New Perceptions of Continental Margin Biodiversity

Chapter 5

New Perceptions of Continental Margin Biodiversity

5.1 Introduction: Diversity Re-examined as Slope Complexity is Disclosed

The Census of Marine Life has promoted synergetic approaches to assess and explain the diversity, distribution, and abundance of life in the ocean, focusing on domains where new approaches allowed discoveries and evident new steps in science. The field project “Continental Margin Ecosystems on a Worldwide Scale”, COMARGE, is one of the five Census projects concerned with the deep ocean. It was launched in 2005 to focus on the complex and active continental margins (Box 5.1), where unique ecosystems including canyons, oxygen minimum zones, cold seeps, and reef-like coral mounds were only recently discovered and studied owing to the development of new oceanographic equipments.

The complexity of the slope seabed has until recently limited the exploration of continental margins to major marine laboratories in developed countries. Such studies shaped our original, sometimes naive, conceptions of what lives on these steep depth gradients. The first impression was that the deep ocean is azoic, owing to the rapid decline in abundances with depth in the Mediterranean (Forbes 1844). This was later disproved by the telegraph cable-laying industry and an ensuing international race to sample to the greatest depths on an ocean scale (reviewed in Mills 1983). Trawl records in the Atlantic off Western Europe revealed that depth ranges of many species were limited to sometimes little more than several hundred meters,
COMARGE focuses on the deep continental margins, excluding the continental shelf. The upper boundary is delineated by the shelf break at ca. 140 m depth over most of the margins except in Antarctica where it can be as deep as 1,000 m. It coincides with a sharp turn-over in species composition. From a geological point of view, the margin ends at the boundary between the continental and oceanic crusts, thus including trenches. From a biological point of view, however, the lower boundary of the margin is more elusive and usually located at the bottom of the continental slope or rise, between 2,000 m and 5,000 m depth. For the purpose of computations and mining in a georeferenced database, we set up the lower boundary at 3,500 m depth. Between these upper and lower boundaries, deep continental margins cover approximately 40 million km² or 11% of the ocean surface. Their width ranges from 10 to over 500 km and their slope from 6° to 1° in active and passive settings, respectively.

What are Continental Margins?

Creating an intricate zonation of populations lining the slope (Le Danois 1948). The true extent of deep-sea biodiversity in the seemingly monotonous sediment environment became evident when Sanders et al. (1965) found that benthic communities along a transect between southern New England and the Bermuda islands were more diverse on the middle of the continental slope than on the shelf or the abyss (Sanders 1968; Rex 1981). Over the past 50 years, biological research on continental margins increased, our perception of deep habitats greatly improved, and descriptive exploration has given way to more functional studies (Fig. 5.1).
Of utmost importance in this evolution of deep-sea science have been the technological developments which disclosed the complexity of the slope environment. These include the use of trawled cameras, manned submersibles, remotely operated vehicles (ROVs), and autonomous underwater vehicles (AUVs), as well as high-resolution sidescan sonar, multibeam bathymetry mapping systems, high-resolution sub-seabed profilers, precision sampling qualitatively and quantitatively, and video and photographic imaging systems. Analyses of these data have been greatly enhanced by advances in digital processing, network databases, and visualization. Geophysical tools have been used to classify and map habitats over large areas because they can discriminate seabed type (mud, sand, rock). Higher-resolution tools have allowed the characterization of ecological features such as coral mounds, outcropping methane hydrate, mud volcanoes, and seabed roughness. Newly developed, near-bottom swath bathymetry operated from ROVs now resolves seafloor structures as small as 20 centimeters. The deep bottom is no longer as remote as it once was. Our perceptions are now of a much higher resolution and reveal that continental margins are both very complex and active regions ecologically, geologically, chemically, and hydrodynamically (Wefer et al. 2003). Collectively, these processes create unique ecosystems such as methane seeps, coral reefs, canyons, or oxygen minimum zones (OMZs). These hot spots are characterized by unusually high biomasses, productivity, physiological adaptations, and apparent high species endemicity (Fig. 5.2).

Fundamental patterns of species distribution first observed and explained in the context of monotonous slopes had thus to be re-evaluated in light of this newly recognized heterogeneity and its interplay with large-scale oceanographic features. The question was timely as the concurrent development of human activities already threatened margin hot spots and triggered urgent needs for sound scientific advice on the evaluation and conservation of continental margin biodiversity (Rogers et al. 2002). Large integrated projects had already begun to address these issues at a regional scale in the European North Atlantic (Weaver et al. 2004), the Gulf of Guinea (Sibuet & Vangriesheim 2009), and the Gulf of Mexico (Rowe & Kennicutt 2008). COMARGE benefited from these programs and expanded their scope to a global scale to address questions that had to be tackled through synergies within an international network of scientists (Box 5.2). This chapter summarizes the progress made so far and underscores in conclusion the major unknowns that may guide future research on continental margins during the next decade and beyond.

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**Fig. 5.2**

Location map of known hot spots sampled for biological purposes and included in COMARGE syntheses.
The COMARGE science plan was discussed and finalized during a community workshop held in 2006. Three main questions have been identified as major unknowns regarding continental margin ecology:

1) What are the margin habitats and what is the relation between diversity and habitat heterogeneity?
2) Are large-scale biodiversity patterns such as zonation or diversity-depth trends ubiquitous and what are their drivers?
3) Is there a specific response of continental margin biota to anthropogenic disturbances?

The strategy to tackle these issues was to create a network of scientists, promote discussions and syntheses through workshops, and foster data integration. The COMARGE network grew to bring together over a hundred researchers and students. Four workshops were organized that addressed: (1) the classification of margin habitats globally, (2) the roles of habitat heterogeneity in generating and maintaining continental margin biodiversity (Levin et al. 2010b), (3) the effects of both large-scale oceanographic features and habitat heterogeneity on nematode diversity (Vanreusel et al. 2010), and (4) the biogeography of marine squat lobsters (Baba et al., 2008). Data integration has been achieved either through the Ocean Biogeographic Information System (OBIS; www.iobis.org) or via the COMARGE Information System (COMARGIS), connected to OBIS. The originality of COMARGIS resides in the fact that it is ecologically oriented. The database has been built on an existing system (Fabri et al. 2006) that allows archiving comprehensive sampling metadata for both biological and environmental data.

5.2 Roles of Habitat Heterogeneity in Generating and Maintaining Continental Margin Biodiversity

Following early exploration, ecological studies were mainly directed at understanding the mechanisms that promote high species richness, with greatest focus on processes that operate at small spatial scales (reviewed in Snelgrove & Smith 2002), or the influence of energy flux on the structure of benthic communities (see, for example, Laubier & Sibuet 1979). In recent years new scientific questions have emerged about the relation between diversity and various forms and scales of margin heterogeneity that are closely linked to growing environmental concern about the deep sea. In the past quarter of a century this interest has focused the study of margins on several key environments. Cold seep communities (see Chapter 9) have been discovered and investigated in conjunction with tectonic studies in active margins and with oil and gas development on passive margins (Sibuet & Olu 1998; Sibuet & Olu-Le Roy 2003). There has been considerable interest in determining the extent of deep coral reef habitats to minimize the impact of deep-sea fisheries (Freiwald 2002). Canyons that cut across margins are now seen not only as novel, and somewhat specialized habitats, but also conduits for pollutant transport into the deeper abyss and sometimes sites of intensive fishing. Of the many environmental gradients that occur on the margins, oxygen minimum zones are seen as special habitats that mirror effects of coastal eutrophication and that may expand in response to climate change (Levin 2003).

COMARGE has brought together scientists working on these and other aspects of margins to evaluate and understand the relations between habitat heterogeneity and diversity.

5.2.1 Types of habitat heterogeneity that affect diversity: scales in space and time

Margin heterogeneity exists in many forms (Figs. 5.3 and 5.4) and on multiple space and time scales; it is also perceived differently depending on the size, mobility, and lifestyles of the species considered. The COMARGE focus on how different sources and scales of heterogeneity influence margin biodiversity has spanned a wide range of taxa, from Protozoa to megabenthos, in diverse settings across the globe. Workshop discussions, synthetic papers, and regional analyses published in a special volume of
the journal *Marine Ecology* (Levin et al. 2010b) have generated several major results.

Perhaps the most universal finding is that heterogeneity acts in a hierarchical, scale-dependent manner to influence margin diversity. At the largest scale with strong effect is hydrography associated with water masses (in particular temperature and oxygen) and overlying productivity. The impingement of water masses on the slope interact with depth and latitude (productivity) to shape levels of diversity and community composition (De Mello E Sousa et al. 2006; Priede et al. 2010; Sellanes et al. 2010; Williams et al. 2010). Productivity influences the water masses and food supply to the sea floor; both positive and negative diversity influences may result (Levin et al. 2001; Corliss et al. 2009).

However, hydrographic influences on diversity are modulated by variations in substrate and flow regime (Williams et al. 2010). At meso-scales (tens of kilometers) there is topographic control in the form of canyons, banks, ridges, pinnacles, and sediment fans. Deposition regimes (canyon floor and deep-sea fan) and substrate vary within these (Baguley et al. 2008; Ramirez-Llodra et al. 2010). At smaller scales there are earth and tectonic processes that control fluid seepage and sediment disturbance forming seeps (Olu-Le Roy et al. 2007b; Cordes et al. 2010; Menot et al. 2010). And at the smallest scales there are habitats formed by ecosystem engineers that influence diversity through provision of substrate, food, refuge, and various biotic interactions. These habitats include coral and sponge reefs, mytilid, vesicomyid, and siboglinid beds (Cordes et al. 2009, 2010). In some cases the biotic influence arises from decay processes at whale, wood, and kelp falls (Fujiwara et al. 2007; Pailleret et al. 2007).
Our focus on specialized margin settings has revealed that stressed habitats associated with hypoxia or high sediment sulfide levels exhibit depressed alpha diversity relative to open slope systems. Importantly, these settings contribute significantly to regional diversity patterns and to beta diversity (species turnover) on margins, ultimately adding to the species richness. This is true for macro- and megabenthos on slopes with oxygen minimum zones (Gooday et al. 2010; Levin et al. 2010; Sellanes et al. 2010), for all taxon sizes on slopes with methane seeps (Cordes et al. 2010; Menot et al. 2010; Van Gaever et al. 2010), and for an even broader range of habitats occupied globally by nematodes (Vanreusel et al. 2010). To address the question of how diversity accumulates across habitats a new analytical approach was developed that examines the change in slopes of species and genus accumulation curves as habitats are included. Analysis of invertebrate diversity at methane seeps from four very different regions illustrates addition of species as hypoxic, microbial mat, vesicomyid clam, and tube worm habitats are added, but with different rates depending on taxon and location (Fig. 5.5). A strong diversity response to habitat heterogeneity was found in Gulf of Mexico habitats; there was a much slower increase in the rate of species accumulation with habitat heterogeneity for the nematode fauna of the Haakon Mosby mud volcano (Cordes et al. 2010).

Several global analyses indicate that there are strong ocean basin and regional differences that preclude the occurrence of identical cosmopolitan species in all habitats (Vanreusel et al. 2010; Williams et al. 2010). Regional patterns can differ from a summed global pattern. This is evident for deep-sea fishes in the North Atlantic, where key roles for the position of the thermocline, local water masses, resuspended organic matter (OM) and seasonality create distinctive diversity patterns (Priede et al. 2010).

Fig. 5.5
Rate of species accumulation for macrofauna or genus accumulation for nematodes across habitats. The CA and OR margin macrofauna include species-level data from near-seep sediments, vesicomyid clam beds, oxygen minimum zones, bacterial mats, and background sediments. Gulf of Mexico macrofauna include species-level data from vestimentiferan tubeworm aggregations, mussel beds, and scleractinian coral habitats. Gulf of Guinea nematodes are genus-level data from seep, transition, canyon, and control sediments. Haakon Mosby mud volcano samples are also genus-level nematode meiofauna from bacterial mats, siboglinid-associated sediments from the outer rim of the volcano, and non-seep influenced sediments. Reproduced with permission from Cordes et al. 2010, copyright 2009 by Blackwell Publishing Ltd.

Fig. 5.4
Continental margin heterogeneity in images: (A) assemblages of mytilids, vesicomyids, and siboglinid tube-worms in a giant pockmark in the Gulf of Guinea (3,200 m depth) (copyright Ifremer, Biozaïre 2 cruise, 2002); (B) authigenic carbonates associated with a hydrocarbon seep are colonized by corals in the Gulf of Mexico (530 m depth) (courtesy of Derk Berquist and Charles Fisher, cruise sponsored by NOAA Ocean Exploration Program and US Mineral Management Service); (C) ophiuroids, antipatharians, and anemones are inhabiting Lophelia-reefs off Ireland (900 m depth) (copyright Ifremer, Caracole cruise, 2001); (D) A cloud of zooplankton around Lophelia reefs off Italy (600 m depth) (copyright Ifremer, Medeco cruise, 2007); (E) filter-feeding organisms such as Brinling asteroids are dominant in the Nazare Canyon off Portugal (1,000 m) (copyright NCCS Southampton and UK Natural Environment Research Council); (F) high sediment loading in the Var Canyon off France favors the sediment-dwelling or burrowing fauna such as squat lobsters (2,200 m) (copyright Ifremer, Medeco cruise, 2007); (G) the “featureless” muddy slope is actually punctuated with small-scale heterogeneities such as fecal pellets of large holothuroids Benthodytes lingua (35 cm in length), Alaminos Canyon, Northern Gulf of Mexico (2,222m depth) (courtesy of Robert Carney, Louisiana State University).
In many instances sources of heterogeneity are superimposed on one another; this can create additional complexity or, if stress or disturbance is involved, it can impose local homogeneity. The influence of heterogeneity has proven to be context-dependent as well. Heterogeneity that adds structure or nutrients often has greater effect at deeper than shallower depths (Levin & Mendoza 2007) because deeper margins tend to be more structurally homogeneous and more food poor. Biotic interactions between substrate provider and epibionts (Dattagupta et al. 2007; Järnegren et al. 2007), between animals and sediment microbes (Bertics & Ziebis 2009), or predation and competition between taxa can generate additional sources of heterogeneity.

5.2.2 Models underlying the heterogeneity–diversity relation

Continued exploration of margins has revealed that any continental margin habitats (for example cold seeps, canyons, deep-water coral reefs) are distributed as patches in a sedimented slope matrix. The resident species are predicted to function as metapopulations and metacommunities. The species-sorting model, in which diversity and metacommunity structure is dictated by different niche requirements (Leibold et al. 2004), appears to explain community patterns for species that occupy methane seep habitats (Cordes et al. 2010) and hypoxic settings (Goody et al. 2010). These niches are defined by substrate (abiotic, biotic), flow regimes, sulfide or methane requirements, and geochemical tolerances to sulfidic or hypersaline fluids (Brand et al. 2007; Levin & Mendoza 2007; Olu-Le Roy et al. 2007a; Levin et al. 2010; Sellanes et al. 2010; Van Gaever et al. 2010). In addition to chemoautotrophic symbioses, reduced compounds (methane and sulfide) also fuel a free-living microbial community that provides nutrition (and possibly settlement cues) for a vast array of smaller grazing, deposit feeding, and suspension feeding taxa, as well as for bacterivores that may specialize on microbes with specific metabolic pathways or morphologies (Levin & Mendoza 2007; Thurber et al. 2009; Van Gaever et al. 2010). Very localized, small-scale variations in geochemical settings may dictate diversity and evenness among meiofauna (Levin & Mendoza 2007; Thurber et al. 2009; Van Gaever et al. 2010; Vanreusel et al. 2010).

Other metacommunity models including mass effects (source-sink dynamics) or patch dynamics (succession based on tradeoffs between dispersalcolonization ability and competition) (Leibold et al. 2004) appear to apply to the canyon and deep-water coral reef settings where many species are not habitat endemics or obligate symbionts (Ramirez-Llodra et al. 2010; Vetter et al. 2010). The communities of deep-water coral reefs and vesicomyid tube worms exhibit clear successional stages on margins (Cordes et al. 2009).

5.2.3 The societal value of continental margin heterogeneity

The recent recognition of a high degree of heterogeneity on single margins and its influence on margin diversity offers new challenges to the assessment, management, and conservation of margin resources (Schlacher et al. 2010; Williams et al. 2010). It becomes essential that this heterogeneity is incorporated into planning for exploration, research, and monitoring (Levin & Dayton 2009). Habitat heterogeneity plays prominently in metapopulation and metacommunity theory, biodiversity–function relations, trophic dynamics, and in understanding roles of ecosystem engineers and invasive species.

Habitat heterogeneity unquestionably influences the key ecosystem services provided by the continental slope. Over 0.62 GtC y⁻¹ settles to the seafloor on margins, of which 0.06 GtC y⁻¹ may be buried in sediments (Muller-Karger et al. 2005). Sequestration occurs by margin biota and through carbonate precipitation (often microbially mediated). Hard bottoms, including those associated with methane seeps, seamounts, canyons, and coral and sponge reefs, are hot spots for fishes and invertebrates and provide major fisheries resource production on margins (Koslow et al. 2000). Oil and methane gas are linked to chemosynthetic environments on margins. The role of microbes and animals in transforming or consuming methane is of considerable interest, given that methane is a powerful greenhouse gas that contributes to global warming.

As we confront increasing pressures on margins from fishing, mineral resource extraction, and climate change, there is much to be gained by combining our newfound understanding of margin complexity with ecological theory into research and management solutions (Levin & Dayton 2009).

5.3 Spatial Trends in Biodiversity

Since the discovery of a diverse deep-sea fauna, deep-sea biologists have debated different hypotheses to explain depth-related patterns of the distribution and diversity of benthic and demersal organisms (Rex 1981), in particular that

- the diversity reaches a maximum at mid- to lower-slope depth,
- the fauna is zoned into bands according to water depth,
- faunal assemblages are dissimilar between depth zones but have a circum-margin distribution within a depth zone,
- and the width of the zones increases with depth.
Since these observations were initially made (1880s–1960s), numerous data have been collected on continental margins, but few syntheses have been attempted. The COMARGE project explored several ways to test those old but still unresolved hypotheses. A major issue has been the lack of taxonomic consistency across studies. Our first approach, thus, was to focus on two taxa that are widespread on continental margins and for which there is an active community of deep-sea taxonomists. For squat lobsters, we first compiled the literature and published a list of 800 known species (Baba et al. 2008), which we have now analyzed to address these questions. We also gathered, standardized, and analyzed individual datasets on deep-sea nematodes to decipher the processes that define global species distributions. The second approach was to undertake meta-analyses across taxa from data either mined from the literature and available in databases, such as OBIS and COMARGIS, or directly provided by members of the COMARGE network.

The role of multiple large-scale oceanographic features that change with latitude on diversity and zonation is more problematic than depth effects. Certainly when shallow-water data predominate analysis there are latitude changes in the ranges of individual species (Macpherson 2002) and in species diversity (Hillebrand 2004). Seeking such patterns below the permanent thermocline removes one of the major consequences of latitude. During the COMARGE project there has been an emphasis upon recognizing the high degree of local and regional heterogeneity on the margins. Until global-scale studies are undertaken, using a uniform design that examines both global and local factors, the actual role of latitude cannot be resolved.

5.3.1 Zonation and distribution on continental margins

Compared with the vast abyssal seafloor and the relatively wide continental shelf the continental margin lies in between as a narrow ribbon of ocean bottom characterized by dramatic transitions. The environment goes from upper slope regions where limited light may actually reach the seabed to a seafloor in total darkness. Except for polar and boreal regions, there is a sharp transition at the thermocline from warmer surface water to deep, cold water (typically less than 3°C). Water pressure increases continuously with depth. Local bottom currents are usually weaker than and decoupled from upper ocean circulation. Importantly, photosynthetically derived food energy in the form of sinking detritus becomes progressively scarcer. Therefore, it is not remarkable that the margin also experiences major biotic transitions. The upper margin experiences a sharp decline in continental shelf fauna as few such species extend into the very different habitat of deeper water. The lower margin transitions to one dominated by abyssal species that extend out across the somewhat similar, larger, but much more food-poor seafloor habitat.

What is remarkable is that the narrow ribbon of margin also harbors a diverse suite of species that seem to be truly margin-endemic. These species occupy restricted bathymetric ranges along any given section of the margin, but often with basin-scale horizontal ranges. The overlap of within-margin species, shelf-to-slope, and slope-to-abyss transitions produces a vertical species change or turnover at specific depths that is known as bathymetric zonation (Carney et al. 1983). The process of describing this zonation is to develop a matrix of similarity values from some taxonomic component of the sampled fauna and then partition that similarity through multivariate analyses. The full process of numerical analysis has several very subjective steps that alter the results. Thus, the sampled depth is dividing into a series of zones that seem to have relatively homogenous biota.

At the beginning of the COMARGE project, a literature survey was undertaken to assess the level of knowledge about bathymetric zonation with three primary objectives (Carney 2005). These were to determine (1) if zonation was the most common distribution pattern found in studies since the 1960s, (2) if there were global similarities in the zonation found, and (3) whether global correlations of zonation help identify most likely causes for the phenomena. Six margin regions were identified as more extensively studied within the context of specific investigation of zonation (Fig. 5.6): Porcupine Sea Bight, Gulf of Mexico, Mediterranean, Cascadia Basin in the northeast Pacific, and Chatham Rise off New Zealand. Studies in these regions, as well as the results from a few single studies produced 33 regional descriptions of zonation. In a meta-analysis it was found that the number of zones reported increased with the depth range sampled (Fig. 5.7). Therefore, fauna underwent species turnover at specific depths in all studies, and zonation did not stop at any depth. The width of the deepest zone was greater than the shallowest zone in all except five cases (Fig. 5.8), suggesting some increased uniformity of faunal composition with depth in most regions. Except for the shelf-to-slope transition, the boundaries of zones did not coincide among the regional patterns. This might indicate the importance of local phenomena or simply be an artifact of inconsistent sampling design and analysis across multiple projects.

There was no indication that the temperature transition from shallow warm water to cold deeper water played a significant role in bathymetric zonation on a global scale. Deep slope species did not emerge extensively into cold shallow water in polar surveys. Similarly, shelf species did not descend into the unusually warm deep water of the Mediterranean. The surveys on Chatham Rise had been undertaken in part to examine the influence of different water masses and productivity regimes on zonation. Unfortunately, both the faunal and oceanographic data
**Fig. 5.6**
The results of thirty-four zonation studies around the world were examined for common patterns. Solid sections were considered homogenous by the authors. White sections were transition regions, and blank areas represent unresolved gaps.

**Fig. 5.7**
(A) Although the execution of each zonation study differed greatly across locations and taxa, (B) the relation between maximum depth samples and homogenous zones recognized indicates faunal change occurs at all depths on the margin.
proved to be equivocal regarding the actual location of fronts and the environmental control of distribution.

The COMARGE literature review and meta-analysis of published conclusions confirmed the ubiquity of bathymetric zonation on all studied continental margins. Another key finding was severe limitations on the extent to which results from different studies can be compared. Some are obvious, such as inconsistent and possibly erroneous identification of specimens. Smaller meio- and macroinfauna comprise the most diverse and abundant metazoan components of these systems (Rex 1981; Rex et al. 2006). Many are new to science and too poorly characterized for consistent identification. This status makes it problematic to compile different datasets to produce accurate species ranges over basin- and global-scale areas. The hypothesis that individual margin species occupy narrow depth ranges over large (thousands of kilometers) horizontal distances requires considerable future study. A less obvious problem is the potential effect that sampling design and data analyses may have on data interpretation and conclusions. The placement and effort of sampling always impose artifacts into the patterns of distribution found. Boundaries between zones are often the result of uneven sampling effort at different depths, especially uneven depth intervals between sampling stations (Carney 2005). Furthermore, the margins and the abyss share a key characteristic of species diversity that demands consideration in future studies of zonation. Species inventories contain a high proportion of very rare organisms, where a given species may be collected only once in an extensive survey (Carney 1997). Even the most abundant species may represent a smaller proportion of the total fauna than is found in many other environments. When inferred from the distributions of species with a low frequency of occurrence, ranges appear to be narrow and the spatial change in fauna on the margin becomes exaggerated.

Developing a definitive zonation map for the global margins is of great practical as well as scientific value. The deep margins are already being exploited, but, because so many areas of the deep ocean are poorly sampled, the data available to regulators are limited. Regulatory agencies that are charged with developing science-based strategies must now rush to catch up with industry. One serious risk with this rush is oversimplification, whereby regulators may ignore the complex set of regulations that has evolved for the more data-rich shallow water environment and develop a single set of regulations for the entirety of the deep ocean. The one uniting theme of COMARGE is that the continental margins are complex and heterogeneous. Zonation studies clearly show that the biota of the upper slope is dissimilar from that of the middle and the lower slope. When zones have been mapped using appropriate sampling, expert taxonomy, and consistent analyses, then regulations can be developed that protect all of the zones present.

5.3.2 Exploring depth–diversity trends along margins: from local patterns to global understanding

5.3.2.1 Expected depth–diversity trends and processes

The relation between diversity and depth is of long-standing interest to deep-sea ecologists, and unraveling the mechanisms underlying its origin and maintenance is of fundamental importance to understanding the determinants of deep-sea biodiversity. Rex (1981) was the first to show that the diversity of dominant macrofaunal and megafaunal groups was unexpectedly high but peaked at intermediate depths in the western North Atlantic, somewhere between 1,900 and 2,800 m depending on taxon. A similar parabolic trend was also observed in the eastern North Atlantic and tropical Atlantic for polychaetes (Paterson & Lambshead 1995; Cosson-Sarradin et al. 1998), thus supporting the hypothesis of a biodiversity peak at mid-slope depth along continental margins. Contradictory patterns have, however, also been found (Stuart & Rex 2009).

In the framework of the COMARGE project, our aim was to question the generality of this pattern and, if confirmed, to identify environmental variables that might explain the relation for well-studied taxa. We gathered data on diversity and sampling depth from 16 cross-margin datasets from the Arctic, Atlantic, Pacific, Indian, Southern
Oceans, and the Gulf of Mexico, each spanning a depth range of 1,000–4,000 m (Fig. 5.9 and Table 5.1). Most datasets represented single transects across a continental margin. The Deep Gulf of Mexico Benthos program (Rowe & Kennicutt 2008) sampled multiple transects to provide data at a regional scale, and Stuart & Rex (2009) compiled diversity values for Atlantic gastropods at the ocean basin scale. Each diversity value was computed from a single quantitative sample.

Once the ubiquity of the diversity–depth relation had been tested, we set out to determine its underlying cause(s). Three environmental variables were tested as significant correlates of diversity: organic carbon flux to the seaﬂoor, temperature, and oxygen. The choice of these variables is based on theoretical considerations.

The relation between diversity and productivity is of central interest to ecologists in many ecosystems including the deep sea (Mittelbach et al. 2001; Stuart & Rex 2009). Past observations and models drawn primarily from the plant ecology literature suggest that a unimodal diversity–productivity relation is ubiquitous (Rosenzweig 1992; Huston & Deangelis 1994). Recent reviews, however, showed that other types of relations without definite maxima (linear increase or decrease) can be equally as common (Mittelbach et al. 2001). For our analysis, estimates for surface primary productivity were obtained from the model of Behrenfeld & Falkowski (1997). The organic carbon that fuels deep-sea benthic communities is only a fraction of surface primary productivity, and it decreases exponentially with depth. Therefore, we used the empirical function given by Berger et al. (1987) to estimate organic carbon fluxes to seaﬂoor from surface primary productivity values.

The metabolic theory of ecology provides a theoretical background for diversity-productivity trends and predicts an exponential increase in species richness with increasing temperature (Allen et al. 2002; Brown et al. 2004). The prediction has been both conﬁrmed and contradicted by observations along latitudinal and longitudinal gradients (Allen et al., 2002; Brown et al. 2004; Hawkins et al. 2007). Along a depth transect off Shetland Islands in the northeastern Atlantic, Narayanaswamy et al. (2005) found a peak in polychaete diversity at the boundary between two water masses. The relation between diversity and temperature was thus parabolic, though the maximum in diversity was explained by the high temperature range rather than temperature per se. For our broad-scale analysis, we did not have bottom temperature data for many of the sampling locations that we wished to include in the analysis. We, therefore, extracted data from the World Ocean Atlas 2005 for each sampling location. Because bottom temperatures in the Atlas are reported in 1° × 1° cells,
Table 5.1

Description of datasets used in the analyses of depth–diversity trends. Location numbering refers to numbers on the map (Fig. 5.9).

<table>
<thead>
<tr>
<th>Location</th>
<th>Depth range (m)</th>
<th>Taxa</th>
<th>Sampling device</th>
<th>Diversity index</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>5. Bay of Biscay</td>
<td>2035–4650</td>
<td>Echinodermata</td>
<td>Beam trawl</td>
<td>ES(57)</td>
<td>Sibuet 1987</td>
</tr>
<tr>
<td>7. Southern Ocean</td>
<td>774–4976</td>
<td>Isopoda</td>
<td>Epibenthic sledge</td>
<td>$H'(\log)$</td>
<td>Brandt et al. 2004</td>
</tr>
<tr>
<td>8. Oman (OMZ)</td>
<td>400–3300</td>
<td>Macrofaunal taxa</td>
<td>Box corer</td>
<td>ES(100)</td>
<td>Levin et al. 2000</td>
</tr>
</tbody>
</table>

we selected the deepest nearby value as an estimate of temperature near the seafloor.

The effect of low oxygen on diversity is obvious in areas where hypoxia imposes a physiological stress on metazoans, such as in OMZs. Oxygen may have a major impact on deep-sea biodiversity below a threshold value of 0.45 ml−1 (Levin & Gage 1998). We therefore predicted a positive, logarithmic relation between diversity and oxygen, and, to test this prediction, we extracted oxygen values from the World Ocean Atlas 2005 as described for temperature.

5.3.2.2 Observed depth–diversity trends and potential drivers

Plots of diversity as a function of depth for each dataset show that in most cases they were significantly correlated and, except in the Goban Spur region, a parabolic curve provided the best data fit (Table 5.2 and Fig. 5.10). Deviations from a common pattern of mid-slope depth maximum in diversity are particularly striking for oxygen minimum zones. Diversity and depth were not correlated off the coasts of Conception, Oman, and Pakistan. The parabolic curves were actually inverted from the predicted pattern. Foraminifers and polychaetes in these cases showed a diversity minimum at mid-slope depth, which coincided with the core of the OMZ (Gooday et al. 2009; Hughes et al. 2009). The unimodal relation between diversity and depth held true at a regional scale in the Gulf of Mexico for polychaetes, isopods, and bivalves but not at an ocean scale for gastropods. The discrepancy in depth–diversity trends at different spatial scales may simply reflect the fact that depth, or pressure, is not the main factor driving the pattern but rather provides a natural interaction term for many environmental variables that co-vary with depth among but not across regions (Levin et al. 2001; Stuart & Rex 2009). The fact that multiple environmental variables and depth are often strongly correlated raises the problem of multicollinearity in multiple regression models (Graham 2003). To limit potential artifacts, we correlated diversity with organic carbon fluxes, temperature, and oxygen at regional to ocean scales only (Table 5.3). For polychaetes, bivalves, and isopods in the Gulf of Mexico, as well as gastropods in the Atlantic Ocean, the diversity–productivity trend is unimodal and peaks at ca. 10–15 gC m⁻² year⁻¹, but it only explains a small portion of the
### Table 5.2

Adjusted $R^2$ for linear, log-linear (ln) and quadratic regression models of diversity as a function of depth. NS, not significant.

<table>
<thead>
<tr>
<th>Datasets</th>
<th>Diversity = $f(depth)$</th>
<th>Diversity = $f(ln(depth))$</th>
<th>Diversity = $f(depth^2)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Arctic Ocean</td>
<td>0.44***</td>
<td>0.35**</td>
<td>0.56***</td>
</tr>
<tr>
<td>2. Faroe–Shetland</td>
<td>0.42***</td>
<td>0.32***</td>
<td>0.42***</td>
</tr>
<tr>
<td>3. Rockall Trough</td>
<td>NS</td>
<td>NS</td>
<td>0.60***</td>
</tr>
<tr>
<td>4. Goban Spur</td>
<td>NS</td>
<td>0.45*</td>
<td>NS</td>
</tr>
<tr>
<td>5. Bay of Biscay</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>6. Gulf of Mexico: Polychaeta</td>
<td>0.22***</td>
<td>0.12**</td>
<td>0.31***</td>
</tr>
<tr>
<td>6. Gulf of Mexico: Bivalvia</td>
<td>NS</td>
<td>NS</td>
<td>0.33***</td>
</tr>
<tr>
<td>6. Gulf of Mexico: Isopoda</td>
<td>NS</td>
<td>NS</td>
<td>0.36***</td>
</tr>
<tr>
<td>7. Southern Ocean</td>
<td>NS</td>
<td>NS</td>
<td>0.34*</td>
</tr>
<tr>
<td>8. Oman</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>9. Pakistan: Foraminifera</td>
<td>0.34*</td>
<td>NS</td>
<td>0.41*</td>
</tr>
<tr>
<td>9. Pakistan: Polychaeta</td>
<td>NS</td>
<td>NS</td>
<td>0.93***</td>
</tr>
<tr>
<td>10. Off Conception</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>11. Off Chiloe</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>12. Atlantic Ocean</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

*p < 0.05;   **p < 0.01;   ***p < 0.001.

Variance (Fig. 5.11 and Table 5.3). Diversity values are especially variable at the lower end of the productivity gradient. Interestingly, temperature was the best predictor of diversity at a global scale. The parabolic relation is heavily driven by low diversity values at temperatures below 0°C in the Norwegian Sea (Fig. 5.12A); however, the depressed diversity in the deep Norwegian basin may be driven by isolation from the deep Atlantic that has slowed recolonization following the last glaciation and catastrophic slides 6,000–8,000 years ago (Bouchet & Warén 1979; Rex et al. 2005). When data from the Norwegian Sea are removed from the analysis, the parabolic relation between diversity and temperature is still statistically significant (Fig. 5.12B), but explains a much smaller portion of variance ($p = 0.02$, adjusted $R^2 = 0.08$). This type of collinearity and confounding among ecological, historical, and biogeographic drivers underlines interplay between local and regional processes that may prove the most difficult to control in quantitative models of large-scale diversity patterns.

#### 5.3.2.3 Limitations and prospects for local and global analyses

As for other large-scale biodiversity patterns on Earth, deciphering depth–diversity trends may provide clues on which mechanisms structure biological communities, but patterns and processes are challenging to establish. The shape of the pattern is better described at local to regional scales because depth provides a natural interaction term for processes that act on benthic diversity. Although not the only pattern observed, a unimodal pattern is the most common outcome. Nonetheless, the collinearity of factors reduces the sensitivity of analyses designed to separate and quantify true predictors against confounding and potentially irrelevant variables. For this reason, meta-analyses at global scale might prove more useful. The single ocean-scale dataset included in this analysis suggests that the diversity of gastropods may be partly explained by geographic variations in food supply and temperature. It should be noted, however, that in addition to multicollinearity, there is also
Fig. 5.10
Plots of diversity as a function of depth and best-fitted regression models when statistically significant; see Table 5.2 for results of the regression models.
Table 5.3

Adjusted $R^2$ for linear, loglinear (ln), exponential (exp), or quadratic regression models of diversity as a function of POC fluxes, oxygen, and temperature on the seafloor. NS, not significant.

<table>
<thead>
<tr>
<th>Datasets</th>
<th>Diversity</th>
<th>Diversity</th>
<th>Diversity</th>
<th>Diversity</th>
<th>Diversity</th>
<th>Diversity</th>
<th>Overall Diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>= f(POC flux)</td>
<td>= f(POC flux²)</td>
<td>= f(O₂)</td>
<td>= f(ln(O₂))</td>
<td>= f(T)</td>
<td>= f(exp(T))</td>
<td>= f(T²)</td>
</tr>
<tr>
<td>6. Gulf of Mexico:</td>
<td>$R^2 = 0.06^*$</td>
<td>$R^2 = 0.14^{**}$</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Polychaeta</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Gulf of Mexico:</td>
<td>$R^2 = 0.20^{**}$</td>
<td>$R^2 = 0.20^{**}$</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.18*</td>
</tr>
<tr>
<td>Bivalvia</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Gulf of Mexico:</td>
<td>$R^2 = 0.20^{**}$</td>
<td>$R^2 = 0.20^{**}$</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.43***</td>
</tr>
<tr>
<td>Isopoda</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12. Atlantic Ocean</td>
<td>$R^2 = 0.05^*$</td>
<td>$R^2 = 0.05^*$</td>
<td>NS</td>
<td>NS</td>
<td>0.06*</td>
<td>0.26***</td>
<td>0.28***</td>
</tr>
</tbody>
</table>

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

---

Concern that the spatial and temporal resolution of available environmental data may limit the utility of these meta-analyses. First, in the World Ocean Atlas, data are reported at grid cells of $1° \times 1°$. At this scale, a steep continental slope at a given locale is only spanned by one or at best two cells, thus potentially masking any down-slope gradient in oxygen or temperature. Second, whereas the spatial resolution of surface primary productivity is much better (ca. 20km), the size and position of the benthic catchment areas that contribute food to particular benthic sites are unknown (Stuart & Rex 2009). Furthermore, lateral inputs of food by cross-slope currents are largely unknown and, therefore, ignored. Finally, the environmental data considered here represent mean annual values over one or two years. Seasonal, annual, or inter-annual variation is not considered. The advent of ocean biodiversity informatics (Costello & Vanden Berghe 2006), coupled with higher resolution global ocean models (see, for example, Chassignet et al. 2006) as well as refined estimates of particulate organic carbon fluxes to the seafloor (see, for example, Seiter et al. 2005) will eventually improve these first predictions on the extent to which these contemporary ecological processes drive diversity patterns.

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Fig. 5.11

Plots of diversity as a function of particulate organic carbon fluxes and best-fitted regression models when statistically significant; see Table 5.3 for results of the regression models.

Fig. 5.12

Plots of gastropod diversity in the Atlantic Ocean as a function of temperature and quadratic regression model (A) with data from the Norwegian Sea, (B) without data from the Norwegian Sea. See text for details.
5.4 Human Influence on Continental Margin Ecosystems

Fifty years ago, as the study of margin ecology began the transition from a descriptive low-resolution to a process-oriented, high-resolution endeavor, there were few recognized environmental threats to the deep sea. In contrast, today, many COMARGE participants are currently actively advising on the environmental management of the deep. Although deep-sea ecology has advanced significantly in the past 10 years, there is much that we still do not know about this vast realm. A great need remains to inform resource developers, policy makers, and even scientists about the diverse life and ecosystems in the deep once thought to be azoic. Deep-sea exploitation is being planned and pursued in the absence of adequate environmental knowledge to ensure protection.

5.4.1 Direct human intrusions in the deep-sea

The impacts of human land-based activities have generally been ignored in the deep sea, but continental slope environments are often closely coupled to events on land. For instance, the composition of sediments in deep water on continental margins is affected directly by drainage areas on land (see, for example, Soh 2003). Toxic wastes such as dichlorodiphenyltrichloroethane (DDT) and polychlorinated biphenyls (PCBs) may eventually concentrate into tissues of deep-sea organisms (Arima et al. 1979; Solé et al. 2001; Thiel 2003; Storelli et al. 2007) after accumulating in coastal deposits (Managaki & Takada 2005) that are transported to the deep sea through canyons and down slopes. Continental margins are, thus, depositional centers for pollutants produced by human activities. Additional contaminants in the deep sea include fluorescent whitening agents (FWAs) that have been detected in high concentrations in sediments at 1,450 m in Sagami Bay (Managaki & Takada 2005), industrial lead in canyon systems (Richter et al. 2009), and trace metals in deep-sea canyon sediment cores that have been correlated with metal inputs associated with industrial activities (Palanques et al. 2008).

Demersal fishing has significant impacts on deep-sea ecosystems. The depletion of shallow water fisheries has progressively pushed fishing activity into deeper water (Davies et al. 2007; Koslow et al. 2000). Compared with their shallow-water counterparts, the growth rates of several commercially valuable deep-sea fish species are much slower, they mature at a late age, their fecundity is much lower, and they exhibit extreme longevity. Collectively, these traits make them extremely sensitive to sustained fishery (Gordon 2005). Because many deep-water fishes, both target and by-catch species, migrate over a wide depth range, demersal trawling affects not only the actual depths fished (ca. 1,600 m) but also extends into deeper waters up to at least 2,500 m (Bailey et al. 2009). Individual fishing vessels can impact a 100 km² area of the seabed in a single 10-day fishing expedition (Hall-Spencer et al., 2002). Demersal fishing has a particularly significant effect on epifaunal coral and sponge habitats (Freiwald et al. 2004; Wheeler et al. 2005; Davies et al. 2007; Reed et al. 2007; UNEP 2007).

The mining of massive polymetallic sulfides and cobalt-rich ferromanganese crusts is becoming increasingly attractive from an economic perspective. Although many potential mineral reserves occur on distant mid-ocean ridges, some of the largest deposits, and those that might be developed first, occur in back-arc rifts and rocky terrain in continental slope settings (ISA 2002). These deposits can be rich in gold, copper, zinc, and silver. The demand for metals from developing nations is expected to rise, raising concerns about the environmental management of near-future mining operations (Hafar & Fujita 2008).

The extraction of hydrocarbons from the deep seafloor will have predictable impacts. Drill cutting spoil may smother organisms, cause organic enrichment, and release toxic chemicals (Currie & Isaac 2005; Jones et al. 2006, 2007; Santos et al. 2009). The effects of exposure to contaminants on deep-sea species is poorly known (Skadsheim et al. 2005). Drill cuttings may pose a greater local environmental hazard in the deep sea than in shallow water because recovery rates will be lower (Glover & Smith 2003).

Other commercial developments may have a profound effect on deep-sea ecosystems. These include the sub-seabed storage of CO₂, water column and sediment surface CO₂ disposal, the use of methane hydrates, submarine mining, tailing disposal, bioprospecting and artificial iron fertilization of surface waters (Glover & Smith 2003; UNEP 2007). Experimental studies on the effects of CO₂ on benthic organisms have been equivocal (Bernhard et al. 2009; Rick- etts et al. 2009; Sedlack et al. 2009). The disposal of mine waste from land into the deep sea, in some cases down canyon systems, has received surprisingly little study (Ellis 2001), although in shallow water the activity has significant smothering and trace metal effects on fauna.

5.4.2 Climate change

The increasing level of CO₂ in the atmosphere over the past century has created a cascading set of effects on ocean environments. Increased atmospheric CO₂ can act as a fertilizer or as a greenhouse gas that warms and increasingly stratifies and acidifies the ocean. Concomitant effects of warming include reduced turnover of oxygen and destabilization of gas (methane) hydrates. Elevated CO₂ in seawater lowers pH and leads to dissolution of carbonate. With its natural steep gradients in water temperature,
salinity, density, and oxygen, the continental margins may exhibit the most pronounced effects of climate change.

### 5.4.2.1 Ocean Warming

Global ocean temperature has risen by 0.1 °C from 1961 to 2003 and may rise by another 0.5 °C over the next century (IPCC 2007). Ocean warming leads to melting of polar ice caps and increased density stratification. Stratification of the world’s oceans is increasing, with the greatest change in the North Pacific. Consequences include decreased surface productivity and organic matter flux to the seabed, as well as reduced mixing of oxygen from surface waters to the interior. Reduced mixing of oxygen is partly responsible for the expansion of OMZs in the world’s tropical oceans (Stramma et al. 2008). The expansion of OMZs will lead to habitat compression in species of plankton and fishes and strong changes in species habitat availability on the upper margins. The stratification of the upper ocean and the increase in the extent of OMZs further alter the flux of materials to the seabed and, thus, impact benthic boundary layer communities indirectly.

Gas hydrates are present along many of the world’s most productive continental margins. The stability of gas hydrate is determined by temperature and pressure (Hester & Brewer, 2009). Warming will decrease stability and may lead to massive dissolution and release of methane into the ocean, although much of this methane is likely to be oxidized by bacteria. Large-scale methane release events are considered to have modified past climate conditions (the clathrate gun hypothesis (Kennett et al. 2003)). Such releases could trigger slope instabilities but also might increase resource availability for slope chemosynthetic communities.

Additional effects of warming may include range expansions and contractions. Examples include the Humbolt (jumbo) squid (Dosidicus gigas), which follows low oxygen waters northward from Mexico in the eastern Pacific and are now routinely found off Oregon, Washington, and Alaska (Zeidberg & Robison 2007). Increasing temperatures may lead species to seek cooler refugia in canyons or down slope. The steep topography of some margins could facilitate range shifts in response to changes in temperature and oxygenation, given that only small distances are required to migrate to suitable conditions.

Less predictable, but also a likely effect of increasing surface temperatures, is a weakening or shifting of ocean circulation (Toggweiler & Russell 2008) leading to different connectivity between populations and, thus, faunal distributions. Certainly, long-term monitoring of deep-sea benthic communities has shown distinct changes in the population size of benthic Foraminifera in relation to changes in organic flux. For instance, in Sagami Bay during El Niño years between 1996 and 1998 average abundance decreased from 4,000 individuals per 10 cm² to 2,000 individuals per 10 cm² (Kitazato et al. 2003).

### 5.4.2.2 Ocean Acidification on Margins

Although the ocean is seen as a sink for atmospheric CO₂ that has absorbed one-third of the anthropogenic CO₂ added to the atmosphere, the ocean carbonate system is slowly being disrupted by this uptake. Enhanced pCO₂ has decreased pH in the water column by 0.1 unit since 1750 (IPCC 2007). This “acidification” effect leads to a lowered calcium carbonate saturation state and is particularly severe in colder waters. On northeast Pacific margins, some of this “corrosive” water is upwelled onto the shelf (Feely et al. 2008). Deep-water coral reefs are highly susceptible to changes in carbonate saturation because their aragonite skeletons are a particularly soluble form of CaCO₃ (Davies et al. 2007). Coral distributions already reflect the acidic conditions in the north Pacific (Guinotte et al. 2006), but the entire ecosystem could be threatened by acidification (Turley et al. 2007). Similarly the magnesium calcite in skeletons of echinoderms represents another easily dissolved form of carbonate. As acidification continues to worsen, mollusks, foraminifera, and other calcifying taxa could also be affected. Notably, low oxygen waters are also low in pH since the respiration processes that deplete oxygen also elevate CO₂. Thus, expansion of hypoxic waters will also bring the stresses associated with acidification.

### 5.5 Achievements and Perspectives: The Unknown Aspects of Margin Biodiversity

Our new, higher-resolution view of the continental margins reveals ecosystems that are unique on Earth. Because continental margins are habitat ribbons that stretch almost continuously along all continents, a diverse array of environmental forcing factors occurs over very small distances. Not so surprisingly, they might harbor among the most diverse faunal communities on Earth. Continental margins cross wide latitudinal and longitudinal swaths, and, when considered in tandem with adjacent trenches, represent the highest variations in depth on Earth, thus crossing gradients in pressure, temperature, oxygen, currents, and food inputs. Moreover, these large-scale gradients are superimposed over a wide range of heterogeneous habitats such as cold seeps, cold corals, canyons, and OMZs, often with their own sets of environmental drivers. These hot spots provide exceptions to the rule of a detritus-based, muddy ecosystem and undoubtedly enhance biodiversity at regional scale. They also provide natural experiments for future study to decipher the processes underlying species distributions and diversity patterns across habitats. It is this integrated
approach of continental margin ecosystems, both in terms of fauna, environmental drivers, and habitats that COMARGE has fostered. This is also the approach needed to describe, predict, and mitigate changes due to human activities.

Through COMARGE, its current participants and future marine ecologists are better prepared to increase knowledge of the system and meet the demands of science-based ocean management. We recognize four critical unknowns that could become knowns, and one major habitat, the trenches, that has been disregarded but is now within sight of new underwater vehicles (Jamieson et al. 2010). The first practical unknown is consistent and correct species identification. Some progress is being made toward synthesizing what is known. Species name compilation accelerated toward the end of the twentieth century through today, with most effort being directed toward WoRMS (World Register of Marine Species: www.marinespecies.org). In many cases, however, comparisons across margin datasets remain impossible, severely limiting integration across habitats and regions. This situation is caused by the taxonomic challenges of the high species richness of the margin combined with declining taxonomic expertise. In addition, the vast geographical coverage of continental margins and the difficulty in accessing them has limited sampling coverage. A large part of the margin taxa is new to science and remains undescribed. For example, surveys of the Australian margins have shown that 90% of 365 species of eastern slope isopods (Poore et al. 1994) and 30% of 524 western slope decapods (Poore et al. 2008) are undescribed. Research expeditions on the continental margin rarely target biodiversity studies or taxonomy specifically, especially as political considerations are increasingly important in funding decisions. The inventory of margin species remains far from complete.

A second key unknown is related to the first. The continental margin is among the least understood of the marine realms biogeographically. Horizontal or geographical distribution patterns are much less understood than depth-related patterns. Surprisingly little information is available about physical and environmental indicators and species composition on which to base biogeographic units on the continental slope. The Census data compilation project, OBIS, goes some way to overcoming this limitation. The Global Open Oceans and Deep Seabed (GOODS) biogeographic classification recognizes 14 lower bathyal provinces defined in terms of geographic or ocean current boundaries (within the depth range 800–3,000 m) on continental slopes and oceanic ridges (Fig. 7 in UNESCO 2009): Arctic, Northern North Atlantic, Northern North Pacific, North Atlantic, Southeast Pacific Ridges, New Zealand-Kermadec, Cocos Plate, Nazca Plate, Antarctic, Subantarctic, Indian, West Pacific, South Atlantic, and North Pacific. The GOODS biogeographic classification did not address upper bathyal depths of the slope (200–800 m), off-shelf areas within marginal seas, and semi-enclosed ocean basins. The UNESCO report acknowledged the need for more species distribution data, improvement of the scientific basis for biogeographic classification, and greater integration of biodiversity data and independent datasets. The question of whether slope species are concentrated in biodiversity “hot spots” remains largely unanswered, but a correlation between species richness and habitat complexity is expected. Biogeographic studies of slope specialist taxa that incorporate an evolutionary component are rare. The evolutionary–historical legacy remains virtually unknown though there is increasing evidence that it may play an important role in present-day species distribution and diversity patterns. Evidence is emerging from taxonomic syntheses, some supported by COMARGE, of some taxa, such as bathyal squat lobsters (Machordom & Macpherson 2004), deep-water scleractinian corals (Cairns 2007), and nematodes (A. Vanreusel et al. unpublished data) that the centre of species richness for bathyal faunas is the same as that for shallow water, namely the Indo-West Pacific “coral triangle”.

A third unknown is how bathyal communities change over ecological timescales. This need is particularly relevant to the assessment of human impacts on continental margins, noting that natural and anthropogenic signals cannot be dissociated. Therefore, there is a strong need for the development of observatory tools for continuous monitoring of bathyal environments and their biological communities.

A fourth unknown is the resilience of margin ecosystem functioning when impacted by natural and anthropogenic perturbations. Ecosystem functioning and dynamics in particular need to be addressed at population-community and ecosystem levels (Levin & Dayton 2009). A positive exponential relation between diversity and ecosystem functioning has recently been shown for deep-sea nematodes (Danovaro et al. 2008). So far, such a diversity–function relation is unique (Loreau 2008) and suggests that ecosystem functioning might quickly collapse in response to biodiversity loss in the deep sea. Further investigations and experiments are needed to corroborate these findings for various habitats and taxa in natural and stressed communities. They also stressed the need for an understanding of recovery processes after a system has collapsed, including the larval dispersal, supply, settlement, and recruitment processes that control the connectivity between populations.

To meet these and additional emerging needs, there must be more sampling undertaken in the context of optimal biogeographic design. There must be increased support of taxonomy including informatics and new technologies. Access to the ocean via HOV (human occupied vehicle), ROV, AUV, and cables must be increased on all margins. And, there must be more effective use of experimentation to understand the causes of patterns. International collaborations as those initiated by COMARGE and an increased partnership with the industry are desirable to achieve these goals.
A conclusion to COMARGE is yet premature. In just four years the project has underscored the complex interplay of large oceanographic features and habitat heterogeneities, acting at a hierarchy of spatial scales to shape distribution and diversity patterns. COMARGE has fostered a holistic understanding of continental margin ecosystems, enhancing international collaborations and increasing the standardization of methodologies that now translates in sampling schemes and cruises specifically addressing its overarching question. Beyond continental margins, the five Census deep-sea projects ( Abyssal Plains (CeDAMar), Seamounts (CenSeam), Vents and Seeps (ChEss), Continental Margins (COMARGE), Mid-ocean Ridges (MAR-ECO); see Introduction for definitions) initiated a large data-mining endeavor in the framework of the synthesis project SYNDEEP (Towards a First Global Synthesis of Biodiversity, Biogeography, and Ecosystem Function in the Deep Sea) to tackle similar issues across all deep-sea habitats. In the years to come, these initiatives will further explore the cumulative and synergistic effects of species turnover among and across habitats to provide new insights on diversity maintenance and ecosystem functioning in the deep sea. Meanwhile, ongoing global analyses on changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries? Proceedings of the Royal Society of London B 276, 1965–1969.


