

*Overview of Recent, Ongoing, and Future Investigations on the*

# *Dynamics and Evolution of European Margins*

BY JÜRGEN MIENERT, PHILIP P.E. WEAVER, SERGE BERNÉ, WOLF CHRISTIAN DULLO,  
DAN EVANS, ANDRÉ FREIWALD, JEAN-PIERRE HENRIET, B.B. JOERGENSEN, GILLES LERICOLAIS,  
VASILIOS LYKOUSIS, JOHN PARKES, FABIO TRINCARDI, AND GRAHAM WESTBROOK

Over the last 15 years marine scientists in Europe have come together to work on a range of scientific problems related to the geological, physical, chemical, and biological processes that control the functioning of the ocean margin system, the most important area for our natural marine resources. These projects have been commissioned due to the increasing need to understand the offshore environment, especially since its exploitation by the hydrocarbon, telecommunication cable, and fishing industries is increasing rapidly. The most recently funded projects have been brought together by two overarching projects that create clusters of related science activities. The EU-

funded OMARC (Ocean Margin Deep Water Research Consortium) project links 13 EU-funded projects on continental margins. The European Science Foundation (ESF)-funded EUROMARGINS (for example Slope Stability on Europe's Passive Continental Margins) program includes 14 projects that study a range of European margin settings from the active margins of the Mediterranean Sea to the passive high-latitude margins of the Northeast Atlantic.

Generally speaking, the European margin can be divided into two different tectonic settings: (1) Atlantic margins, consisting of rifted and shear margin segments where continental break up has

led to the formation of new lithosphere, and (2) convergent Mediterranean margins where lithosphere has subducted beneath continental crust, causing frequent and high-amplitude earthquakes. In addition, major contrasts in geological processes exist due to the formerly glaciated margin setting in the north and a river-dominated margin in the south (see Canals et al., this issue).

As scientists discovered more about different areas of the European margin, it has become clear that we may be able to achieve a much better understanding of strata formation and related physical and biological processes by integrating climate and tectonic variability. So far,



Norwegian Margin

Vøring Plateau

Faeroe-Shetland Margin

Rockall Margin

Porcupine Margin

Celtic Margin

Aarmorican Margin

Iberian Margin

Europe

Mediterranean Sea

Canary Islands

Africa



Over the last 15 years marine scientists in Europe have come together to work on a range of scientific problems related to the geological, physical, chemical, and biological processes that control the functioning of the ocean margin system, the most important area for our natural marine resources.

the major controlling processes investigated include changes in global sea level, oceanographic regime, and sediment fluxes that are strongly influenced by climate variability. Another important study was to understand the controlling processes from the deep to the shallow biosphere and the biosphere's coupling to the geosphere, which may be influenced by tectonic variability.

The most recently funded projects are briefly described below. Each project involves a number of partner laboratories from a range of European countries. These projects are in various stages of progression; some have recently been completed, while others have barely started.

#### ACTIVE SEDIMENTARY PROCESSES AND THE STRATAL RECORD

A number of projects within the OMARC cluster are related to sediment dynamics. These projects aim to understand a complete sedimentary system from source to sink, and contribute to better modelling of inorganic and organic particle transport along transects from rivers to the shallow shelf and from canyons to the deep sea. These projects

focus efforts at contrasting sectors of the Northeast Atlantic and Mediterranean margins. Major goals of this cluster of projects are: determine the temporal and spatial variability of the governing sediment transport processes, pathways, and fluxes; determine their contribution and role in the construction of the margin's sedimentary strata; and understand the architecture of the sedimentary record.

#### EURODELTA (European Coordination on Mediterranean Prodeltas)

Prodeltas are large, shallow-marine features located seaward of river mouths that are characterized by significant mud accumulation at water depths below the level that storm waves can destroy. On the Mediterranean and Black Sea shelves (Figure 1), prodelta deposits up to tens of meters thick are extensive, shore-parallel, and mud-dominated. These deposits formed approximately 5 kyr Ma (thousand years ago) under the influence of fluvial supply and marine processes and constitute shallow areas of rapid sediment accumulation and intense exploitation (e.g., trawling, mussel cultivation, cables, pipelines, platforms).

In view of the considerable economic and societal importance of European

coasts, it is necessary to establish how prodeltas developed and evolved, how vital they are to the long-term stability of coastal regions, and how they can be best managed to sustain economic activities and the natural environment. The

---

**Jürgen Mienert** (*juergen.mienert@ig.uit.no*) is Professor, Institute of Geology, University of Tromsø, Norway. **Philip P.E. Weaver** is Professor, Southampton Oceanography Centre, United Kingdom. **Serge Berné** is Senior Research Scientist, Institut français de recherche pour l'exploitation de la mer (IFREMER), Plouzané Cedex, France. **Wolf Christian Dullo** is Professor, Leibniz-Institut für Meereswissenschaften (Ifm-GEOMAR), Kiel, Germany. **Dan Evans** is Science Manager of the European Consortium for Ocean Drilling Research, British Geological Survey, Edinburgh, United Kingdom. **André Freiwald** is Professor, Institut für Paläontologie, Universität Erlangen-Nürnberg, Erlangen, Germany. **Jean-Pierre Henriët** is Professor, Renard Centre of Marine Geology, University of Gent, Belgium. **B.B. Joergensen** is Head, Biogeochemistry Group, Max Planck Institute for Marine Microbiology, Bremen, Germany. **Gilles Lericolais** is a researcher, Institut français de recherche pour l'exploitation de la mer (IFREMER), Plouzané Cedex, France. **Vasilios Lykousis** is Director of Research, Institute of Oceanography, Hellenic Center for Marine Research (HCMR), Greece. **John Parkes** is Professor, School of Earth, Ocean and Planetary Sciences, University of Cardiff, United Kingdom. **Fabio Trincardi** is Senior Research Scientist, Istituto di Scienze Marine-Consiglio Nazionale delle Ricerche (ISMAR-CNR), Bologna, Italy. **Graham Westbrook** is Professor, School of Earth Sciences, University of Birmingham, United Kingdom.

EURODELTA project is reconstructing the recent growth of prodelta systems by integrating knowledge ranging from river-discharge and flood dynamics (magnitude, recurrence, offshore impact), to estimates of sediment-accumulation rates based on short-lived radionuclides and/or sedimentological analyses of sediment cores from delta plain and prodelta environments, to physical stratigraphy in shallow waters revealed by high-resolution geophysical surveys. This data integration also includes key information from historical maps constraining the phases of delta construction over the last few centuries and will lead to a better evaluation of climate and human forcing.

For the first time in Europe, a specific river flood event, the Po River flood in October 2000, has been quantitatively related to a depositional event and the construction of a sedimentary body (i.e.,

the prodelta) in the nearshore environment (Figure 2). This new knowledge will facilitate better predictions of where and how much river-borne pollutants tend to accumulate nearshore. EURODELTA is advancing the understanding of the processes, stratigraphy, sediment budget, and geophysical characteristics of prodeltas. Significant contributions are made to shallow water surveying technology, prodelta risk-assessment strategies, and prodelta modelling.

### EUROSTRATAFORM (European Margin Strata Formation)

This project takes the results from EURODELTA and extends the work into a more complete source-to-sink approach following marine sediment dispersal from source to sink (i.e., river output to deposition on the shelf, slope, or basin floor), and the conversion of this sedi-

ment into strata. The EU-funded project EUROSTRATAFORM has a U.S. counterpart that is also called EuroSTRATAFORM and is funded by the U.S. Office of Naval Research. The EU project focuses on the Adriatic, Gulf of Lions, Portuguese, and northern Norwegian margins while the U.S. project is limited to the Adriatic and Gulf of Lions. Scientists from both projects work closely studying the Adriatic and Gulf of Lions; their efforts include joint cruises and meetings, data exchange, and numerous joint publications. Several articles of this issue are devoted to the results of these collaborations.

### ASSEMBLAGE (Assessment of the Black Sea Sedimentary System Since the Last Glacial Extreme)

ASSEMBLAGE is a European collaborative project focused on the assessment

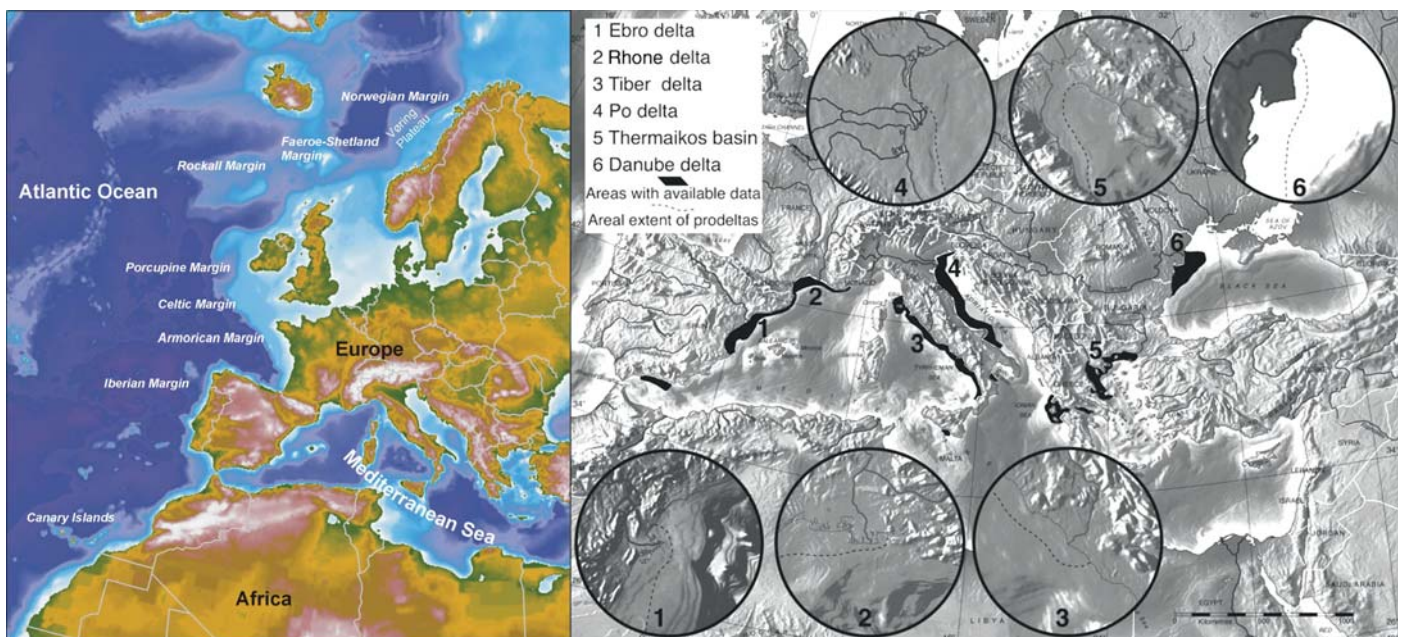


Figure 1. Major delta systems studied at the northern margin of the Mediterranean Sea and the Black Sea (more information available at [www.pangaea.de/Projects/EURODELTA](http://www.pangaea.de/Projects/EURODELTA)).

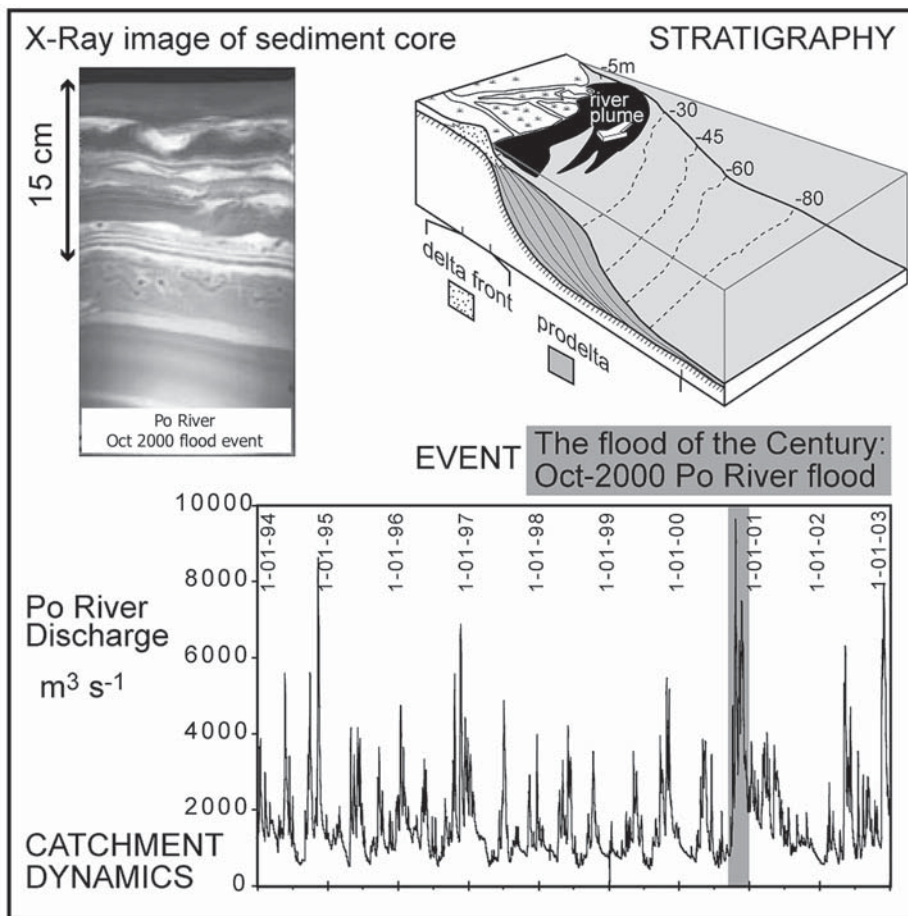


Figure 2. EURODELTA data has, for the first time, quantitatively related a specific depositional event to the construction of a sedimentary body (i.e., the prodelta) in the near-shore environment. This figure shows river discharge data from the centennial Po River flood in October 2000 and the resulting sediment record on the Po prodelta.

of the Black Sea sedimentary system from its northwestern part, including the continental shelf and slope, down to the deep sea zone. The western Black Sea is a unique physiographic setting characterized by a particularly wide shelf (100 to 150 km). The northwestern Black Sea receives water and sediment discharge from some major European rivers (Danube, Dniepr, Dniestr); the sea is characterized by high sedimentation rates, which present favorable conditions for paleoclimatic studies of this region. Its geographic position and that

of its drainage basin makes it sensitive to changes in the ice cap during the last glacial period. These changes are recorded in the sedimentary record.

Two cruises (BlaSON 1 and BlaSON 2) provided detailed images of the seafloor by swath mapping, side-scan sonar, and very-high-resolution seismic profiling. These cruises have increased our understanding of the timing of and the processes controlling Holocene sea-level rise on the shelf and have allowed reconstruction of the outbuilding of the Danube delta and deep-sea fan. To

characterize the last transgression (invasion of saltwater into a giant low salinity lake?), sediments were sampled from the coast to the deep basin; these samples covered sediment history from the Late Pleistocene lacustrine phase to the Holocene marine phase of the Black Sea. Core samples retrieved by the R/V *Marion Dufresne*, which have not yet been analyzed, will provide detailed age determinations. By studying the stable isotopes, pollen, molluscs, ostracods, foraminifers, diatoms, and clay mineralogy of these cores and by using proxies delivered via rivers that drain the interior of Asia and Europe, it will be possible to understand the history of climate change at a very high resolution. The abrupt Holocene reconnection of the Black Sea to the Mediterranean is perhaps one of the most dramatic climatic events that occurred in Europe in the last 18,000 years, and this research can be used as a proxy for possible future scenarios.

### PROMESS 1 (Profiles Across Mediterranean Sediment Systems: Part 1)

Continental margins' outer shelf development is complex. Scientific drilling is needed to understand how sedimentary processes create continental margin strata, how fast and under what conditions strata creation is achieved, and how knowledge of these processes and margin stratigraphy can be formulated into predictive and diagnostic models. Because the best places to study are often those with the highest net accumulation of sediment, sampling by relatively short piston cores is often precluded. PROMESS1 fills this knowledge gap by involving scientific drilling on continental shelves and slopes in the Mediter-



ranean Sea and emphasizing sampling of long sections (50 to 300 m) and *in situ* measurements of shelf and upper slope sedimentary sequences deposited during the last 500 kyr, at 50 to 300 m water depth. Data gathered through PROMESS1 will provide high-resolution records of sea-level changes, slope stability, canyon history, and climate variability in physiographic settings with high sedimentation (glacial and interglacial prodeltas) and exceptional preservation of depositional sequences.

The first drill site in the Gulf of Lions was situated on the interfluves of the Bourcart and Herault canyons, at a water depth of 298 m. Seismic data show continuous sedimentation during the Late Pleistocene. The targeted penetration was 300 meters below seafloor (mbsf), which was supposed to correspond to the last four 100-kyr cycles. The occurrence of *Pseudoemiliana lacunosa* below 270 mbsf indicates that Marine Isotope Stage (MIS) 12 was reached at the bottom of the hole. It is already possible to confirm that the seismic bounding surfaces do not represent local changes in sedimentation processes. They are linked to 100-kyr glacial-interglacial cycles that modify lithology and sedimentation rates on the upper slope. The presence of coarser sediment at the end of each “forced regression” (sedimentary sequence formed during a sea-level fall) and the occurrence of some biogenic gas trapped by the overlying clayey sediments deposited during the ensuing warm period are causing seismic anomalies. These seismic patterns repeat during each glacial cycle. These anomalies can be tracked at the regional scale and studying these cores enable researchers to determine the age

of buried shorelines.

A second drill site was situated at the seaward termination of the Last Glacial Maximum shoreline, at a water depth of 103 m. The targeted depth was 100 mbsf in order to sample shelf sequences that were deposited during the same time interval as the first site. The major difference from the first site (where continuous sedimentation occurred) was successively emerged and submerged areas characterized by discontinuities related to submarine and/or subaerial erosion. Preserved dipping sedimentary units up to 35 m thick were interpreted as evidence of former shorefaces and shorelines formed during a sea-level lowstand of glacial periods.

PROMESS 1 also included two drill sites on the Adriatic shelf and slope. The shelf site offers an unprecedented high-resolution record of the Holocene (about 30 m) and will be exploited to reconstruct short-term changes in sediment supply driven by climate change and/or human impact. The slope site penetrated about 70 m of mud in the distal part of “forced-regression” deposits that are expected to represent a finer-grained correlative to those penetrated in the Gulf of Lion. Although the Gulf of Lion and the Adriatic slope sites are different in terms of tectonic setting and supply regime, comparing them should help us separate eustatic fluctuations from regional and local components of relative sea-level change.

### **STRATAGEM (Stratigraphical Development of the Glaciated European Margin)**

To go beyond the range of shallow drilling and to extend our scientific knowl-

edge both back in time through the whole Neogene and laterally along a margin transect requires the integration of vast data sets. Mainly through the provision of vast quantities of seismic data generated by 29 oil companies, the STRATAGEM project has achieved this margin-wide study in the Northeast Atlantic from Norway to southwest of Ireland. Through this endeavor, scientists have learned that even though the glaciated European margin is tectonically classified as passive, the post-rift history of the margin has been physically dynamic.

The resulting stratigraphic atlas presents a unified stratigraphic framework for the margin from Miocene to the lower Pliocene and the lower Pliocene to the Holocene epochs, respectively. The seismic stratigraphic framework is based on unconformity-bound megasequences informally termed the “lower” and “upper” Neogene successions. The lower Neogene succession mainly preserves a record of basinal deep water. The fully established thermohaline circulation in the Northeast Atlantic Ocean is a Neogene phenomenon. The upper Neogene succession records a major seaward progradation of the margin, as well as a change in the oceanographic circulation pattern. This change in sedimentation style occurred at about 4 million years ago (Ma) and is marked by margin-wide erosion. Although glacial sediments form a major component of the prograding wedges, the onset of late Neogene change pre-dates Northern Hemisphere glaciation by at least 1.5 million years. The latter may have been accelerated by uplift. A change from restricted to expansive glaciation occurred in the early to mid-Pleistocene.

As scientists discovered more about different areas of the European margin, it has become clear that we may be able to achieve a much better understanding of strata formation and related physical and biological processes by integrating climate and tectonic variability.

Plate tectonics is the main long-term instigator of change and has underpinned the shaping of the ocean margin. Climate change, ocean currents, and sea level have all responded to tectonic change, and have interacted among themselves to sustain and further modify the shape of the margin. However, large-amplitude tilting cannot be accounted for by intra-plate stress variations, but is consistent with a dynamic topographic response to upper mantle convection, in particular, edge-driven flow beneath the continental margin. Sedimentary and oceanographic changes resulting from dynamic topographic responses to the evolution of upper mantle convective flow during ocean widening may be characteristic of the development of “passive” continental margins (Stoker et al., in press).

#### **COSTA (Continental Slope Stability)**

One of the primary concerns about exploitation of the margin is the threat of submarine landslides, which is widespread in some sectors. The COSTA project has investigated strata formation and submarine slope failures along the European margin. It has allowed scientists to determine which type of strata formation contributes to preconditioning a submarine slope failure, therefore

to the potential for geohazards. Detailed images of seafloor failures provided by swath mapping, side-scan sonar, and three-dimensional seismic imaging have provided an understanding of the complex processes and resulting impacts. To properly analyze slope stability and submarine flow dynamics, sediments were sampled in and around failure-prone areas to beyond the depth of the failure plane. This type of sampling allowed detailed examination of the physical and chemical makeup of destabilized sediments and of the known or potential failure surfaces they bound. Furthermore, the effect of earthquakes and gas hydrates on slope stability is of importance to the understanding of the variability of slope stability. An excellent example of a giant submarine landslide comes from the mid Norwegian margin, where the hydrocarbon industry worked jointly with academia (Mienert, in press; Solheim et al., in press) (more information available at [www.offshore-technology.com/projects/ormen/](http://www.offshore-technology.com/projects/ormen/)).

The giant Storegga slide developed as a retrogressive slide in a passive continental margin setting, where the shelf is approximately 100 km wide (Figure 3). It is located immediately south of the Vøring Plateau where it was discovered in 1979. The nearly 300-km-long

headwall is located in water depths from 150 to 400 m along the shelf break. The headwall reaches maximum heights of between 150 to 200 m. The maximum run out of slide material reached 400 to 800 km, and the final deposition occurred at 3800 m water depth. It is now well documented that the Storegga slide consists of lobes from more than 50 individual slide events ranging from the first phase of 2400 km<sup>3</sup> to minor slides of less than 1 km<sup>3</sup> at the headwall. The slope gradient along the failure planes is between 1 degree and 1.5 degrees, but reaches 23 degrees or more at the head wall. The slides affected an area of approximately 95,000 km<sup>2</sup> and they took place almost concurrently around 8250 years ago. Therefore, it is appropriate referring to the “Storegga slides” of Holocene age (Haflidason et al., in press).

The stratigraphy of the area prone to the Storegga slides is characterized by glacial-interglacial sedimentary cycles. During interglacials, thick deposits of fine-grained marine clayey sediments are deposited parallel to the warm, northward-directed Norwegian current, which produces a sediment drift with sorted marine clay layers. The glacial sedimentary units are composed of unsorted diamicton and /or ice-proximal meltwater deposits on the upper slope. Glacial sediments were rapidly deposited on the interglacial sediments, creating an excess pore pressure. However, layer-parallel slip surfaces and jumps between various stratigraphic levels have been observed, for example, in the Storegga slide scar area (Figure 3). Slip surfaces in Storegga are developed in the interglacial marine clays. These clays are weaker and have higher sensitivity than glacial clays, and

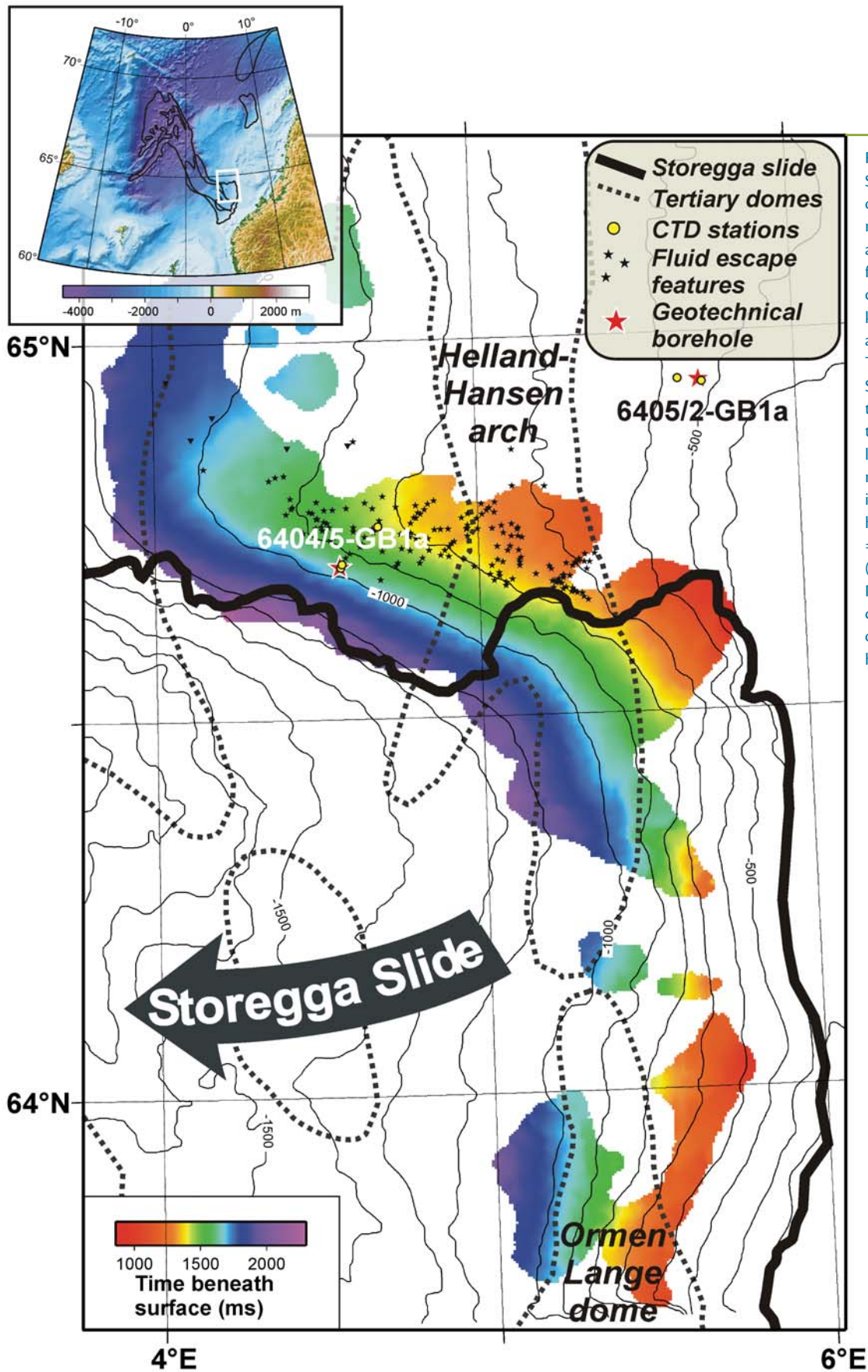


Figure 3. Location of the giant Storegga submarine landslide on the passive Norwegian continental margin (left top) and the area with geophysical evidence for gas hydrates. Storegga is one of the largest submarine slides known on continental margins affecting an area of ~ 95000 km<sup>2</sup>. The bathymetric map of the Storegga slide shows the location of the headwall (solid line), the northern sidewall, the Helland Hansen arch and the Ormen Lange dome (stippled area) including the area of inferred gas hydrate occurrence (color scale = time beneath the sea surface) (after Büinz and Mienert, 2004). Pock marks indicating fluid escape (black stars) concentrate on the northern zone of the gas hydrate field.



show contractant behavior upon loading, which creates failure planes.

### HYDRATECH (Techniques for the Quantification of Methane Hydrate in European Continental Margins)

Methane hydrates are important because they hold vast reserves of hydrocarbons, may cause submarine landslides, and can pose a hazard to offshore drilling. It is difficult to identify them beneath the seafloor, and even more difficult to quantify the amount of methane locked within the hydrate itself.

Methane hydrate is an ice-like solid composed of water and methane. It occurs in sediments up to a few hundred meters beneath the seafloor often on continental slopes where water depths exceed a few hundred meters. Any increase in temperature or decrease in pressure will cause hydrate to dissociate and release methane gas, which can weaken the host sediment, rupture overlying sediments, and hence, make seafloor slopes prone to landsliding. Large slides can generate tsunamis with catastrophic consequences for coastal populations. Hydrates may also pose

a clear need to find out the distribution of hydrates on continental margins so that environmental protection and geo-hazard mitigation strategies can be put in place.

The aim of the HYDRATECH project was to evaluate and develop marine remote sensing (seismic) techniques that can be used to identify the presence of methane hydrate beneath the seafloor, and to quantify the amount of hydrate present. Seismic data sets were acquired at three sites (off Northwest and Southwest Svalbard, and adjacent to the Storegga Slide off Norway) using state-of-the-art seafloor seismometers and high-resolution seismic reflection methods. Modelling of seismic ray paths and inversion of travel times from these high-resolution data allowed us to detect and measure the spatial variations in the seismic properties of the underlying sediments. The measured properties include the velocities of compressional and shear waves, and the attenuation of compressional waves, through the underlying sediments. Known relationships among these seismic properties and hydrate content allowed us to predict the amount

that traps free methane gas beneath it. The results from Northwest Svalbard indicate a 100-m-thick zone of gas hydrate immediately above the BSR at a depth of 200 m below the seabed; we predict the hydrate is present in low concentrations here. By contrast, the results from Southwest Svalbard indicate the absence of any significant hydrate concentrations above seismic bright spots that are associated with accumulations of free gas. However, locally developed BSRs are seen at shallower depths around possible gas migration pathways. The results from Storegga show that the distribution of hydrate is strongly controlled by the migration of gas through locally permeable sediments, producing some areas with hydrate above a strong BSR, and other areas where hydrate is undetectable above a weak or absent BSR.

Seismic properties were interpreted in terms of hydrate content based on theoretical or empirical relationships. Several existing techniques were evaluated and new approaches were developed before applying the most promising of these methods to the data acquired from the Svalbard and Storegga sites. These approaches were also tested against laboratory experimental results of variations in seismic properties of sediments with hydrate grown under conditions simulating nature. This laboratory work involved a study of how methane hydrates grow in sediments, including Nuclear Magnetic Resonance imaging of hydrates formed in samples, and the development of a resonant-column system to measure seismic properties of hydrates under similar frequencies and strain amplitudes against those used in the marine experiments. These were the first mea-

### The HYDRATECH project demonstrated a successful marine seismic technique for detecting and quantifying hydrate content beneath the seafloor on continental margins.

problems for petroleum-production wells that tend to warm the surrounding sediments, thus releasing methane gas from the destabilized hydrate and weakening the platform foundations. There is

of hydrate within the sediments there.

Continental-margin hydrates are often seen on seismic sections as bottom-simulating reflectors (BSRs). This is where the solid hydrate forms a blanket

surements to be made of seismic properties of sediment containing hydrate at seismic frequencies in the laboratory. A theoretical model can be used to make good predictions of the known hydrate contents of laboratory samples based on the known resonant column seismic parameters.

The HYDRATECH project demonstrated a successful marine seismic technique for detecting and quantifying hydrate content beneath the seafloor on continental margins. The main sources of error are: the uncertainty about the manner in which hydrate forms inside the host sediment, which depends on sediment type; and, in the absence of boreholes, the uncertainty over the actual sediment types present. Progress on resolving the former will depend on further investigation of natural and laboratory-created samples containing hydrate, especially of clay-rich sediments that are prevalent in the marine environment.

## BIOSPHERE-GEOSPHERE INTERACTIONS

### METROL (Methane Flux Control in Ocean Margin Sediments)

Understanding the controls and mechanisms of methane production and breakdown in ocean-margin sediments is the key aim of the METROL project (more information available at [www.metrol.org](http://www.metrol.org)). METROL mainly deals with shallow-water environments and will make important contributions in understanding the distribution, turnover, and emission of methane in coastal seas, including the North, Skagerrak, Kattegat, Western Baltic, and Black seas.

Methane is one of the most important energy sources in the industrialized

**Methane is one of the most important energy sources in the industrialized world, but is also an effective greenhouse gas when emitted into the atmosphere. Vast amounts of methane are created in European margin sediments leading to the formation of free gas, to complex carbonate structures, and to methane emission.**

world, but is also an effective greenhouse gas when emitted into the atmosphere. Vast amounts of methane are created in European margin sediments leading to the formation of free gas, to complex carbonate structures, and to methane emission. These processes are not only important for offshore operations of the hydrocarbon industry, but also for ecosystem diversity and for climate development. Most importantly, it has been found that a high percentage of the entire methane flux through the sediments, maybe greater than 90 percent, is retained in the seafloor through anaerobic oxidation by microorganisms (Boetius et al., 2000; Michaelis et al., 2002). METROL aims to explore the microbiological and geochemical controls of this methane barrier in subsurface coastal sediments to quantify current methane fluxes and evaluate the effect of environmental change on seafloor methane release.

Estimates of the total methane flux in the seafloor range from 85 Tg C/yr (teragrams of carbon per year) for the entire ocean to 120 to 248 Tg C/yr for estuarine and shelf sediments, which constitute 8 percent of the ocean floor. The contribution of methane fluxes from slope and deep-sea sediments is poorly

known. However, the global methane flux is assumed to be equivalent to 10 to 20 percent of the total subsurface sulfate reduction, which accounts for the oxidation of 370 Tg C/yr. The total anaerobic oxidation of methane in the ocean floor should therefore be 37 to 74 Tg C/yr (i.e., significantly less than the above estimate for shelf sediments alone). Thus, the numbers are still highly uncertain. The total emission of methane from the ocean to the atmosphere is estimated to be only 10 Tg C/yr (Reeburgh et al., 1993), much of which is presumably produced in the water column. Thus, the seafloor is currently highly efficient in retaining methane, although accumulated gas may occasionally be released by eruptive events. Although published reports on natural gas seepages suggest that they are very rare, the petroleum industry has identified, but not publicly reported, many more. This discrepancy is partly due to the lack of high-performance and expensive geophysical techniques within the scientific community. There are still too few data on the flux of gas from seabed seepages and even fewer on the contribution of seepages to atmospheric concentrations of gases such as methane.

At the METROL study sites investigated in 2003 and 2004, it was confirmed that the microbiological key process of subsurface methane oxidation plays a critical role as a barrier against methane emission. Regulating factors are the methane and sulfate fluxes but also the geological characteristics of the sites (Figure 4a, b). Even at methane seeps, an unknown but probably major portion of a methane deposit is biologically oxidized before it can escape into the water column. The efficiency of this process must be understood if researchers are to quantify current methane fluxes in marine sediments and predict the effect of environmental change on seafloor methane release.

### ANAXIMANDER (Exploration and Evaluation of the Eastern Mediterranean Sea Gas Hydrates and the Associated Biosphere)

This project studies methane-bearing sediments and associated gas hydrates in the Anaximander area east of the Rhodes Basin in the eastern Mediterranean. The overall objective is the investigation of the deep biosphere (bacteria) related to presence of methane and/or to the formation/dissociation of gas hydrates. The deep-biosphere environment will be studied by sampling and by fully characterizing the microbial communities in gas hydrate and/or other methane-rich sediments. Anaerobic methane oxidation carried out by consortia of archaea (methanotrophs) and sulfate reducing

bacteria as well as biogenic methane production through methanogenesis is under investigation. In addition, the metabolic activity, distribution, and composition of the organic matter found in the biogenic communities associated with the gas-hydrate environment are being examined. A second objective involves the development of pressure-sampling techniques to collect pristine sediment cores without the dissociation of gas hydrates during sample collection and handling. Comparison of the field data on the equilibrium phase of the gas hydrates with those from the experiments will enable understanding of the condition and the rate of their dissociation during handling and sample treatment.

Data collected during the project will

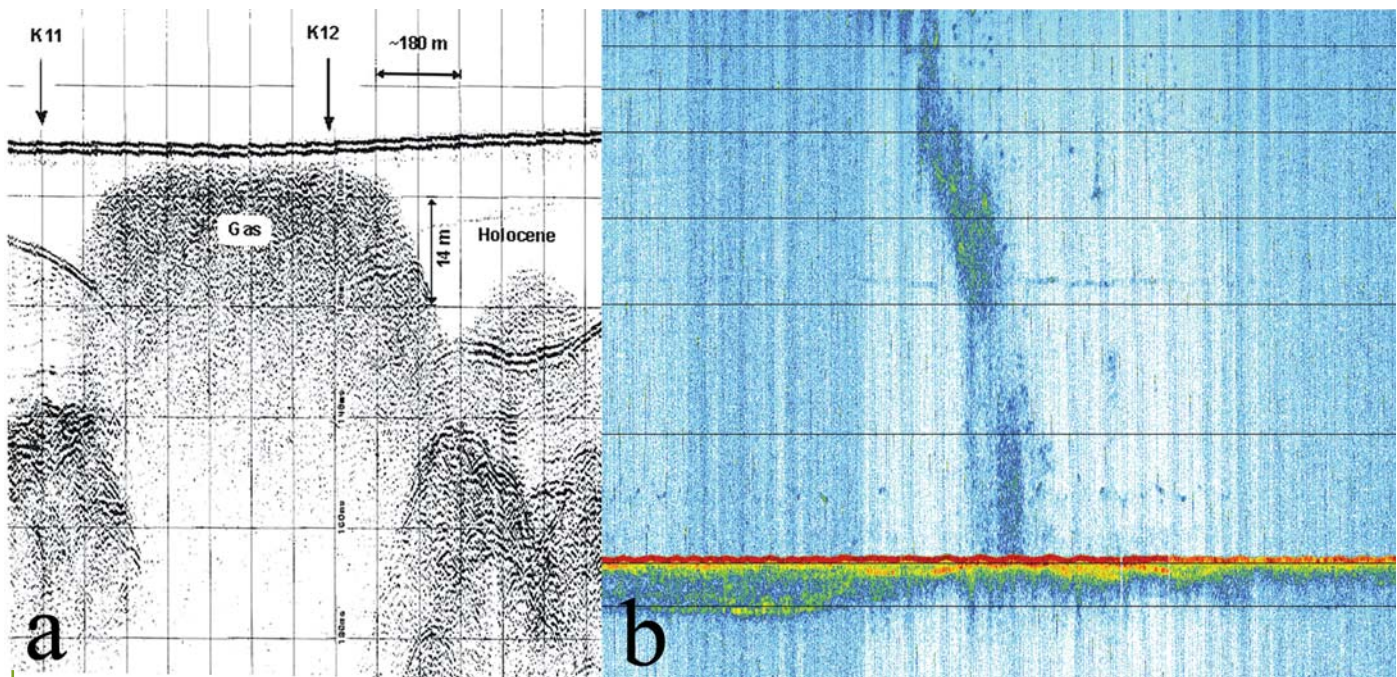


Figure 4. (a) A seismic profile through the METROL study site in the Kattegat (North Sea, Danish sector). The gas rising from the deep source is completely consumed by anaerobic methanotrophic microorganisms. (b) Hydroacoustic imaging of a gas flare above the METROL study site Tommeliten (North Sea, Norwegian Sector). Gas is escaping from the seafloor despite the presence of a methanotrophic community. The image was kindly provided by G. Wendt (University Rostock, Germany).



be used to define the stratigraphy, morpho-sedimentary features, deformational structures, and depositional bodies based on seismic and acoustic imaging, in order to establish the tectono-sedimentary framework where the gas hydrates are hosted. Important goals are to determine the distribution of the gas hydrates in pore space, their properties at unsaturated conditions, and their transport in the liquid phase by diffusion and convection. All information gathered from this study will contribute to the evaluation of the role of gas hydrate as a potential contributor to global warming, the possibility of its exploitation as an energy source, and its role in environmental risk assessment in the Eastern Mediterranean.

### **DeepBUG (Development and Assessment of New Techniques and Approaches for Detecting Deep Sub-Seafloor Bacteria and their Interaction with Geosphere Processes)**

Marine sediments cover 70 percent of Earth's surface and contain the largest global reservoir of organic carbon. Surprisingly, high bacterial populations are present in these sediments, to a depth of at least hundreds of meters (current deepest sample 842 m, oldest 14 Ma). These bacteria are not just surviving, they are thriving in extreme conditions at these depths; they have high diversity and are well adapted to life in the subsurface. Bacterial biomass in these sediments represents about 10 percent of the total surface biomass; the sub-seafloor biosphere is a substantial habitat on Earth. Existing microbiological techniques are inadequate for the investigation of these deeper samples, and there-

## **Marine sediments cover 70 percent of Earth's surface and contain the largest global reservoir of organic carbon. Surprisingly, high bacterial populations are present in these sediments, to a depth of at least hundreds of meters**

fore the EU's DeepBUG research project aims to develop new techniques and approaches for detecting sub-seafloor bacteria and their interaction with geosphere processes.

The DeepBUG project designed and tested a range of new sampling and subsampling systems that enable consolidated sediments in excess of 1000 m deep to be processed effectively for microbiological analysis. These new systems were central to handling on Ocean Drilling Program (ODP) Leg 201, the first dedicated "deep biosphere" ODP drilling leg. Detection limits for microscopic detection of sedimentary bacteria have been improved by a factor of 25, down to 2,400 cells/cm<sup>3</sup>, and new approaches using <sup>13</sup>C-substrate incorporation to detect active bacteria have identified the ability of a major division of uncultured bacteria to use acetate under sulfate-reducing conditions. This represents a major advance and may lead to the eventual isolation of members of this group. In addition, the sensitivity of the radiotracer method for measuring rates of bacterial sulfate reduction has been greatly improved (less than 1 picomole [pmol] SO<sub>4</sub><sup>2-</sup>/cm<sup>3</sup>/day) (Kallmeyer et al., 2004) and used to demonstrate the presence of sulfate reduction in deep and ancient sediments, including the lowest rates ever measured in any marine environment.

A new high-temperature, high-pressure apparatus has been developed (Kallmeyer et al., 2004), which has shown that sulfate reduction rates can be highest up to 80 to 100°C and are stimulated by elevated pressure (220 and 450 bar). In contrast, initial investigation of methanogenesis indicates that the process is not influenced by pressure. Bicarbonate methanogenesis was confirmed as the major methanogenic pathway in marine sediments, and indications of deep bacterial methanogenesis to 1,100 mbsf and about 125°C provides evidence for the deepest and hottest deep biosphere so far.

A range of different approaches demonstrate an overlap between biosphere and geosphere processes, including the role of bacteria in deep, high-temperature alteration of organic matter, and in aspects of fossil-fuel formation and geosphere processes providing deep (bacteria-related) energy sources. In the subsurface and to temperatures up to 50°C, methane was shown to be a significant energy source for sulfate reduction, whereas, at higher temperatures other energy sources dominate.

The range of different genetic approaches used (16S rRNA gene libraries, Polymerase Chain Reaction [PCR] profiling, Denaturing Gradient Electrophoresis [DGGE] profiling, and functional

gene libraries), combined with bacterial activity, total bacterial numbers, Stable Isotope Probing (SIP), determination of viable populations, and characterization of deep sediment isolates has enabled the most robust and comprehensive assessment of biodiversity (bacterial and Archaea) and function in the sub-seafloor biosphere to date. Direct bacterial populations were enumerated from 15 new sites (27 percent increase in global data) representing a range of oceanographic, diagenetic, and geological conditions, which further confirms that deep bacteria are globally present in marine

sediments (Figure 5). Detailed spatial sampling through deep geochemical interfaces has demonstrated marked elevation of bacterial processes (especially methanogenesis and bacterial productivity) biodiversity and bacterial numbers (Parkes et al., 2004). If this is widespread in sediments, it may lead to an increase in the global estimate of the biomass in the sub-seafloor biosphere. New deep bacterial isolates have been obtained, and they greatly extend our knowledge of the physiology of sub-seafloor bacteria (Tofin et al., 2004).

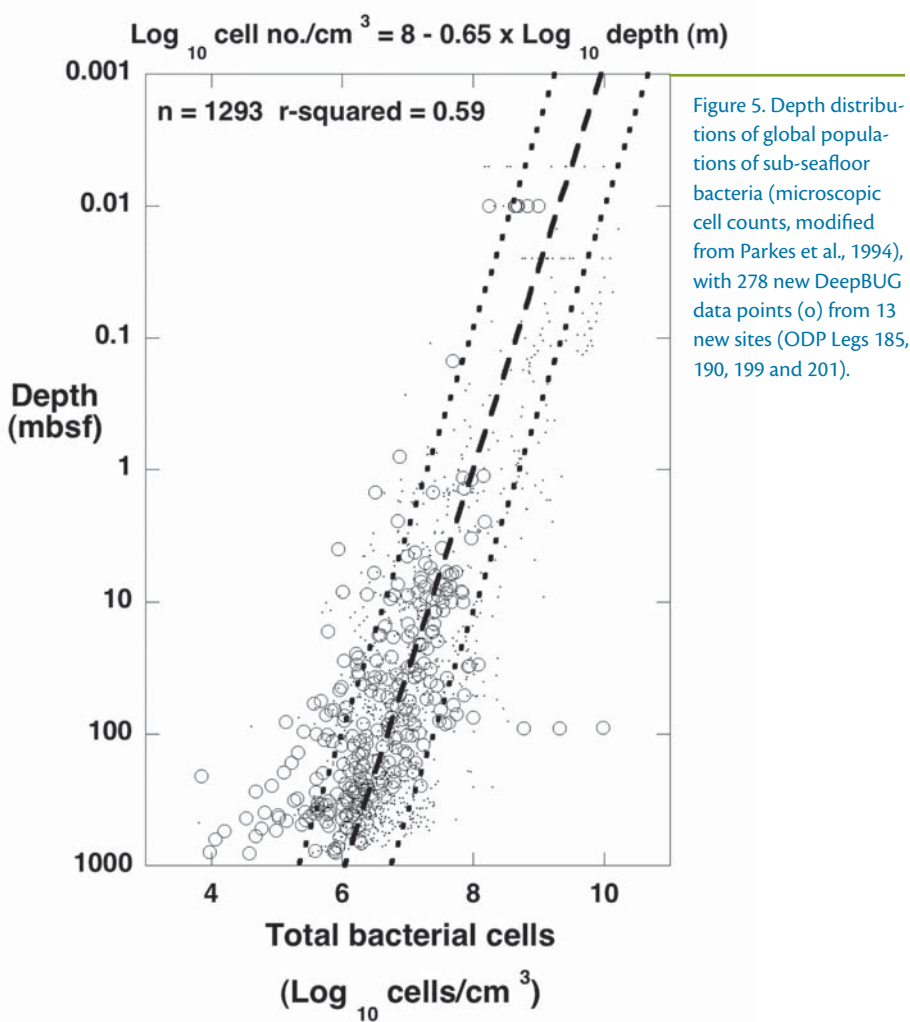
## DEEP CORAL REEFS AND CARBONATE MOUNDS

Coral reefs are usually associated with warm, tropical waters, not with the cold, deep, dark waters of the North Atlantic where corals were once regarded as oddities on the seafloor. Only recently has it become known that cold-water coral species also produce reefs that may rival their tropical cousins in terms of the species richness of associated marine life. Increasing commercial operations in deep waters and the use of advanced offshore technology have slowly revealed the true extent of Europe's and other hidden coral ecosystems (Freiwald et al., 2004). Three closely linked EU projects—Environmental Controls on Mound Formation along the European Continental Margin (ECOMOUND), GEOMOUND (The Mound Factory-Internal Controls), and Atlantic Coral Ecosystem Study (ACES)—aim to expand our knowledge of Europe's deep-water coral communities.

### ECOMOUND

Cold-water carbonate mounds along the European continental margin have been investigated in the ECOMOUND project to understand the external oceanographic control and forcing mechanisms on carbonate mound formation and development. The main target areas were the Porcupine Seabight, the Rockall Trough margins, and offshore the northernmost part of Norway where clusters of carbonate mounds have been reported, and which are densely colonized by the cold-water coral *Lophelia pertusa*.

Deep-water coral associations and reef formations have been known to occur along the European Margin for sev-



eral decades. However, these carbonate mounds are unique reef structures for the modern cool-water European seas, even though they were much more common in the geological past. They provide the most diverse ecosystem of deep ocean margins and are possibly one of the most important sites for fish recruitment.

Carbonate mounds with cross sections between 100 to 1800 m at their base, rising up to 350 m above the seabed and surrounded by a 60 to 90 m deep circular moat have been reported in the Porcupine Seabight in water depths of 650 to 1000 m. More recently, carbonate mounds of a similar height were discovered on the continental slope north of the Porcupine Bank in water depths of 500 to 1100 m. Carbonate mounds have also been described in a zone up to 15 km wide in water depths of 500 to 1000 m in the southwestern Rockall Trough (Kenyon et al., 2003). These mounds also rise up to 350 m above the seabed and appear associated with slumped or faulted margin sediments. Only offshore Norway do the coral reefs occur on elevated ridges shallower than 400 m.

High-resolution acoustic imaging and video documentation show a prolific coral cover on many of the mounds, which are mostly confined to an uppermost seismic unit of Early Pleistocene age (De Mol et al., 2002). But, a simple model for mound formation is unsatisfactory owing to the observed variation in size, morphology (e.g., linear ridges, ring shapes), and number of these mounds showing very localized clustering.

The oceanographic regime is governed by different water masses displaying a density gradient in the vicinity of the mounds, where organic carbon from

...these carbonate mounds are unique reef structures for the modern cool-water European seas... They provide the most diverse ecosystem of deep ocean margins and are possibly one of the most important sites for fish recruitment.

the sea surface prevails and provides nutrients for the corals. The environmental setting of the mounds shows a strong diurnal tide influence. The mounds consist of a high proportion of biogenic carbonate material, where sandy and silty clays are baffled and then accumulated within the biogenic framework. Particulate-organic-material dynamics of the benthic boundary layer at this specific setting indicates enriched flow rates at the sediment surface. The activity of benthic fauna associated with the deep-water coral ecosystem causes emplacement of fresh organic material into the sediments, consequently enriching the mound sediments in organic carbon relative to off-mound sites, but no evidence for hydrocarbon venting is reported.

Detailed analyses of sediment cores reveal that coral growth occurs only during interglacial times. Glacial oceanography does not support the formation of a density gradient in the vicinity of the mounds, and therefore insufficient nutrients existed for the deep-sea coral ecosystem. These observations finally lead to a model describing the growth and development of carbonate mounds controlled by environmental changes (Figure 6).

## GEOMOUND

Large clusters of carbonate mounds on the seabed have appeared time and time

again throughout Earth's history, mostly forming spatially confined clusters. It is believed they reflect a key process in the biogeochemical dynamics of the ocean and atmosphere. The earliest so-called stromatolitic mounds, which appeared billions of years ago in the Precambrian seas, had very modest dimensions, not much higher than a few meters, but they provided all of Earth's atmospheric oxygen that humans breathe today.

The GEOMOUND project, closely associated with ECOMOUND, has quantified the carbon sink represented by the giant mound provinces discovered in the Irish Porcupine and Rockall Basins, and has defined their broad basinal setting and their link to large-scale fluxes of matter and energy. Giant carbonate mounds seem to be systematically confined to offshore hydrocarbon basins; advanced basin modelling has revealed potential pathways of methane, which may have played a role in the initiation of mound formation. Bright spots in the sediment layers just below a number of mounds may represent the "smoking gun"—residual patches of gas arguing for a degassing event. Pockmarks also frequently occur close to mound clusters, and a spectacular buried slope failure underlies a large cluster of around 1,000 small, buried mounds called the Magellan mound province. It is possible that slides and mounds are different ex-



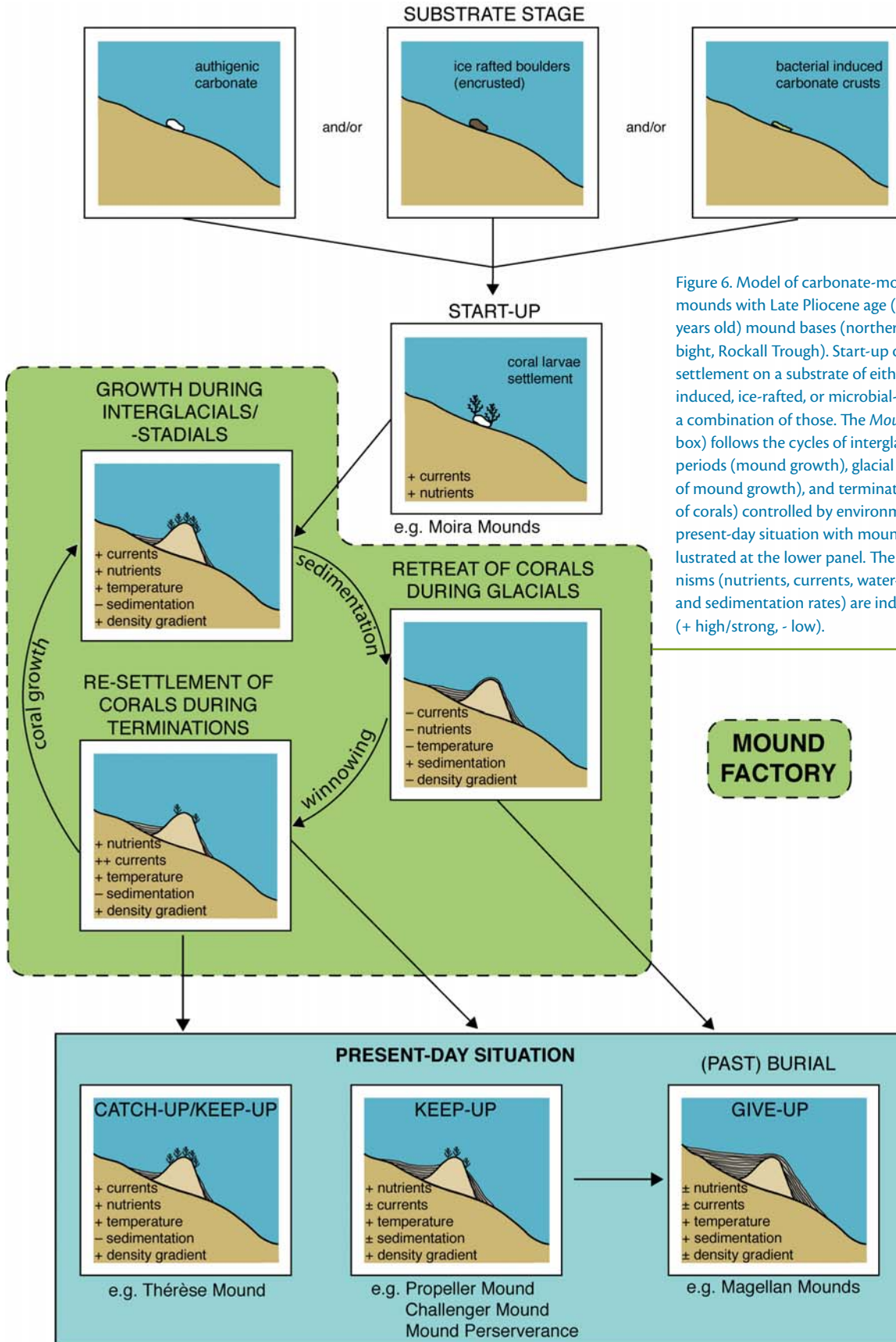


Figure 6. Model of carbonate-mound genesis for mounds with Late Pliocene age (about 2 million years old) mound bases (northern Porcupine Sea-bight, Rockall Trough). Start-up of coral larvae settlement on a substrate of either fluid-migration-induced, ice-rafted, or microbial-induced origin, or a combination of those. The *Mound Factory* (green box) follows the cycles of interglacial/interstadial periods (mound growth), glacial periods (stagnation of mound growth), and terminations (resettlement of corals) controlled by environmental factors. The present-day situation with mound examples is illustrated at the lower panel. The controlling mechanisms (nutrients, currents, water-mass characteristics and sedimentation rates) are indicated in the boxes (+ high/strong, - low).

© A. Rüggeberg

pressions, at different times and under different oceanographic conditions, of one intermittent gas migration pathway. However, no active seeping has been observed in the Porcupine Basin.

Mounds also appear to be prolific hot-spots in ecosystem diversity, particularly rich in deep-water coral species such as *Lophelia* and *Madrepora*. GEOMOUND has directly led to the discovery and survey of one of the most prolific deep-water coral ecosystems in the Atlantic: the Thérèse mound group in the Belgica mound province. Intriguingly, this group of mounds, covered by true forests of deep-water corals and associated species, occurs adjacent to totally barren mounds.

### ACES

The EU ACES project has concentrated on the coral ecosystems and investigated coral hotspot areas off mid Norway (Sula Reef), the Skagerrak (Kosterfjord reefs), the northern Rockall Trough (Darwin Mounds), the southern Rockall Trough (Logachev and Pelagia carbonate mound provinces), the Porcupine Seabight (Belgica and Hovland carbonate mound provinces), and the Galicia Bank.

The ACES project has successfully mapped cold-water coral ecosystems in all study sites stretching from the Galicia Bank to the Norwegian Sula Reef. The framework constructing potential of the locally reef-forming coral *Lophelia pertusa* is variable and is controlled by the following factors: (1) intrinsic controls are determined by the skeletal ultra-structural composition of the skeleton and the lifespan of the polyps, which can be estimated as 10 to 15 years on average; (2) extrinsic factors are determined

by the trophic condition of the ambient water mass, which is correlated with the skeletal growth rate. The more nourished the water mass, the higher the skeletal growth development. The molecular genetic mapping indicates an existing gene flow along the continental margin but also high degrees of interbreeding because of the existence of long-lasting clonal colonies. Scandinavian fjord corals show a significantly different genetic signature as a matter of genetic isolation from the open-ocean coral populations.

The hydrographic regime in all ACES sites is characterized by a strong current regime, driven by tides; this regime becomes accelerated at topographic highs such as moraines and carbonate mounds. The role of submerged oceanic banks (Porcupine Bank, Rockall Bank) and the interaction with the oceanic circulation and particle flow has been recognized as a prime control for the nourishment of extensive coral growth at the continental margin. Submerged banks force the surface currents to form an anticyclonic vortex around the bank, which in turn entraps cold and relatively eutrophic waters for a prolonged period of time. This plankton soup sinks, driven by tidal pumping, and becomes concentrated at the bathymetric position of the coral ecosystems. This modified benthopelagic coupling process fits with the analysis of particulate organic carbon in the benthic boundary layer and demonstrates the importance of both oceanographic and hydrographic controls.

During the lifetime of ACES, the number of verified *Lophelia* sites in the Northeast Atlantic increased from 416 to 846. To date, the number of identified species that belong to the reef-associated

fauna (Figure 7) is 1300. The biodiversity indexing is underway but must be regarded as a difficult task due to the sampling techniques used in this habitat. The analysis of the soft tissue of *Lophelia pertusa* showed that the coral produces lecithotrophic larvae and spawns in winter. The reaction of *Lophelia* polyps to different exposures of sedimentation was obtained from aquarium experiments. To conclude, *Lophelia* ecosystems indeed attract a large number of species and biomass compared to the background environment.

ACES generated status reports focusing on the human impact to cold-water reefs for the Kosterfjord, the Darwin Mounds, the southern Rockall Trough, and Porcupine Seabight coral ecosystems. Damage of different degrees by the fishing industry is observed on many ACES study sites. The topic of cold-water coral ecosystem protection is now anchored in many international political conventions and culminated in a comprehensive report on the global status of cold-water coral ecosystems (Freiwald et al., 2004).

### EUROMARGINS

EUROMARGINS is a new activity of the ESF that started in 2003. It has as its principal focuses the imaging, monitoring, and modeling of the physical, chemical, and biological processes that are occurring in the passive continental margin. The program comprises 14 projects covering a range of topics including the crustal “architecture” of conjugate volcanic margins; studies of slope stability in the Arctic north of Svalbard and on glacier-fed margins and in the Mediterranean on river-fed margins; detailed



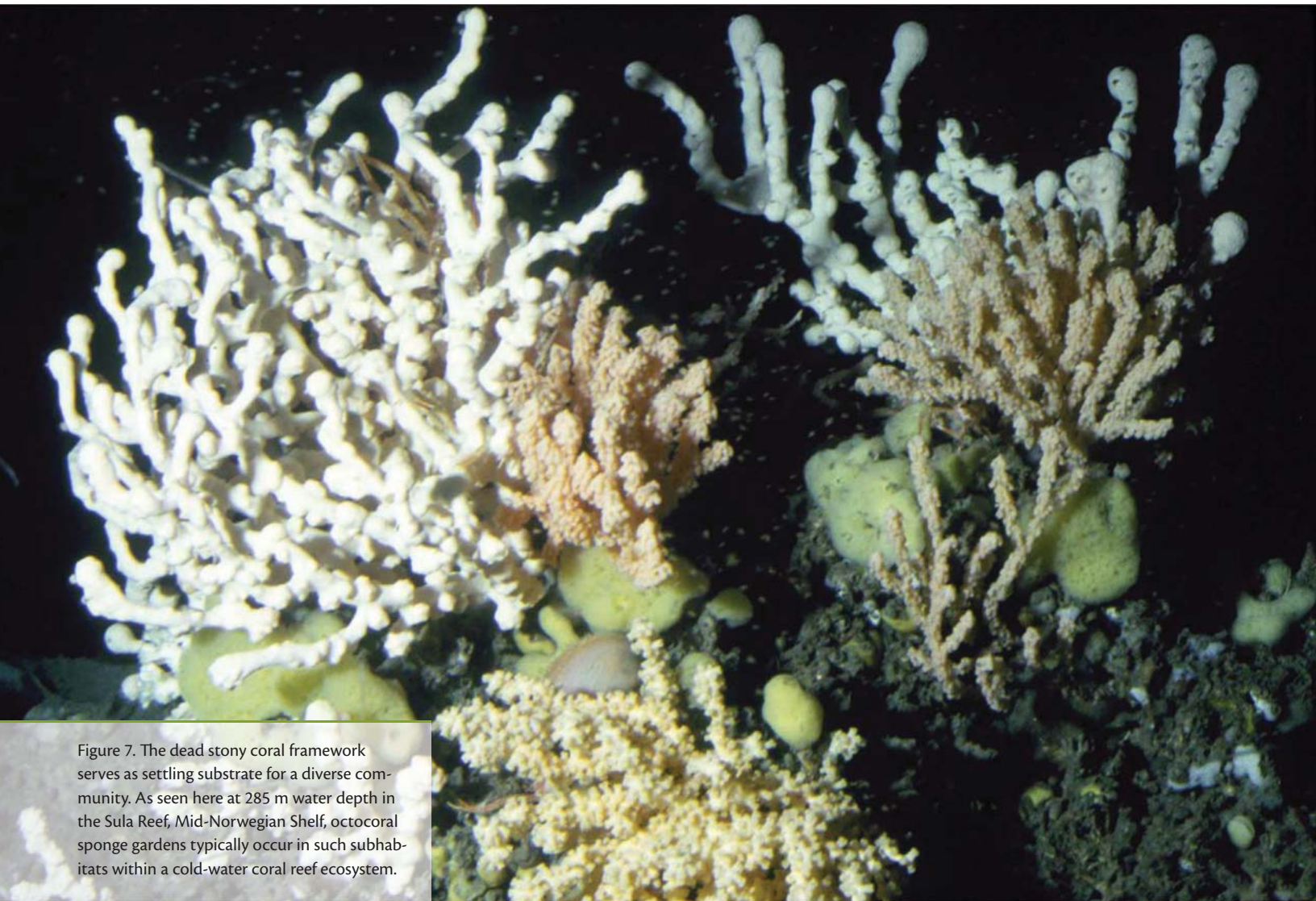


Figure 7. The dead stony coral framework serves as settling substrate for a diverse community. As seen here at 285 m water depth in the Sula Reef, Mid-Norwegian Shelf, octocoral sponge gardens typically occur in such subhabitats within a cold-water coral reef ecosystem.

studies of seepages through the seabed; and carbonate mounds and deep-water coral reefs and their relationship to fluid flow in margins. The program will run for five years and includes national research funding and a European networking component.

Passive continental margins, which are one of the most distinctive morphological features of the world's ocean basins, mark the transition between continental and oceanic crust. They are also the sites

of some of the world's largest accumulations of sediments and are one of the few remaining frontiers for natural resources. The nations of Europe share one of the longest margin systems in the world. Understanding the processes that have shaped this passive continental-margin system will require broadly based interdisciplinary studies. EUROMARGINS will seek to encourage the development of both new technologies and conceptual models for passive-margin evolution

with the expressed aim of advancing, in a major way, integrated research into the mechanisms that are responsible for continental break-up and the formation of ocean basins and their margins. The pooling of human resources, the training of a new generation of geoscientists, and the optimal sharing of national observational platforms (e.g., ships), and analytical and modelling facilities are considered important "value-added" ingredients of the EUROMARGINS program.



## CONCLUDING REMARKS

There has been a considerable amount of research on Europe's continental margin, but much more needs to be done. As techniques develop and more areas are surveyed, researchers see a gradually evolving picture where the geosphere, biosphere, and hydrosphere all interact to produce a range of complex environments. The long-term effects of human-kind's impact on these environments through exploitation of fish and minerals remain unknown, but more research, and more integration of this research, is urgently needed to measure these impacts and to map a route to sustainable development. Europe needs to make such decisions in line with its strategic objective of sustainable development. Guidance documents on sustainable development have been developed at various conferences and by various organizations, including: EU's Gothenburg European Council, who met in 2001 (more information available at [http://europa.eu.int/comm/gothenburg\\_council/sustainable\\_en.htm](http://europa.eu.int/comm/gothenburg_council/sustainable_en.htm)); EU legislation was enacted in 1998 called the Biodiversity Action Plan for the Conservation of Natural Resources (available at <http://europa.eu.int/scadplus/leg/en/lvb/l28023.htm>); principles developed at the World Summit on Sustainable Development in 2002 (available at <http://www.johannesburg-summit.org>) and the commitments to mitigate the loss of biodiversity created at the Convention on Biological Diversity in Rio de Janeiro in 1992 (available at <http://www.biodiv.org/convention/articles.asp>), and the biodiversity strategy to prevent biodiversity loss at the regional level developed at the OSPAR Convention for the Protection of the Marine

Environment of the North-East Atlantic in 2000 (available at <http://www.ospar.org/eng/html/welcome.html>).

## ACKNOWLEDGEMENTS

We thank the European Commission, European Science Foundation, U.S. Office of Naval Research, and the U.S. National Science Foundation for supporting the ongoing research projects including the seagoing activities with research vessels. This publication was supported by EC contracts EVK3-2002-00513 (OMARC), RTN2-2001-00281 (EURODOM), EVK3-CT-2002-00079 (Eurostrataform), EVK3-CT-2002-40024 (PROMESS1), EVK3-CT-2001-20001 (EURODELTA), EVK3-CT-1999-00006 (COSTA), EVK3-CT-2000-00043 (HYDRATECH), EVK3-CT-1999-00017 (DeepBUG), EVK3-CT-2002-00090 (ASSEMBLAGE), EVK3-CT-2002-00080 (METROL), EVK3-CT-2002-00068 (ANAXIMANDER), EVK3-CT-1999-00011 (STRATAGEM), EVK3-CT-1999-00008 (ACES), EVK3-CT-1999-00013 (ECOMOUND), EVK3-CT-1999-00016 (GEOMOUND) and the EUROMAR-GINS program of the European Science Foundation 01-LEC-EMA14F, NFR contract number 158733/420. ☐

## REFERENCES

- Boetius, A., K. Ravenschlag, C.J. Schubert, D. Rickert, F. Widdel, A. Gieseke, R. Amann, B.B. Jørgensen, U. Witte, and O. Pfannkuche. 2000. Microscopic identification of a microbial consortium apparently mediating anaerobic methane oxidation above marine gas hydrate. *Nature* 407:623-626.
- Bünz, S., and J. Mienert. 2004. Acoustic imaging of gas hydrate and free gas at the Storegga Slide. *Journal of Geophysical Research* 109(B4):B04102.
- De Mol, B., P. Van Rensbergen, S. Pillen, K. Van Herreweghe, D. Van Rooij, A. McDonnell, V. Huvenne, M. Ivanov, R. Swennen, and J.P. Henriët. 2002. Large deep-water coral banks in the Porcupine Basin, southwest of Ireland. *Marine Geology*

- 188:193-231.
- Freiwald, A., A. Grehan, J.M. Roberts, T. Koslow, and J.H. Fosså. 2004. Cold-water coral reefs. UNEP-WCMC Report. *Biodiversity Series* 22:1-84.
- Hafliðason, H., H.P. Sejrup, A. Nygård, J. Mienert, P. Bryn, R. Lien, C.F. Forsberg, K. Berg, and D. Masson. In press. The Storegga slide: Architecture, geometry, and slide development. *Marine Geology* (special issue).
- Kallmeyer, J., T.G. Ferdelman, A. Weber, H. Fossing, and B.B. Jørgensen. 2004. A cold chromium distillation procedure for radiolabeled sulfide applied to sulfate reduction measurements. *Limnology and Oceanography: Methods* 2:171-180.
- Kenyon, N.H., A.M. Akhmetzhanov, A.J. Wheeler, T.C.E. Van Weering, H. de Haas, and M. Ivanov. 2003. Giant carbonate mud mounds in the southern Rockall Trough. *Marine Geology* 195:5-30.
- Michaelis, W., R. Seifert, K. Nauhaus, T. Treude, V. Thiel, M. Blumenberg, K. Knittel, A. Gieseke, K. Peterknecht, T. Pape, A. Boetius, R. Amann, B.B. Jørgensen, F. Widdel, J. Peckmann, N.V. Pimenov, and M.B. Gulin. 2002. Microbial reefs in the Black Sea fueled by anaerobic oxidation of methane. *Science* 297:1,013-1,015.
- Mienert, J. In press. COSTA: Continental slope stability: major aims and topics. *Marine Geology* (special issue).
- Parkes, R.J., B.A. Cragg, G. Webster, J.C. Fry, and A. J. Weightman. 2004. Deep subsurface habitats in the equatorial Pacific and Peru margin sediments. In: *The 10th Annual International Symposium on Microbial Ecology ISME-10, Microbial Planet; Sub-Surface to Space*, held in Cancun, Mexico August 22-27. International Symposium on Microbial Ecology, Geneva, Switzerland.
- Reeburgh, W.S., S.C. Whalen, and M.J.H. Alperin. 1993. The role of methylo-trophy in the global methane budget. Pp 1-14 in *Microbial Growth on C1 Compounds*, J.C. Murrell, and D.P. Kelly, eds. Intercept, Andover, United Kingdom.
- Solheim, A., P. Bryn, H.P. Sejrup, J. Mienert, and K. Berg. In press. Ormen Lange: An integrated study for the safe development of a deep-water gas field within the Storegga Slide Complex, NE Atlantic continental margin. Executive summary. *Marine and Petroleum Geology* (special issue).
- Stoker, M.S., D. Praeg, P.M. Shannon, B.O. Hjelstuen, J.S. Laberg, T. Nielsen, T.C.E. van Weering, H.P. Sejrup, and D. Evans. In press. Neogene evolution of the Atlantic continental margin of NW Europe (Lofoten Islands to SW Ireland): Anything but passive. In: *Petroleum Geology: North-west Europe and Global Perspectives—Proceedings of the 6th Petroleum Geology Conference*, A.G. Dore, and B. Vining, eds. Geological Society of London.
- Toffin, L., G. Webster, A.J. Weightman, J.C. Fry, and D. Prieur. 2004. Molecular monitoring of culturable bacteria from deep-sea sediment of the Nankai Trough, Leg 190 Ocean Drilling Program. *FEMS Microbiology Ecology* 48:357-367.