I - EXECUTIVE SUMMARY

This summary, initiated during the workshop discussions, was consolidated over several months thereafter as participants and CIESM colleagues each provided inputs in their particular area of expertise: Joan Batista and Joan Moranta (ichthyofauna), Bella Galil (biogeographic trends, megafauna, macrofauna), Cristina Gambi (meiofauna), Rolf Koppelmann (zooplankton) and Tassos Tselepides (macrofauna) all contributed ideas and words to the sections concerning the deep-sea fauna; Laura Giuliano – in collaboration with Christian Tamburini and Mikhail Yakimov – to microbiology, brine pools and pollution, Gerhard Herndl to prokaryotes diversity, David Billett (abyssal plains), Daniel Desbruyères (cold seeps), Paul Snelgrove (continental slopes; emerging technologies) to patterns and processes, Anna Metaxas to technologies and, along with Aline Fiala Medioni, to cold seeps. Frédéric Briand took care of what was left and of the overall synthesis, thankfully assisted in the final editing and in the writing up of the introduction by Paul Snelgrove.

1. INTRODUCTION

The Workshop was held in Heraklion, Greece, from 2 to 5 July 2003, at the Institute of Marine Biology of Crete. In welcoming the participants, Frédéric Briand, Director General of CIESM, first expressed his gratitude to Tassos Tselepides, Acting Director of the Center and one of the pioneers of deep sea ecology in the Cretan Sea, for facilitating the venue and the logistics, and to Angelo Tursi, Chair of the CIESM Committee on the Marine Ecosystem, for his early, enthusiastic support in selecting this theme. He then presented the general background and objectives for the workshop.

Background and objectives

Today much more is known about planet Mars than about life in the deep sea regions of our own planet. Despite our powerful fascination – since ancient times – about undersea worlds, deep-ocean exploration lags very far behind the exploration of outer space, and the global number of scientific deep-sea submersibles looks pale in comparison to that of satellites and spaceships. In the Mediterranean, deep-sea exploration is truly in its infancy, and our knowledge of the bathyal biota, dismal. To draw attention to this perplexing state of affairs, CIESM brought together some of the best experts in the discipline in order to summarize the scant, but developing knowledge on Mediterranean deep-sea biology and to identify the most crying gaps.

It is in the Mediterranean that deep-sea organisms were first discovered and studied: Antoine Risso, an apothecary from Nice published a series of papers between 1810 and 1827 on fish and crustaceans collected by fishermen at depths of 600 to 1,000 m in the Gulf of Genoa. Risso’s papers were thoroughly ignored at the time for they contradicted the “paradigm” formulated by Edward Forbes that below 550 m the deep ocean was a lifeless zone. It was only in 1861, when Alphonse Milne-Edwards identified molluscs and corals attached to a piece of telegraph cable.
brought up from 1,800 m deep between Algeria and Sardinia, that Risso’s findings were vindicated.

Today we know several species that live below 4,500 m, deep in Mediterranean trenches. Yet our current level of knowledge of Mediterranean deep-water communities remains extraordinarily limited as very few biologists have sampled deep-sea regions. Few deep-sea habitats in the world ocean are thoroughly known, but in those areas that have been studied scientists did find a plethora of new species (Grassle and Maciolek, 1992), new habitats, and even new types of ecosystems (e.g. Grassle, 1986). New data on deep-sea seamounts and deep-water reefs elsewhere in the world (e.g. Koslow et al., 2001; Hall-Spencer et al., 2002) suggest that these environments often support taxonomically unique communities that are highly vulnerable to human-induced disturbance; there is every reason to expect that seamounts in the Mediterranean will be as distinct and vulnerable.

More generally, in view of the small sampling effort invested so far in deep areas of the Mediterranean Sea, there is little doubt that future investigations will generate exciting new discoveries. At the very least, many species that are new to science will be discovered. It is also possible that completely novel processes and environments will be found and that we have only scratched the surface with some of our recent discoveries. The discovery of hydrothermal vents in the Eastern Pacific, hardly 30 years ago, has revolutionized the way that ecologists view the Earth. Given the very limited state of our knowledge of the Mediterranean, it is quite possible that discoveries of equal magnitude await.

There is also a real sense of urgency: surrounded by dense coastal human populations and cities, subjected to intense fishing, fast-growing maritime traffic, the Mediterranean deep sea may be among the most heavily impacted deep-sea environments in the world. Yet it is also among the least known areas in terms of biodiversity resources. It may well be that a significant loss of biodiversity is currently taking place before scientists have had a chance to document its existence. In the following pages we will share our concerns over the initial commercial exploitation of deep water species; over the mounting threats posed by oil drilling, gas and mineral exploration. In fine a significant, complex issue looms large: given the unknown level of sustainability of deep-sea ecosystems, what would be the wisest policy for their conservation?

The Mediterranean Deep-Sea: a major research opportunity

The morphology of the Mediterranean Sea, its geological history, and proximity of research laboratories make it an ideal location for innovative deep-sea research. The Mediterranean deep-sea is unique among deep-sea environments in being uniformly warm (>13°C), which in itself offers opportunities for testing fundamental concepts about deep-sea communities (e.g. reduced rates of metabolism, links between physiological adaptations and diversity patterns, colonization, etc.). The contrasting material flux in western and eastern basins (described below) offers an ideal mensurative experimental opportunity to evaluate how material flux influences patterns of diversity, whereas the unusual complexity of bottom habitats (see below) offers an excellent framework in which to examine how habitat heterogeneity influences rates of species turnover. The topographic and hydrological isolation, the frequent extinction and reinvasion cycles, also provide an intriguing background for biogeographic studies, particularly in tandem with novel techniques (e.g. molecular clocks, phylogenetic analyses, etc.).

Perhaps the most compelling aspect of the Mediterranean as a research locale for deep-sea investigations and explorations is the proximity of many well-equipped laboratories. Process-oriented studies in other areas of the world are seriously constrained by the cost and logistics of mounting major seagoing expeditions to deploy and retrieve experiments. In the Mediterranean it is possible to access deep-water environments in day trips, thereby greatly increasing the range of possible experiments. In short, the Mediterranean Sea has the potential to become a major focal point for deep-sea diversity studies.
2. MAPPING DEEP-SEA HABITATS

In the past few years, the access of the oceanographic community to multibeam echo-sounding technologies has allowed the mapping of vast areas of the deep Mediterranean Basin, revealing a sea bottom of far greater complexity than that known from standard bathymetric maps, and providing a tremendous resource – rarely available over such a large scale – for biodiversity studies.

In 2001 a joint campaign of French and Dutch researchers on board the IFREMER R/V L’Atalante collected data that led to the co-production by CIESM and IFREMER of two important compilation maps – bathymetry and acoustic imagery – of the Mediterranean Ridge and adjacent areas in the Eastern Mediterranean Basin. Both maps offered, with a degree of resolution never achieved before, a brand-new vision and understanding of the vast bulge created at the subduction zone between the African and European plates. This effort was followed in 2003 by the co-production by CIESM and Geosciences Azur (Observatory of Villefranche s/mer, France) of maps of bathymetry and acoustic imagery of the Nile deep-sea Fan (see http://www.ciesm.org/publications/misce.html).

In recent months, swath mapping data have been collected and analysed for most areas of the Western Mediterranean Basin – from the Alboran Sea, the Algerian margin, the Balearic Sea, the Gulf of Lions, to the Tyrrhenian and Ionian Seas. Spanish, French and Italian research teams (from the University of Barcelona, IEO, IFREMER, University of Brest, Geosciences Azur, IGM Bologna) are currently cooperating under the aegis of CIESM and IFREMER, to produce a new compilation map which will synthesise these new findings at a scale of 1:200,000 with a grid resolution of 500 m. This map should be available by the end of 2004.

Before long, by integrating additional data collected by Eastern Mediterranean Institutes and French teams in the Aegean Sea, the Gulf of Lybia, the Nile system and Levantine waters, CIESM will be able to produce a comprehensive map of the entire Deep-Sea Mediterranean. A formidable challenge will be then to couple this knowledge with our emerging, fragmented picture of deep-sea biodiversity.

3. BIODIVERSITY PATTERNS

Investigations of the Mediterranean deep-sea fauna are at a very early stage: below 1,000 m, where systematic quantitative sampling has been extremely limited, most faunal groups remain largely unknown and there are basins in the Eastern Mediterranean and in southern waters where effectively nothing is known about deep-sea biology. At depths shallower than 800 m the sampling effort is considerably better, except in the southern Mediterranean which remains largely unsampled for any deep-sea fauna. While the basis of our knowledge of deep-sea zooplankton and microbes is somewhat stronger – at least in the Western Basin – the pelagic ichthyofauna is hardly known. Indeed meso- and bathypelagic fishes represent a wide-open area for research.

3.1. Megafauna

Our knowledge of deep megafaunal communities (fishes, crustaceans and cephalopods) in the Mediterranean is mainly limited to the bathymetric range over which commercial fishing operates, usually down to 800 m. Below this range we have only fragmented data on the bathyal biota of the Western and Levantine basins.

Although there are past collections of megafauna in the Mediterranean, most of these have either been non-quantitative or have collected scattered samples without any systematic coverage. For example, the scientific exploration of the Levantine bathyal biota commenced with the extensive voyages of the Pola (1890-1893). In 1910 the Danish Oceanographic Expedition to the Mediterranean, aboard the Thor, sampled nine sites along the western limits of the Levantine Sea, from Cyrenaica to Rhodes. However, as that expedition focused mainly on plankton, and “dredgings were only occasionally made … the result will thus necessarily be but poor” (Stephensen, 1915). The Lamont Geological Observatory research vessel Vema collected few deep benthic
samples in 1958 (Barnard, 1964). The German research vessel Meteor in 1987 collected benthic samples at sites between Crete and Israel at depths ranging between 95 and 4396 m during a ten-day sojourn (Janssen, 1989). The handful of deep-sea fishes gathered persuaded Klausewitz (1989) that “this collecting trip confirmed the paucity of the deep-sea fish fauna in the eastern basin of the Mediterranean”. The total of 167 trawl hauls conducted since 1988 by the Israel Oceanographic and Limnological Research, down to 1,550 m, have not significantly altered this perception (Galil, in press).

Further down, photographic investigations have collected valuable qualitative information on the Levantine bathyal ichthyofauna. Two surveys conducted at a 15-year interval utilized bait, thus attracting facultative or obligate scavengers. Gilat and Gelman (1984) employed a free-fall camera positioned on top of a bait holder, taking still photographs at 5 minutes intervals for 18 hours, at six sites between Israel and Cyprus. Off Cyprus, at a depth of 1490 m, they found that the sharks Centrophorus granulosus and Etmopterus spinax were the most abundant species, constituting over 83% of the records. More recently Jones used an autonomous unmanned lander platform equipped with cameras and sonars for tracking movements of fish attracted to bait in the Cretan sea, Rhodos basin, and Ierapetra Basin (see Jones et al., 2003). In the Cretan Sea (1,500-3,850 m) and Rhodos Basin (2,300-3,850 m), again sharks (Hexanchus griseus, Galeus melastomus, Centrophorus spp., Centroscymnus coelolepis, and Etmopterus spinax) predominated, together with the teleost fishes Chalinura mediterranea and Lepidion lepidion (Jones, in Priede and Bagley, 2000).

In a recent survey transacted without resorting to bait, Galil (in press) documented the site-typical faunal complement. She concluded that “there is no doubt that the abundance of the Levantine deep water megafauna is remarkably low: in 80 hours of video documentation only three fishes, B. mediterraneus, Cataetyx laticeps, and Chauliodes sloani, were recorded. Although the methods utilized were not sufficient for quantitative comparison with studies made in the Western Mediterranean, the small number of species and specimens confirms the ichthyofaunal scarcity of the Levantine Sea, not only compared with the adjacent Atlantic Ocean (Haedrich and Merrett, 1988), but also with the Western Mediterranean”.

In the Western basin valuable quantitative information is available on the bathymetric distribution and community structure of deep megafaunal groups in the north-western area, essentially down to 2,200 m. This has been complemented recently by a few samples (only 10 bottom trawls were conducted) taken as far down as 4000 m in western and central deep-sea areas (Sardà, 2001).

### 3.2. Zooplankton

Although temporal variability is insufficiently covered, the sampling effort for zooplankton is better than in most other groups. Since the Straits of Gibraltar act as an ecological barrier to the immigration of many deep Atlantic species (see Scotto di Carlo et al., 1984), the Mediterranean Sea is characterized by an impoverished bathypelagic fauna. Thus, in contrast to the rather diverse zooplankton found down to ca. 200 m (e.g. Mazzochi et al., 1991; Siokou-Frangou et al., 1997; Deudero and Morales-Nin, 2001; Fernández de Puelles et al., 2003) in the Mediterranean epipelagic zone, only few typical bathypelagic species have been identified so far and the deep waters appear to be populated by several midwater species adapted to living at anomalously great depths (Vinogradov, 1968; Lapernat and Razouls, 2001).

Table 1 lists some of the main references published on deep-sea zooplankton of the Mediterranean Sea in the last forty years. As there are more publications and reports (several in non-English language) available, the list is only suggestive and does not claim for completeness. The reader is refered to Scotto di Carlo et al. (1991) for a summary of investigations on copepod communities until the end of the 1980s, to Gasser et al. (1998) for updated information from the Western Mediterranean, and to Andersen et al. (2001a,b), Laval et al. (1992) and Mills et al. (1996) for data on gelatinous zooplankton down to mesopelagic depths. Information on deep mesozooplankton from the Eastern Mediterranean will be found in Pancucci-Papadopoulou et al.
(1992), Weikert and Koppelmann (1993) and Weikert et al. (2001) plus in studies cited therein. Microzooplankton investigations down to 1,850 m were conducted by Böttger-Schnack (1994, 1997) in Levantine waters.

Overall, deep-sea zooplankton abundance and diversity decrease from west to east. Two taxa are dominant in the deep water of the Levantine Sea: *Eucalanus monachus* at mesopelagic depths and *Lucicutia longiserrata* in the bathypelagic zone. Scotto di Carlo et al. (1991) stated that the deep community structure showed only little or no diel and seasonal variability. However, significant changes occur occasionally or on time-scales not assessed so far. Weikert et al. (2001) found high amounts of zooplankton in the deep water body of the Levantine Sea in 1993. This change in zooplankton composition and abundance is likely associated with a change in hydrography, the Eastern Mediterranean Transient (see CIESM Workshop n°10, 2000; Klein et al., 1999), which started in 1988/1989. Since the available data are sparse and fragmentary, all studies suffer from the lack of time-series investigations.

### 3.3. Macrofauna

Despite the thorough review of Fredj and Laubier (1985) on qualitative aspects of the benthic macrofauna composition of the deep Mediterranean Sea, quantitative data remain generally

Table 1. Major deep-sea zooplankton investigations in the Mediterranean Sea

<table>
<thead>
<tr>
<th>Region</th>
<th>max. Depth</th>
<th>Group</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balearic Sea</td>
<td>2800 m</td>
<td>Zooplankton</td>
<td>Furnestin and Arnaud, 1962</td>
</tr>
<tr>
<td>Balearic Sea</td>
<td>2800 m</td>
<td>Copepoda</td>
<td>Mazza, 1962</td>
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<tr>
<td>Ionian Sea</td>
<td>3000 m</td>
<td>Microzooplankton</td>
<td>Greze, 1963</td>
</tr>
<tr>
<td>Eastern Mediterranean Sea</td>
<td>2000 m</td>
<td>Zooplankton</td>
<td>Kimor and Berdugo, 1967</td>
</tr>
<tr>
<td>Mediterranean Sea</td>
<td>3000 m</td>
<td>Zooplankton</td>
<td>Vinogradov, 1968</td>
</tr>
<tr>
<td>Tyrrhenian, Adriatic Seas</td>
<td>1000 m</td>
<td>Copepoda</td>
<td>Hure and Scotto di Carlo, 1974</td>
</tr>
<tr>
<td>Tyrrhenian Sea</td>
<td>2000 m</td>
<td>Zooplankton</td>
<td>Scotto di Carlo et al., 1975</td>
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<tr>
<td>Levantine Sea</td>
<td>4400 m</td>
<td>Zooplankton</td>
<td>Kimor and Wood, 1975</td>
</tr>
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<td>Alboran Sea</td>
<td>1000 m</td>
<td>Zooplankton</td>
<td>Vives et al., 1975</td>
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<tr>
<td>Western Mediterranean Sea</td>
<td>1000 m</td>
<td>Copepoda</td>
<td>Vives, 1978</td>
</tr>
<tr>
<td>Tyrrhenian, Ionian Seas</td>
<td>2000 m</td>
<td>Copepoda</td>
<td>Vaisièrre and Seguin, 1980</td>
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<td>Tyrrhenian Sea</td>
<td>3000 m</td>
<td>Copepoda</td>
<td>Ianora and Scotto di Carlo, 1981</td>
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<tr>
<td>Tyrrhenian Sea</td>
<td>3000 m</td>
<td>Mesozooplankton</td>
<td>Scotto di Carlo et al., 1984</td>
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<tr>
<td>Eastern Mediterranean Sea</td>
<td>4000 m</td>
<td>Near-bottom Plankton</td>
<td>Christiansen 1989</td>
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<td>Ligurian Sea</td>
<td>700 m</td>
<td>Gelatinous Zooplankton</td>
<td>Laval et al. 1989</td>
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<tr>
<td>Levantine Sea</td>
<td>4000 m</td>
<td>Micronekton</td>
<td>Weikert, 1990</td>
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<tr>
<td>Levantine Sea</td>
<td>4000 m</td>
<td>Mesozooplankton</td>
<td>Weikert and Trinkaus,1990</td>
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<td>Mediterranean Sea</td>
<td>2500 m</td>
<td>Mesozooplankton</td>
<td>Scotto di Carlo et al., 1991</td>
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<td>Micronekton</td>
<td>Andersen and Sardou, 1992</td>
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<td>Western Mediterranean Sea</td>
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<td>Pancucci-Papadopoulou et al., 1992</td>
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<td>Mesozooplankton</td>
<td>Weikert and Koppelmann, 1993</td>
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<td>Microcopepoda</td>
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<td>Alboran Sea</td>
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<td>Western Mediterranean Sea</td>
<td>1000 m</td>
<td>Macropl. Micronekton</td>
<td>Sardou et al., 1996</td>
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<td>Levantine Sea</td>
<td>1850 m</td>
<td>Microzooplankton</td>
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<td>Ligurian Sea</td>
<td>1000 m</td>
<td>Mesozooplankton</td>
<td>Gasser et al., 1998</td>
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<tr>
<td>Ligurian, Tyrrhenian Seas</td>
<td>700 m</td>
<td>Macropl., Micronekton</td>
<td>Andersen et al., 1998</td>
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<tr>
<td>Western Mediterranean Sea</td>
<td>1355 m</td>
<td>Near-bottom Plankton</td>
<td>Cartes, 1998</td>
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<td>Ionian Sea</td>
<td>3700 m</td>
<td>Copepoda</td>
<td>Lapernet and Razouls, 2001</td>
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<td>Levantine Sea</td>
<td>4250 m</td>
<td>Mesozooplankton</td>
<td>Weikert et al. 2001</td>
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<tr>
<td>Western Mediterranean Sea</td>
<td>1000 m</td>
<td>Mesozooplankton</td>
<td>Andersen et al., 2001a,b</td>
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<td>Levantine Sea</td>
<td>4250 m</td>
<td>Mesozooplankton</td>
<td>Koppelmann et al., 2003</td>
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scarce, when not completely lacking. It is not an exaggeration to state that the vast majority of the deep Mediterranean basin is virtually unknown. Indeed, the Eastern Mediterranean which is the deepest of the two basins, long remained one of the most poorly studied areas of the world. During the second half of the 20th century some general ecological and faunal surveys provided valuable but scattered information on various areas (e.g. Pérès and Picard, 1958; Chukhtchin, 1964; Lédoyer, 1969; Guille, 1970; Desbruyeres et al., 1972; Vamvakas, 1970 and 1973; Di Geronimo, 1974). In the deepest area – the Cretan Sea – the earliest records of macrobenthic organisms were those given by Forbes (1844), Raulin (1870) and Jeffreys (1881,1883). With the establishment of the Institute of Marine Biology of Crete a number of benthic studies appeared in the last twelve years (e.g., Tselepides and Eleftheriou, 1992; Koutsoubas et al., 1992; Karakassis and Eleftheriou, 1997; Koutsoubas et al., 2000; Tselepides et al., 2000), contributing new information on the macrobenthic fauna distributed from the outer continental shelf to the upper and mid-slope of Crete.

Until recently, however, knowledge of the deep (bathyal to abyssal) macrobenthic fauna remained sparse, derived primarily from material collected from the early Pola Expedition (Sturany, 1896) to the Eastern Mediterranean. In recent years (1987-2000) a more coherent, quantitative sampling effort was undertaken, largely through EU-funded projects and the logistic support of national deep sea initiatives such as the German Meteor Expeditions (see Janssen, 1989; Fiege et al., 1994; Ben Eliahu and Fiege, 1996; Fiege et al., 2000). Even so the number of quantitative macrobenthic samples acquired is very low (probably less that 100), as most of these studies were conducted as part of large multidisciplinary biogeochemical projects and therefore little effort and time was devoted to sampling the benthic community. The western basin remains also grossly understudied as very few quantitative studies did focus on the bathyal and abyssal macrofauna. A recent comprehensive quantitative investigation, undertaken by Stora et al. (1999) analysed samples from within and along the flanks of the Toulon Canyon. Valuable quantitative information on the community structure of the bathyal suprabenthos in the Catalan Sea, showing relatively high diversity at mid-bathyal depths, has been added by Cartes et al. (2001).

“The florofaunistic impoverishment of the Eastern Mediterranean compared with the Western Mediterranean richness in species” (Sarà, 1985) has been generally accepted, as well as the perception of a gradational decrease from west to east that is more conspicuous for the deep benthos than for the whole fauna (Fredj and Laubier, 1985). Thus the Levantine deep water fauna has long been presumed the poorest in species and abundance in the whole Mediterranean (Fredj, 1974), although Bellan-Santini (1990) recognized that particularly “limited amount of sampling [was] carried out in the eastern basins”, even suggesting that “the relative species richness of (…) faunas of the different sectors of Mediterranean is better correlated with the level of research effort than the true species richness”. It seems realistic, however, to assume that the low number of species and specimens recorded does not stem solely from limited effort or inefficient gear.

Information on biogeography can be extracted from non-quantitative historical studies, but considerable caution is neeed. Although Marenzeller (1893) reported that species occur deeper in the Levant than elsewhere in the Mediterranean, his records were later considered suspect, an artifact resulting from a “systematic mistake on the depth measurements” that “needs to be cleared up in the future” (Fredj and Laubier, 1985: 128). Recent studies published greater depth records in the Levantine Sea than in the Western Mediterranean for 14 serpulid species, with a third of the depth extensions > 400 m (Ben Eliahu and Fiege, 1996). Several molluscs have been collected from greater depths in the Levantine Sea than in the southern Tyrrenian Sea (Di Geronimo et al., 2001). Extension of the depth records were also reported for five of the bathyal amphipods, in one case for as much as 1,100 m (Sorbe and Galil, 2002). The Levantine Sea benthofaunal scarcity – theoretical ecologists might evoke a “niche vacuum” – may cause such extensions of the bathymetric distributions.

The present-day Mediterranean deep water fauna is less closely related to the Atlantic bathyal than was the case in the Pleistocene (Barrier et al., 1996). This disparity is attributed in part to
the shallow Gibraltar sill that bars the deep water of the Atlantic Ocean from entering the Mediterranean, and to the Mediterranean outflow that bars the entry of the deep water Atlantic fauna into the Mediterranean (see Salas, 1996). The onset of warmer climates led to the demise of many cold stenothermic and stenohaline species and to the eventual impoverishment of the bathybenthos. In addition, the extreme oligotrophy of the Levantine Sea prevented settlement by members of the Atlantic bathyal that would have been able to cross the shallow Gibraltar Straits and the Siculo-Tunisian sill (<400 m) (Pérès, 1985). The recurring stagnant (dysoxic and anoxic) Quaternary episodes resulted in a reduction, or even extinction of deep bottom-living fauna unable to avoid annihilation by adapting to shallower depth: Van Harten (1987) reported that “several species of deep-water ostracodes that are still common in the Western Mediterranean became extinct in the Eastern Mediterranean basin at the onset of early Holocene S1 sapropel deposition”. Bacescu (1985) believed that the bathyal bottoms of the Levant are still “unfavourable”, or even “azoic”, after the last sapropelic event, dated between 9,000 and 6,000 years B.P., following the suggestion (George and Menzies, 1968) “that sufficient time has not elapsed to allow colonization of the deep-sea floor”.

Bouchet and Taviani (1992) suggested that much of the Mediterranean deep-sea fauna is made-up of non-reproducing pseudopopulations that have entered the Mediterranean as meroplankton with the Atlantic inflow at Gibraltar. However, the populations of the most common benthic molluscs in depths greater than 1,000 m in the Levantine Sea are composed of both adult and juvenile specimens. Moreover gravid benthic decapod crustaceans and fish have been collected repeatedly from the depths of the Levantine Sea (Galil and Goren, 1994; Goren and Galil, 1997; Fishelson and Galil, 2001). Though much reduced in diversity and richness compared with the deep sea fauna of the western and central basins of the Mediterranean, the Levantine bathy-benthos appears to be composed of autarchontous, self-sustaining populations of opportunistic, eurybathic species that have settled there following the last sapropelic event.

Often considered a “biological desert”, the deep Mediterranean Sea certainly holds many surprises: it was recently found that certain areas display such high activity as to be characterised as “benthic hotspots” (see Fiege et al., 2000; Danovaro et al., 2001; Tselepides and Lampadariou, in press). It appears likely that other areas, relatively rich in species – including some new ones to science – await discovery.

3.4. Meiofauna

Literature on meiofauna assemblages and nematode diversity in deep-sea Mediterranean is very scant. The only available information on meiofauna concerns the continental shelf and upper slope of the Western Mediterranean Basin and the Cretan Sea (Vivier, 1978; Guidi, 1987; Soetaert et al., 1991; Bovée de et al., 1990; Danovaro et al., 1999; Grémare et al., 2002; Dinet, 1976; Danovaro et al., 1995, 1999). It appears that the Western Basin is characterised by significantly higher meiofaunal densities. In spite of this, meiofaunal assemblages display exactly the same community structure and indeed are strongly dominated by nematodes (80-90% of total meiofaunal density) followed by harpacticoid copepods and polychaetes (Danovaro et al., 1999).

Nematodes are the most abundant metazoans on Earth, accounting for 80% of all multicellular animals on the planet; they are ubiquitous in marine habitats and sensitive to environmental changes. Moreover, nematodes become increasingly important with increasing water depth (Carmen et al., 1987; Cook et al., 2000). This phylum is characterised by a very high species number: more than 20,000 have been described on morphological and anatomical features, and potential species richness is in excess of 1 million (Lambshead and Boucher, 2003). As nematode genera and species are often cosmopolitan (the same genera can be found at tropical and polar latitudes), nematodes provide interesting “models” for investigating benthic biodiversity patterns.

However, despite their ubiquity and dominance, the knowledge of nematode diversity in the deep-sea sediments is limited to few areas such as the upper abyssal zone of the North and Central Atlantic, the eastern Central and Southern Pacific, the Arctic and the Weddell Sea, Antarctica.
Information on nematode biodiversity in the Mediterranean is scant and limited to the Western Basin (Cassidaigne Canyon, Vitiello, 1976; transect off Calvi, Corsica by Soetaert et al., 1991). Moreover, long-term times series on deep-sea meiofaunal diversity are completely lacking and almost no information is available for extreme environments such as the Mediterranean abyssal plain, cold seeps, brine pools and sea-mounts or along the Mediterranean latitudinal and longitudinal gradients. No information is available yet on meiofaunal or nematode diversity in deep-sea sediments of the Southern Mediterranean sector, and a single study has been conducted across the Mediterranean to investigate the role of the longitudinal gradient at depths of ca 3,000 m (work in progress).

3.5. Prokaryotes

Since prokaryotic organisms largely lack distinct morphological features, assessment of prokaryotic species diversity relies on the use of molecular tools such as fingerprinting techniques, cloning and sequencing of the ribosomal RNA gene (see Stahl et al., 1984; Giovannoni et al., 1990; Muyzer et al., 1993, CIESM Workshop n°11, 2000). Over the past decade it became clear that marine environments harbour an enormous phylogenetic diversity of prokaryotes. It is estimated that only less than 1% of all the marine prokaryotic species have been isolated thus far.

Diverse members of the two domains of life, *Bacteria* and *Archaea*, make up the prokaryotic component of marine plankton. *Bacteria* are phylogenetically more diverse than *Archaea* and about 80% of the *Bacteria* clones fall among nine phylogenetic groups (Giovannoni and Rappé, 2000). As indicated by fingerprinting techniques such as denaturing gradient gel electrophoresis (DGGE) and terminal restriction fragment length polymorphism (T-RFLP), the composition of the bacterioplankton community changes significantly between adjacent strata of the water column, even in the Mediterranean Sea despite the comparatively high temperature of Mediterranean deep waters. Thus depth is one of the major factors affecting bacterial community structure (Massana et al., 1997; Murray et al., 1998; Acinas et al., 1999; Massana et al., 2000).

The generally slightly higher richness of bacterial species in the euphotic layer is probably a reflection of the higher dissolved organic matter concentration and diversity as compared to deeper layers (Moeseneder et al., 2001). In the euphotic layer, phytoplankton are releasing parts of the photosynthetically fixed organic matter directly into the water and grazing on phytoplankton by the proto- and metazoan food web also contributes to the production of fresh dissolved organic matter which can be utilized efficiently by the bacterioplankton consortia. Remarkably, the richness of bacterial species declines only by about 25% from the surface waters to the lower mesopelagic and bathypelagic realm (Moeseneder et al., 2001) while overall bacterial abundance declines concurrently by about one order of magnitude. This paradox calls for more extensive investigations on the substrate requirements of deep water bacteria under *in situ* pressure conditions.

High-pressure conditions typical of the deep-sea have long been known to affect the metabolism of marine bacteria (see for instance Zobell and Oppenheimer, 1950; Jaenicke, 1987; Straube et al., 1990; Bianchi and Garcin, 1994; Poremba, 1994; Yayanos, 1995; Tholosan et al., 1999; Tamburini et al., 2003). Even if these conditions are not necessarily lethal for bacteria (Sharma et al., 2002), they will likely affect the bacterial community composition. Due to the homeothermic features of its deep-sea layers (around 13°C), the Mediterranean Sea offers an unique opportunity to study the effects of the high pressure on the deep sea microbial communities without the compounding effects of low temperature which characterize all other deep oceanic environments.

The metabolic activities of deep-sea bacteria are strictly depending on the particle flux through the water column (Nagata et al., 2000; Tamburini et al., 2003). A large fraction of the bacterial
consortia (>32 x 10^9 cells m^{-2} d^{-1}; Turley and Mackie, 1995) are transported into the deep-sea by settling particles (Turley and Mackie, 1994; Turley and Mackie, 1995). Attached bacteria play an important role in the degradation of aggregates. They convert the particulate organic carbon (POC) to dissolved organic carbon (DOC), bacterial carbon and carbon dioxide (CO2) through ectoenzymatic hydrolysis (Cho and Azam, 1988; Smith et al., 1992; Turley, 1993). In order to better understand how attached bacteria contribute to POC mineralization through the water column, the biological mechanisms controlling dissolution of ballast minerals should be studied (Armstrong et al., 2001). Preliminary essays simulating the descent of diatoms through the water column have demonstrated that enzymatic hydrolysis rates of attached bacteria are strongly affected by the increase in pressure during particles sinking. There is evidence now that particle-associated bacterial consortia are phylogenetically remarkably different from free-living bacterial communities (Moeseneder et al., 2001) at any given depth stratum of the Mediterranean Sea water column. Thus, the concept that free-living bacteria are becoming entrapped in particles and exhibit high metabolic activity there and releasing their progeny into the ambient water might not always reflect the actual situation. Thus studies on the phylogenetic composition of bacterial communities have to be combined more intensively with metabolic rate measurements in the future to shed light onto the complex interactions between free-living and particle-associated bacteria.

The second prokaryotic domain of life, the Archaea, are ubiquitously distributed throughout the global ocean. Planktonic Archaea fall almost invariably in two phylogenetic groups, the Crenarchaeota and the Euryarchaeota. Recently it has been shown that the relative abundance of Crenarchaeota increases with depth, equating roughly bacterial abundance in the layers below 1,000 m (Karner et al., 2001). Euryarchaeota generally make up no more than 15% of the total prokaryotic cells and do not vary in abundance with depth. At present the energy sources of the Archaea are still unknown, due to the lack of culturing these organisms. There is indication, however, that they may take amino acids (Ouverney and Fuhrman, 2000) and utilize inorganic carbon as well (Wuchter et al., 2003). The relatively larger contribution of Archaea to total prokaryotic abundance in the deep ocean than in surface layers suggests that they are better competitors for available substrate than Bacteria in deep waters.

In summary, information available on microbial diversity in the deep oceans is still scarce, as is information on the regulating mechanisms (CIESM Workshop n°21, 2003). Deep-sea environments are likely to contain numerous novel and widespread major prokaryotic lineages. Given the enormous volume represented by this habitat and typical bacterial abundances, the previously unknown Archaeal and Bacterial groups may well be the most abundant organisms on Earth (Fuhrman and Davis, 1997).

### 3.6. Extreme environments

#### 3.6.1. Cold seeps

Seepage of cold fluids, enriched in sulfide, methane, hydrocarbons, as well as nutrients are common both in active and passive margins from 400 to 7,326 m. They are known to sustain exuberant deep-sea, chemosynthesis-based communities, which are usually dominated by bacterial mats, bivalves (mussels and clams) and tube worms, both metazoans associated with endosymbiotic chemo-autotrophic bacteria (see review in Sibuet and Olu, 1998; Kojima, 2002; Tunnicliffe et al., 2003). At all sites, chemosynthesis-based communities are restricted to areas where methane seep out along tectonic features leading to accumulation of hydrogen sulfide in the sediment through microbial sulfate reduction processes (Fiala-Médioni et al., 1993; Henry et al., 1996; Guézenec and Fiala-Médioni, 1996). Mud volcanoes have been identified as one of the geological contexts favoring the exploitation by chemosynthesis-based symbioses of cold seeps rich in methane (Henry et al., 1996).

Although exploration is still in its infancy, several cold-seep communities have been located and described in the Eastern Mediterranean Sea, south of Crete and Turkey, on mud volcanoes or...
along faults associated with high flux of methane (Camerlenghi et al., 1992; Charlou et al., 2003) and observed from 1,700 to 2,000 m (MEDINAUT/MEDINETH Shipboard Scientific parties, 2000; Olu et al., 2001). These observations followed the discoveries on the Napoli mud volcano (1,900 m) of abundant thanathocoenoses of bivalves attributed to Myrtea sp. (Lucinidae) and Vesicomya sp. (Vesicomidae) (Corselli and Basso, 1996). More recently similar communities were also observed north of Egypt in the Nile delta (Nautilin cruise, 2003).

The communities are dominated by small bivalves belonging to four families often encountered at seeps (Lucinidae, Vesicomidae, Mytilidae and Thyasiridae) and by pogonophorans including a large vestimentiferan Lamellibrachia sp. Associated fauna included a Suberitidae sponge Rhizaxinella pyrifera, Polychaeta (other than pogonophorans), galatheids Munidopsis marionis and M. acutispina, one large crab, Chaceon mediterraneus and a sea urchins belonging to the genus Echinus (Olu-Le Roy et al., 2001).

3.6.2 - Brine pools microbiology

The deep hypersaline anoxic basins (DHABs) of the Eastern Mediterranean Sea are unique environments created by the flooding of ancient evaporites from the Miocene period (5.5 Million years B.P.). Compared to smaller hypersaline ponds, the composition of these basins, ranging in area from 5 to 20 km², is fairly constant perhaps due to their deep location (deeper than 3,300 m). The DHABs are characterised by a total salinity above 30% (close to the saturation point of NaCl which would mark the upper limit of resistance of all biological forms) (De Lange et al., 1990a), absence of light, elevated pressure (>30 MPa), variable pH values and ionic composition. The transition from normal seawater to brine occurs at about 3,300 m depth. At this transition, salinity increases sharply with depth, whereas the concentration of dissolved oxygen drops rapidly to zero. This change is likely to occur within a depth of 1 m. The sharp density difference between brines and the upper normal deep seawater acts as a barrier to the oxygen exchange between water and brines. Several reports indicate that the seawater-brine interface is a very stable physical configuration (Wiesenburg et al., 1985; De Lange et al., 1990b).

The DHAB environments represent one of the last frontiers that challenge the life sciences today. A great diversity of microorganisms have been detected by cultivation-independent methods along the seawater-brine gradient, and hundreds of individual isolates were obtained in pure cultures. Compared to other anoxic marine hypersaline lakes that have been more largely studied for their bacterial diversity, namely the Kebrit Deep and the Shaban Deep basins (Red Sea) (Antunes et al., 2003; Eder et al., 1999, 2002), the DHABs showed a highly complex structure and a very high abundance of newly described prokaryotic taxonomic groups, particularly in the interface. According to these findings, both the Bacteria and Archaea domains are well represented in the different layers of the DHABs, particularly at the interface where the hydrolysis rates of biopolymers appear clearly higher than in the immediately overlying oxygenated water (BIODEEP data).

4. NEW RESEARCH DIRECTIONS - PATTERNS

The Mediterranean Sea offers a fascinating location for studying issues in deep-sea biodiversity because of its unique geological history, its physiography and easy access of its deeper areas (see Fig. 1). Unlike the open ocean, the Mediterranean Sea has been subjected to drying out and then inundation from the Atlantic, a process that may have occurred as many as 17 times (Maldonado, 1986). The most recent event occurred about 5 million years ago, making the Mediterranean abyssal zones very “young” (biologically speaking) in comparison to the oceans. In addition, since the shallow sill (300 m) at the Strait of Gibraltar has prevented migration of abyssal species into the Mediterranean Sea (see section 3.3), unique opportunities exist of studying the influence of migration vs speciation in influencing species richness. The presence of a number of abyssal basins at varying distances from the connection to the Atlantic, and the separation of the deep Eastern and Western Mediterranean by the Strait of Sicily sill (400 m) provides further opportunities of assessing the effects of topographic separation on biodiversity.
Apart from unique geological features, the Mediterranean Sea has a number of hydrographic features that will also have a different effect on biodiversity in comparison to “normal” abyssal settings. Most notable of these is the temperature of the water, which does not fall below 13°C making the Mediterranean the warmest abyss in the World’s oceans. Normal rules that apply to cold abyssal fauna elsewhere are not found in the Mediterranean, offering novel comparisons on the combined physiological effects of temperature and pressure. The deep Mediterranean is also affected by temporal variation in the formation of cold water during winter months at a number of locations, but most notably in the Aegean Sea, off Rhodes and the Adriatic (see CIESM Workshop n° 10, 2000; Lascaratos et al., 1999).

4.1. Bathyal patterns on continental slopes
Continental slope environments include some of the most heterogeneous sedimentary environments in the deep sea. Bathymetry is an overriding variable that must be considered in any comparison between slope communities and likely contributes significantly to broad-scale patterns. Process-related studies will be considered separately (see section 6 below), but in terms of pattern there are several questions that are particularly compelling in the Mediterranean.

One key question is how patterns of diversity change as a function of depth along the continental slope and rise, and how the quality, quantity, and frequency of organic input contribute to this pattern. Different areas of the Mediterranean are known to vary in terms of surface production, sedimentation rates, and morphology (e.g. Danovaro et al., 1999). The degree to which the faunas of these areas differ remains poorly known, beyond the recent comparative study of Galil (in press) on the biodiversity patterns of bathyal mega- and macro-benthos in the Western and Levantine basins.

Among other questions:
1) Does diversity peak at intermediate depths (as e.g. in the north Atlantic, Rex, 1983) in all of these areas or do areas with different material flux show different depth-diversity relationships?
2) What is the extent of bathymetric zonation (e.g. Cartes and Sarda, 1993) in different taxonomic groups in all areas of the Mediterranean? Comparative studies between regions with nearby geographic regions with contrasting flux regimes (e.g. Levin and Gage, 1998) are likely to be particularly informative.
3) Do topographic features such as canyons support unique faunas within and adjacent to canyon areas (see 4.4. below)? This should be linked to zooplankton studies, given the potential zooplankton may play in influencing material flux.
4) Are there latitudinal or longitudinal gradients within the Mediterranean?

Another area of interest is whether specific areas of the Mediterranean slope represent “hotspots” of diversity, and therefore should be prioritized for conservation efforts. Because this region is poorly sampled for most groups, except in a few key areas, representative, quantitative sampling for different faunal groups (e.g. megafauna, macrofauna, meiofauna, microbes) is urgently called for in areas where these data are completely lacking. Topographic features (e.g. canyons, seamounts) should also be targeted given that these areas are likely to support relatively distinct faunas. Ideally, studies of different groups should be undertaken collaboratively, so that it may be possible to test whether groups such as macrofauna and meiofauna are similar in diversity pattern; evidence from the ocean basins suggests possible conflicting patterns among groups (Snelgrove and Smith, 2002), but comparisons are difficult because collaborative studies that examine different size groups from the same location are extremely rare.

4.2. Abyssal plains patterns
Although the abyssal basins occur at more or less the same latitude, there are significant differences in surface productivity between the eastern and western basins. In the Western
Mediterranean seasonal changes occur with maximum (mesotrophic) production of about 400 mgC m\(^{-2}\) d\(^{-1}\) (Morel and André, 1991) in May. In contrast, the Eastern Mediterranean is oligotrophic with a maximum surface production in offshore areas of about 60 mgC m\(^{-2}\) d\(^{-1}\) (Danovaro et al., 1999) leading to a much lower flux of organic matter to the seabed in the two regions (Kerhervé et al., 1999). There are distinct differences therefore in the quantity and quality of organic matter deposited on the seabed which will have important biological consequences. In addition, recent observations reported elsewhere in this volume highlight that, as in the major oceans (Smith and Druffel, 1998; Billett et al., 2001), there are long-term radical changes in the deep-sea fauna, which may be related to variation in hydrography and organic matter flux.

The Mediterranean deep-sea clearly offers a variety of different and unique environmental settings in a continuum that stretches longitudinally from 4° to 36°W. Yet, as emphasized in section 3, little scientific use has been made of these different settings, and we face a striking lack of information on species richness and community structure. The apparent low diversity of the deep Mediterranean Sea has not encouraged sampling. A concerted effort, therefore, is needed in relation to the major gradients (environmental, geological and historical) and would yield rich rewards. Such a programme should focus on all size classes from bacteria to fish, with the greatest effort on the smaller size fractions. It should also use molecular and morphological techniques. The former would be especially useful in the study of small size fractions and for studying speciation in relation to the environmental and physical gradients.

With reference to the location of the abyssal basins in the Mediterranean (see Fig. 1) the following questions should be addressed:

1) What changes occur in species richness, species dominance and community structure between the Algero-Provencal, Tyrrenian, Ionian and Levantine Basins?
2) How do these patterns differ between taxa, size classes (micro-, meio-, macro- and mega-fauna) and functional groups?
3) How do these patterns differ in relation to reproductive strategies of the fauna?
4) What is the level of endemism within each basin?

In terms of pattern it is particularly important to characterise regional biodiversity, within each basin, in the Western and Eastern Mediterranean, and in the whole Mediterranean in comparison with the Atlantic Ocean, particularly abyssal plain regions in close proximity to the Strait of Gibraltar.

4.3. Deep-sea zooplankton

If we have some knowledge about the vertical distribution of the mesozooplankton main taxa in various basins, there is a dearth of information on temporal changes. The information on microzooplankton including protozoans is very sparse in the Western and Eastern Mediterranean (see Tanaka and Rassoulzadegan, 2002) and the same holds true for gelatinous organisms. Quantitative information available for the latter group is from mesopelagic depths in the western part of the Sea, only. To gain better insights into the distribution and dynamics of the deep-sea zooplankton, the temporal and spatial distribution of different size classes of zooplankton from protozoa over micro-, meso- and macrozooplankton to micronekton and gelatinous organisms must be investigated. The sampling design should cover diurnal to decadal time scales to detect daily and ontogenetic migrations as well as changes associated with global change. The spatial resolution should cover the full-depth vertical distribution in different basins. These investigations will help to define key species for process studies.

Zooplankton sampling should be combined with investigations of the benthos. Information on the abundance, composition and ecological role of the near bottom fauna as a linking element between the plankton and the benthos (pelago-benthic and bentho-pelagic coupling) should be gained. Moreover, fine-mesh samples in the near-bottom environment are needed to investigate the dispersal of benthic larvae.
Fig. 1. General bathymetry of the Mediterranean Sea (adapted from GEBCO data).
4.4. Canyons
Several submarine canyons cross the continental slope of the Western and Central Mediterranean (Reyss, 1971). These submarine features are viewed as hotspots of species diversity and endemism (Gili et al., 1998, 1999), likely to play an important role on structuring the populations and life cycles of the planktonic fauna (Macquart-Moulin and Patriti, 1993, 1996; Gili et al., 2000) and benthic megafauna fishery resources dwelling on their influence (Cartes et al., 1994; Sardà et al., 1994a,b; Stefanescu et al., 1994). Faunal density and biomass are usually higher inside the canyons when compared to similar depths in the surrounding habitat, but individual size is significantly smaller than on the adjacent open slope. Although information relating submarine canyons and biological aspects of the fauna is still very scarce, morphologic and oceanographic features of the canyons are understood to be the main factors of this linkage (Gardner, 1989; Vetter and Dayton, 1998).

4.5. Extreme environments
4.5.1. Cold seeps
Extensive exploration and characterization of these communities along geological structures which can be located by multibeam echosounding and other geophysical tools have yet to be initiated. Due to their spatial patterns, the distribution and characteristics of these highly fragmented habitats could be only assessed using large facilities, including oceanographic vessels and manned or remotely operated deep-sea vehicles in a framework of an interdisciplinary approach (geophysics, geochemistry, biology and microbiology). A large section of the bottom mapping has been published and provides a very important base for upcoming benthic exploration (see section 2 above).

The isolation of the Mediterranean seeps and vent habitats from the Atlantic Ocean after the Messinian crisis led to the development of unique communities, which are likely different in composition and structure from those in the Atlantic Ocean. For example, the bivalve mollusc populations found in Mediterranean cold seeps are very specific, with species much smaller in size than those from other seep sites. The use of modern molecular markers, as well as more classical taxonomy, would lead to a better understanding of the origin and evolution of these communities (e.g. their relationship to shallow water sulfuretum organisms and/or to cold seep communities in the Atlantic Ocean).

Once the major spatial patterns in community structure are established, the food web structure should be described using enzymatic and isotopic methods, as well as “in situ simulated” techniques, aboard research vessels. Bacterial symbioses and consortia which form the base of chemo-autotrophic functioning can be described using both ultrastructural methods, as well as molecular markers. The relationship between the microdistribution of biota and fluid patterns can be examined using in situ analysis, microsensors, flow meters, and water sampling associated to optical imagery. The Mediterranean Sea provides a unique opportunity to understand the relative roles of temperature and pressure in adaptive ecophysiology, particularly for organisms inhabiting high sulfide environments.

4.5.2. Brine pools
A number of DHABs isolates and individual DNA clones from the metagenomic expression libraries have been selected as candidates for potential biotechnological applications. All the organisms from those samples were derived from enrichment cultures set under the conditions simulating the DHAB environments (temperature, chemical composition etc.) except for the pressure. Therefore apparent baro/piezophilic organisms cannot be uncovered with that cultivation strategy. The lack of isolates belonging to the new taxonomic groups that were described by means of culture independent methods could support the hypothesis of their pressure dependence. Almost no attempts have been made to detect the possible presence of fungi and viruses and to study their influence on the microbial population dynamics in the DHABs.
5. DEEP-SEA SAMPLING METHODS AND EMERGING TECHNOLOGIES

Our capacity to quantify biodiversity in deep-sea environments is most severely constrained by the sheer size and remoteness of the habitat, the cost of sample collection and processing, and a shortage of qualified taxonomists. If, for the most part, the technologies necessary to sample deep-sea organisms for diversity studies have been developed, there are recognized deficiencies with any single approach. Moreover, a given sampling approach usually targets specific size groupings of organisms, integrates over specific spatial and temporal scales, and typically underestimates certain taxa because of behavioural response or physical disturbance of individuals. Deep-sea ecologists are aware of these shortcomings and try to minimise their effect, recognizing the limitations of their samples.

For megafaunal organisms, various types of trawls and nets can provide quantitative, though not absolute, estimates of species abundance. Submersibles (e.g. Uzmann et al., 1977) and towed still and video camera systems (e.g. Russel et al., 1986) have been used for ground truthing. These approaches are particularly useful in rugged or fragile habitats where trawling is not possible (e.g. Kreiger et al., 2000). Imaging quality is constantly improving and facilitating identification, and the advent of digital imagery has allowed quantification at mm scales. However, still and video camera images are limited in that they do not provide voucher specimens. For this reason, combining trawl efforts with photography, video, or sampling by submersible provides the most accurate measurements of diversity and abundance.

A variety of approaches have been developed for sampling organisms associated with bottom sediments. The first semi-quantitative sampling of deep-sea macrofaunal benthos was the epibenthic sled (Hessler and Sanders, 1967) which is dragged through the surficial sediment on the seafloor. Although epibenthic sleds are known to significantly undersample sedimentary fauna, they are still used to sample small hyperbenthos – the organisms that live just above the seafloor (e.g. Mees and Jones, 1997). Alternative quantitative approaches for sampling hyperbenthos include novel applications of moored plankton pumps (e.g. Garland et al., 2002) and video plankton recorders (e.g. Davis et al., 1992) that can provide quantitative time series data in situ. Interestingly, in deep-sea systems there is still a constraint that sampling volume may be a limiting factor for some organisms because concentrations (e.g. meroplankton of some taxa) may be too low to be effectively sampled by current versions of these instruments.

For sedimentary macrofauna, box corers have been a standard quantitative sampler since their development in the early 1970s (Hessler and Jumars, 1974). Nonetheless box corers create a bow wave that can disperse meiofauna and light surficial sediments, resulting in underestimates of meiofauna and lost “fluff” layer from the sediment-water interface. A multiple corer that is engineered to enter the sediment slowly and produce no bow wave was therefore developed to resolve this problem (Barnett et al., 1984). Very recent comparisons of macrofaunal samples collected with box corers and multiple corers reveal the alarming finding that box corers may underestimate macrofauna in several instances (Horton et al., 2003). A large multiple corer (megacorer) may represent the next generation of sediment sampler. A distinct disadvantage with all such samplers is that samples are collected blindly, and the immediate neighbouring spatial environment is not known. In mixed environments or areas with rough topography, sampling with bulky and not highly targeted equipment may be particularly difficult. One solution is to combine a corer or grab with a video system (e.g. Mortensen et al., 2000). Another approach is to use submersibles or remotely operated vehicles (ROVs) equipped with manipulators to push small box corers or tube corers into the sediment (e.g. Grassle and Morse-Porteous, 1987). The limitation of this latter approach is the relatively small number of samples that can be collected, and the high cost of submersibles and ROVs.

For hard substrate environments ranging from bedrock to mixed gravel, towed video and photographs from submersibles (e.g. Grassle, 1985) or remotely operated vehicles (e.g. Sarrazin et al., 1999) are effective for megafauna, whereas grab and suction samplers offer a mechanism for
obtaining voucher specimens and sampling smaller organisms (e.g. Tsurumi and Tunnicliffe, 2001). Whereas video and still imagery can provide quantitative descriptors of biodiversity, grab and suction samples have been strictly qualitative. As with sedimentary habitats, plankton pumps and video plankton recorders can be utilized to quantify the hyperbenthos on hard substrates.

Process studies that aim to address regulation of biodiversity often require different types of approaches that are not adequately represented in the brief “snapshots” provided by trawl or video transects from discrete cruises. Bottom time-lapse camera (e.g. Lampitt and Burnham, 1983) and lander vehicles (e.g. Smith et al., 2001) that remain in situ for extended periods can provide key data on variables such as particle flux and respiration. However, except for megafauna that can be enumerated by in situ cameras, a physical sample for faunal analysis is still required. At present, a ship or submersible/ROV is required to accomplish that task. Continuous access to shallow-water ecosystems has been achieved with the development of ocean observatories, fixed stations that are linked to shore by a fiber optic cable which provides power to sensors and transmits data to land (e.g. Van Alt et al., 1997). Based on the same concept, project NEPTUNE, currently underway in the Northeast Pacific (www.neptune.washington.edu), will run a network of 3,000 kilometers of fiber optic cables throughout the Juan de Fuca plate at depths up to ~3,000 m, and instrument multiple areas with suites of sensors. This approach will provide two-way interactive sampling and has significant potential to advance our understanding of deep-sea diversity regulation and the role of biodiversity in ecosystem function.

One other area where new technologies have the capacity to accelerate efforts to map abundance patterns of fishes is the use of acoustics. Acoustics is being used increasingly in fisheries stock assessments and has the advantage of covering large swaths of relatively deep sea-bottom while enumerating individual fishes (e.g. Boyer et al., 2001). The main drawbacks of this approach are very poor taxonomic resolution and significant underestimates of abundances of fishes living above rugged topography (e.g. Starr et al., 1996).

The issue of taxonomy remains one of the great challenges in assessment of deep-sea diversity. The development of molecular techniques has greatly improved our capacity to resolve taxonomic patterns in difficult groups such as microbes (e.g. Lopez-Garcia et al., 2003), and population structure in metazoans (e.g. France, 1994), as well as biogeographic relationships (e.g. Baco et al., 1999). The pairing of morphological taxonomists with molecular biologists is the most effective means of moving forward in taxonomy of deep-sea organisms and ultimately improved understanding of patterns and regulation of biodiversity in deep-sea ecosystems.

6. PROCESSES – PRIORITY STUDIES

6.1. Slope environments – Process studies

Deep-sea continental slope studies in the Mediterranean should focus on several key areas. Description of bathyal patterns of diversity (see section 4.1 above) should be complemented by process-oriented studies that address why patterns of diversity exist and what factors are responsible for these patterns.

Patterns of diversity and why they exist

The Mediterranean offers an ideal environment in which to test the role of seabed heterogeneity, both in terms of morphological features such as canyons and slump areas, as well as biological features such as feeding disturbances and patches of organic matter. This question requires combined observational efforts and experimental approaches, where effects of disturbance and organic input are manipulated at small scales in order to infer how broad-scale variation in disturbance and organic input regimes influence maintenance of biodiversity pattern. Particularly for experimental work, the Mediterranean has a tremendous advantage over most deep-sea settings; the proximity of research laboratories and scientific expertise to slope environments facilitates repeat visits to recover experiments and resample areas to a degree that has never been achieved elsewhere.
The relatively small scale of the Mediterranean in comparison with ocean basins also facilitates comparison of local versus regional diversity and rates at which species turn over spatially. This question is wide open for all deep-sea systems, but is more tractable in the Mediterranean than elsewhere because of the proximity of environments. Specific questions include: How do slope species compare between the Eastern and Western Mediterranean, and how does this relate to organic input? Do rates of species turnover change with depth in contrasting these regions? Can experimental manipulation of organic input alter species composition to make local compositions similar among regions? Does the comparatively warm Mediterranean deep sea influence rates of species change with depth, since the temperature variable is significantly reduced in importance? Are there physiological differences in the temperature tolerances of species inside and outside the Mediterranean, and can this explain diversity patterns? Does this relationship affect affinities of different depth slope communities with Atlantic fauna?

**Biogeographic links to the Atlantic**

An obvious question regarding geographic patterns in Mediterranean slope communities is the degree to which they are “self-seeding” or dependent upon colonizers supplied from the Atlantic, and whether the degree to which this happens is depth-dependent. This work feeds in directly to abyssal communities (see below). A two-pronged approach is warranted. First, molecular studies could help address the distinctness of Mediterranean organisms. A more complex, but intriguing approach, would be to look at flux of reproductive propagules through the Strait of Gibraltar. How does self-seeding vary from one taxonomic group to the next, particularly as a function of reproductive mode?

**Time series**

The deep sea is perhaps the most deficient marine environment in terms of time series data to evaluate role of processes that change on seasonal or decadal basis. The use of cabled observatories in shallow water areas (e.g. LEO-15; www.marine.rutgers.edu/mrs/) is now being extended into the deep sea through international collaboration (www.Neptunecanada.ca, www.neptune.washington.edu), and a similar approach in the Mediterranean could help to address how seasonal flux of organic and inorganic material to slope environments influences patterns of diversity. Long-term changes, such as those caused by climate change or changes in land use practices (e.g. hydrology changes) would also benefit from this type of approach. The importance of long-term time series data is becoming increasingly apparent in all ecosystems as human footprints expand, and the deep sea is no exception (see CIESM Workshop n°22, 2003). Such data could also address the sensitivity of slope systems to human perturbations, either land-based or related to seagoing activities. Although a cabled observatory would provide the most temporally comprehensive data set to address these questions, the proximity of slope environments to multiple marine laboratories does suggest the alternative approach of establishing long-term monitoring stations that could be visited on at least a yearly basis.

**Biodiversity and ecosystem function**

Slope environments receive higher levels of organic input than abyssal regions, and may therefore play a more critical role in remineralization or organic matter. Natural patterns in diversity within the Mediterranean could be utilized to conduct experimental studies that examine the effects of diversity on rates of carbon metabolism and nutrient efflux from sediments.

**Historical issues**

The unusual geological history of the Mediterranean also offers opportunities to utilize paleo-oceanographic records to enhance our understanding of modern distribution patterns. Taxa particularly well preserved in geological records (e.g. Ostracoda, Foraminifera, Mollusca) could be particularly enlightening.

**6.2. Abyssal plains – process studies**

Once the basic patterns of species richness, dominance, endemism and community structure are known in relation to environmental gradients, then more specific sampling and experimental...
programmes can be formulated to study critical processes, such as downslope migration and speciation processes; whether the reduced diversity of the Mediterranean Sea has an effect on ecosystem functioning; or whether the Mediterranean Sea is more vulnerable to anthropogenic and catastrophic (e.g. turbidite) impacts because of its reduced biodiversity?

A way forward is to develop Mediterranean deep sea biodiversity research within the framework of the Census of Marine Life (CoML) international research programme. This project has a specific field programme to compare species richness, species distributions, dominance and community structure in major abyssal basins in all the World’s oceans. A CoML workshop was held recently to coordinate research in all deep-sea sediment environments. Its report (Horton, Wigham and Billett, in prep.) will be made available on: www.coml.org. Mediterranean researchers could contribute unique data to this programme, thus allowing to compare the diversity of the Mediterranean region with the major Atlantic abyssal plains.

6.3. Zooplankton

The role of deep-sea zooplankton within the ecosystem should be assessed by determining the synecological significance of functional groups and key species for remineralisation processes. Energetic and somatic material fluxes have to be determined to estimate the role of these faunal elements in biogeochemical cycles. Remineralisation processes are difficult to observe and quantify, and they remain poorly characterized throughout the entire water column. The depth dependence of nutrient remineralisation and of the controlling factors are important features of biogeochemical cycles. The character of organic and inorganic material transported to the deep-sea reflects the ecological structure in the upper ocean and influences the remineralisation rate. Furthermore, the sensitivity of the deep pelagic community to climate change has to be investigated to predict changes in remineralisation at depth and feedback mechanisms to the surface. To obtain such data, needed for individual-based models and in oceanic and global material flux budgets, in situ measurements and observations and experiments under in situ conditions are necessary.

6.4. Canyons

The deep-sea grounds of the western and central basins of the Mediterranean exhibit several submarine canyons of varying size that may form an important link between the coastal zone and the deep sea zone. These canyons may act as conduits of coastal detritus (organic and inorganic) to the deep-sea grounds (Gardner, 1989). However, geological and biological processes related to canyons remain largely unstudied and consequently poorly understood. Enhanced productivity (Macquart-Moulin and Patriti, 1996; Vetter and Dayton, 1998) and the local currents related to canyons may play a role in larval drift and juvenile recruitment because of the relationship between canyons and the formation of intermediate nepheloid layers (Company and Sardà, 1997; Puig et al., 2001).

6.5. Extreme environments

6.5.1. Cold seeps

In these extreme environments, some of the most interesting processes occur at the organismal level. For example, molecular, enzymatic, and physiological adaptations can be expected in relation to the low oxygen concentration and the possibly toxic levels of compounds such as H2S, CH4 and trace metals in the seeping fluid, and to the extremely high salinity of the fluids in brine pools. Since the communities in these habitats are most likely chemosynthetically fueled, the understanding of chemosynthetic metabolic pathways in the microbes, and of microbe-metazoan interactions, is imperative. In cases of symbiosis, modifications in the metabolic pathways of the metazoans are most likely present. The co-evolution of the host-symbiont complex has probably resulted in efficient mechanisms of nutrient uptake and delivery by the host to the symbiont, and of carbohydrate reduction and distribution from the symbiont to the host. Trophic strategies other
than symbiosis, such as grazing, detritivory and suspension feeding, will also be present, perhaps adapted to the source, density and availability of particulates on the substratum and in the water column.

Interestingly the structure and function of populations in these chemosynthetic environments are strongly influenced by fluid-fauna interactions. Spatial and temporal patterns in the distribution of metazoan species are directly related to the spatial pattern and temporal fluctuations in fluid flux (e.g. Juniper and Sibuet, 1997). However, faunal individual growth and population proliferation can alter (or even inhibit) the direction and rates of fluid flux, thus deteriorating access to their required source of nutrition.

Trophic structure, carbon and material flows are particularly interesting in these extreme environments. While most of the carbon that flows through the ecosystem originates chemosynthetically, photosynthetically-derived carbon also enters in the form of sinking particulates, such as phytodetritus, marine snow, fecal pellets, as well as dead plankton and fish. The relative importance of the two sources of carbon in these systems is not understood and should be investigated.

Chemosynthetic environments, such as cold seeps and brine pools, are patchily distributed on the ocean floor and can be separated by distances of hundreds to thousands of kilometers (Sibuet and Olu, 1998). Additionally, most organisms that inhabit these environments are highly endemic and sessile (Sibuet and Olu, 1998). Thus the processes of larval dispersal, colonization and recruitment on which little is known (Young, 2003), are of particular interest in these habitats. Most likely the larval life history stage lasts for periods of weeks to months, and dispersal occurs along the direction of the dominant flow, since most metazoan larvae are weak swimmers. It is possible that other chemosynthetic environments, such as wood and whale falls, are used as stepping-stone habitats to extend the dispersal range of these larvae (Smith et al., 1989, Sibuet and Olu, 1998; Smith and Baco, 1998; Distel et al., 2000). Molecular markers are extremely useful tools in determining range of dispersal through patterns in relatedness (e.g. Vrijenhoek, 1997). The processes of invertebrate colonization and recruitment, and of vertebrate migration have not been studied in these systems to date. Understanding their importance will allow a better assessment of connectivity among these chemosynthetic, extreme environments.

6.5.2. Brine pools

Very little is known concerning the biological changes that characterise the DHABs. Different hypotheses have been made about the origin of the bacteria inhabiting the Basins that could (i) sink with the particulate matter through the upperlying water column, accumulate first at the interface, and then continue a slow flowing through the brine layers; (ii) precipitate during landslide of the DHABs surrounding oxygenated sediments; (iii) descend from populations that became trapped in salt when the evaporites formed (Hübner, 2002; McGenity et al., 2000).

The DHABs are undersampled with respect to bacterial functional diversity so that, in spite of the evidence for diagenetic production of several elements (e.g. sulphur, iodine, phosphate) (Henneke et al., 1997; Hübner, 2002; Luther et al., 1990; Ullman et al., 1990), nothing is known about the bacterial intervention in the DHABs biogeochemical cycles. The bacterial phylogenetic diversity of four DHABs was investigated by means of 16S rDNA based analyses and the results suggested the presence of novel Bacteria and Archaea thriving under extreme environmental conditions. Interestingly, some correspondence with similar environments (Orca and Cariaco basins in the Gulf of Mexico; Shaban and Kebrit basins in the Red Sea) has been found concerning several eubacterial taxa, mainly members of the g, d, and e subdivisions of the Proteobacteria, and archaeal sequences falling into the marine groups of the Crenarchaeota and Euryarchaeota. Compared to the other hypersaline anoxic basins, the DHABs and therefore the Urania Basin harbour a much higher diversity of unknown sequences, most of which belonging to new candidate divisions.
Up to date, neither representatives of the novel detected bacterial taxa nor the majority of deeply branching \textit{e-Proteobacteria}, and the marine groups of the two above-mentioned archaeal kingdoms have ever been obtained in culture. Therefore their metabolic features and their role within their natural source ecosystems are still unknown. Evidence of the active role of some novel Bacterial and Archaeal taxa (e.g. KB1-related clones, similar to those obtained from the Kebrit Deep basin) natural microbial populations has been obtained by preliminary RT-PCR based analyses of the whole community 16S rRNA at the interface of the Urania Basin. The presence of prokaryotic activities in all the sampled layers (interface and brines) of the four DHABs has been detected by measurement of functional hydrolytic ectoenzymes activities, bacterial biomass production and $^{14}$C-glutamic acid assimilation and respiration rates.

7. ARE DEEP-SEA RESOURCES SUSTAINABLE?

At a time when the Mediterranean Sea is confronted to unprecedented, cumulative “assaults” ranging from global climatic change to oil drilling, from overfishing to massive pollution, it is no longer possible to simply brush off the question.

7.1. Hydrological change

Changes in surface water hydrology will also affect intermediate and deep-water masses on decadal to centennial scales. Because it is a sensitive ecosystem (Turley, 1999), hosting a deepsea fauna well adapted to live under a combination of high pressure, high temperature and high salinity (see Scotto di Carlo \textit{et al.}, 1984), the Mediterranean Sea is particularly worth monitoring to detect early warning signals of change. Hydrological data collected in past decades from the surface down to the greatest depths in many areas, plus several one-year time series collected since 1999 (as deep as 3,400 m) in the Tyrrhenian and the Ionian sub-basins, point with few exceptions to a continuous increase in both temperature and salinity. Whether this is a long-term trend, whether it reflects climatic changes at a Mediterranean scale (see Bethoux \textit{et al.}, 1999), at a global scale via the influx of Atlantic water at Gibraltar (C. Millot, pers. com.), or is driven more directly by man through changes in the water budget following river diversions and damming in Mediterranean riparian countries (Bryden \textit{et al.}, 1994), are open questions. The new Hydrological Programme launched by CIESM will hopefully cast light on this issue, through a grid of autonomous CTD stations deployed in key areas of the Mediterranean Sea – straits, channels, zones of dense water formation, deeper areas (see CIESM Workshop n°12, 2002 and http://www.ciesm.org/ people/task2.html).

7.2. Pollution

Massive urban development, industrialization and touristic development on its shores, fast-growing maritime transport, plus oil, mineral and gas exploration in its deeper areas, all seriously threaten the quality of Mediterranean waters. Many international Agreements – notably the 1978 Barcelona Convention – Protocols and Action programmes aim to regulate the management of Mediterranean pollution. Yet deep-sea environments are not included into the available legislation, despite evidence (see Fig 2; and Galil \textit{et al.}, 1995) that litter can reach the Mediterranean seabed at great depths. In general, the impact of new types of contaminants – primarily persistent, hydrophobic compounds that are nonvolatile, relatively insoluble, and resistant to biodegradation – on the deep sea ecosystem remains unknown.

Developing oil and gas exploration in the deep waters off the southeastern Mediterranean coast is a cause of further concern. Unfortunately no information is actually available on the natural oil biodegradation mechanisms active at the deep-sea layers as was highlighted during the recent, dramatic heavy-fuel oil spill caused in 2001 by the \textit{Prestige} accident off Galicia.

Exploration and production activities place stresses upon the offshore ecosystems: gas production platforms are point sources of chronic contamination and disturbance. Drilling discharges are composed of cuttings and drilling fluids. The large cuttings descend directly to the bottom,
where in areas of relatively low current speed, piles of up to 30 m in diameter and 1 m in height have been observed (Zingula and Larsen, 1977). The effects of drilling discharges on the benthic biota can be profound. The biota in the immediate vicinity of the operation is smothered by the rapid accumulation of the cuttings. Those mounds of cuttings alter the local physical environment. The cuttings may be later colonized by a variety of organisms, many of which are capable of living only on hard substrates and therefore are not naturally present in the area.

Deep-sea tailings placement of mines located close to the coast is now one of several options available for disposing of mine wastes. While there is yet no generally accepted definition for deep-sea tailings placement, several proposals have been made for placing such tailings at depths below the upper mixed layer or upwelling zone. There is an urgent need to develop improved or additional evaluation and monitoring techniques to assess and demonstrate conclusively where and when this form of tailings placement is environmentally safe, where it is the preferred and lowest risk option, and where and when it is not acceptable.

Among the minerals of economic interest, the occurrence of metaliferous oxides and metaliferous sulfides in the deep ocean has long been known. Thus manganese nodules were collected by the HMS *Challenger* in 1872 and their untapped potential has generated grandiose plans ever since. Yet deep ocean mining of these minerals is still in its infancy. Polymetallic sulfide deposits are produced by seawater circulation through the hot volcanic rocks which well up along spreading ridges of the oceans and back-arc basins. Upon coming in contact with cooler water, the minerals precipitate, producing mineral deposits of zinc, copper, lead, barium, silver, and gold in widely varying proportions in sulfides and oxides. Some deposits in heavily sedimented environments appear to contain several millions of tons of ore, which compare well with some of the largest massive sulfide deposits that are being mined on land. Except for the Atlantis II Deep in the Red Sea, none of the deposits have been surveyed and sampled sufficiently to determine their

Fig. 2. Solid waste collected from a trawl conducted at 2,200 m deep off the Peloponese, Greece, during the DESEAS campaign (2001).
grade and tonnage. Deposits are known from about one hundred locations in the Pacific, two in the Atlantic, one in the Mediterranean, one in the Indian Ocean, and in several “deeps” of the Red Sea. Today there are many specialists who believe that polymetallic sulphides will be extracted from the sea before mining of ferromanganese crusts and nodules takes place. While the resource is plenty, unfavorable metal prices plus problems linked to recovery, processing and environmental concerns make it unlikely that exploitation will begin soon.

7.3. Fisheries
Most living marine resources are exploited on the continental margins at depths less than 400 m, but recently deep-sea fisheries have been developed all over the world. Traditional trawl and longline fisheries capable of reaching depths down to nearly 1,000 m have been operating in the Mediterranean Sea for many years, mainly in the western basin. These fisheries target shrimps as well as hake and sharks. In this context, the development of a deep-water fishery in terms of sustainability is a legitimate, major concern. The key questions are how deep-sea fisheries exploitation may affect the deep-sea grounds and whether Mediterranean deep-sea resources can sustain a commercial exploitation. The answers to these questions well extend beyond the biological realm.

Some Mediterranean deep-sea species may attain, at present, high biomass levels between 1,000 and 1,400 m depth, making attractive as resources to fishermen. Indeed construction of trawlers capable of working depths below 1,000 m is now getting under way. Based on limited available knowledge, it appears that the deep-sea bed is inhabited by generally slow-growing species that are less dependent on the production pulses that occur closer to the surface. Such species tend to be more specialised feeders, partly because of their morphological and functional adaptations to great depth, low light levels, and low food availability. Their populations will typically have lower densities. As these environments are subjected to more constant conditions than the coastal environment, they are presumably more vulnerable to (i.e., less able to recover from) exploitation and other anthropogenic disturbances.

8. SELECTED KEY RESEARCH QUESTIONS
By way of conclusion the following, clearly non exhaustive, list of key research questions or issues is suggested:
• How do faunal dominance and diversity vary as a function of depth across different regions of the Mediterranean?
• What is the rate of spatial turnover of species, and how does this vary with habitat heterogeneity? Does reproductive strategy within groups influence biogeographic turnover rate?
• Is nanism – the size differential of conspecific Atlantic and Mediterranean deep sea biota – a general rule?
• Do some areas of the Mediterranean represent “hotspots” of diversity that should merit some degree of protection from human-related disturbance? How do natural forms of disturbance, such as seasonal pulsing of food or predator feeding, influence these patterns? Can this input explain between-basin differences in pattern, as well as depth-related differences?
• Is high endemism a general pattern in the Mediterranean deep sea? To what extent is recruitment local? How do Atlantic, Mediterranean abyssal and slope communities influence one another in this respect? Do some regions serve as sources and others as sinks? What are the sources of reproductive propagules?
• Can the geological record of past events in the Mediterranean tell us how patterns have changed in the past, and thus how they are currently regulated, and how global climate change and other perturbations may affect these environments in the future?
• What sampling protocols/strategies are required to ensure quantitative collection of biological data (spatial and temporal scales)?
• How is deep-sea ecology impacted overall by surface conditions?
• What are material and process links between chemosynthetic ecosystems and the surrounding deep-sea?
• What is the connectivity among individual chemosynthetic habitats?
• Does pressure affect contaminant toxicity to deep-sea organisms (Are deep-sea organisms any more/less sensitive to contaminants than surface water organisms)?
• What is the bioavailability/toxicity of dissolved and particulate materials to deep-sea organisms?