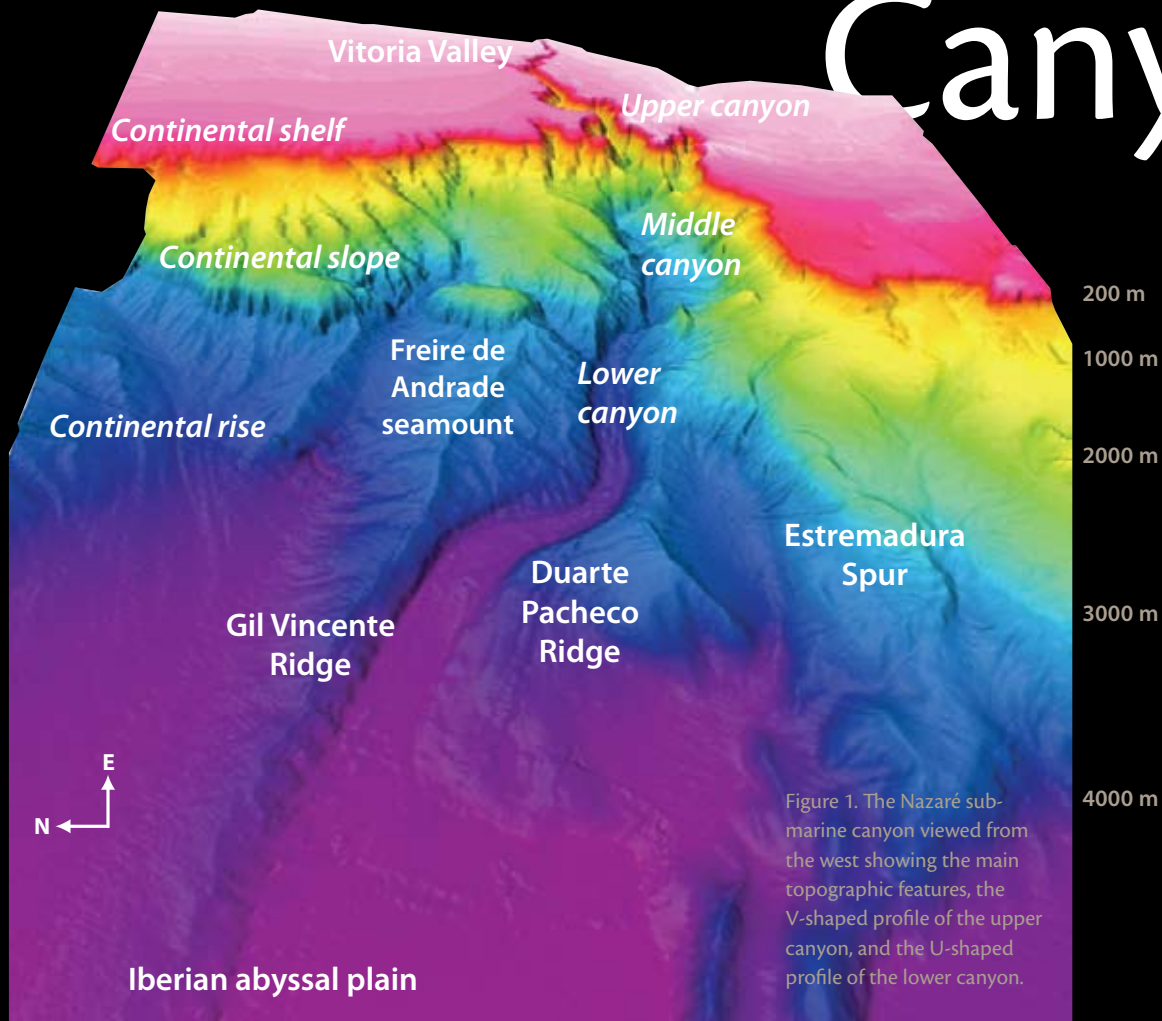


Europe's Grand Canyon **Nazaré** Submarine Canyon



BY PAUL TYLER, TERESA AMARO, RAQUEL ARZOLA, MARINA R. CUNHA,
HENKO DE STIGTER, ANDREW GOODAY, VEERLE HUVENNE, JEROEN INGELS,
KOSTAS KIRIAKOULAKIS, GALDERIC LASTRAS, DOUGLAS MASSON,
ANABELA OLIVEIRA, ABIGAIL PATTENDEN, ANN VANREUSEL, TJEERD VAN WEERING,
JOAO VITORINO, URSULA WITTE, AND GEORGE WOLFF

ABSTRACT. *The Nazaré submarine canyon extends ~ 210 km westward from the coast of Portugal, down to a water depth of > 4500 m. The considerable habitat heterogeneity found throughout the canyon is affected by strong currents and high turbidity, especially in the upper parts of the canyon. The canyon morphology comprises steep slopes, scarps, terraces, and overhangs, and a deeply incised thalweg is found in the lower part of the canyon. The seabed within the canyon is composed of varying proportions of rock and sediments that range from sand to fine mud. This great variation in physical environment is reflected by the varied fauna inhabiting the canyon. Diversity tends to decrease with depth, but there is also continual replacement of species with increasing water depth. Certain groups, such as the gorgonians and sea lilies, tend to be found on rocky surfaces, while large protozoans dominate the sediments at 3400-m depth. In addition to describing the fauna of Nazaré Canyon, we discuss experiments undertaken as part of the HERMES project to elucidate the ecosystem function processes operating in the deeper parts of the canyon.*

INTRODUCTION

The continental shelf along the west coast of Portugal and Spain is only 20–60-km wide and slopes gently seaward. At about 200-m depth, there is a significant increase in slope to about 6° that extends down to the abyssal plain. The shelf and slope region is cut by several extensive submarine canyons, the longest of which is Nazaré Canyon, which extends from shallow water less than 1 km off the coastline to a depth of 5000 m at 210 km offshore (Figure 1). Unlike many submarine canyons, Nazaré Canyon is not connected to a major river system, but, even so, it is recognized as a major sediment pathway among European canyons. Nazaré Canyon was chosen as a focus for determining canyon biodiversity during the EU-HERMES program because of its size and putative habitat heterogeneity. Because canyons are heterogeneous on a variety of scales, we will describe the

canyon using the upper/middle/lower classification (Vanney and Mougenot, 1990; de Stigter et al., 2007; Lastras et al., in press).

The upper part of Nazaré Canyon runs east-northeast to west-southwest, changing to an east-west orientation in the middle and lower parts (Figure 1). There is a subsidiary canyon known as the Vitória valley on the upper northern flank, and the main channel in the lower canyon is bordered to the north and south by Gil-Vicente and Duarte Pacheco ridges, respectively. The middle and lower part of the canyon follow the line of a reactivated Hercynian fault zone (the Appalachian-Hercynian orogeny sutured Lurussia and Gondwana and closed the Tethys Sea), and it is likely that basement structure controls the present canyon geomorphology. The epicenter of the devastating 1755 Lisbon earthquake was located only 100 km away.

MORPHOLOGY AND SEDIMENTOLOGY

A wide variety of features contributes to the high morphological heterogeneity of Nazaré Canyon, and ultimately impact its biodiversity. In the upper and middle canyon, in water < 4000-m deep, the canyon is distinctly V-shaped and deeply incises the continental shelf and slope, with an average axial gradient of ~ 6° (Figure 1). Along this section, the deepest part of the canyon (called the thalweg) is < 100-m wide.

Slopes in the upper and middle canyon have a rugged topography, with numerous gullies and semicircular erosional scarps. The latter are related to landsliding, mainly debris flow and rock avalanching, which are key processes in sculpting the canyon walls. External forcing, such as earthquakes (Weaver et al., 2000), sea-level changes, and higher sediment flux related to climatic variation (Arzola et al. 2008), probably

triggers the landslides.

Bedrock commonly outcrops at the seafloor on steep slopes (Figure 2A, B). Less-steep areas are covered by a drape of fine-grained sediments (Figure 2B). Terraces, believed to be cut into the surrounding bedrock by migrating meandering currents, are found mainly in the middle canyon and generally parallel the canyon axis. Thick sequences of muddy turbidites are presently accumulating on these terraces (Figure 2C), with sediment cores indicating accumulation rates of 0.4–1.4 cm yr⁻¹ over the last few hundred years. This terraced area defines a distinct depocenter within the middle canyon, with little sediment passing beyond this zone to the lower canyon (de Stigter et al., 2007). The thalweg floor is comprised of coarse gravel and large boulders often draped with soft sediment that appears to be constantly reworked by tidally driven near-bottom currents.

At about 120 km from the canyon head at water depths greater than 4000 m, the canyon opens into a wider, U-shaped channel that has a flat floor

reaching 7.5 km in width, an average axial gradient of 0.5°, and a second-order thalweg that is up to 500-m wide (Lastras et al., in press). Here, seafloor sediments range from mud to coarse gravel. A mud layer a few centimeters thick overlying sandy, turbiditic sediments covers much of the wide, flat canyon floor. Sand and gravel floor the narrow, second-order thalweg channel.

Little sediment appears to be reaching this part of the canyon at present, suggesting a markedly lower-energy environment. However, coarse gravel exposed in the walls of the second-order thalweg channel indicates a much more active past, with catastrophic processes capable of transporting boulders up to 1-m across (Figure 2D, E). The age of these sediments is unknown, but they are almost certainly pre-Holocene, suggesting a canyon environment very different from the present during Pleistocene low sea-level stands. The flanking terraces are covered by fine sediment with numerous individuals of the xenophyophore *Galatheammima* sp. (Figure 2F).

Figure 2 (opposite page). Photographic observations of Nazaré Canyon geological and sedimentary structures overlaid on the canyon topography at 3400-m and 4500-m depth. (A) Massive rock outcrop on a near-vertical cliff bounding the thalweg (deepest) channel at 3400-m depth. (B) Rock outcrop mantled by a thin layer of the soft, unconsolidated, muddy sediment typical of areas of moderate slope in the upper and middle canyon (3400 m). (C) Soft muddy sediment with abundant evidence of bioturbation typical of terraces in the middle canyon (3400 m). (D) Cliff composed of partially consolidated conglomerate marking the edge of the second-order thalweg channel at 4500-m depth. The largest boulder (bottom right) is ~ 1 m across. (E) Sand dune overlying large boulders or rock outcrop on the floor of the second-order thalweg channel at 4500 m. (F) Muddy sediment colonized by abundant xenophyophores (*Galatheammima* sp.) on the broad flat canyon floor at 4500-m depth. The 3400-m bathymetry has no vertical exaggeration; the 4500 bathymetry has a twofold exaggeration. All photos copyright NERC/NOG

PHYSICAL OCEANOGRAPHY

As the result of strong topographical control, residual currents inside the canyon are aligned in an along-channel direction. This alignment extends to near-surface depths, well above the 150-m depth canyon rim, suggesting

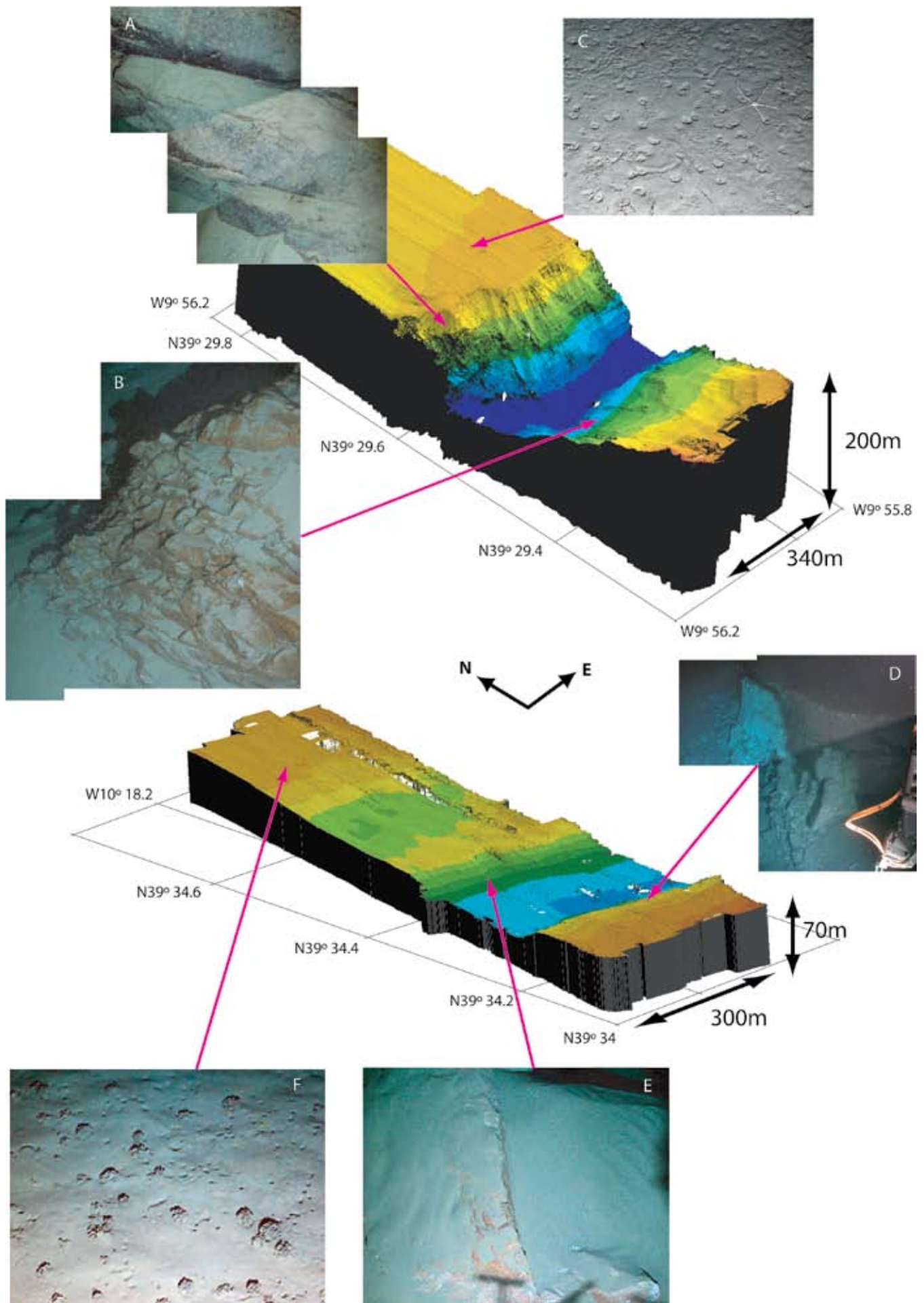
Paul Tyler (pat8@noc.soton.ac.uk) is Professor, National Oceanography Centre, University of Southampton, Southampton, UK.

Teresa Amaro is Postdoctoral Researcher, Center for Environmental and Marine Studies (CESAM) and Department of Biology, University of Aveiro, Aveiro, Portugal. **Raquel Arzola** is a postgraduate researcher at the National Oceanography Centre, University of Southampton, Southampton, UK. **Marina R. Cunha** is Auxiliary Professor, CESAM and Department of Biology, University of Aveiro, Aveiro, Portugal.

Henko de Stigter is a researcher at the Royal Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands. **Andrew Gooday** is Professor, National Oceanography Centre, University of Southampton, Southampton, UK. **Veerle Huvenne** is a researcher at the National Oceanography Centre, University of Southampton, Southampton, UK. **Jeroen Ingels** is PhD Candidate, Department of Marine Biology, University of Ghent, Ghent, Belgium. **Kostas Kiriakoulakis** is Research Fellow, Department of Earth Sciences, University of Liverpool, Liverpool, UK. **Galderic Lastras** is Associate Professor, GRC Geociències Marines, Universitat de Barcelona, Barcelona, Spain.

Douglas Masson is Senior Researcher, National Oceanography Centre, University of Southampton, Southampton, UK. **Anabela Oliveira** is a researcher at the Instituto Hidrográfico, Lisboa, Portugal. **Abigail Pattenden** is PhD Candidate, National Oceanography Centre, University of Southampton, Southampton, UK. **Ann Vanreusel** is Lecturer, Department of Marine Biology, University of Ghent, Ghent, Belgium. **Tjeerd Van Weering** is Researcher, Royal Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands. **Joao Vitorino** is a researcher at the Instituto Hidrográfico, Lisboa, Portugal. **Ursula Witte** is Professor, Oceanlab, University of Aberdeen, Aberdeen, UK.

George Wolff is Professor, Department of Earth Sciences, University of Liverpool, Liverpool, UK.



“ MARINE CANYONS ARE JUST AS SPECTACULAR AS THEIR SUBAERIAL COUNTERPARTS, AND NEED CAREFUL, SUSTAINABLE MANAGEMENT. ”

that the canyon substantially disturbs the predominantly north-south slope-parallel circulation. Within the canyon to depths of about 300 m, the residual currents correlate well with the winds affecting the western Portuguese margin. Northerly winds promote upwelling conditions and southward flow across the shelf. During strong northerly wind events, an onshore (up-canyon) flow up to 10 cm s^{-1} has been observed inside the canyon, with upwelling occurring near the canyon head. During cessation of northerly winds, or during periods of predominant southerly winds that promote downwelling on the shelf, the residual flow near or just above the canyon rim depth is down-canyon.

Below 300-m depth, flow inside the canyon is independent of wind-forcing conditions and shelf circulation. Other forcing mechanisms, such as the interaction of the north-flowing Mediterranean Outflow Water (MOW) with the canyon, play a role in controlling circulation dynamics. Off the western Portuguese coast, the MOW is observed as a tongue of high-salinity water that follows the continental slope and extends to depths between 600 m and 1500 m. Off Nazaré, the main core of MOW occurs at 1200-m depth, with a second (less-saline but warmer) core observed at about 700-m depth. High-salinity MOW bodies were found inside the upper section of the Nazaré Canyon out to about 20 km from shore, where the canyon floor is 600-m deep but the nearby shelf is only 100-m deep. Although only weak

and variable flows were measured at the depths of the MOW cores, observations revealed sustained and relatively strong ($10\text{--}20 \text{ cm s}^{-1}$) residual flows at the upper and lower boundaries of the MOW. Close to the Vitória tributary, near the bottom (700-m depth), a persistent onshore (up-canyon) flow was observed for at least one year. During the same period, a persistent offshore (down-canyon) residual flow was observed at 1700-m depth, close to the bottom, at the outer part of the upper section of the canyon (personal observations of authors Oliveira and Vitorino).

In addition to residual circulation, tidal currents are important in Nazaré Canyon, where they maintain a high-energy environment near the bottom at several locations. The external (barotropic) tide off the western Portuguese coast is dominated by the lunar semi-diurnal (M_2) constituent and modulated by the solar semi-diurnal (S_2) constituent with a clear spring-neap tide cycle. The interaction of the barotropic tide with the canyon topography, in the presence of water-column stratification, leads to the generation of internal waves of tidal period (internal tides) that radiate from the generation point, propagating the tidal energy up- and down-canyon. This generation mechanism is particularly effective at the canyon rim, where critical conditions for internal wave reflection occur. Like most submarine canyons, Nazaré serves as a trap for internal waves, and particularly internal tides. The steep walls of

the upper section of Nazaré Canyon are supercritical to incident internal waves at a semi-diurnal (M_2) period, leading to reflection toward the bottom of internal tides generated at the rim. The canyon axis slope, however, is subcritical to these frequencies, allowing up-canyon propagation of internal-tide energy. HERMES observations revealed that these processes contribute at some locations along Nazaré Canyon to the development of very high bottom currents, which have a profound effect on sediment and faunal distributions. Observations from the outer part of the upper section of the canyon, just north of the Berlengas Islands, revealed the downward intensification of tidal current fluctuations, which reached about 50 cm s^{-1} near the bottom (1700-m depth) during the spring tides, with the total current (residual plus tidal) attaining up to 70 cm s^{-1} . These high current fluctuations near the bottom provide an erosive environment that leads to resuspension of bottom sediment, as clearly seen in near-bottom turbidity measurements. These observations suggest that, during extended time periods (one year or more), a mechanism at the outer part of Nazaré Canyon promotes the continuous erosion of bottom sediments (by bottom-intensified, semi-diurnal internal tides) and sediment export to the deeper areas of the mid section of the canyon (due to the sustained down-canyon residual flow observed at the seafloor in this area).

SUSPENDED MATERIAL IN THE WATER COLUMN AND AT THE SEABED

To assess the nature of suspended particulate organic matter (POM_{susp}) through the canyon system, samples

were collected at discrete depths in the upper, middle, and lower canyon.

Concentrations of suspended particulate organic carbon (POC_{susp}) decreased with water depth from maximum near-surface values of $198 \mu\text{g L}^{-1}$ ($16.5 \mu\text{M}$) to $< 1 \mu\text{g L}^{-1}$ ($0.025 \mu\text{M}$) at abyssal depth ($\sim 4300 \text{ m}$) (Figure 3). Nevertheless, there is a clear enrichment in POC_{susp} at the benthic boundary layer (BBL; $\sim 10 \text{ m}$ above bottom) in the canyon axes when compared to mid-water samples from the same depths (i.e., $\sim 400\text{--}2000 \text{ m}$).

There is strong evidence of particle-laden layers, so-called nepheloid layers close to the seabed (de Stigter et al., 2007; Oliveira et al. 2007); in all parts of the canyon, suspended sediment loads increase toward the seabed, especially in the upper part of the canyon (Figure 4). In fact, during a dive with the remotely operated vehicle (ROV) *Isis* in June 2007, the currents were so strong and the suspended sediment load so high that it was impossible to use the ROV near the seabed. In the upper part of the canyon, down-canyon sediment transport was $5.6 \times 10^3 \text{ g m}^{-2} \text{ d}^{-1}$, with a sediment-deposition rate of $64.5 \text{ g m}^{-2} \text{ d}^{-1}$. In the middle part of the canyon, this rate diminished to $1.9 \times 10^3 \text{ g m}^{-2} \text{ d}^{-1}$ down-canyon, countered by a $0.7 \times 10^3 \text{ g m}^{-2} \text{ d}^{-1}$ rate up-canyon, resulting in a net downward sediment transport of $1.2 \times 10^3 \text{ g m}^{-2} \text{ d}^{-1}$. The sediment-deposition rate in the middle part of the canyon is $46.5 \text{ g m}^{-2} \text{ d}^{-1}$ (de Stigter et al., 2007). In the lower canyon, sediment fluxes are much lower, $0.1 \times 10^3 \text{ g m}^{-2} \text{ d}^{-1}$ both up- and down-canyon, implying no significant net transport of suspended material.

Within the sediment, total oxidation of the organic fraction was greater in the

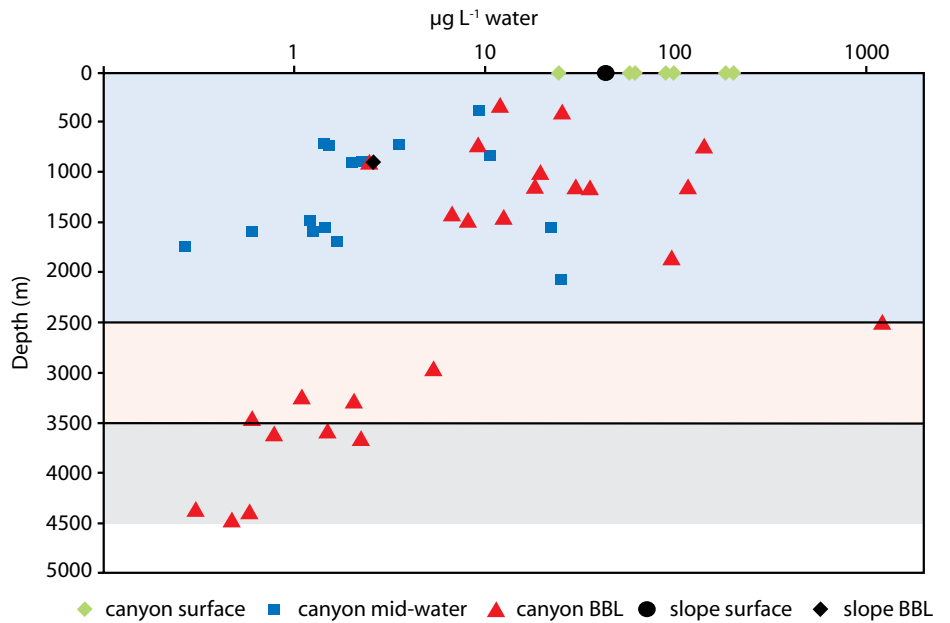


Figure 3. POC_{susp} concentrations at the Portuguese margin. Black diamonds = surface water samples; black squares = mid-water samples; black triangles = BBL (benthic boundary layer) samples at canyon axes; open triangle = BBL open-slope sample. Note logarithmic x-axis scale.

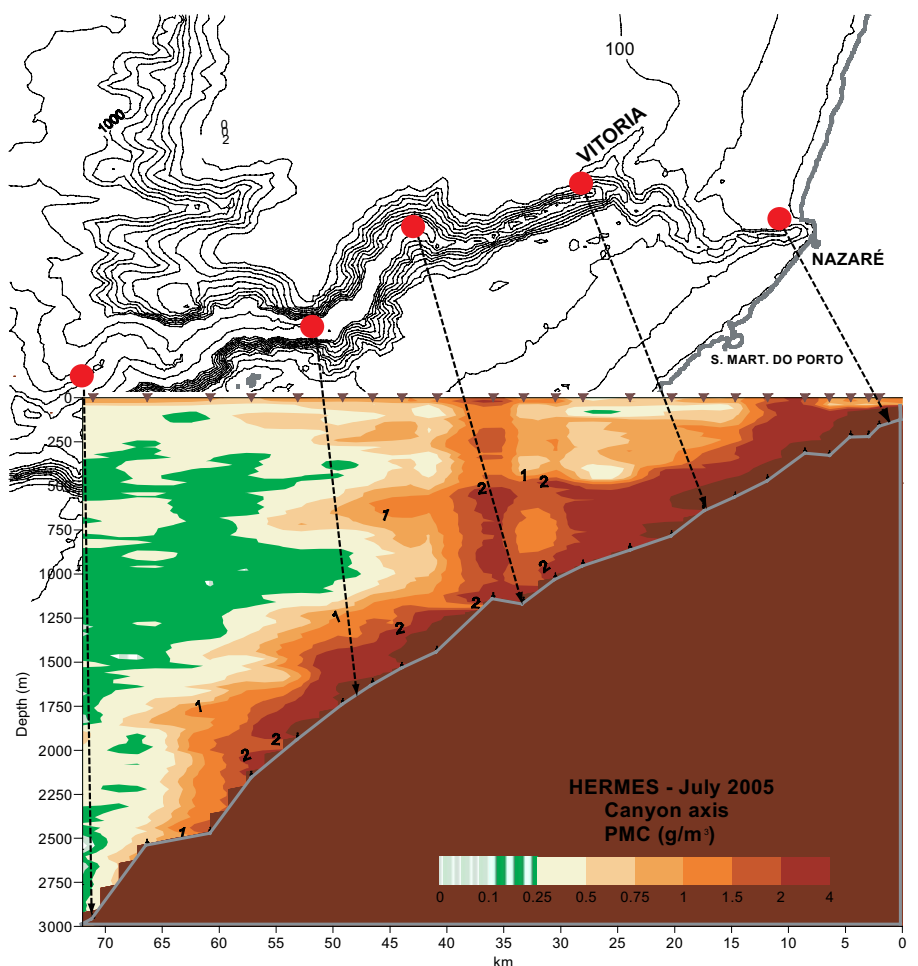


Figure 4. Suspended particle load above the seabed in the axis of Nazaré Canyon.

canyon compared with the nearby margin (Epping et al., 2002). However, burial of refractory organic matter is greater in Nazaré Canyon than on the margin, but the reactivity of canyon-buried organic matter is less than that on the local margin. Epping et al. (2002) suggest that the canyon is enriched in older, laterally advected organic matter.

FAUNAL VARIATION WITHIN THE CANYON

Protozoa and Meiofauna

Benthic foraminifera vary throughout the length of the canyon (Koho et al., 2007), with low standing stocks in the disturbed canyon axis. In the upper canyon, the foram standing stock is dominated by a species of *Technitella*. The dominant species on the terraces of the upper canyon is the tubular *Bathysiphon* sp., contributing to the highest standing stock in the canyon. Deeper stations in the lower canyon are dominated by the agglutinated *Saccorhiza ramosa*. Middle and lower canyon terraces are dominated by *Melonis barleeanum* and *Chilostomella oolina*, indicative of low pore water oxygen and high labile organic matter (Koho et al., 2007).

Meiofauna (32–1000 µm) is the most abundant eukaryotic size class in the marine sediments, with small samples yielding thousands of individuals of many different species. Garcia et al. (2007) investigated the distribution of meiofauna in canyon sediments compared to the adjacent continental slope, concentrating on the canyon axis where physical disturbance is considered highest. In the upper and middle parts of the canyon axis, the phytodetritus is fresher and of higher nutritional value for the

meiofauna. However, they seem unable to exploit fully the high amounts of food resources the canyon provides. The low abundance of meiofauna in the canyon axis is a result of local high-velocity bottom currents and unstable sedimentary conditions that hinder their settlement (Garcia et al., 2007). Conversely, on the sediment-draped terraces and the flat-floored canyon valley in the middle and deep canyon (3000–5000-m water depth), meiofauna seem to thrive on abundant food. Large amounts of fresh marine and more recalcitrant terrigenous organic matter are episodically flushed to the deeper canyon and the abyssal plain. Both the high quantity and quality of sedimentary organic matter, which are determined by canyon hydrography and heterogeneity, increase meiofauna densities and biomass, and directly and indirectly regulate, for example, the nematode assemblages (as the most abundant taxon within the meiofauna) (J. Ingels, University of Ghent, *pers. comm.* 2008). Here, the current flow is less pronounced and more episodic relative to the active canyon axis and more disturbed upper part of the canyon, and hence meiobenthic communities are better established, even in sediment layers 0–5-cm deep (J. Ingels, University of Ghent, *pers. comm.* 2008).

Nematode biodiversity was low in the upper and middle parts of the canyon, especially in the canyon axis, while in

the deeper canyon biodiversity was only slightly lower than on the adjacent open slope. Nevertheless, because of its heterogeneity and contrasting conditions compared to the slope, Nazaré Canyon shows high rates of genera turnover and contributes significantly to total western Iberian margin diversity. Furthermore, nematode assemblages in the canyon are characterized by higher numbers of predatory and scavenging nematodes, and certain genera (e.g., *Sabatieria*) are more able to withstand less-favorable conditions. The high quality and amount of bio-available food is able to sustain a more complex trophic community, thus enhancing trophic diversity in the canyon system.

Macrofauna

Macrofauna (those animals retained on a 500-µm sieve but not visible in photographs) have been identified for the upper (~ 1000-m depth), middle (3400-m depth), and lower (4300-m depth) parts of Nazaré Canyon (Figure 5). Samples collected on three separate HERMES project cruises of RRS *Discovery*, RRS *Charles Darwin*, and RV *Pelagia* show that the fauna vary greatly with depth.

At 1000 m, faunal density was the lowest (485 ± 96.9 ind. m⁻²) with equal contributions of polychaetes (45% of the total) and crustaceans (40%), followed by molluscs (14%). Polychaetes

“MANY ASPECTS OF CANYONS ARE STILL UNKNOWN OR ONLY PARTLY UNDERSTOOD, HOWEVER, AND CONTINUED RESEARCH EFFORTS WILL FOCUS ON THESE IMPORTANT COMPONENTS OF OUR CONTINENTAL MARGINS.”

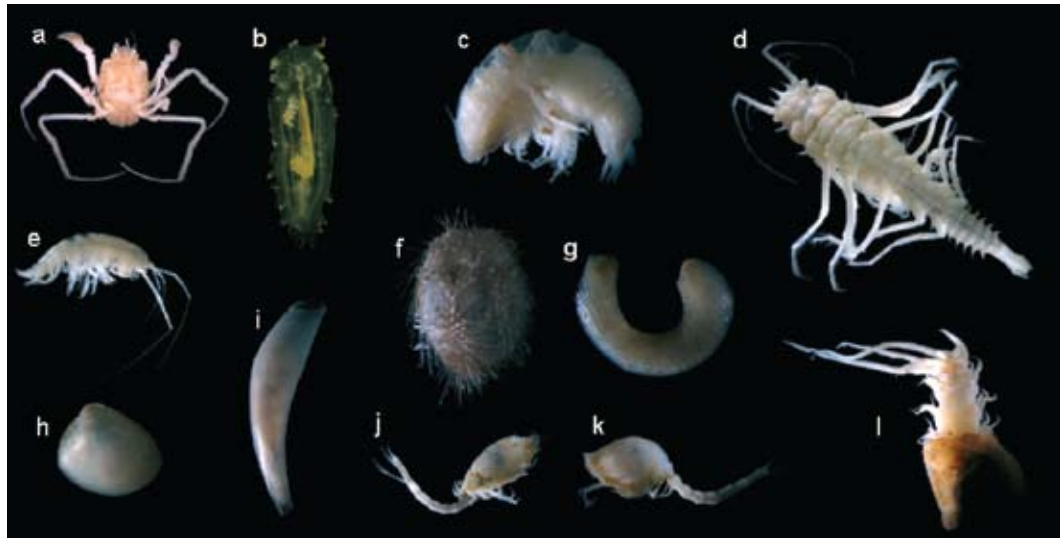


Figure 5. Specimens of macrofauna collected in the Portuguese canyons and adjacent open slopes at approximately 1000-m depth during the research cruise *Pelagia 64PE252* in 2006: (a) *Cymonomus granulatus*, (b) *Laetmogone violacea*, (c) Cirolanidae, (d) *Apeudes grossimanus*, (e) Amphipoda, (f) *Brissopsis lyrifera*, (g) Caudofoveata, (h) Bivalvia, (i) Scaphopoda, (j) and (k) Dyastilidae, and (l) Onuphidae.

were mostly represented by the orders Aciculata (mobile carnivores and omnivores), in particular, families Onuphidae and Lumbrineridae, which dominate in terms of biomass, and Canalipalata (low-mobility surface and subsurface deposit feeders). Crustaceans were mostly represented by the orders Amphipoda and Tanaidacea.

At 3400 m, the assemblages attained the highest faunal densities (up to 4325 ± 287.7 ind. m^{-2}), with a strong dominance of molluscs (up to 56%), followed by polychaetes (up to 33%) and crustaceans (up to 13%). The Aplacophora, Canalipalata (mostly Spionidae), and Tanaidacea, respectively, were the major representatives of these three faunal groups, and the occurrence of Aciculata and Amphipoda strongly declined.

At 4300 m, the assemblages decreased in density (up to 1152 ± 194.7 ind. m^{-2}) but changed again towards a very strong dominance of polychaetes (up to 82%),

accompanied by a decrease in molluscs and crustaceans. The three faunal groups were represented mainly by the orders Canalipalata (mostly Spionidae), Bivalvia, Isopoda, and Tanaidacea.

At the two deeper locations, the assemblages sampled in 2005 and 2006 showed an increase of approximately 1.5 in total faunal density (2695 ± 942.1 ind. m^{-2} in 2005 to 4325 ± 287.7 ind. m^{-2} in 2006 at 3400-m depths, and 825 ± 69.7 ind. m^{-2} in 2005 to 1152 ± 194.7 ind. m^{-2} in 2006–4300-m depths), although without significant changes in faunal composition and community structure.

Nazaré Canyon benthic macrofauna previously sampled during the OMEX II cruise (Curdia et al., 2004) showed similar features, although much higher densities (over 14,000 ind. m^{-2}) were found at depths of 2900 m. During OMEX II and HERMES cruises, faunal densities in Nazaré Canyon assemblages were compared to open-slope assemblages and

showed consistently higher values, supporting the view of canyons as hotspots of faunal abundance and biomass.

Assemblages were characterized by the predominance of opportunistic surface and subsurface feeders usually associated with organically enriched areas. The occurrence of these assemblages may be explained by the existence of detritus and particulate organic carbon (POC), which are major carbon sources in canyons, and suggests that these sources are major natural drivers for the composition and structure of Nazaré Canyon benthic assemblages. Spatial (different depths) and temporal (either seasonal or interannual) differences in the benthic assemblages appear to be a response to fluctuations in the transport of particulate material and the associated amount of organic matter reaching the seafloor.

Megafauna

The steep sides of the upper Nazaré Canyon were dominated by a mixture

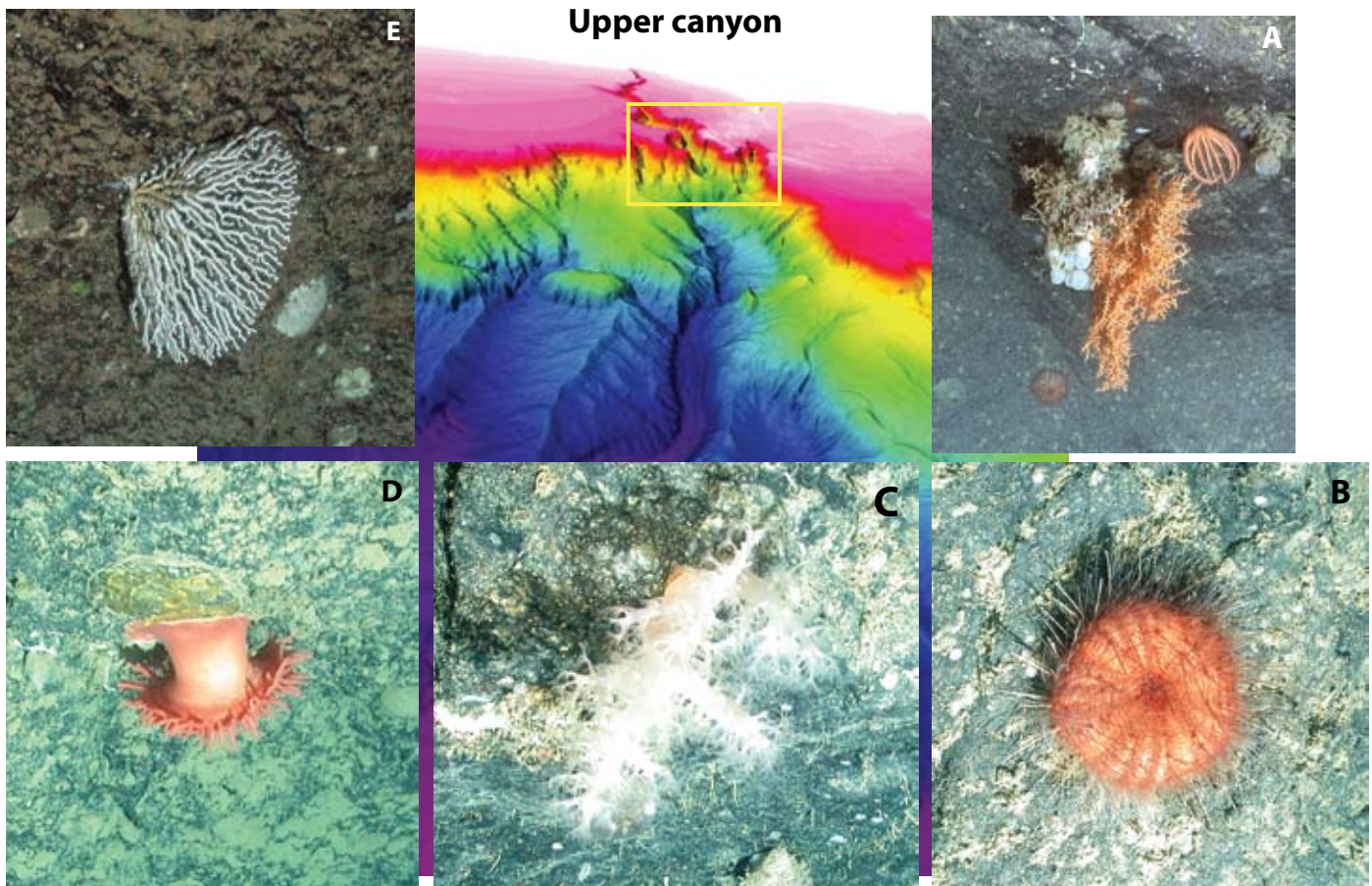


Figure 6. Rock fauna in the upper part of Nazaré Canyon. Clockwise from top right: (A) the cold water coral *Madrepora* sp., (B) the echinothurid sea urchin *Calveriosoma hystrix*, (C) the soft coral *Gersemia* sp., (D) an unidentified anemone, and (E) a gorgonian coral. All photos © NERC/NOC

of suspension and deposit feeders, and organisms living on rock or in sediment. Megafauna include hard and soft corals, sea fans, anemones, and echinothurid sea urchins all living on or attached to rock (Figure 6A–E). Slightly deeper in the canyon among the nektonic (swimming) fauna is the octopus *Benthoctopus johnsoniana* (Figure 7A), though it was rarely seen swimming but usually resting instead in its characteristic pose on the seabed. Deposit-feeding echinoids include the pencil urchin *Cidaris cidaris* (Figure 7B). An unidentified anemone was common on rock surfaces, and a very distinctive but unnamed cerianthid sea anemone with purple

tentacles was found in sedimentary areas (Figure 7C and D). Suspension feeders living on rocks include the brisingid sea-stars *Brisinga* sp. (Figure 7E).

Megafauna are more sparse in the middle and lower parts of the canyon. However, the large xenophyophore *Galatheammima* was particularly common on the canyon floor where it occurred in very high densities, though it was not found in the thalweg (Figure 2F). This single-celled protozoan grows to a considerable size, often exceeding 10 cm in diameter. Other megafauna inhabiting these sedimentary areas were the holothurian *Benthoctopus* and the ophiuroid *Ophiura concreta*

(Figure 8A and B). The floor of the thalweg, comprised of sand with scattered boulders, contained no obvious megafauna, but where the thalweg had incised the sediments to expose bedrock, a suspension-feeding community dominated by the alcyonean *Anthomastus* and the crinoid *Anachalypsicrinus nefertiti* was found (Figure 8C and D).

PROCESS EXPERIMENTS IN NAZARÉ CANYON

The availability of new research equipment such as ROVs now makes it possible to study biological and ecological processes in situ within canyon systems. A variety of seabed experiments

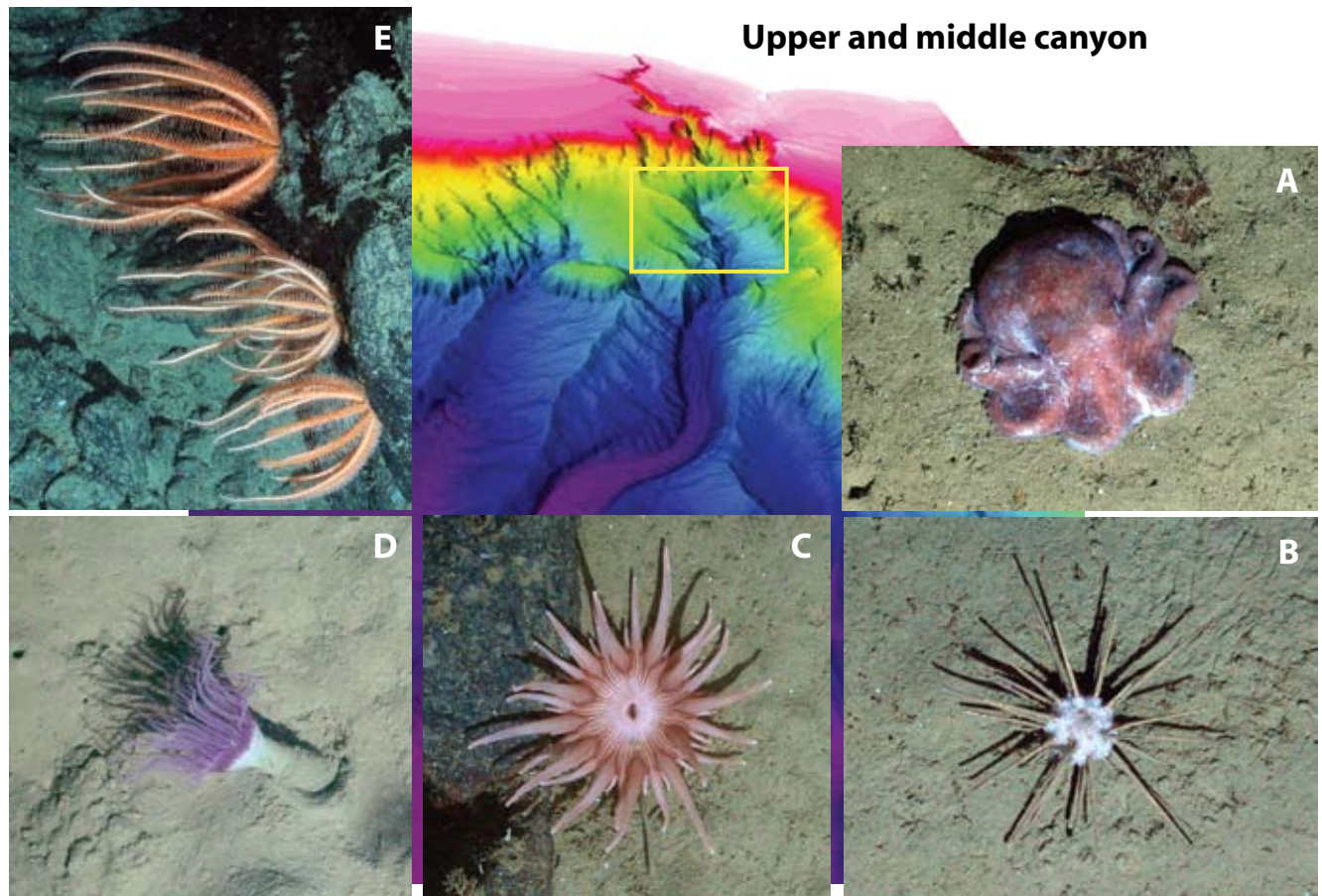


Figure 7. Fauna of the upper and upper middle part of Nazaré Canyon. Clockwise from top right: (A) the octopus *Benthoctopus johnsoniana*, (B) the urchin *Cidaris cidaris*, (C) an unidentified anemone, (D) the cerianthid anemone *Cerianthus*, and (E) the bringingid seastar *Brisinga* sp. All photos © NERC/NOC

were recently conducted within Nazaré Canyon.

Feeding Experiments

An in-situ ^{13}C feeding experiment conducted in Nazaré Canyon is revealing selectivity and anomalous feeding patterns in nematodes. A ^{13}C pulse-chase experiment (*Feedex*) was used to investigate the selective uptake of different food sources by free-living nematodes in the canyon. Results from in situ addition of ^{13}C -labeled bacteria and diatoms (*Skeletonema* sp.) to specially designed core tubes in a random array (Figure 9A) are unraveling differences in structural and functional nematode

diversity reflected in natural ^{13}C isotope abundances; they are showing how the nematode community reacts to different food sources. After the addition of food, the experiment was allowed to incubate and then both experimental and control cores were retrieved. Preliminary results indicate that the canyon nematode community is able to react quickly to the input of algae, but there was a delay in the response of bacteria to enrichment.

Sediment Community Oxygen Consumption

Measuring the turnover of organic carbon at the seabed is technically challenging. An ROV-deployed benthic lander

was set in Nazaré Canyon (Figure 9B) to measure oxygen uptake and sample the sediment both after deployment and immediately before recovery in the area under investigation to quantify the micro-, meio-, and macro-biota. Unfortunately, the equipment was lost in bad weather.

Bacterial Activity in Megabenthic Holothurians

Molpadiid holothurians (Figure 9D) are extremely abundant at ~ 3400 m in Nazaré Canyon. These high abundances are unusual for deep-sea burrowing species at this depth, because they occur in lower abundances in noncanyon systems

Lower canyon

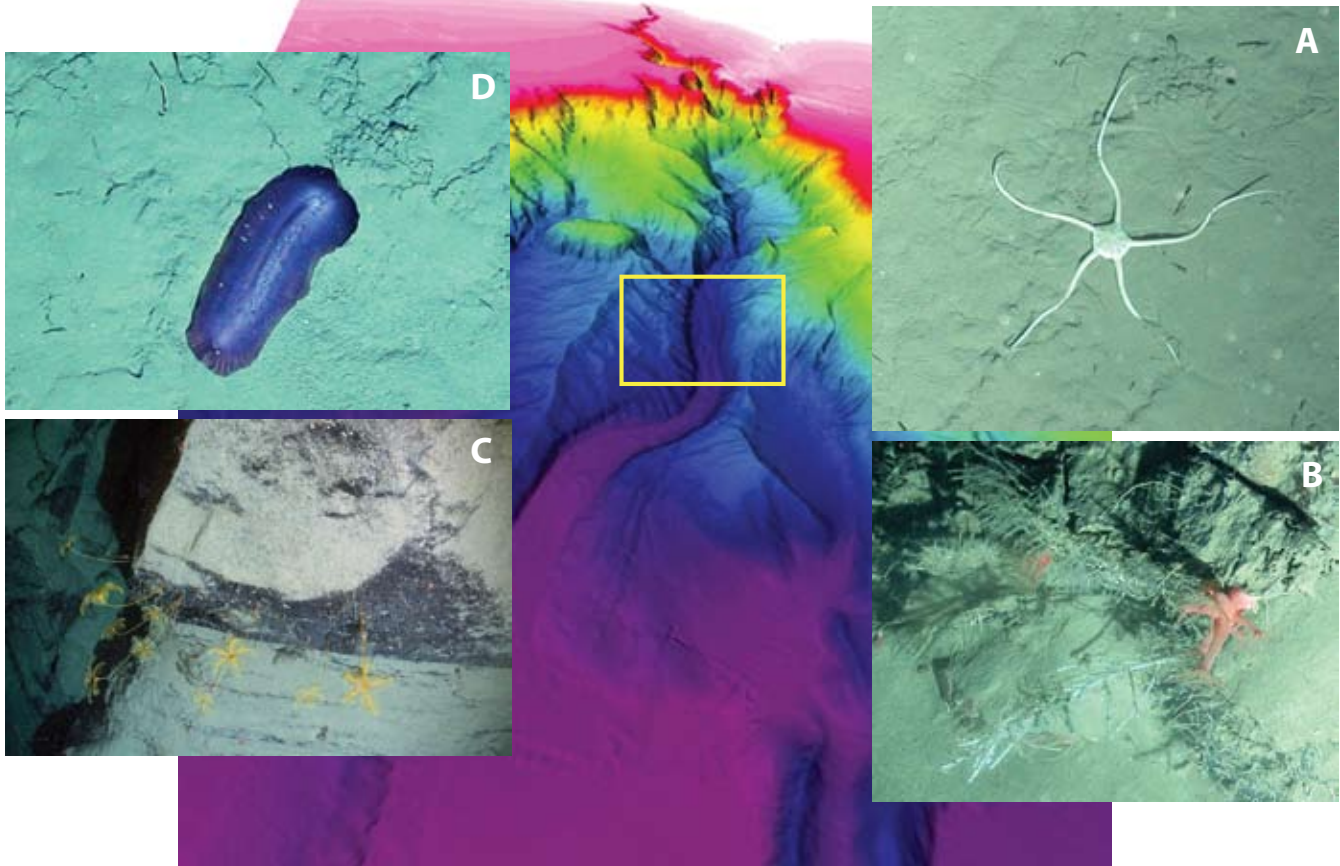


Figure 8. Fauna of the lower part of Nazaré Canyon. Clockwise from top left: (A) the holothurian *Benthodytes typicus*, (B) the ophiuroid *Ophiura concreta*, (C) the soft coral *Anthomastus*, and (D) the stalked crinoid *Anachalypsicrinus nefertiti*. All photos © NERC/NOC

(Weaver, 2005). Sediment ingested from the surface by these deposit-feeding holothurians includes dissolved organic matter (DOM), micro-organisms, meiofauna, decaying organic debris, and inorganic components (Roberts et al., 2001). But what are they feeding on? Is food the controlling factor for such high abundances in Nazaré Canyon? In order to investigate these questions in more detail, two main hypotheses have been posed: (1) the bio-availability of potential food sources controls the abundance of molpadiid holothurians, and (2) possible trophic interactions with prokaryotes enhances this holothurian's ability to digest sediment.

To test these hypotheses, the composition of sediment samples and holothurian gut content and fecal material were compared (Figure 9C and D). The experimental circular chamber (fondly known as the “holothurian toilet”) placed on the seabed (Figure 9C) allowed the *Molpadia* (Figure 9D) to be maintained in situ independent of contaminating sediment, thus allowing feces to be collected free of sedimentary bacteria. Results show that at 3400 m in Nazaré Canyon, the main compounds being used by the deep-sea holothurian *M. musculus* appear to be proteins, which are degraded through the gut. Lipids are also used, but to a lesser extent, and carbohydrates

were not broken down or used at the time of sampling. Prokaryotes help the holothurians degrade sediment in the first part of the gut and produce a high-nutritional-quality food source for consumption (recent work of author Amaro and colleagues). Moreover, molecular fingerprinting analyses provide evidence for the presence of a distinct bacterial community in both Nazaré Canyon sediment and within *M. musculus* guts (recent work of author Amaro and colleagues).

CONCLUSION

Nazaré Canyon investigations have provided the opportunity for HERMES

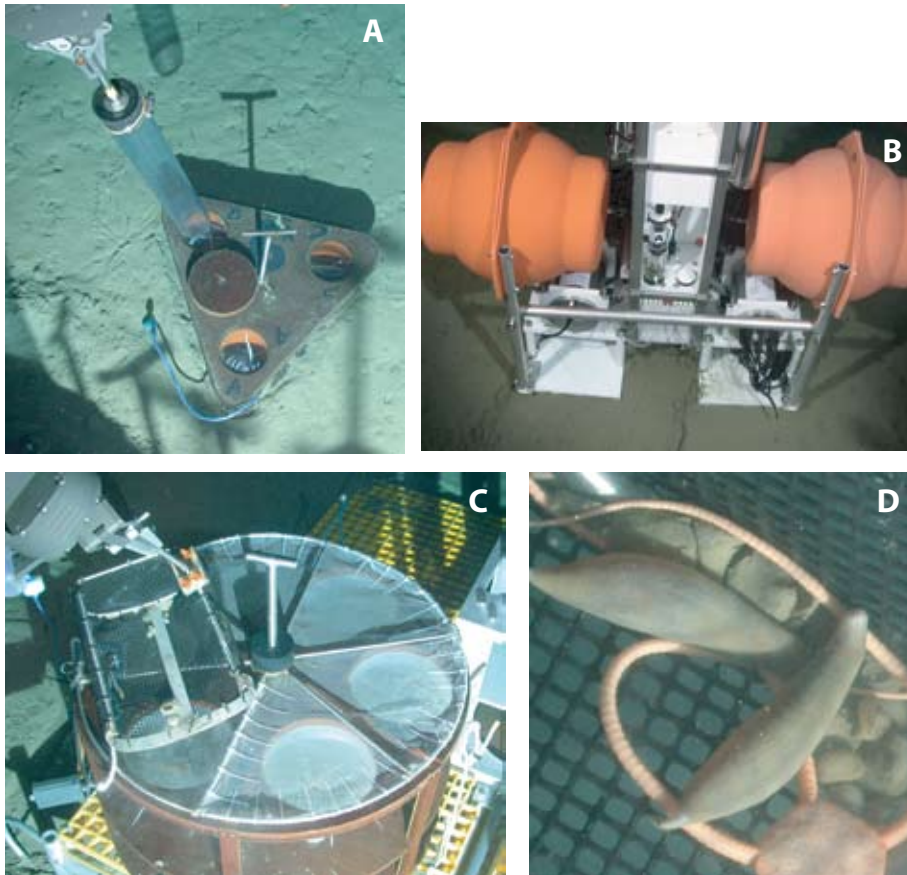



Figure 9. Process studies in Nazaré Canyon at 3400 m. (A) Experimental feeding of canyon nematodes. Courtesy of University of Ghent (B) Sediment community oxygen consumption. Courtesy of University of Aberdeen. (C) and (D) Bacterial production in the gut of *Molpadia blakei*. Courtesy of University of Aveiro/NOC

researchers to examine habitat heterogeneity determined by physical and sedimentary processes, and the faunal response to this heterogeneity. Evidence to date suggests that faunal diversity throughout the canyon is high and thus represents a biodiversity hotspot, especially for such an active canyon. Marine canyons are just as spectacular as their subaerial counterparts, and need careful, sustainable management. Many aspects of canyons are still unknown or only partly understood, however, and continued research efforts will focus on these important components of our continental margins.

ACKNOWLEDGEMENTS

This work was funded by the HERMES project (EC contract number GOCE-CT-2005-511234) under the European Commission's Framework Six Programme. 

REFERENCES

- Arzola, R.G., R.B. Wynn, G. Lastras, D.G. Masson, and P.P.E. Weaver. 2008. Sedimentary features and processes in the Nazaré and Setúbal submarine canyons, west Iberian margin. *Marine Geology* 250:64–88.
- Curdia, J., S. Carvalho, A. Ravara, J.D. Gage, A.M. Rodrigues, and V. Quintino. 2004. Deep macrobenthic communities from Nazaré Submarine Canyon (NW Portugal). *Scientia Marina* 68:171–180.
- de Stigter, H., W. Boer, P.A. de Jesús Mendes, C.C. Jesús, L. Thomsen, G.D. van den Berg, and T.C.E. van Weering. 2007. Recent sediment transport and

- deposition in Nazaré Canyon, Portuguese continental margin. *Marine Geology* 246:144–164.
- Epping, E., C. van der Zee, K. Soetaert, and W. Helder. 2002. On the oxidation and burial of organic carbon in sediments of the Iberian margin and Nazaré Canyon (NE Atlantic). *Progress in Oceanography* 52:399–431.
- Garcia, R., K.A. Koho, H.C. De Stigter, E. Epping, E. Koning, and L. Thomsen. 2007. Distribution of meiobenthos in the Nazaré canyon and adjacent slope (western Iberian Margin) in relation to sedimentary composition. *Marine Ecology Progress Series* 340:207–220.
- Koho, K.A., T.J. Kouwenhoven, H.C. de Stigter, and G.J. van der Zwaan. 2007. Benthic foraminifera in the Nazaré canyon, Portuguese continental margin: Sedimentary environments and disturbance. *Marine Micropaleontology* 66:27–51.
- Lastras, G., R. Arzola, D.G. Masson, R.B. Wynn, V.A.I. Huvenne, V.A.I. Hühnerbach, and M. Canals. In Press. Geomorphology and sedimentary features in the central Portuguese canyons, Western Iberian Margin. *Geomorphology*.
- Oliveira, A., A.I. Santos, A. Rodrigues, and J. Vitorino. 2007. Sedimentary particle distribution and dynamics on the Nazaré canyon system and adjacent shelf (Portugal). *Marine Geology* 246:105–122.
- D. Roberts, H.M. Moore, J. Berges, J.W. Patching, M.W. Carton, and D.F. Eardly. 2001. Sediment distribution, hydrolytic enzyme profiles and bacterial activities in the guts of *Oneirophanta mutabilis*, *Psychropotes longicauda* and *Pseudostichopus villosus*: What do they tell us about digestive strategies of abyssal holothurians? *Progress In Oceanography* 50 (1–4): 443–458.
- Vanney, J.R., and D. Mougénot. 1990. A Gouf-type canyon, the Canhão-da-Nazaré (Portugal). *Oceanologica Acta* 13(1):1–14.
- Weaver, P.E. 2005. The geobiology of the Nazaré and Setúbal Canyons, Portuguese Continental Margin. Cruise report No. 1 RRS *Discovery* cruise D297 27 Jul–16 Aug 2005. National Oceanography Centre, Southampton, 41 pp.
- Weaver, P.P.E., D.S.M. Billett, A. Boetius, R. Danovaro, A. Freiwald, and M. Sibuet. 2004. Hotspot ecosystem research on Europe's deep-ocean margins. *Oceanography* 17(4):132–143.
- Weaver, P.P.E., R.B. Wynn, N.H. Kenyon, and J. Evans. 2000. Continental margin sedimentation, with special reference to the north-east Atlantic margin. *Sedimentology* 47(s1):239–256, doi:10.1046/j.1365-3091.2000.0470s1239.x