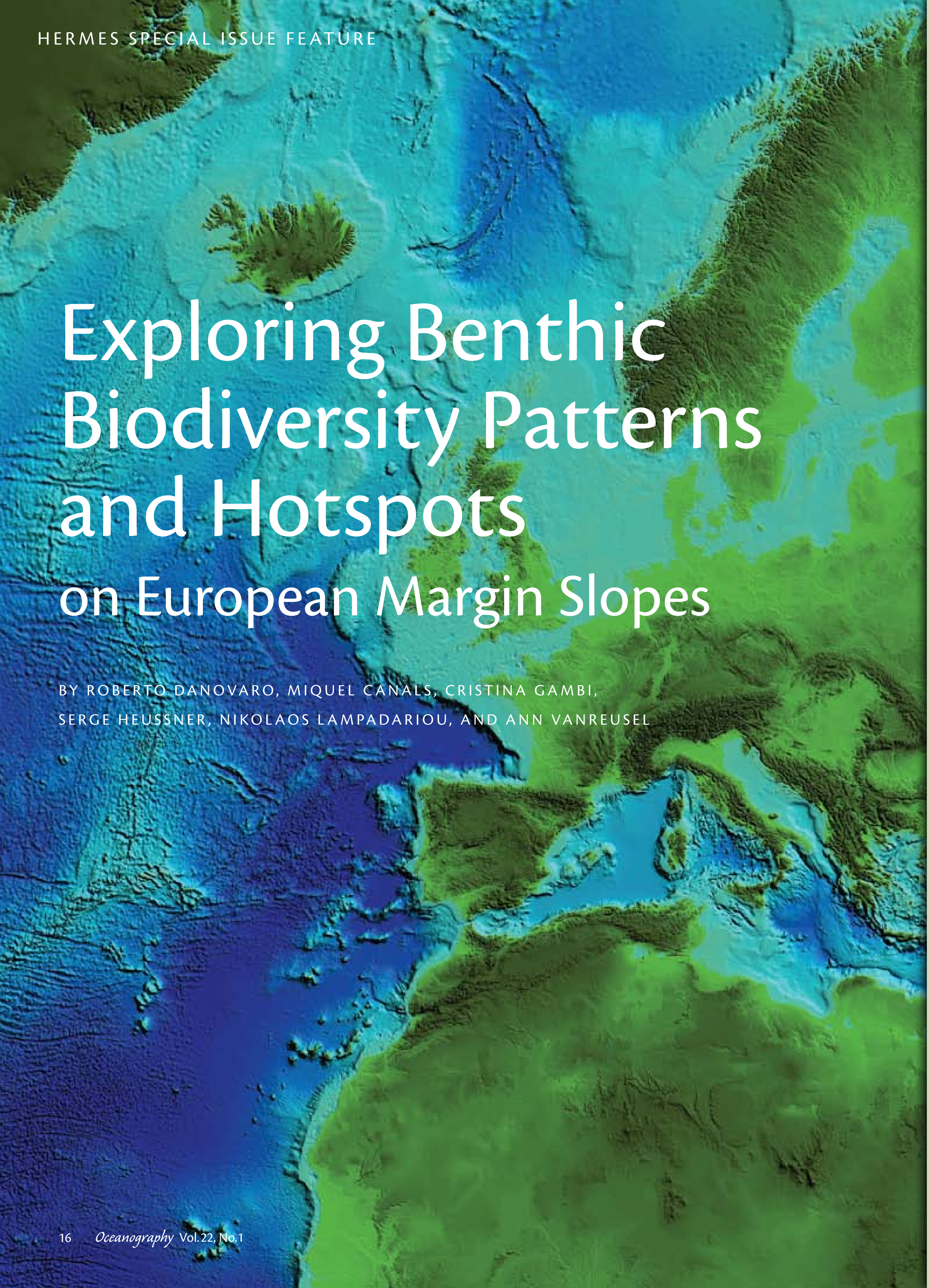

Exploring Benthic Biodiversity Patterns and Hotspots

on European Margin Slopes

BY ROBERTO DANOVARO, MIQUEL CANALS, CRISTINA GAMBI,
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ABSTRACT. There is increasing evidence that continental slope ecosystems represent one of the major repositories of benthic marine biodiversity. The enhanced levels of biodiversity along slopes are hypothesized to be a source of biodiversity for continental shelves and deeper basins. Continental margins are increasingly altered by human activities, but the consequences of these anthropogenic impacts on benthic biodiversity and ecosystem functioning are almost completely unknown. Thus, there is an urgent need to gather sufficient information to enable us to understand patterns and drivers of deep-sea biodiversity along continental margins. Although the local diversity of some deep open slope ecosystems is moderately well documented, very little is known about the biodiversity of these systems at greater spatial scales. Topographic setting, hydrodynamic forcing, and the biogeochemical characteristics of the deep-sea floor may play key roles in promoting and sustaining high biodiversity along the open slopes of continental margins. HERMES provided the opportunity to acquire a significant volume of information on the biodiversity, trophic conditions, and topographic characteristics of open slopes across European margins, increasing our knowledge of the latitudinal, longitudinal, and bathymetric patterns of benthic biodiversity, and extending our comprehension of the mechanisms driving deep-sea biodiversity and its potential loss. Improved knowledge of these processes is needed to inform policy decisions for promoting sustainable management of open slopes and deep-sea ecosystems along continental margins.

VULNERABILITY OF SLOPE ECOSYSTEMS TO LOSS OF BIODIVERSITY

The continental slope connects the continental shelf and the deep sea; all exchanges of matter and energy, including anthropogenic inputs, between these two broad domains occur across the continental slope. Although continental slopes constitute less than 20% of the world's ocean real estate, they may be quantitatively important sources of the organic matter that fuels respiration in the open ocean's interior (Bauer and Druffel, 1998; Canals et al., 2006). Their profound involvement in global biogeochemical and ecological processes makes continental slope ecosystems essential to the sustainable functioning of our biosphere. Several goods (biomass, bioactive molecules, oil, and gas) and services (climate regulation, nutrient regeneration, and food) provided by deep-sea ecosystems are produced and/or stored along the open slopes of continental margins. At the same time, slope ecosystems are principal repositories of deep-sea biomass and likely host a large proportion of Earth's as-yet undiscovered biodiversity. Assessing their vulnerability to anthropogenic inputs is therefore crucial to defining specific policy actions aimed at preserving deep-sea biodiversity.

Protecting deep-sea biodiversity is not only ethical but also timely from a socio-economic perspective, as some recent global-scale studies demonstrate the existence of a close link between benthic biodiversity and ecosystem functioning (Danovaro et al., 2008a). These studies show that deep-sea ecosystem functioning and efficiency increase exponentially where there is higher biodiversity (Figure 1). The exponential nature of that relationship suggests that open slope systems and deep basins are characterized by positive functional interactions between different deep-sea benthic species (ecological facilitation). These findings also indicate that the consequences of biodiversity loss to the functioning of these ecosystems can be dramatic. Danovaro et al. (2008b) estimate that a biodiversity loss of ~ 20–30% can result in a 50–80% reduction of deep-sea ecosystems' key processes and their consequent collapse. Because deep-sea ecosystem functioning is crucial to global biogeochemical cycles (Dell'Anno and Danovaro, 2005), it is of paramount importance to define deep-sea biogeographic domains, identify the sources of deep-sea species diversity, and increase understanding of the mechanisms driving and/or threatening that biodiversity. In HERMES, we examined the patterns of meiofaunal diversity and, particularly, of nematode diversity. Nematodes account for three-fifths of all metazoans on Earth—and 80–90% of total faunal abundance in deep-sea sediments. Moreover, nematodes are one of the most diverse metazoan phyla in the ocean (Lambshead and Shalk, 2001; Lambshead and Boucher, 2003).

THE ENIGMA OF DEEP-SEA BIODIVERSITY

The discovery of longitudinal and latitudinal gradients of species richness in terrestrial ecosystems (see Rosenzweig, 1995) has recently been transposed to marine systems, but with conflicting results; observations on latitudinal trends of marine biodiversity are rare, and several taxa do not display any trend (Rex et al., 1993, 2000; Clarke and Crame, 1997; Roy et al., 1998; Crame, 2000). The existence of latitudinal patterns of biodiversity from the tropics to the poles (decreasing species richness for macrofauna, increasing richness for nematodes) is still largely debated (Lambshead et al., 2000; Rex et al., 2000); thus, the use of meiofauna as a proxy for all faunal size groups in the deep sea is still being validated (Danovaro et al., 2008a). These patterns are generally explained by different factors, including species-area hypothesis (i.e., species richness increases with surface area), energy productivity, species ranges, and historical (evolutionary) factors (Gray, 2000). There are, however, still large gaps in information on latitudinal patterns in the Northern Hemisphere, especially regarding the diversity of small metazoans (including nematodes). In other words, a huge knowledge gap remains, making it difficult to compare the information available on patterns of terrestrial versus marine biodiversity, which limits our ability to define a general theory of biodiversity patterns and regulating factors.

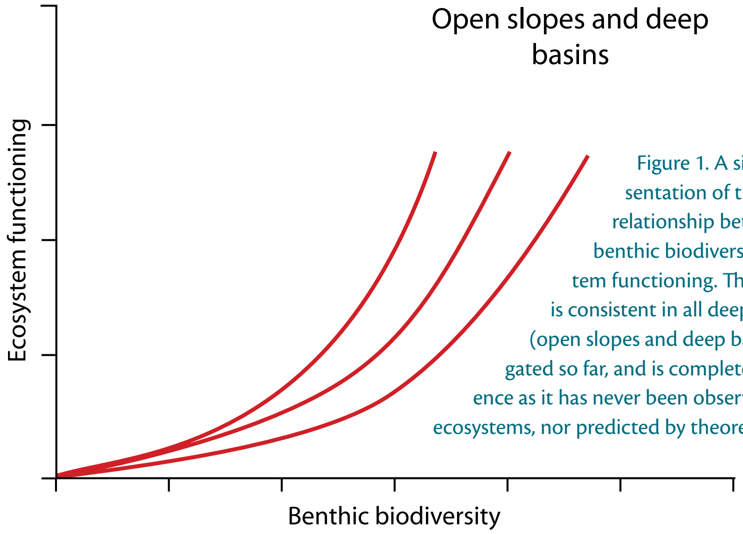

Figure 1. A simplified representation of the exponential relationship between deep benthic biodiversity and ecosystem functioning. This relationship is consistent in all deep-sea systems (open slopes and deep basins) investigated so far, and is completely new for science as it has never been observed in terrestrial ecosystems, nor predicted by theoretical models.

A central paradigm of marine diversity is that species richness increases with increasing water depth to a maximum around 2000 m and thereafter decreases (Rex, 1981; Levin et al., 2001). The enhanced levels of biodiversity along slopes are possibly a source for biodiversity of deeper basins and shelves through radiation and dispersal processes closely coupled with benthic topography and the hydrodynamic, physical, and biogeochemical characteristics of the deep sea. The "source-sink hypothesis" (Rex et al., 2005) suggests that abyssal biodiversity is a subset of bathyal biodiversity (in particular, the biodiversity of the slopes at depths typically between 1000 and 2500 m), but this hypothesis has so far only been tested for gastropod bivalves (McClain, 2005; McClain and Etter, 2005). We do not know to what extent this hypothesis applies to other faunal groups or phyla.

In open slope systems, bathymetric gradients of species diversity have been more widely documented than latitudinal gradients (Rex, 1981; Etter and Grassle, 1992; Gray et al., 1997; Rex et al., 1997; Levin and Gage, 1998; Stuart et al., 2003). However, there is now increasing evidence that unimodal biodiversity patterns with a peak at intermediate depths may not be the rule. Further studies are needed to understand the interconnection between open slopes and bathyal-abyssal ecosystems.

The mechanisms that potentially control bathymetric patterns in species richness are still largely unknown. A variety of biological and environmental factors have been proposed to explain why

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species diversity changes with depth, including speciation rates, competition, predation, patch dynamics, boundary constraints, environmental heterogeneity, climatic variability, productivity, and various combinations of these factors (Ricklefs and Schluter, 1993; Levin et al., 2001; Stuart et al., 2003). However, a deep-sea zonation (zones with similar ecological conditions) simply based on depth ranges is clearly insufficient to explain diversity and in some cases is misleading. We are approaching a phase of deep-sea research that will require redefinition of the criteria for the identification of "eco-regions" at the deep-sea floor (Danovaro et al. 2008b). Defining the borders, extent, and interconnections of deep-sea regions with specific ecological, biogeographic, and environmental characteristics is essential for building a deep-sea biogeography, which is needed—as in terrestrial ecosystems—to identify the deep-sea areas deserving of special protection and monitoring, and thus for responsible management of deep-sea resources.

If spatial patterns of biodiversity in the deep sea are far from being clarified, even more uncertain is our understanding of the mechanisms driving these patterns. Among them, those more frequently invoked are: (1) sediment grain size and substrate heterogeneity; (2) productivity, organic content, and/or microbial features; (3) food resources; (4) oxygen availability; (5) current regimes; and (6) catastrophic disturbances (Etter and Grassle, 1992; Jahnke, 1996; Levin and Gage, 1998; Levin et al., 2001). However, in each specific deep-sea area, all of these factors can act in different combinations and can be superimposed onto other local or regional conditions, causing as-yet unpredictable biotic responses (Levin et al., 2001).

HOTSPOTS OF BIODIVERSITY ALONG EUROPEAN SLOPES

Within the framework of the HERMES project, a significant body of information on local diversity, trophic conditions, and topographic characteristics was acquired at a large spatial scale along bathymetric patterns on various European open slopes, from the Arctic Ocean to the Black Sea (Figure 2). These data are of paramount importance for understanding factors controlling the distribution of biodiversity along latitudinal, longitudinal, and bathymetric gradients on open slopes.

Ten open slope systems were investigated with the same sampling strategy: a series of bathymetric transects were run along the slopes, with additional transects extending to adjacent topographic settings in order to compare slope biodiversity with that of canyons, unstable slopes, and coral banks (Figure 3). This sampling strategy allowed us to define open slope biodiversity as a reference for

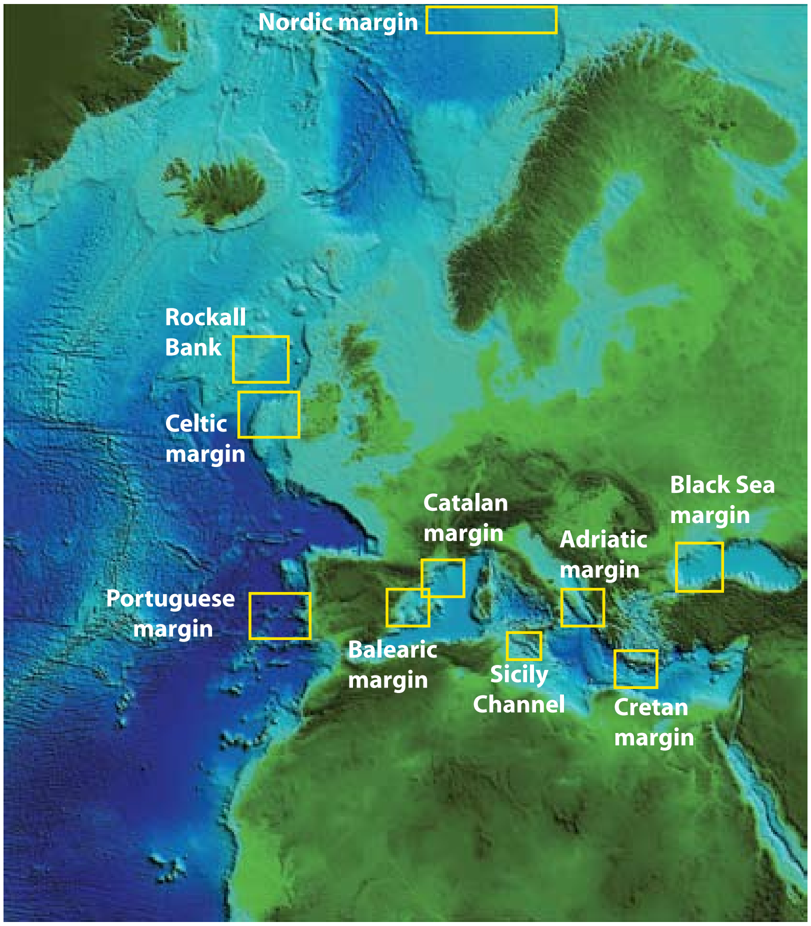

Figure 2. Sampling areas along the European open slopes. Biodiversity sampling across European margins was carried out using the following research vessels: *Polarstern*, *Discovery*, *Pelagia*, *Endeavor*, *Tethys II*, *Universitatis*, *Urania*, and *Aegaio*. Overall, 218 sites (depth range: 150–5500 m) were sampled along 20 slopes and nine adjacent canyons during more than 20 sampling cruises.

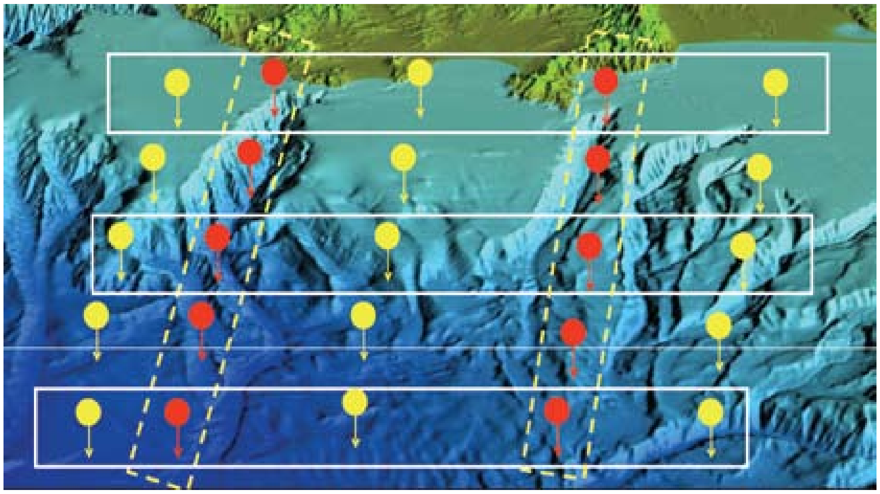

Figure 3. An example from the Catalan margin of the sampling strategy adopted in all continental margins under investigation. Yellow symbols mark the open slope stations sampled for biodiversity analysis and red symbols the stations located along transects in adjacent topographic settings (e.g., canyons, unstable slopes). The map is not to scale.

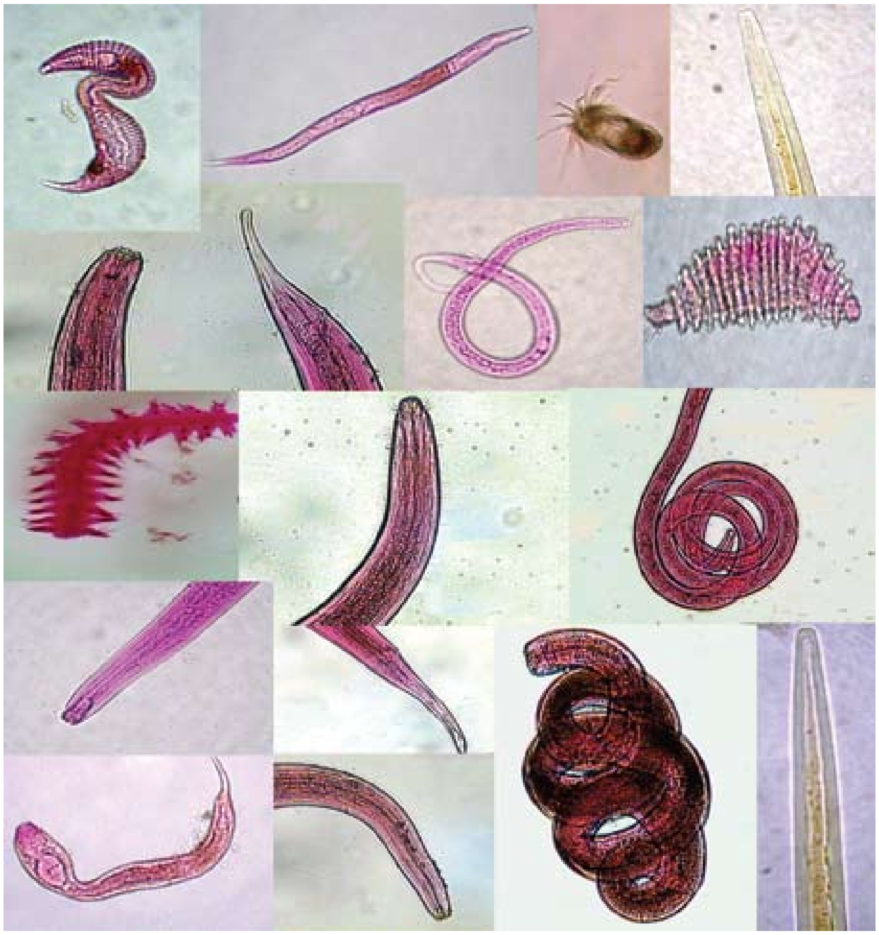

Figure 4. An example of the diversity of life forms of the small metazoan fauna (meiofauna) inhabiting and numerically dominating open slope sediments.

the biodiversity levels observed in other specific ecosystems.

Metazoan meiofauna, and nematodes in particular, were used to describe the biodiversity patterns in the deep sea (Figure 4). Benthic biodiversity was measured as the total number of meiofaunal taxa present and as nematode species richness (the total number of species identified at each site), expressed as E(51) (the expected number of nematode species for a theoretical sample of 51 specimens). Deep-sea nematode diversity appears to be related to that of other benthic components such as foraminifera (Gooday et al., 1998), macrofauna (Levin et al., 2001), and the richness of higher meiofaunal taxa in the deep sea (Danovaro et al., 2008a). The results for nematode biodiversity suggest that slopes can be considered hotspots of benthic biodiversity (sensu Myers et al., 2000) and that they are optimal systems for investigating large-scale and bathymetric patterns, potentially representing a model for planning biodiversity conservation in deep-sea areas.

LATITUDINAL PATTERNS OF BIODIVERSITY ALONG EUROPEAN SLOPES

Investigation of deep-sea metazoan species richness along latitudinal gradients is relatively new and, so far, is restricted to a few macrofaunal taxa (Rex et al., 1993, 1997, 2000), modern and fossil foraminifera (Thomas and Gooday, 1996; Culver and Buzas, 2000), and nematodes (Lambshead et al., 2000). Contrasting results are reported from these few studies such that latitudinal trends of marine biodiversity cannot be discerned for several taxa (Macpherson and Duarte, 1994; Rohde, 1999). Sometimes trends are determined using the available, limited deep-sea diversity data, which are never collected with the specific intention of assessing large-scale diversity gradients. Until now, studies on faunal diversity along latitudinal gradients have used data assembled from a variety of projects that used different collecting protocols and methods. This problem has contributed to increasing the degree of uncertainty in the interpretation of results.

Preliminary results gathered by the HERMES project, using a large data set collected under the same sampling strategy and laboratory protocols, are providing new insights into the knowledge of latitudinal patterns. Although limited data were collected along the European open slopes for comparison, the results are significantly different from those expected. The richness of total meiofaunal taxa and nematode diversity (as E[51]) displays a pattern in which the highest biodiversity is reached at intermediate to high latitudes (Figure 5). However, the very limited information available between 42°N and 70°N or more, and the peculiar characteristics of the deep Mediterranean, suggests that adequate, spatially replicated, intensive sampling might change the picture. These new observations beg for new hypotheses based on the combined effect of regional productivity and efficiency of shelf export in different slope areas. In this respect, it is now evident that the quality of food sources can play a key role in driving the observed spatial patterns of biodiversity, and each area appears to be driven by different factors. In particular, the labile components of organic matter (as proteins, carbohydrates, and lipids) can influence species distribution and the biodiversity of open slope systems.

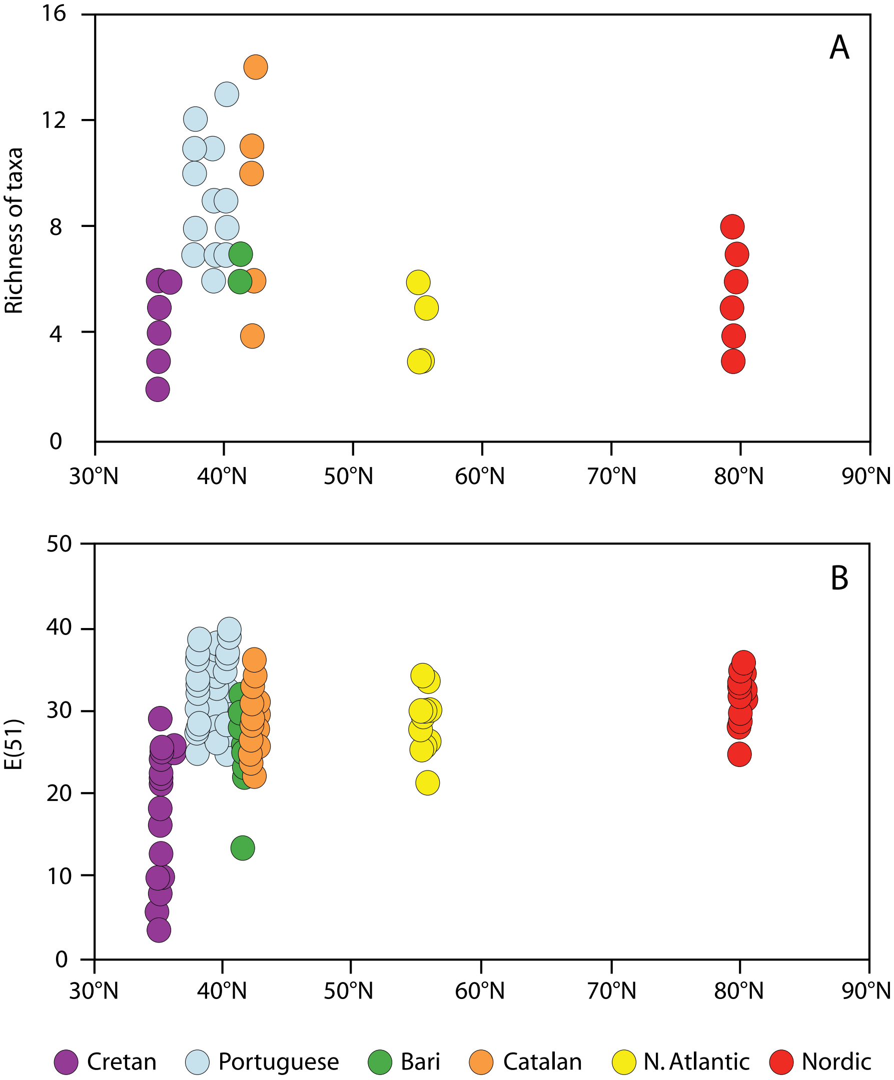

Figure 5. Latitudinal patterns of benthic biodiversity along the open slopes of the European margins. Patterns of biodiversity are illustrated as: (A) number of higher meiofaunal taxa and (B) nematode biodiversity expressed as expected species number E(51).

LONGITUDINAL PATTERNS OF BIODIVERSITY ALONG EUROPEAN SLOPES

Little is also known about the longitudinal gradients across the deep-sea regions and the continental margins. Although the Mediterranean basin is recognized as one of the most diverse on the planet, in terms of both terrestrial and coastal marine species (Myers et al., 2000), its deep basin seems to contain much lower diversity than equivalent deep-sea regions of the Atlantic and Pacific oceans (Lambshead et al., 2000). The reasons for this low diversity are related to: (1) the complex paleoecological history characterized by the Messinian salinity crisis and the almost complete desiccation of the basin, and (2) the high deep-sea temperature (ca 10°C higher than the Atlantic Ocean at similar depths), which makes the settlement of deep-Atlantic fauna in the deep-Mediterranean basin difficult. These conclusions are based on the analysis of macrobenthos, whereas little information is available on meiofaunal diversity. Our preliminary findings suggest that biodiversity (as number of meiofaunal taxa) is highly variable in open slope systems located at the same longitude (Figure 6A). Similar results were observed in terms of E(51) (Figure 6B).

Within the Mediterranean region, biodiversity displays a clear longitudinal gradient along open slopes, with values decreasing eastward, from the Catalan to the southern Cretan margins. The observed longitudinal gradients both in the Atlantic Ocean and the Mediterranean Sea are also evident when the biodiversity of all open slopes is compared at similar depths. Due to the existence of a decreasing west-east productivity gradient, it was further suggested that the longitudinal gradient observed in the deep Mediterranean could be influenced by changes in food availability (Danovaro et al., 1999, 2008b). The results suggest that the spatial variability of food quality along the European margins, from the Nordic to the southern Cretan margins, influences the biodiversity spatial patterns at large scale.

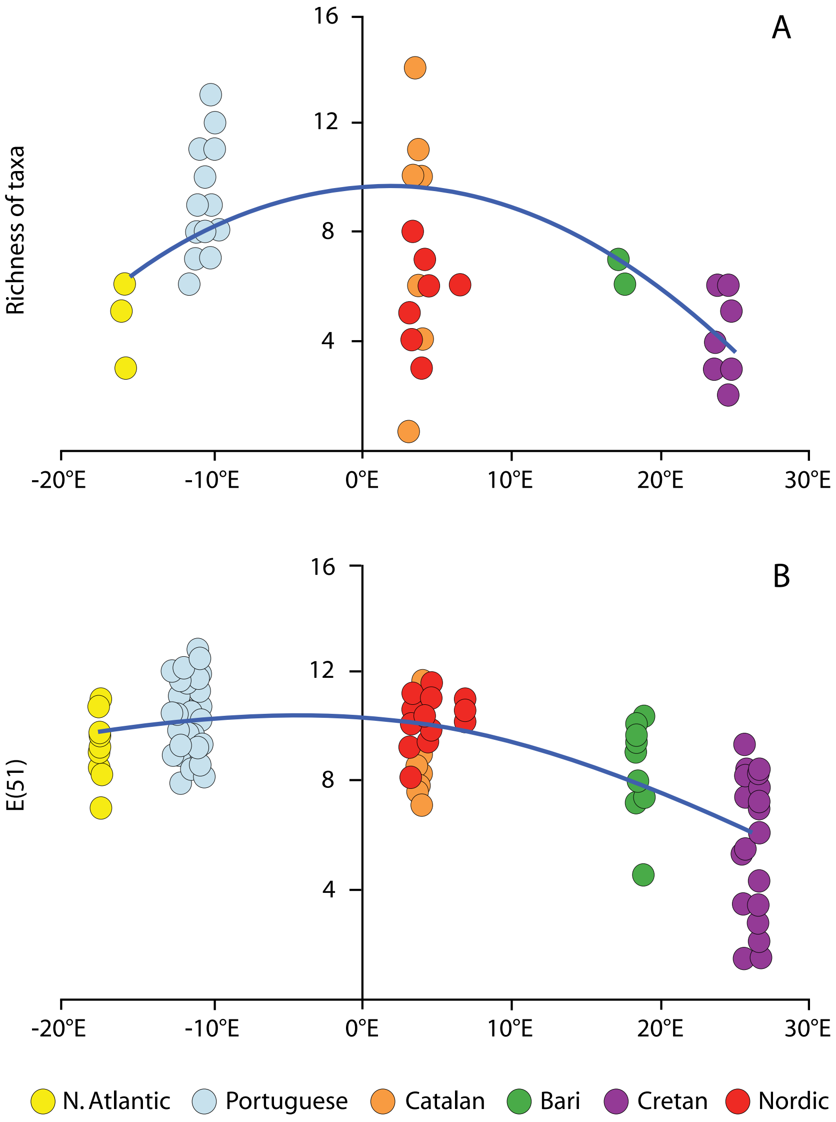

Figure 6. Longitudinal patterns of benthic biodiversity along the open slopes of the European margins. Patterns of biodiversity are identified as: (A) number of higher meiofaunal taxa and (B) nematode biodiversity expressed as expected species number E(51).

BATHYMETRIC PATTERNS OF BIODIVERSITY ALONG EUROPEAN SLOPES

Species diversity varies strongly with depth, and diversity-depth patterns vary geographically from basin to basin (Rex et al., 1997). Although diversity-depth trends are not completely understood, it seems likely that they are shaped by complex interacting factors that operate at different temporal and spatial scales (Levin et al., 2001; Stuart et al., 2003). Knowledge of bathymetric gradients of diversity is largely based on studies conducted in the bathyal zone (i.e., from the shelf break at 200 m down to 4000 m). HERMES results reveal that nematode communities are characterized by high biodiversity values, but the expected strong unimodal trend over the bathymetric gradient with a diversity peak at 2000-m water depth put forward by Rex (1981) is not always evident. Therefore, a bell curve cannot be used to describe the general patterns of meiofaunal biodiversity along the European open slopes under investigation. Moreover, different taxa display different spatial patterns with increasing depth. In accordance with previous studies (Vincx et al., 1994; Hoste et al., 2007), the number of taxa decreases with increasing depth along the open slopes in all study areas except the North Atlantic (Rockall Trough; Figure 7A). However, no clear spatial pattern in nematode diversity, as E(51), can be identified in any of the study areas, except the southern Cretan margin where diversity decreases with depth (Figure 7B). These results suggest that biodiversity patterns also depend on topographic and ecological features. This outcome underlines the importance of acquiring a better understanding of specific topographic features and the need for new approaches to investigate deep-sea biodiversity that are tightly linked to geosphere characteristics.

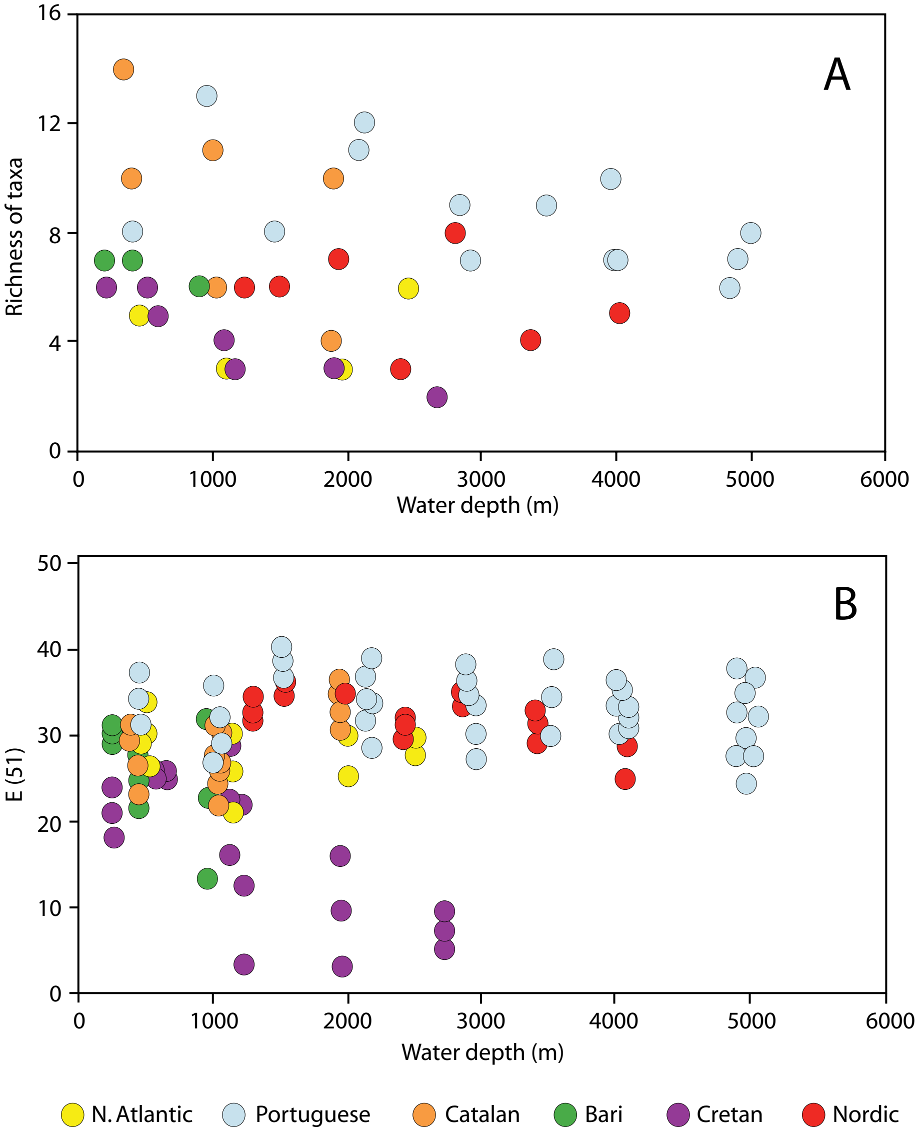

Figure 7. Bathymetric patterns of benthic biodiversity along the open slopes of the European margins. Benthic biodiversity is expressed as: (A) number of higher meiofaunal taxa and (B) nematode biodiversity expressed as expected species number E(51).

BIODIVERSITY TURNOVER IN OPEN SLOPE SYSTEMS

Given the complexity of the factors driving benthic biodiversity on open slopes, the simple measurement of local (alpha) diversity is not sufficient to draw a clear picture of the mechanisms involved. Analysis of turnover (beta) diversity (Gray, 2000) is useful for providing further insight as it reflects the degree to which a number of species are replaced by other species when moving from one site to another (Figure 8). Beta diversity was analyzed during HERMES by comparing (1) different open slope environments and (2) open slope environments with adjacent canyons, unstable slopes, or coral banks. Although alpha diversity is often similar among different open slopes, beta diversity was found to be extremely high in some regions, reaching values up to 90% (e.g., between slopes in Rockall Trough and southern Crete). A partial exception is represented by high-latitude slopes that, along with the presence of a large number of closely related species, also displayed lower turnover diversity. Nonetheless, where turnover diversity is calculated among regions and slopes at different latitudes along European margins, the values are always extremely high. Turnover diversity values reported from the HERMES project are among the highest reported so far in the deep-sea literature, suggesting that open slopes could be preferential sites for the high specialization and possibly speciation of deep-sea fauna. Such high beta diversity is likely to be associated with a high substrate heterogeneity and topographic complexity, a postulate still being carefully examined.

CONCLUSIONS AND PERSPECTIVES

The multidisciplinary HERMES project represents one of most comprehensive

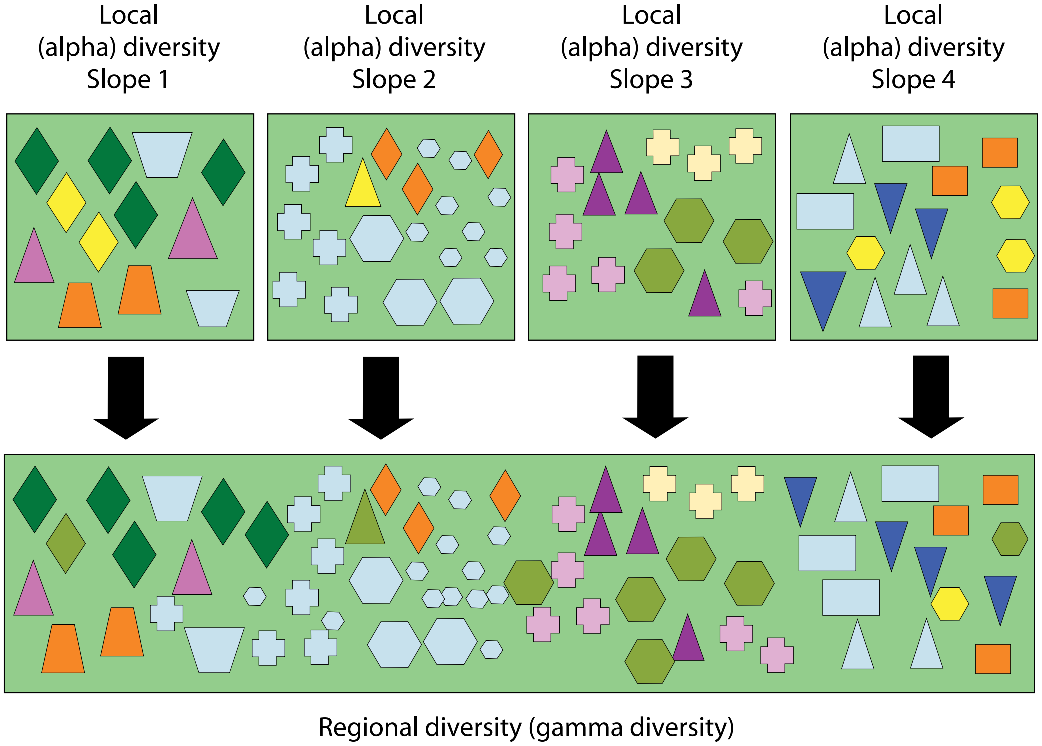

Figure 8. A schematic example of how turnover biodiversity (beta diversity) can enhance biodiversity at larger spatial scales. The shape and color of the various symbols reflect the diversity of the benthic species in deep-sea sediments along the slopes. If the number and identity of the species within each box (slope) are identical in all slopes, the beta diversity is 0, and the total regional diversity (gamma diversity) is equal to the local diversity (i.e., the diversity present in a single box). Conversely, if the number and identity of the species within each box differ more or less between the different slope areas, the overall diversity will increase according to the equation: $\gamma = \alpha \times \beta$ (where beta diversity is the fraction of unshared species). In the example illustrated here, the beta diversity is 100% (i.e., no shared species among different slopes).

attempts to understand patterns and drivers of benthic biodiversity along continental margins. The approach used, based on the cooperation of scientists from different countries and integrating a range of expertise and disciplines (i.e., deep-sea biology, microbiology, geology, and physical oceanography), is creating the most relevant, consistent, and innovative data set ever on open slope biodiversity and ecosystem functioning at the global scale. The results briefly illustrated here reveal that open slopes are "hotspots" of biodiversity in which species richness is higher than that reported for bathyal and abyssal plain ecosystems. However, a unique, general driver capable of explaining the spatial patterns of biodiversity was not identified. This result is not surprising, considering the multiplicity of interactions among "local" ecological characteristics, environmental factors, and topographic and textural conditions in each specific slope environment. This complexity probably has considerable influence on the conditions, allowing settlement of a high number of species. The patterns of deep-sea biodiversity along the slope are different from those hypothesized so far, drawing a mosaic of life more complex and varied than previously imagined. Further efforts should be devoted to increasing the spatial resolution of deep-sea investigations along open slopes. Understanding the mechanisms controlling deep-sea biodiversity within and across these attractive environments will open new perspectives for the conservation and sustainable management of these systems crucial to the functioning of the global ecosystem.

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