	TOBI (Towed Ocean Bottom Instrument) is one of the UK deep sidescan sonars used to produce acoustic maps of the deep seafloor. © Eva Ramírez Llodra/NOC Southampton	82
Photo 3.11:	Examples of the international fleet of piloted submersibles and remote operated vehicles used for deep-sea research. A: © H. Luppi/NOCS; B: © D. Desbruyères/IFREMER; C: © Gouillow/IFREMER; D: © Bremen University; E: © Eva Ramírez Llodra/HBOI; F: © C. German/WHOI	84
Photo 3.12:	The underwater vehicle ABE from the Woods Hole Oceanographic Institution, USA. © C. German/WHOI	85
Table 3.1.	Human-Occupied Submersibles (SUB) and Remote Operated Vehicles (ROV) currently used for research in chemosynthetic ecosystems	83
Map 3.1:	Bathymetric map of a section of the Catalan Sea (Eastern Mediterranean) showing canyon systems	70
Map 3.2:	The mid-ocean ridge system showing the known hydrothermal vent biogeographic provinces	77

ABOUT THE AUTHORS

David Billett is head of the DEEPSEAS Group at the National Oceanography Centre, Southampton, UK. He is interested in how climate change affects deep-sea ecosystems, the biodiversity of continental margin and abyssal plain ecosystems and applying knowledge on deep-sea ecology to the management of deep ocean resources.

e-mail: dsmb@noc.soton.ac.uk

Eva Ramírez Llodra is currently a research fellow working between the Institute of Marine Sciences (CMIMA-CSIC) in Barcelona, Spain and the National Oceanography Centre (NOC), Southampton, UK. Her main research interests are the reproductive patterns and larval ecology of deep-sea species with attention to the forces driving these communities, their geographic distribution and the effects of increasing anthropogenic pressure on a poorly known ecosystem.

e-mail: ezs@icm.csic.es