Part 1

The Mediterranean deep-sea ecosystems
An overview of their diversity, structure, functioning and anthropogenic impacts

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1. Introduction

Once considered as lifeless domains, deep-sea habitats are at present, from a biodiversity viewpoint, considered exceptional ecosystems that harbour singular trophic webs. This perspective has arisen from pioneering research carried out in Earth's major oceanic areas, particularly the Pacific and the Atlantic, since the mid 19th and during the 20th centuries. A major landmark was the discovery in 1977 in the eastern Pacific of ecosystems based entirely on chemosynthetic* primary production, linked to deep-sea hydrothermal vents* (Corliss *et al.*, 1979). Moreover, deep-sea ecosystems are now the ultimate target of industrial fisheries worldwide, following the relentless depletion of fish communities on the continental shelves, in a sort of "(over)fishing down the bathymetric range" effect (Merrett and Haedrich, 1997).

The first data on the presence of organisms living in the bathyal* domain was presented by Risso (1816) examining specimens delivered to him by local fishermen in Nice (France), obtained at depths between 600 and 1000 m. Other data collected during the 19th century points to the presence of life at bathyal and abyssal* depths, despite the long-standing extrapolation by Forbes from observations in the Aegean sea in 1841 claiming the existence of an azoic, or lifeless, domain deeper than 600 m (Gage and Tyler, 1991). The first systematic oceanographic expeditions to the deep-sea were the *Challenger* expedition (1872-1876, Gage and Tyler, 1991) and, in the Mediterranean, the *Pola* (1890-1893),

the *Dana* (1908-1910) and *Thor* (1921-1922) expeditions (Bas, 2002).

The Mediterranean contains sea-beds up to 5000 m deep. The maximum depth is 5121 m in the Matapan-Vavilov Deep, off the Southern coast of Greece, with an average depth of 2500 m. The Mediterranean sea harbours most of the same key geomorphologic structures – such as submarine canyons, seamounts, mud volcanoes or deep trenches – that have proven to translate into a distinctive biodiversity makeup in other regions in the world; recent findings have indeed confirmed this (including the presence of chemosynthetic trophic webs). A further unique feature of the Mediterranean is that it harbours one of the few warm deep-sea basins in the world, where temperatures remain largely uniform at around 12.5-14.5ºC at all depths, with high salinity (38.4-39.0 PSU) and high oxygen levels (4.5-5.0 ml l^{-1}; Miller *et al.*, 1970; Hopkins, 1985). The constant temperature and salinity regime of the Mediterranean contrasts with the Atlantic at comparable latitudes, where temperature decreases and salinity increases with depth. Another important issue is the relative isolation of deep-sea communities, not only with respect to those of the Atlantic (the maximum depth of the sill of Gibraltar is *ca.* 300 m), but also between those in the Eastern and Western Mediterranean, separated by the shallow Sicily Channel (*ca.* 400 m, fig. 1). All these features reinforce the potential for unique deep-sea communities in the Mediterranean, and the importance of precautionary action to limit the impact of human activities on these fragile habitats.
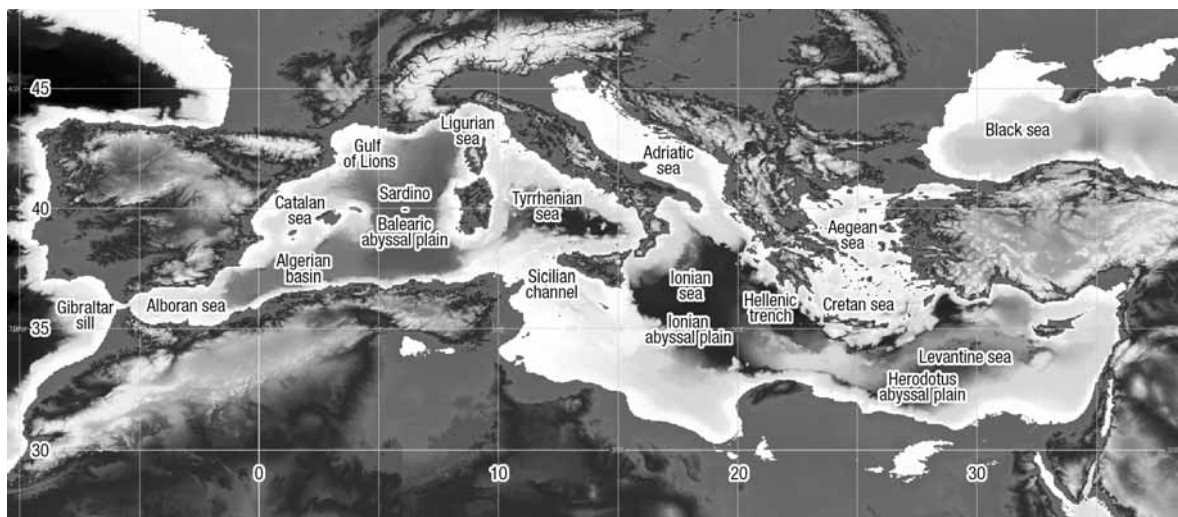

Fig. 1. Geography of the Mediterranean sea.
Credits: International Bathymetric Chart of the Mediterranean, published 1981 by the Head Department of Navigation and Oceanography, St. Petersburg, Russia, on behalf of the International Oceanographic Commission (GEBCO, 2003).
Modified. **See colour plate, p. 57.**

* Key ecological concepts are marked with an asterisk the first time they appear, and defined in the Glossary.

The Eastern and Western Mediterranean display important geological and biological differences. First, the Eastern Mediterranean is geologically more active, because it is a contact zone between 3 major tectonic plates: African, Eurasian and Arabian. For this reason, it features a wide array of interesting cases of unique biocenoses*, such as mud volcanoes, seamounts or cold seeps*. The Western Mediterranean is relatively featureless in comparison, although still not devoid of unique environments. Biologically, the Western Mediterranean, whilst still oligotrophic* by North Atlantic standards, has relatively high primary production, especially in the Gulf of Lions, due to the river Rhone runoff and wind mixing (fig. 2). The Eastern Mediterranean has very low primary production, particularly in the Levantine sea.
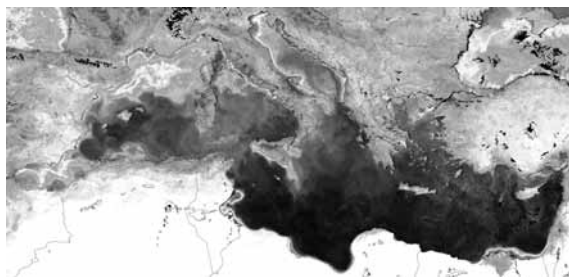

Fig. 2. Chlorophyll *a* map (Monthly composite for Apr. 2000) produced by the Inland and Marine Waters Unit (JRC-EC) using SeaWiFS raw data distributed by NASA-GSFC.
See colour plate, p. 57.

The continental shelves, where most commercial fishing activity is conducted, cover only 30% of the Mediterranean sea surface, while the bathyal domain covers 60% and the abyssal plain the remaining 10% (approx.) (fig. 3). Continental shelves are only extensive near the major river mouths (the Rhone in the Gulf of Lions, the Nile in the Levantine sea), or on the Adriatic and Tunisian coasts. A large part of the Mediterranean coast has deepwater beds very near shore, typically a few hours away by commercial vessel.

Although fishing for continental shelf resources dates back to ancient times, commercial fisheries in the bathyal domain started only in the early decades of the 20th century, and have increased in importance since the 1950's, especially on the Ligurian, Catalan and Balearic coasts (Sardà *et al.,* 2004a). The development of deepwater commercial fisheries was linked, as in other seas, to the development and motorization of trawler vessels. Deep-water fisheries in the Mediterranean target red shrimps (*Aristeus antennatus* and *Aristaeomorpha foliacea*) between 400 and 800 m (sporadically down

to 1000 m.) Beds deeper than 1000 m can be considered virgin from the viewpoint of commercial exploitation of living resources.

Throughout the world, commercial fisheries, based mostly on predatory fish, are suffering serious depletion (Myers and Worm, 2003). Given the state of continental shelf fish resources, the fishing industry is directing more attention towards the potentially exploitable living resources of the deep-sea. Waters deeper than 1000 m cover around 60 % of our planet, and their unique ecosystems have been discovered only recently (since the 1970's). Hydrothermal vents, cold seeps, and cold-water coral reefs can be found in deep waters. Other habitats, such as seamounts (Rogers, 1994; Koslow, 1997; Galil and Zibrowius, 1998) and submarine canyons (Bouillon *et al.,* 2000; Gili *et al.,* 1998; 2000), have been identified as diversity hotspots. Considering their unique features and low turn-over rates, deep-sea ecosystems are highly vulnerable to commercial exploitation (Roberts, 2002). Globally, around 40% of trawling fishing grounds are now on waters deeper than the continental shelf (Roberts, 2002) and many seamount fisheries have been depleted in short periods of time (Lack *et al.,* 2003).
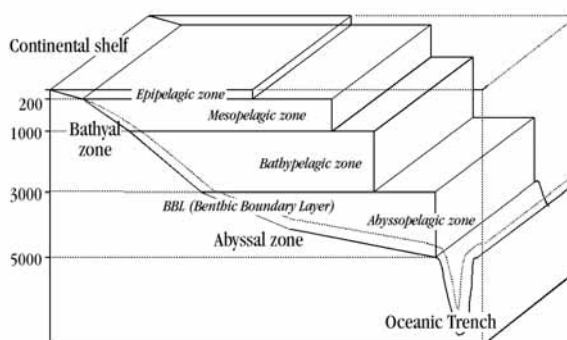

Fig. 3. Schematic representation of the marine depth zones, with emphasis on concepts presented in this document.

2. Deep-sea diversity patterns

2.1. Fauna

2.1.1. Overview

The deep Mediterranean fauna displays a number of characteristics that differentiate it from other deep-sea faunas of the world's oceans (Bouchet and Taviani, 1992): *i)* the high degree of eurybathic* species; *ii)* absence (or low representation) of typical deep-water groups, such as macroscopic foraminifera (Xenophyophora), glass

sponges (Hexactinellida), sea-cucumbers of the order Elasipodida, primitive stalked sea-lilies (Crinoidea) and tunicates (sea-squirts) of the class Sorberacea (Pérès, 1985; Monniot and Monniot, 1990); and *iii)* the number of endemisms (26.6% of species in the Mediterranean fauna: Ruffo, 1998) declines with increasing depth, with comparatively low endemisms below 500 m (see also Fredj and Laubier, 1985). The number of endemisms depends, however, on the taxon and, for instance, among Amphipoda a high percentage (49.2%) of the bathyal species are endemic (Ruffo, 1998), even higher than in coastal zones. In the case of amphipods, the absence of pelagic free larvae (as compared to other peracarid taxa) helps explain this high rate of deep-sea endemisms.

The Mediterranean deep-sea is very 'young' compared to other oceans. During the Messinian (Upper Miocene) the water flow between the Atlantic and the Mediterranean was cut off, as a result of tectonic movements of the European and African plates, precipitating an almost complete drying out of the Mediterranean between 5.7 and 5.4 million years ago (Messinian salinity crisis). The water exchange between the two seas was restored in the Lower Pliocene, giving rise to a Mediterranean sea fauna remarkably similar to that of the Atlantic in the Pliocene and Pleistocene. The current Mediterranean deep-water fauna is less related to the Atlantic bathyal fauna than it was in the Pleistocene (Barrier *et al.,* 1989), due to the lack of Atlantic deep water (and fauna) entering the Mediterranean (Salas, 1996). Bouchet and Taviani (1992) postulated that the impoverishment of the Mediterranean deep-sea fauna is relatively recent (post-glacial Pleistocene), and that the onset of current hydrological conditions in the Holocene led to an almost complete extermination of the richer glacial deep-sea fauna, which was more similar to the present Atlantic fauna, particularly affecting the cold stenohaline* taxa.

Some faunistic groups are poorly represented in the deep Mediterranean compared to the NE Atlantic: fish (Stefanescu *et al.,* 1992), decapod crustaceans (Cartes, 1993), mysids (Cartes and Sorbe, 1995), echinoderms (Tortonese, 1985), and gastropods (Bouchet and Taviani, 1992). Fredj and Laubier (1985) reported that *ca.* 2100 species of benthic* macrofauna* are found deeper than 200 m in the Mediterranean, and only 200 species have been recorded deeper than 2000 m, although the lower sampling effort below 2000 m could certainly bias this result. Bouchet and Taviani (1992) pointed to the paucity of deep Mediterranean benthic macrofauna in terms of abundance, species and endemisms.

Systematic deep-sea samplings have shown that the deep Mediterranean basin (along with the Norwegian and Caribbean basins) harbours impoverished deep Atlantic fish faunas (Haedrich and Merrett, 1988).

Certain areas of the Mediterranean deep-sea are benthic diversity hotspots because they harbour special faunas rich in endemic taxa (see section on unique habitats below). Submarine canyons are also considered as hotspots of species diversity and endemisms (Gili *et al.,* 1998; 2000).

Additionally, a floro-faunistic impoverishment of the Eastern Mediterranean compared with the Western Mediterranean richness in species is accepted (Sarà, 1985), through a gradational decrease from west to east, which is more conspicuous for the deep benthos. The Eastern basin is separated from the Western one by the Siculo-Tunisian sill (*ca.* 400 m), and the Levantine bathyal benthos appears to be composed of autochthonous – self-sustaining populations of eurybathic species that settled after the Messinian event.

2.1.2. Megafauna*

Scientific knowledge of deep megafaunal communities (mainly fish, crustaceans and cephalopods) was limited to the bathymetric range exploited by fishing (down to 800-1000-m) until the early 1980's, when scientific expeditions began quantitatively sampling the bathyal grounds in the Mediterranean.

Based on extensive samplings in the Levantine sea, Klausewitz (1989), Galil and Goren (1994) and Galil and Zibrowius (1998), reported the scarcity of deep-sea fish fauna in the Mediterranean eastern basin, but at the same time revealed the discovery of new and rare taxa. During the 1980's and 1990's, a series of surveys were conducted in the Catalano-Balearic and Algerian Basins, focussing on more ecological aspects (biomass and size-depth distribution, feeding ecology). These samplings were carried out in lower-slope bathyal communities between 1000 and 2300 m in depth, paying special attention to the dominant megafaunal groups, fish (Stefanescu *et al.,* 1992, 1993; Moranta *et al.,* 1998) and decapod crustaceans (Cartes and Sardà, 1992, 1993; Cartes, 1994, 1998b; Maynou and Cartes, 2000; Cartes and Carrassón, 2004).

Standardised comparisons point to clear differences between Mediterranean and Atlantic deep-sea demer-

sal fish fauna (Moranta *et al.,* 2003). Fish population densities are lower in the Mediterranean (fig. 4), a feature that can be related to the much lower availability of organic matter* on the Mediterranean seabed in comparison to the Atlantic, due to the oligotrophic characteristics of the Mediterranean sea (fig. 2). In the same way, Atlantic fish assemblages are composed of a larger number of species than those of the Mediterranean. This might owe to the recent origin of Mediterranean deep-sea fauna, after the Messinian salinity event. Comparing the Eastern and Western Mediterranean basins, the Levantine Sea has a particularly low number of species and low abundance (Stefanescu *et al.,* 1992; Kallianotis *et al.,* 2000), and the assemblage composition is also qualitatively different. For instance, deep-sea sharks (*Centrophorus* spp., *Etmopterus spinax* and *Hexanchus griseus*) are among the most abundant fish species in Levantine bathyal communities.

A characteristic feature of Mediterranean deep-sea megafauna is the numerical importance (in terms of abundance and number of species) of decapod crustaceans which, together with fish, are the dominant taxa in deep Mediterranean assemblages. In the deep Mediterranean, decapod crustaceans are the dominant invertebrate taxon, whilst they are of little importance in biomass in the Bay of Biscay. Additionally, species of tropical or subtropical origin (e.g. *Aristeus antennatus*, *Aristaeomorpha foliacea*, *Acanthephyra eximia*) dominate in deep Mediterranean decapod assemblages (Cartes, 1993).

Suspension feeders* (e.g. hexactinellid sponges, pennatulids) are dominant in terms of invertebrate biomass on the upper and middle slope (to 1400 m) in the Atlantic, whilst echinoderms are important at all depths and dominant on the middle and lower slope (Lampitt *et al.,* 1986). Suspension feeders are of relatively little importance in the Mediterranean, due to its ologotrophic waters, and they are important only locally. Probably due to their low levels of food consumption, crustacean decapods are more important in the deep Mediterranean (an oligotrophic region, Cartes and Sardà, 1992) than in the deep Atlantic, where echinoderms dominate (Billett *et al.,* 2001).

Etmopterus spinax.
Drawing by M. Würtz © Artescienza 1994.
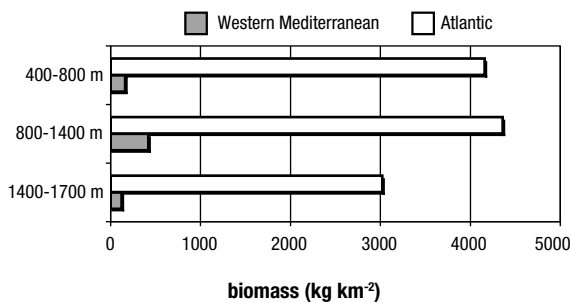**See colour plate, p. 61.**

Fig. 4. Comparison of biomass by depth interval between the Western Mediterranean (Balearic sea) and the Atlantic (Rockall trough), based on Moranta *et al.* (2003).

- **Megafauna abundance and species richness decreases with depth, but there exists a secondary peak of biomass between 1000 and 1500 m.**

- **Dominant megafaunal groups in the deep Mediterranean are fishes and decapod crustaceans**

- **The levels of megafaunal biomass in the deep Mediterranean are 1 order of magnitude lower than in the Atlantic, at comparable depths, due to the low primary production of the Mediterranean sea.**

- **Important differences exist between the eastern and the western Mediterranean, both in species composition and abundance**

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Box 1. Species composition of megafauna in the Western Mediterranean

Otter trawl surveys in the Western Mediterranean carried out between 1988 and 2001 (Stefanescu *et al.,* 1994; Cartes, 1993; Sardà *et al.,* 2004b) provide an accurate picture of the decapod crustacean and fish species composition and biomass distribution with depth.
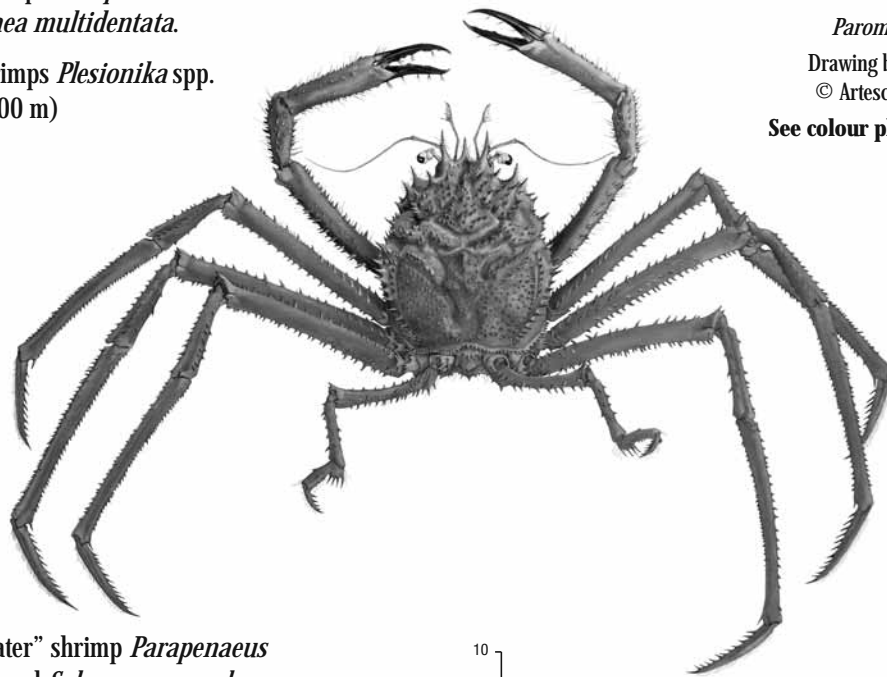
Decapod crustaceans

Seventy species of decapod crustaceans have been reported from 200 to 4000 m. From these, 20 are of commercial interest at present (including some species dwelling predominantly in shallow waters):

- the red shrimps: mainly *Aristeus antennatus*, but locally also *Aristaeomorpha foliacea*.

- other red shrimps: *Acanthephyra eximia* and *Acanthephyra pelagica*.

- the glass shrimps: *Pasiphaea sivado* and *Pasiphaea multidentata*.

- Pandalid shrimps *Plesionika* spp. (down to 1000 m)

Among these species, only 4 reach significant densities (> 0.1 kg/h in the experimental sampling gear) between 1000 and 1600 m depth: *Aristeus antennatus*, *Geryon longipes*, *Acanthephyra eximia* and *Munida tenuimana*. Below 1600 m the total biomass of decapod crustaceans is very low (< 1 kg/h).

The distribution of biomass with depth of decapod crustaceans is shown in the figure below. There is an important increase in biomass from 200 to 400 m, followed by a sharp decrease to 1000 m, where the decapod biomass is practically one tenth of the biomass at the shelf break. A secondary peak of biomass occurs between 1300 and 1500 m, though reaching much lower levels of biomass. The high abundance of *Aristeus antennatus* at around 1500 m is partly responsible for this secondary peak (Sardà *et al.,* 2003b).

Paromola cuvieri.
Drawing by M. Würtz
© Artescienza 1977.
See colour plate, p. 61.

- the "deep water" shrimp *Parapenaeus longirostris* and *Solenocera membranacea* (down to 400 m only)

- the anomuran crabs *Munida* spp.

- the Norway lobster *Nephrops norvegicus* (present down to 700 m only) and the spiny lobster *Palinurus mauritanicus* (400 m only)

- crabs: *Geryon longipes*, *Paromola cuvieri*, *Chaceon mediterraneus*, and *Macropipus tuberculatus* (the latter down to 600 m only).

Relative abundance of decapod crustaceans with depth, elaborated from data from experimental samplings in the western Mediterranean from 1988-2001.

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Fishes

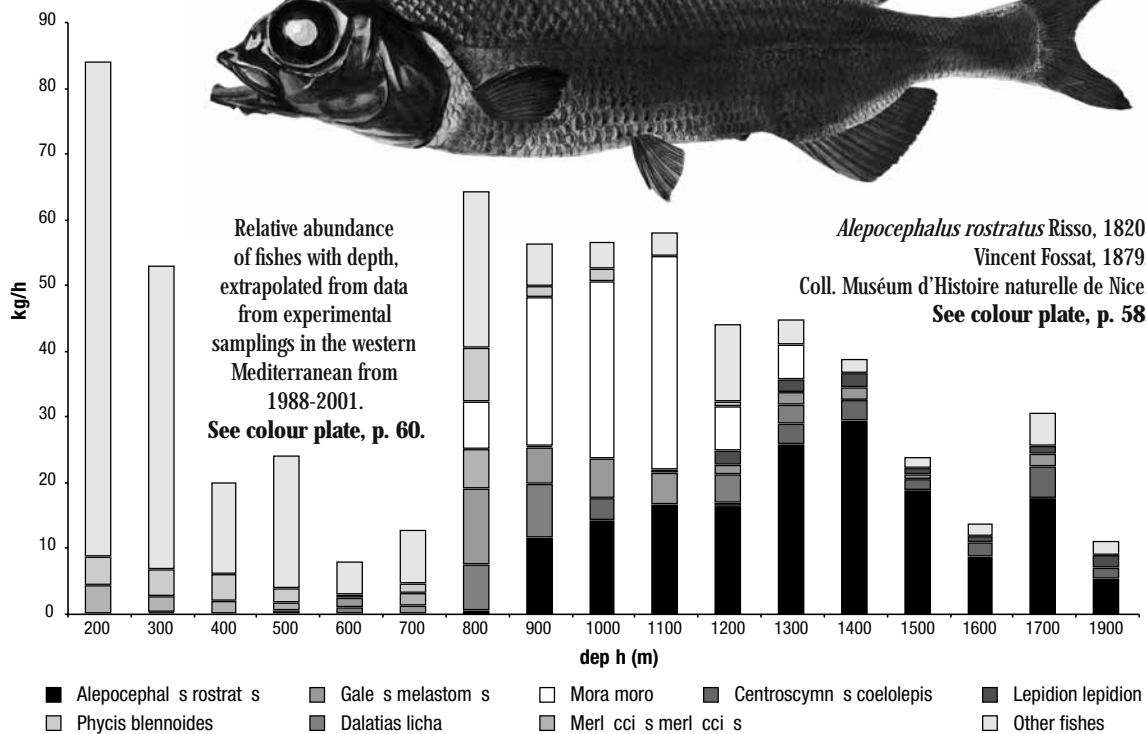The fish assemblage from 200 to 2250 m (Stefanescu et *al.,* 1993; 1994, Moranta *et al.,* 1998) comprises *ca.* 90 species in the western Mediterranean. As shown in the figure below, fish biomass strongly decreases from 200 m to 800 m (i.e. ~10:1). Fishes are very diverse at these depths, and the commercial species are represented by *Merluccius merluccius* and *Phycis blennoides*, among others. From 800 m to 1800 m, important fish biomasses are again present. The dominant species at 800-1100 m are the sharks *Dalatias licha* and *Galeus melastomus*, and the teleostean fishes *Alepocephalus rostratus* and *Mora moro*. The latter are dominant from 900 to 1100 m. From 900 m *A. rostratus* becomes very important, whilst between 1300 and 1700 m it forms more than 70% of the fish biomass (see also table below). It is important to note that while standing biomass stocks are relatively important between 800 and 1500 m, the productivity of fish at these depths is expected to be very low (see Chapter 3).

Stefanescu *et al.* (1992) showed that in the NW Mediterranean, fish size (mean fish weight) decreases for some dominant species with depth between 1000 and 2250 m. This trend is especially significant below 1200 m, due to a faunal shift whereby large or medium-sized species (gadiforms such as *M moro, P. blennoides, T. trachyrhynchus* or sharks such as *Hexanchus griseus*) are replaced by small ones (such as the macrourids *Coryphaenoides guentheri* and *Chalinura mediterranea* or the chlorophthalmid *Bathypterois mediterraneus*). The authors pointed to the impossibility of large or medium-sized fishes to satisfy their energetic requirements in a progressively more restrictive trophic environment. Similar results have been obtained for the Eastern Mediterranean down to 4000 m (D'Onghia *et al.,* 2004).

Relative abundance of fishes with depth, extrapolated from data from experimental samplings in the western Mediterranean from 1988-2001.
See colour plate, p. 60.

Alepocephalus rostratus Risso, 1820
Vincent Fossat, 1879.
Coll. Muséum d'Histoire naturelle de Nice.
See colour plate, p. 58.

Legend:
- ■ Alepocephal s rostrat s
- □ Phycis blennoides
- ■ Gale s melastom s
- ■ Dalatias licha
- □ Mora moro
- ■ Merl cci s merl cci s
- ■ Centroscymn s coelolepis
- ■ Lepidion lepidion
- □ Other fishes

Depth interval (m)	Biomass dominance (30% of total fish weight)	Abundance (>30% of total fish number)
<1000	*G. melastomus*	*T. scabrus*
1000-1200	*A. rostratus*	*A. rostratus*
1200-1500	*A. rostratus*	*B. mediterraneus*
1500-2500	*C. cœlolepis*	*B. mediterraneus*
>2500	*Ch. mediterranea*	*Ch. mediterranea*

2.1.3. Macrofauna

In the deep Mediterranean, macrofaunal biomass varies considerably across areas (Pérès, 1985) and also seasonally. Macrofaunal abundance and biomass decrease generally with depth, and most likely also, as in meiofauna, along a west-east gradient. Close to submarine canyons or other areas of local high productivity, macrofaunal biomass may increase. Macrofaunal density in the Mediterranean is about 1/10 of the densities reported for the Atlantic at comparable depths (Cosson *et al.,* 1997; Flach and Heip, 1996).

In the Western Mediterranean, Stora *et al.,* (1999), reported values between 2.54 g/m² dry weight (at 250 m) and 0.05 g/m² (at 2000 m), in the Toulon canyon. Macrofaunal biomass differed also between the canyon axis (2.54 g/m²) and the canyon flanks (0.70 g/m²) at the same depth. Richness of species decreased also with depth, from 124 species at 250 m to 31 at 2000 m. A combination of grain size and geochemical composition of the sediments was suggested as possible explanatory causes of the patterns observed. Deposit feeders were the dominant guild in the Toulon canyon instead of suspension feeders and carnivores, which were dominant in the upper and middle slope in oceanic regions.

In the more oligotrophic Cretan sea, Tselepides *et al.* (2000) reported comparable values of macrofaunal biomass: 1 g/m² dry weight at 200 m depth and 0.06 g/m² at 1570 m. Instead, species richness was considerably lower in the Cretan sea than in the NW Mediterranean, with around 35 species at 200 m and around 8 at 1570 m.

The small average size of species (most animals between 0.5 and 10 mm) seems to be a characteristic of the deep Mediterranean macrofauna. As a consequence, the deep Mediterranean features a more marked decrease in the biomass than in the density of macrobenthos with depth (Pérès, 1985).

The diversity and distributional patterns of the swimming macrofauna (suprabenthos* or hyperbenthos*) have been studied in the western (Cartes and Sorbe, 1996, 1999; Cartes *et al.* 2003), and, to a lesser extent, the eastern Basin (Madurell and Cartes, 2003). Different taxa of bathyal suprabenthic fauna showed diversity peaks at mid-bathyal depths in the Catalan sea and in the Algerian Basin, with some variation depending on the taxon considered (around 600 m for amphipods; around 1200 m for cumaceans). Comparisons of suprabenthic assemblages in terms of number of species between the Ionian sea (eastern Basin) and the Catalan sea (western Basin) suggest a lower impoverishment in the Eastern Mediterranean peracarid assemblages than would be expected (Madurell and Cartes, 2003).

Regarding near-bottom zooplankton, Scotto di Carlo *et al.* (1991) reported the existence of homogenous copepod assemblages from the deep Mediterranean (600-2500 m), with no differences in faunal composition, and higher copepod biomass in the Western basin than in the Eastern basin. Due to the relatively warm temperature (13-14.5ºC) of deep Mediterranean waters, one might expect low biomass levels of near-bottom zooplankton. For instance, the biomass of near-bottom deep-sea zooplankton (10 m above the sea bed) was anomalously lower in the deep Red Sea (where the temperature of deep water reaches 22 ºC) than in the typical oceanic regions (Atlantic and Pacific: Wishner, 1980), a trend attributable to increased decomposition rates of organic matter in a warm water mass.

- **Macrofaunal abundance and species richness decreases generally with depth, but local environments with increased levels of biological production may increase macrofaunal abundance and diversity.**

- **Macrofauna species are typically very small in the Mediterranean, compared to the Atlantic.**

Bathymedon longirostris, Eusirus longipes, Lepechinella manco, Rachotropis grimaldii.
© J. E. Cartes. **See colour plate, p. 60.**

2.1.4. Meiofauna

While densities of meiofauna* (or meiobenthos) on the Mediterranean continental shelf are comparable to those in other oceans (Danovaro *et al.,* 2000), deep-sea meiobenthos densities are one order of magnitude lower in the Mediterranean than in the northeast Atlantic (Bouchet and Taviani, 1992; Danovaro *et al.,* 2000; and especially below 1700 m: De Bovée *et al.,* 1990).

Meiofaunal abundance (excluding foraminiferans) diminishes with increasing depth (De Bovée *et al.,* 1990), along with environmental indicators of food resources. This pattern is even more pronounced in the Eastern basin (Danovaro *et al.,* 2000) (fig.5) and the extremely oligotrophic eastern Mediterranean shows one of the lowest meiofaunal standing stocks in the world (Tselepides and Lampadariou, 2004).
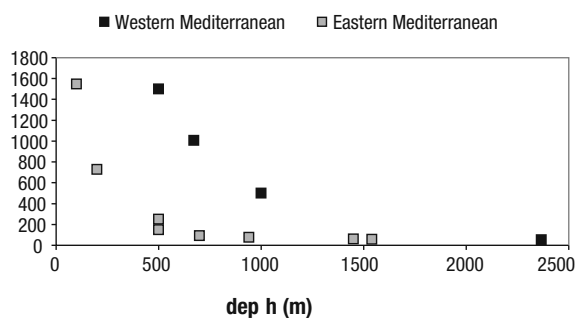

Fig. 5. Meiofaunal abundance by depth, combining data from De Bovée *et al.* (1990), Danovaro *et al.* (1999; 2000).

In general, meiofaunal abundance is dominated by nematodes, with important fractions of harpacticoid copepods and polychaetes. In the Western Mediterranean (Gulf of Lions and Catalan Sea), the meiofauna is dominated by nematodes (92.4%). In the Catalan Sea meiofaunal density varied seasonally from 296 (September) to 746 (March) ind · cm-2 (Cartes *et al.,* 2002) at around 1200 m depth. Nematode biodiversity below 500 m in the Eastern Mediterranean is lower than in other equally deep sediments worldwide, and even lower than within a Mediterranean canyon at 1500 m depth (Danovaro *et al.,* 1999).

Below 500 m depth in the Eastern Mediterranean, the contribution of bacteria to organic matter degradation is significant (bacteria represent 35.8% of the living biomass, Danovaro *et al.,* 1995) and the bacterial to meiofaunal biomass ratio is very high (20 times, Danovaro *et*

al., 1999; 2000); in the Western Mediterranean it is lower (2.5 times). The combination of low primary production and bacterial dominance of secondary production in the east is also of significance as it could account for the low fisheries production (Turley *et al.,* 2000).

The rapidly diminishing meiofaunal abundance is explained not only by the oligotrophic nature of the Mediterranean, but also by the rapidity of organic matter degradation in a relatively warm deep-water environment (De Bovée *et al.,* 1990; Bouchet and Taviani, 1992).

Information on meiobenthos from trenches of the abyssal or hadal zones is still limited, but Tselepides and Lampadariou (2004) showed that meiofaunal abundance in Eastern Mediterranean deep-sea trenches (with depths exceeding 3750 m) was unexpectedly high (45-156 ind/10 cm^2); higher than in surrounding abyssal plains and comparable to mid-slope (1500 m) depths. The accumulation of organic matter in deep sea trenches could explain the high meiofaunal abundance reported.

- **The abundance of meiofauna diminishes with increasing depth, and is lower in the eastern Mediterranean than in the western**

- **Local high abundance of meiofauna has been reported for very deep environments, such as deep-sea trenches**

- **The combination of low primary production and bacterial dominance of secondary production may account for the low fisheries production in the eastern Mediterranean**

2.1.5. Endemism

By its special oceanographic structure and paleoecology, the Mediterranean Sea has a particular fauna compared to the nearby Atlantic ocean. Different theories about the origin and evolution of deep Mediterranean fauna have been suggested and documented. Examples are the Tethys hypothesis, which postulates that the origin of some Mediterranean endemisms are faunal relicts surviving the Messinian crisis (Pérès, 1985), and the pseudopopulation hypothesis by Bouchet and Taviani (1992), explaining the occurrence of some species in the Mediterranean not as reproducing populations, but as maintained by the periodical influx of larvae trough
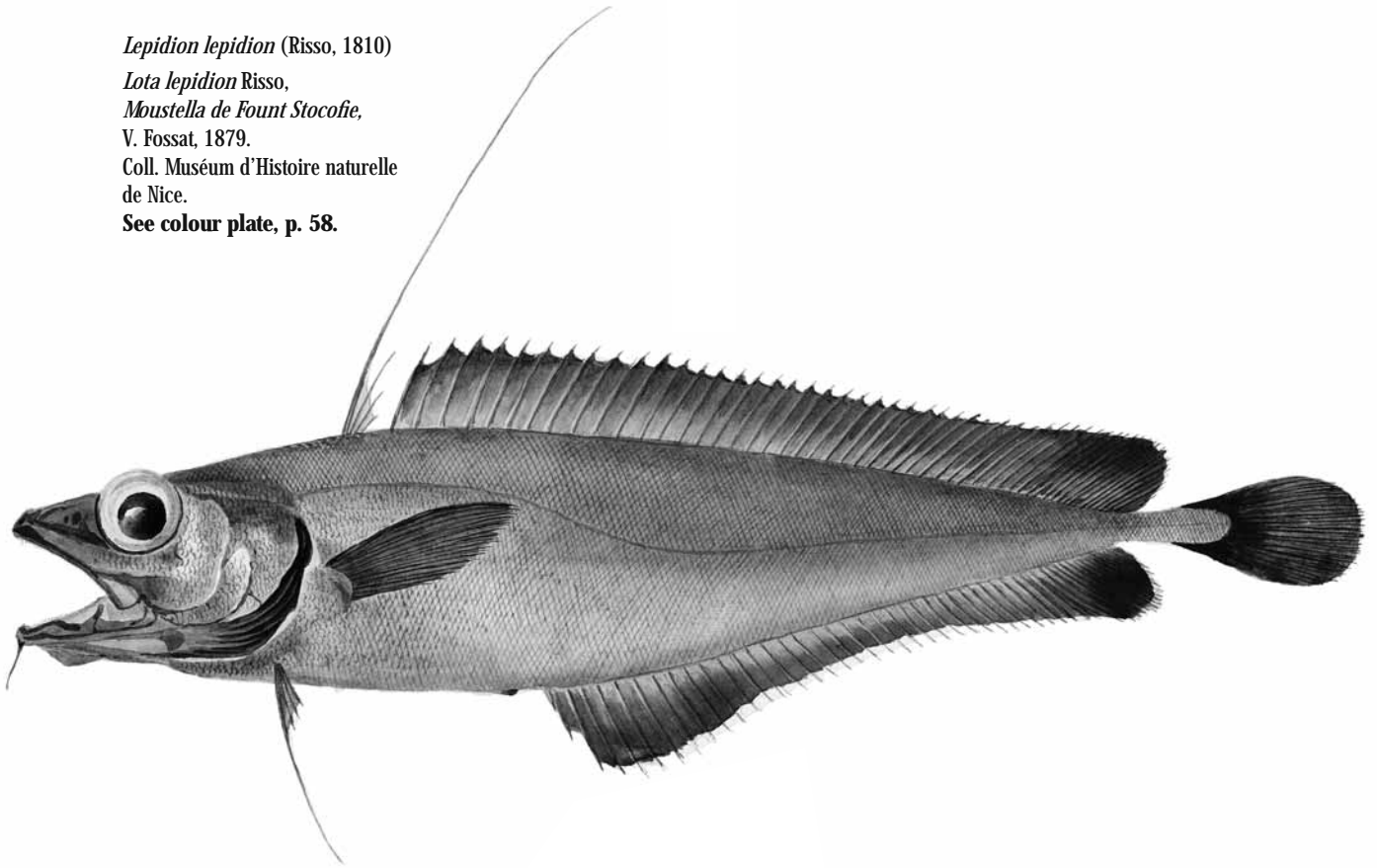
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Lepidion lepidion (Risso, 1810)

Lota lepidion Risso,
Moustella de Fount Stocofie,
V. Fossat, 1879.
Coll. Muséum d'Histoire naturelle
de Nice.
See colour plate, p. 58.

the Straits of Gibraltar. Most components of the Mediterranean deep-water fauna (deeper than *ca.* 200 m) basically derive from impoverished communities of Atlantic origin.

It has been estimated that around 26.6% of the total Mediterranean marine fauna (4238 species: Fredj *et al.,* 1992) are endemic. Though no similar overall balances exist specifically for the deep-sea fauna, the percentage of endemisms is higher than the mean above cited for some taxa (*e.g.,* 49.2% Amphipoda, Ruffo, 1998). For some taxa, even endemic genera can be found (*e.g.,* in decapod crustaceans: *Levantocaris, Zariquieyon*), while in other taxa with a higher number of endemic species (amphipods), no endemic genera are reported. As explained above for Amphipoda, the proportion of endemisms by taxon is probably closely related with life strategies. For example, no endemic cephalopods are reported in the deep Mediterranean (R. Villanueva, pers. comm.), probably due to the possession of free-pelagic larvae distributed in the entire water column.

Tortonese (1985) reported 6 endemic fishes below 1000 m: *Bathypterois mediterraneus, Paralepis speciosa, Rhynchogadus hepaticus, Eretmophorus kleinenbergi, Lepidion lepidion* and *Paraliparis leptochirus.* Only two of these species are found both in the eastern and western Mediterranean.

Among decapod crustaceans, *Levantocaris hornungae* (Galil and Clark, 1993), and the large crabs *Chaceon mediterraneus* (Manning and Holthuis, 1989; Cartes, 1993), and *Zariquieyon inflatus* (Manning and Holthuis, 1989) are endemic. Only 2 of the 28 species of decapods collected in the Catalan Sea between 862-2265 m were endemic (Cartes, 1993). 2 of the 3 endemic decapods are found both in the eastern and western Basins, while *Z. inflatus* has been collected only in the western Mediterranean.

Tortonese (1985) reported 4 endemic echinoderms below 200 m, 1 dominant (*Leptometra phalangium*) and 3 rare species (*Prototrochus meridionalis, Irpa ludwigi, Hedningia mediterranea*).

In the case of macrofauna, although the depth distribution of endemisms is more or less acknowledged, it is hardly known if these endemisms are uniformly distributed along all deep Mediterranean Basins. In the case of peracarid crustaceans, between 552 and 1808 m in the Catalano-Balearic Basin, Cartes and Sorbe (1995) reported 3 endemic Mysidacea of the total of 16 species collected, 4 of the 32 species of Cumacea (Cartes and Sorbe, 1996), and 26 of the 82 species of Amphipoda (Cartes and Sorbe, 1999). Therefore, 25.4% of bathyal peracarids in the Catalano-Balearic Basin can be considered as endemics. Previously, a similar propor-

18

tion (24.2% of the 99 species collected) of bathyal-suprabenthic Peracarids were cited as Mediterranean endemics in the same area (recalculated from Cartes and Sorbe, 1993) at similar depths (from 389 to 1859 m). In the Algerian Basin, at depths between 249 and 1622 m, the percentage of endemisms among suprabenthic Peracarids was slightly lower than in the Catalan Sea (18.2%: calculated from Cartes *et al.,* 2003).

The number of endemisms is low, particularly in the deep bathyal domain and below 2500-3000 m. This boundary has been suggested by some authors (Pérès, 1985; Bellan-Santini, 1990) as the upper limit of distribution of the true abyssal fauna. However, the number of Mediterranean deep-sea endemisms could have been overestimated simply by differences in sampling between the deep Mediterranean and surrounding biogeographic areas; some deep amphipods (e.g. *Rhachotropis caeca*, *Lepechinella manco*, or *Pseudotiron bouvieri*), catalogued as endemic Mediterranean species, have in recent years been found in the Bay of Biscay and the Cantabric Sea (Bachelet *et al.,* 2003).

Conversely, new sampling programmes are increasingly reporting new endemic taxa in the deep Mediterranean, and the faunal composition of deep-sea communities is far from being completely recognized , especially for small faunal groups.


- **The number and type of endemisms in the deep Mediterranean are the result of its particular paleoecology. They should be an important criterion in defining future MPAs in deep Mediterranean ecosystems.**

- **Some faunistic groups such as amphipods present high rates of endemism in the deep Mediterranean.**

- **The number of endemic species among megafaunal taxa in the deep Mediterranean are 6 for fishes, 4 for decapod crustaceans and 4 for echinoderms.**

2.2. Structure of deep-water Mediterranean communities

2.2.1. Continental slope

Two main biocenoses ("facies") in the bathyal Mediterranean have classically been defined (Pérès, 1985): *i)* soft-bottom communities; *ii)* hard-bottom communities. Pérès and Picard (1964) established the transition between the circalittoral and bathyal domains in the Mediterranean at around 180-200 m depth. Depending on the nature of the sediment (which depends in turn on factors such as hydrodynamism and mainland influence), three horizons were established by Pérès (1985) in the soft-bottom communities: the upper, middle and lower slope horizons. The upper slope horizon is a transition zone between the coastal zone and bathyal domains, comprising a large share of eurybathic forms and extending to 400-500 m deep. The sea pen *Funiculina quadrangularis* and the crustaceans *Parapenaeus longirostris* and *Nephrops norvegicus* are characteristic species of this horizon. The middle slope horizon, characterized by firmer and more compact muds, is the zone where most taxa achieve maximum diversity. For fish and decapods, in the NW Mediterranean, this horizon extends to a depth of 1200-1400 m. The cnidarian *Isidella elongata*, the crustaceans *Aristeus antennatus*
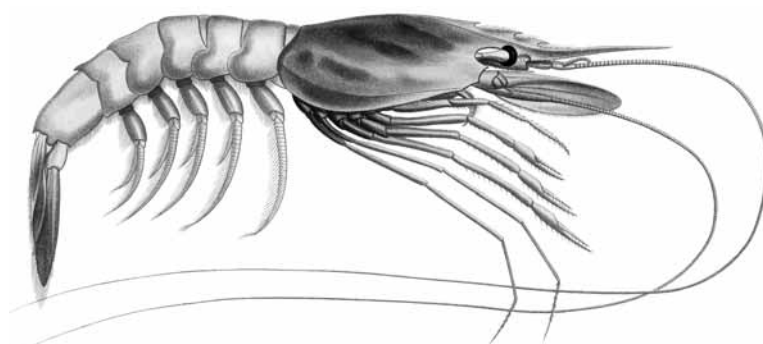
Aristeus antennatus

Albert Ier Prince de Monaco. Camp. scient. Pénéidés pl. III.
EL. Bouvier del, M. Borrel pinx.
Coll. Oceanographic Museum, Monaco.
See colour plate, p. 59.

natus and *Aristaeomorpha foliacea* are characteristic examples. The lower slope horizon is not so well studied, but some characteristic megafaunal species can be listed: decapods, such as *Stereomastis sculpta*, *Acanthephyra eximia* and *Nematocarcinus exilis*, and fishes, such as *Bathypterois mediterraneus*, *Alepochephalus rostratus*, *Lepidion lepidion* and *Coryphaenoides guentheri*. Hard bottoms are represented below 300 m and down to 800-1000 m, in areas where high hydrodynamism precludes sedimentation and exposes bare rock. In the northern Ionian sea (Santa Maria di Leuca) a unique biocenose of white corals has been reported from 450-1100 m depth (Mastrototaro *et al.* 2002; Tursi *et al.* 2004). Live colonies of *Madrepora oculata* and *Lophelia pertusa* were found, with a rich epibiont fauna. These species occur elsewhere in the Mediterranean as fossils or subfossils (Pérès, 1985), **see Box 6**.

In the marine environment, depth is assumed as the major forcing factor structuring communities: species assemblages and communities show more variability vertically, as a function of increasing depth, than over the horizontal dimension (Rowe and Menzies, 1969; Haedrich *et al.,* 1975; 1980; Hecker, 1990a; Cartes and Sardà, 1993; Stefanescu *et al.,* 1994). This observation suggested the idea of the zonation phenomenon: depth bands of high faunal homogeneity separated by boundaries of faunal renewal. Species are usually distributed along ecological gradients in a bell-shaped curve, and this is also observed with diversity. Ecological theory and observations show that species are distributed along environmental gradients (see e.g. ter Braak and Prentice, 1988), having a different *habitat amplitude* or *centre of gravity* in their distribution (Stefanescu *et al.,* 1994, for a Mediterranean deep-sea example). Along a depth gradient, species show also a minimum and maximum depth of occurrence, with an intermediate depth, the Depth of Optimal Abundance (DOA), where their density is the highest. Species may find better living conditions, i.e. trophic requirements, at this DOA, as a consequence of an adaptive success to the environment. In deep-Mediterranean fish assemblages, for instance, most fish species showed an increase in their trophic diversity* associated with the DOA (Carrassón and Cartes, 2002).

Boundaries of faunal change have been described in deep ecosystems, both at bathyal and abyssal depths. Most deep-Mediterranean species have an eurybathic distribution. This is probably due to the high thermal (13-13.5ºC in the western basin; 14-14.8 ºC in the eastern basin) and saline (38.5-38.6 PSU) stability of the water mass below 150 m in the deep Mediterranean (Hopkins, 1985). Pérès (1985) already proposed a pattern of change with depth for deep Mediterranean fauna. Although with important local variations, a faunal renewal belt between the upper and middle part of the slope appears recurrently between 300 and 700 m for megafaunal assemblages, both in oceanic regions and in the Mediterranean, and in the deep Catalan Sea (northwestern Mediterranean) at *ca.* 500 m depth (Abelló *et al.,* 1988; Cartes *et al.,* 1994). A second, deeper, boundary between 1000 and 1400 m has also been reported in deep sea ecosystems (Haedrich *et al.,* 1980; Wenner and Boesch, 1979; Cartes and Sardà, 1993) and, in the deep Mediterranean, it separates the middle and lower slope assemblages (Pérès, 1985; Cartes and Sardà, 1993). Due to the particular paleoecolgical conditions of Mediterranean biota, and the lack of a thermal gradient below 150 m, the boundary between bathyal and abyssal depths has not been clearly identified. The abyssal communities in the deep Mediterranean are extremely impoverished in species, and boundaries are masked by the eurybathic character of deep Mediterranean species; some authors even question the existence of a truly abyssal fauna in the deep Mediterranean (Pérès, 1985).

Each depth assemblage is characterized by its own levels of biomass, production and faunal diversity. In the deep-bathyal Mediterranean, a decrease in species richness below 1300 m has been reported to occur in different taxa (e.g. in amphipods, Cartes and Sorbe, 1999). Most studies available are descriptive in nature, with little data trying to relate changes in faunal assemblages with environmental variables that could explain possible zonation patterns. Therefore, possible causes for species distribution are far from being fully established. Some differences in zonation patterns have been found depending on the trophic level of each taxon. Zonation rates regularly increase with trophic level (Rex, 1977; Cartes and Carrassón, 2004), and, in the western Mediterranean, lower rates of zonation were found in peracarids (belonging to a low trophic level) compared to fish and decapods. Trophic and biological causes may explain, in a thermally stable environment, patterns of distribution and zonation of deep-sea Mediterranean species.

The bathymetric location of boundaries of faunal renewal also shows local variations, accompanied by changes in the location of peaks of biomass with depth. Concerning faunal zonation, mid and low bathyal communities (where the dominant taxa are fish, decapods and peracarids) are distributed deeper in more eutrophic areas (the continental side of the Catalan Sea) than in the insular area of the SW Balearic Islands, a more oligotrophic zone (Cartes *et al.,* 2004). The displacement of the depth where boundaries are located seems a consequence of variations in trophic factors (e.g. organic matter enrichment by river discharges). Thus, within the same community, this trend is most evident among species situated at the lowest trophic levels – species with a higher sensitivity to changes in the quality of primary sources of food (primary production and detritus).

2.2.2. Submarine canyons

A factor inducing local changes in zonation is the occurrence of active submarine canyons (fig. 6), which present a physical discontinuity of the continental slope. Active submarine canyons are important pathways channeling advective inputs of mainland origin, such as river outflow, mediated by nepheloid* layers (Durrieu de Madrón *et al.,* 1999; Puig *et al.,* 2001). Canyons have a higher organic carbon content than surrounding areas (Buscail and Germain, 1997), and preferential trans-
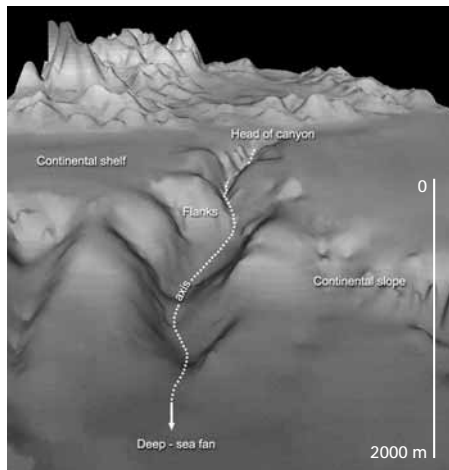
Fig. 6. Topography of a submarine canyon.
Credits: GRC Geociències Marines (Universitat de Barcelona) and RMR Institut de Ciències del Mar (CSIC), modified.
See colour plates, p. 63-64.

port of material within the canyons compared with adjacent open slope areas has been documented (Monaco *et al.,* 1999). Local sedimentary events of high intensity have been reported on the continental slope, displacing large masses of particulate material over considerable distances. These phenomena are the origin of disturbance* at small time and space scales (Crassous *et al.,* 1991). Concerning the response by organisms, high macro- and meiofaunal biomass has been reported in canyons (Cartes, 1998a), and they are also important to megafaunal commercial fisheries (e.g. red shrimp fisheries in the vicinity of western Mediterranean submarine canyons: Sardà *et al.,* 1994; Stefanescu *et al.,* 1994; presence of *Aristeus antennatus* at shallow depths in the canyons of the Nile delta, B. Galil, pers. comm.).
In the deep Mediterranean, submarine canyons are important for ecosystem structure and functioning because:

1) Canyons can act as a source and reservoir of endemic species. A number of highly specific populations of Hydromedusae, collected by sediment traps, have been recently described from submarine canyons in the western Mediterranean (Gili *et al.,* 1998; 2000), with different species found in each canyon, separated by less than 100 km.

2) canyons can act as a pathway for littoral species to colonize the deep water, when they are carried down by advective inputs (colonization of bathyal depths by species living in harbours in the Toulon canyon: Stora *et al.,* 1999; littoral species found below 1000 m, e.g. *Psammogammarus caecus* in the Catalan Sea: Cartes and Sorbe, 1999).

3) migratory micronektonic* crustaceans (hyperiids, euphausiids) tend to accumulate in the canyon head (Macquart-Moulin and Patriti, 1996). A biomass accumulation of suprabenthos (Cartes, 1998a) and decapod crustaceans (Cartes *et al.,* 1993) has also been reported, with more or less evident seasonal fluctuations.

4) Species inhabiting canyons or their vicinity (e.g. the red shrimp *Aristeus antennatus*, Cartes, 1994; Sardà *et al.,* 1994) show temporal changes in abundance, probably as a consequence of the seasonally-varying accumulation of food resources in canyons. Higher recruitment of macro- and megafaunal species into or in the vicinity of canyons has also been documented (Sardà *et al.,* 1994; Stefanescu *et al.,* 1994; Cartes and Sorbe, 1999).

5) By changing the vorticity of underwater currents, canyons are responsible for local upwelling, resulting in an enrichment of the water column and pelagic systems. Important concentrations of small pelagic fish, cetaceans and birds are observed in the epipelagic* layer in waters near submarine canyons (Palomera, 1992; Abelló *et al.,* 2003).

In decapod crustacean communities, however, species composition was similar between canyons and surrounding areas, and only some secondary species were preferentially distributed, or more abundant, in canyons (e.g. *Ligur ensiferus, Plesionika edwardsi*: Cartes *et al.,* 1994).

In conclusion, the biological differences between canyons and surrounding areas result from differences in biomass, rather than the establishment of distinct communities or species (excluding perhaps the endemic jellyfish species reported by Gili *et al.,* 1998; 2000), probably as a consequence of the high hydrodynamism of these type of environments.
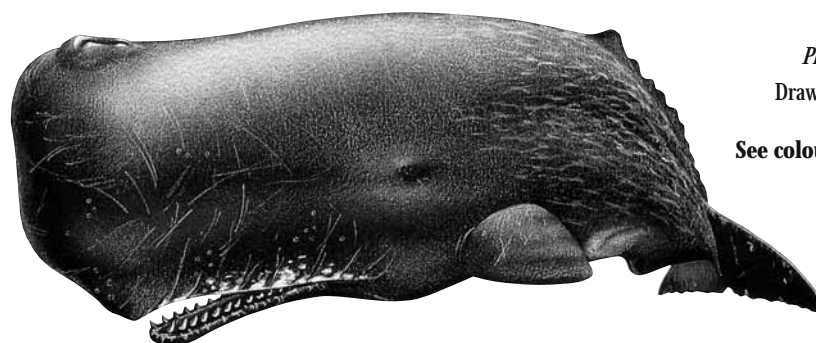
Physeter catodon.
Drawing by M. Würtz.
© Artescienza.
See colour plate, p. 61.

3. Functioning of deep-sea Mediterranean food webs

3.1. Overview

Early investigations pointed to a high stability of bathyal ecosystems, regarding both their structure and dynamics (Grassle, 1977). Stability was also assumed at seasonal and interannual time scales. This view, however, has progressively changed in recent decades with the increasing evidence of aspects such as the seasonal influx of phytodetritus to deep sea environments (Hecker, 1990b) and the non-continuous reproduction or peaks in the recruitment reported for deep sea species **(see Box 2).** Changes have also been reported on an interannual scale (e.g. over a period of 10 yr in Porcupine Abyssal Plain: Billett *et al.,* 2001 or in hydrothermal vents: Lutz and Haymon, 1994), and it has also been suggested that climate change is influencing the quantity and quality of food reaching deep-sea Mediterranean ecosystems (Danovaro *et al.,* 2001).

Globally, the Mediterranean sea is considered an oligotrophic region. Based on satellite imagery data (SeaWiFS, fig. 2), the mean annual surface primary production, as indicated by the Chlorophyll-a pigment, ranges between 1 and 2 mg /m³/yr in the most productive areas, such as the Gulf of Lions or the Alboran Sea, and 0.1-0.2 mg/m³/yr in the SW Balearic Islands, 0.05 mg/m³/yr in the Tyrrhenian sea, and only 0.02-0.03 mg/m³/yr in the most oligotrophic areas in the Levantine sea, to the south of Crete and Cyprus. The primary production, the flux of particles along the water column (total particle flux between 32.9 and 8.1 g/m²/yr at 80 and 1000 m, respectively: Miquel *et al.,* 1994 in the Ligurian Sea) and the concentration of (total or labile) organic matter on deep-sea bottoms follow a seasonal pattern with peaks that seem to be coupled with the spring peak of primary production (Carpine, 1970; Danovaro *et al.,* 1999; Cartes *et al.,* 2002). Surface primary production often peaks around April (Cartes *et al.,* 2002), while organic matter flux is at a maximum in June (Miquel *et al.,* 1994) in the Ligurian sea. For organics in deep sediments, there is only discontinuous data available (Cartes *et al.,* 2002). Peaks seem to occur also around June (Medernach, 2000; Cartes *et al.,* 2002). Primary production, phytoplankton pigment concentration and flux of particles are, for instance, lower in the Catalan sea (NW Mediterranean) than in the Bay of Biscay (NE Atlantic), located at similar latitude (Buscail *et al.,* 1990, summarized by Cartes *et al.,* 2001b). Particulate organic matter (POM) in deep bottoms, although varying depending on local conditions, is also low in the deep Mediterranean, particularly in the Eastern Basin (Danovaro *et al.,* 1999).

Danovaro *et al.* (1999) reported that mass fluxes at equal depths are up to two orders of magnitude higher in the Western Mediterranean (Gulf of Lions) than in the Eastern Mediterranean (Cretan sea). 10% of the carbon in surface waters is exported to 1000 m depth in the Western Mediterranean, but only 2-3% in the Eastern Mediterranean, whilst bacterial densities are 4 times higher in the former than in the latter. The same authors also reported different efficiencies in the transfer of organic matter to the deep sea between the west and the east – 10% and 1% respectively. This has profound implications in terms of bentho-pelagic coupling.

The high thermal stability of the deep Mediterranean probably contributes to a rapid degradation of the POM reaching the deep bottoms, resulting in poor quality (or refractory) food for the benthos. In the absence of changes in abiotic factors such as temperature, food availability and local productivity regimes might explain important biological features (e.g. species composition and size distribution) of the Mediterranean fauna. The trophic level of species and the dietary diversity explain patterns of distribution overlap (i.e. possible competence between species), and the depth range occupied by Mediterranean top predators below 1000 m (Cartes and Carrassón, 2004). In the context of a generally oligotrophic region, such as the deep Mediterranean, it is of particular significance to understand the functioning of areas of comparatively higher production, such as canyons and upwelling regions.

With the exception of some extreme environments (cold seeps), most deep ecosystems in the Mediterranean are allochthonous (i.e., they depend on POM originating in the photic zone or of terrigenous origin). At present, most of the information on the structure and functioning of trophic webs concerns megafauna dwelling on muddy bottoms. Detailed information on diets and resource partitioning of fish and decapod crustaceans available from the Catalano-Balearic Basin (western Mediterranean) indicates:

1) Diets are generally highly diversified (Shannon index reaching 5.3 bits in the diet of the red shrimp *Aristeus antennatus*: Cartes, 1994);

2) Fish and decapods are organized in three different trophic levels, as reported from isotopic analyses (Polunin *et al.,* 2001);

3) The occurrence, both among decapods and fish, of 3 basic trophic guilds (functional groups), composed of meso-bathypelagic*, benthopelagic* and benthic feeders, which respectively prey on macroplankton, suprabenthos and macrobenthos compartments;

4) There is a high degree of resource partitioning* (low dietary overlap) among deep-sea fish and decapod crustaceans (Macpherson, 1979; Cartes, 1998b; Carrassón and Cartes, 2002). Prey size and prey mobility are the two main factors explaining this trend;

5) Decapods are not only detritivores or scavengers, as previously assumed, but active predators selecting, as fish do, the size of their prey (Cartes, 1993; Fanelli and Cartes, 2004). Among decapod crustaceans, however, there is an increase of detritivore habits below 1200 m coinciding with the rarefaction of some important prey (euphausiids, macrofauna such as *Calocaris macandreae*) at that depth, and with a boundary of community change at that same depth level (Cartes and Sardà, 1993; Cartes, 1998b); and

6) There is a trend to a decrease of feeding intensity with depth (between 500-2200 m) both for decapods (Cartes, 1998b) and fish (Carrassón and Cartes, 2002), which suggests a reduction of metabolic activity with increasing depth (in connexion with the extensive work by Childress (e.g., 1995), showing the same trend for oxygen consumption data). This general pattern, however, may vary depending on seasonality (prey availability) and the reproductive state of species (Maynou and Cartes, 1998). As a general conclusion, in deep environments trophic relationships are complex, indicating that we are working more within the structure of a trophic web than in a trophic chain (as occurs, for instance, in epipelagic environments).

A similar degree of resource partitioning is more difficult to establish for benthic macro- or meiofauna. It has been documented for macrofauna (e.g. suprabenthos: Cartes *et al.,* 2001a; 2001b) and even for meiofauna (foraminiferans: Gooday *et al.,* 1992) with direct (e.g. consuming labile/refractory organic matter), or indirect (e.g. via consumption of foraminiferans by isopods) responses to POM fluxes probably depending on the trophic level occupied by each species or taxon.

- **Surface primary production is low in the Mediterranean sea and extremely low in the more oligotrophic areas, such as the Cretan sea.**

- **Seasonal peaks in primary production are reflected in seasonal peaks of secondary produc-**

tion in the deep sea, as well as other seasonal changes of food consumption and reproduction.

- **The low food input to the deep-sea results in scarce food resources, high food partitioning, highly diversified diets, and very complex trophic webs.**

3.2. Mesoscale* variations in the dynamics of deep-sea ecosystems

In addition to temporal changes, deep-sea ecosystems also vary on a spatial scale. Differences between the eastern and western Mediterranean are more evident for fish: certain dominant species are found only in the western basin (e.g. *Centroscymnus coelolepis, Polyacanthonotus rissoanus, Chalinura mediterranea, Lepidion lepidion, Alepocephalus rostratus, Nemichthys scolopaceus, Nettastoma melanurum*, Whitehead *et al.,* 1989; D'Onghia *et al.,* 2004; Lloris, pers. obs.). In other cases, it has been suggested that the small differences between the eastern and western basins should be simply attributed to differences in sampling effort (Bellan-Santini, 1990). At mesoscale, deep Mediterranean fauna regularly show a high similarity between neighbouring areas. Thus, only 11.6 % of the hyperbenthic peracarid crustaceans found in the SW Balearic slope had not been reported previously 350 km away in the Catalan Sea (Cartes and Sorbe 1993, 1995, 1999).

In addition to the biogeographical variations cited, changes in the functioning of food webs have been reported at mesoscale (350 km) in the western basin. Depending on the distance to the coast (and thus, to the influence of advective fluxes of mainland origin), the trophic resources of deep sea fauna are based more on the benthic or pelagic compartments. For instance, on the middle slope of the continental side of the Catalan Sea, benthos was the main contributor to the food supply for megafauna (crustaceans and fish), after a study on the food consumption-food supply balance (Cartes and Maynou, 1998). In contrast, in a more open-sea area (e.g. the SW Balearic Islands) bathyal fish relied more on pelagic prey as a food resource. A western-eastern increase in oligotrophic conditions in the Mediterranean seems to have similar consequences, and fish assemblages in the Ionian Sea exploit preferentially pelagic prey, a feature consistent with the low abundance

Box 2. Reproductive strategies of deep-water species: recruitment patterns in productivity hotspots

Although most studies were originally focused on commercial species of fish and decapod crustaceans (e.g. the red shrimp *Aristeus antennatus*), there is now detailed information on the biological cycles of a number of deep Mediterranean species. Suprabenthic peracarid crustaceans (Cartes and Sorbe, 1999; Cartes *et al.,* 2001b), and non-commercial, though ecologically important, fish and decapods have been the topic of these studies (e.g. Macrouridae: Massutí *et al.,* 1995; D'Onghia *et al.,* 1999; Pandalidae: Company and Sardà, 2000; Pasiphaeidae: Company *et al.,* 2001; Polychelidae: Abelló and Cartes, 1992). Both continuous and non-continuous reproductive patterns have been documented, with some trend towards seasonality, or annual restricted periods of maturity, in mid-slope dwelling species with increasing depth, both among Cumacea (Cartes and Sorbe, 1996), and Pandalidae (Company and Sardà, 2000). Biological trends with depth have also been studied in the last decade (Stefanescu *et al.,* 1992; Sardà and Cartes, 1993). Some dominant species follow a bigger-deeper and smaller-shallower trend (e.g. *Phycis blennoides*, *Mora moro*, *Plesionika martia*) preferentially on the upper and middle slope, while some show a smaller-deeper trend (e.g. *Aristeus antennatus*), on the lower slope, and some species do not show any significant size-related trend with depth at all (Morales-Nin *et al.,* 2003). Probably the depth of recruitment and reproductive aggregations by deep-water species depend on a number of physical and trophic factors which may vary between species. A link has been suggested, for example, between phytodetritus* deposition and recruitment for small suprabenthic species (Cartes *et al.,* 2001a, 2001b). In megafauna, a link between recruitment and the occurrence of nepheloid layers (Puig *et al.,* 2001) has been shown for pandalid shrimps.

Puig *et al.* (2001) showed that the larval and recruitment processes of three deep-water pandalid shrimps (genus *Plesionika*) were related to nepheloid detachments at the continental margins, along a narrow bathymetric range of *ca.* 400 m depth. The existence of a nepheloid layer is the result of the overall water mass circulation in the NW Mediterranean area (frontal structure). Frontal structures located at around 400 m depth are widespread in the oceans worldwide (Puig *et al.,* 2001) and suggest the existence of a preferential recruitment habitat for some continental slope species.

…/…

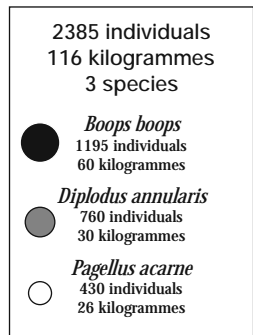Fon *et al.* (1988)

Puig *et al.* (2001)
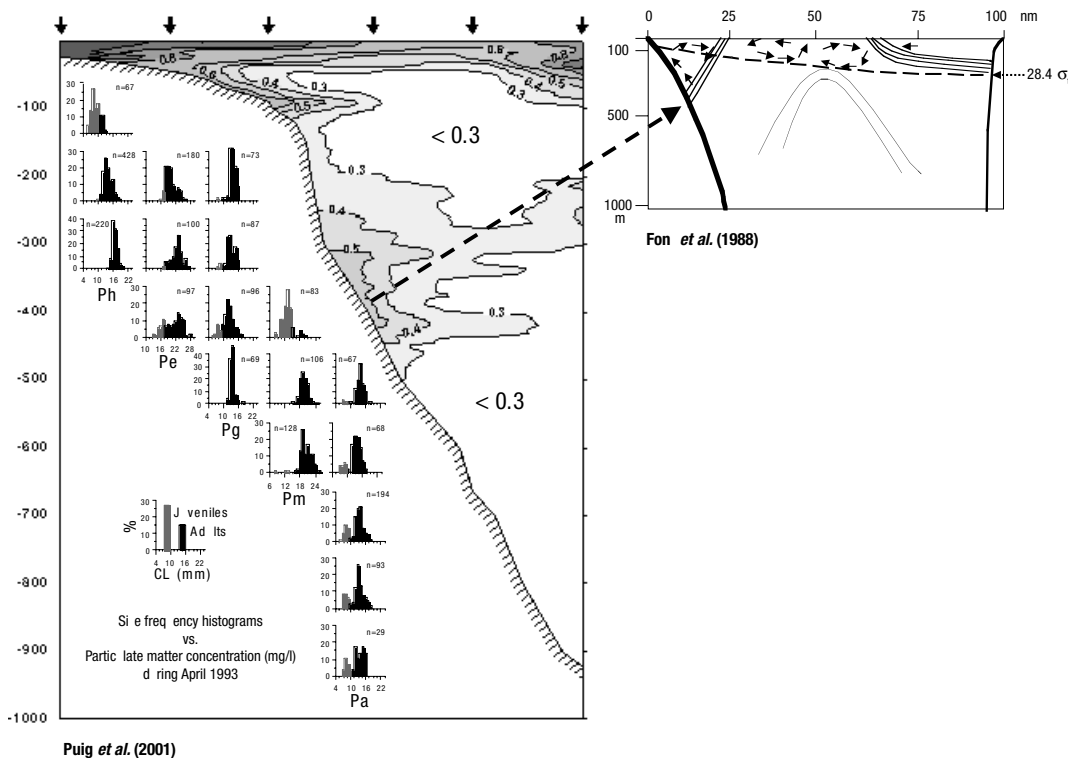
Another important aspect of the population dynamics of deep-water species is the presence of seasonal reproduction peaks, despite the apparent stability of ecological conditions in the deep sea. A study on the duration of the reproductive periods of 17 deep-water decapod crustaceans (some of them dwelling below 1000 m) showed that their reproductive periods were more clearly seasonal than those of species dwelling along the shelf and upper-slope continental margins (Company *et al.,* 2003). The *shorter* reproductive periods shown by deep-sea dwelling species (Fishelson and Galil, 2001; Company *et al.,* 2003) are an aspect of their life histories that might affect their commercial exploitation. The reproductive output of deep-sea species could be compromised if any exploitation is undertaken during their short reproductive period.

Box 3. Diversity, biodiversity and species richness

Diversity

2385 individuals
116 kilogrammes
3 species

● *Boops boops*
1195 individuals
60 kilogrammes

⬤ *Diplodus annularis*
760 individuals
30 kilogrammes

○ *Pagellus acarne*
430 individuals
26 kilogrammes

Diversity
refers to *the absolute number of species present, or any other measurement that incorporates the number of species as well as its relative abundance* (Norse *et al.,* 1980 *in* Wilson, 1988).
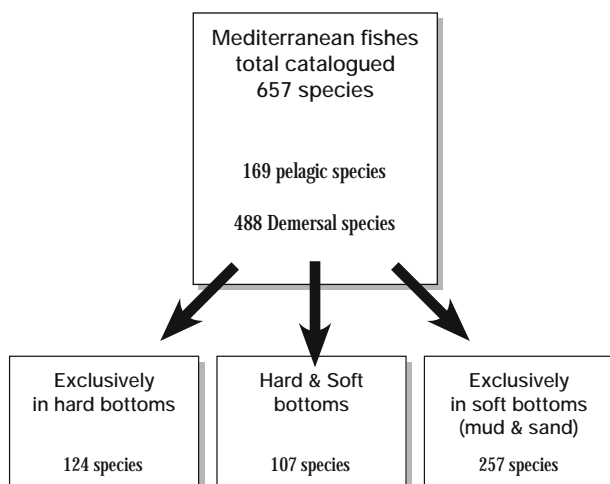
Biodiversity

1 Family
1 Genus
3 species

⬤ *Scorpaena notata*

⬤ *Scorpaena porcus*

⬤ *Scorpaena scrofa*

<

1 Family
3 Genus
3 species

● *Boops boops*

⬤ *Diplodus annularis*

○ *Pagellus acarne*

Biodiversity
refers to *the variety of organisms considered at all the levels, from the genetic variants pertaining to the same species, to varieties, species, genera, families and even superior taxonomic levels, including the variety of ecosystems, that includes the communities of organisms that live in certain habitats as well as the physical training conditions under which they live* (Wilson, 1992).

Species richness

Mediterranean fishes
total catalogued
657 species

169 pelagic species

488 Demersal species

Species richness
refers to a list of species
at a given location or community
(Puttman, 1994).

Exclusively in hard bottoms	Hard & Soft bottoms	Exclusively in soft bottoms (mud & sand)
124 species	107 species	257 species

Graphical synthesis of the three forms to understand the term *biodiversity.*

of macrobenthos and meiobenthos biomass in the eastern Mediterranean below 400 m (Tselepides and Eleftheriou, 1992; Danovaro *et al.,* 1999).

As a result of these ecological patterns, it is important to note that:

(i) Fish assemblages can change depending upon the trophic characteristics of the area they inhabit. Thus, dominant species in the eastern Ionian Sea, mainly depending on pelagic resources (e.g. *Hoplostehtus mediterraneus* and *Chlorophthalmus agassizi*), are rare or absent in more eutrophic areas, such as the continental side of the Catalan Sea (Madurell *et al.,* 2004); and

(ii) a comparison between areas under mainland influence and far from this influence (insular areas) in the deep Mediterranean evidenced local changes in the bathymetric distribution and zonation of deep sea fauna (Maynou and Cartes, 2000; Cartes *et al.,* 2004).

In conclusion, an increase in oligotrophic conditions (in terms of primary production in surface waters) favours the exploitation of pelagic resources, instead of benthos, by deep sea top predators. In these oligotrophic areas (e.g. the Ionian Sea), fish tend towards a strategy of caloric maximization consuming prey from the mesopelagic compartment, more energy-rich than benthos.

Food availability decreases even more below 1000 m in the deep Mediterranean, despite the biomass increase reported at around 1200 m in the NW Mediterranean for fish. This peak of biomass **(see Box 1)**, first described as a general trend in the North Atlantic (Gordon and Duncan, 1985) was also found in the western Mediterranean (Stefanescu *et al.,* 1993; Moranta *et al.,* 1998), though it has not conclusively reported for the Eastern Basin. Some species responsible for this peak that are recorded in the western Mediterranean are absent (e.g. *Alepocephalus rostratus*) in the Eastern Basin, where studies of megafaunal biomass distribution are particularly scarce (Kallianotis *et al.,* 2000; Politou *et al.,* 2003), reaching only 1000 m depth. On the Cretan slope, megafaunal biomass showed a peak at 500 m (Kallianotis *et al.,* 2000) and did not show a significant decrease with depth between the two deepest strata sampled (800 and 1000 m), even showing a non-significant biomass increase at 1000 m. Some fish species responsible for the biomass peak in the western Basin are still dominant in fish assemblages (e.g. *Mora moro, Galeus melastomus*: Kallianotis *et al.,* 2000) at 1000 m depth in the Eastern basin. In the western Mediterranean, below 1000 m, dominant species such as *Alepocephalus rostratus* base their diet on macroplankton, adopting the strategy of species inhabiting low productive regions. Consistently, benthic biomass also decreases at those depths (Cartes *et al.,* 2002). Further, a number of fish species (e.g. *Phycis blennoides, Mora moro, Trachyrhynchus trachyrhynchus*) are represented around these depths almost exclusively by large specimens, with a clear bigger-deeper trend in their size distributions (Stefanescu *et al.,* 1993), and with a progressive dependence on benthopelagic resources with increasing size. Food consumption also decreases with increasing fish size, and the bathymetric aggregation of these large sizes for these species around a narrow depth range around 1200 m probably indicates the increasing scarcity of food resources with increasing depth below 1000 m.

The general principle that it is essential to know the carrying capacity of ecosystems before any exploitation begins, is even more crucial in the case of deep-water, low productive, ecosystems. Temporal studies, following not only the dynamics of commercial species, but the whole functioning of the ecosystem, are essential. In particular must be addressed: (1) the productive capacity of the lowest trophic levels – macrofauna, including the swimming compartment (suprabenthos, macrozooplankton); and (2) the complexity of food webs – number of trophic levels involved – and the food consumption of top predators.

Depth-distribution balances based on production rather than biomass constitute a more realistic approach to better understanding the dynamics of deep-water ecosystems. The evidence presently available points to the

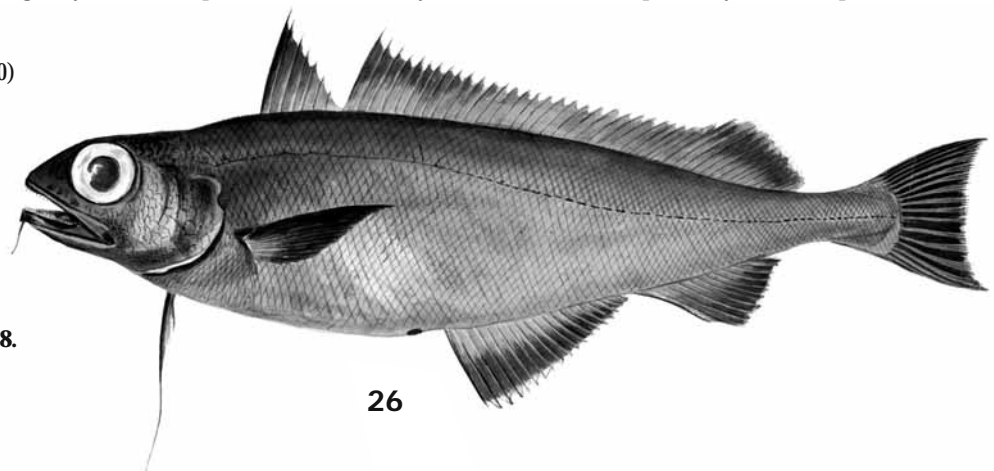*Mora moro* (Risso, 1810)

*Mota mediterranea,
Mora,*
V. Fossat, 1878.

Coll.
Muséum d'Histoire
naturelle de Nice.
See colour plate, p. 58.

conclusion that in the Mediterranean, depths below 1000 m (or most appropriately, we should refer to the lower slope assemblages: Pérès, 1985) are particularly poor and especially sensitive to future human intervention, for instance fishing.

- **Depths below 1000 m in the Mediterranean are particularly fragile and especially sensitive to future human intervention, for instance fishing.**

- **The general principle that it is essential to know the carrying capacity of ecosystems before any exploitation begins, is even more crucial in the case of deep-water, low productive, ecosystems.**

3.3. Human alteration of trophic webs

Anthropogenic impacts on deep Mediterranean communities (e.g. fisheries, trawling, and waste disposal) may have a strong influence on the dynamics of such fragile ecosystems, although the number of studies addressing this issue is still limited. Present knowledge of trophic dynamics available for the deep Mediterranean shows that:

1. Gorgonian communities (e.g. *Isidella elongata*) and other sessile organisms are immediately removed from soft bottoms after trawling, changing the associated biocoenosis, which may comprise species of commercial interest (such as red shrimps) in the case of *Isidella* biocenose. From a trophic perspective, communities may change from those dominated by filter feeders (e.g. sponges, brachiopods such as *Gryphus vitreus*) and low-trophic level predators (gorgonians) towards other communities dominated by deposit feeders and top predators. Trawling may also have a negative impact on colonies of other hard-bottom dwelling corals (e.g. *Lophelia pertusa* and *Madrepora oculata*) , some rare, living in the deep Mediterranean.

2. Trawling may also alter the secondary production of benthic communities, with increasing dominance of species of higher P/B ratio, by decreasing the mean individual size. Additionally, a decrease in the mean trophic level of food webs is also expected.

3. The influence of discards and the damage induced on benthic species has received less attention, but it may change the food consumption patterns of species that are, only potentially, opportunists and scavengers. Discards of non-commercial species are a non-trivial part of the catch biomass in fisheries of the red shrimp *Aristeus antennatus* (27%: Carbonell *et al.,* 1998; Bozzano and Sardà, 2002). Therefore, the feeding behaviour of species and the whole dynamic of such low-productive ecosystems can also be altered.

4. Marine pollution can be channelled to the deep-sea by submarine canyons, as reported for the Toulon Canyon in the western Mediterranean (Stora *et al.,* 1999). As a result of dredge spoil dumping at the canyon heads, strong concentrations of heavy metals and organic matter have accumulated deeper. This enrichment in organic matter even favours the colonization of bathyal depths by some species living in harbours, in shallow water. Organochlorinated compounds are another source of pollution of the deep Mediterranean, evidenced by the enzymatic xenobiotic activities detected in deep-sea fish living between 1500-1800 m depth, which indicate the ability of such organisms to cope with these pollutants (Porte *et al.,* 2000). Differences between the responses by species were suggested in relation to the feeding behaviour of each species. Accumulation of solid waste (plastics, etc.) is important in the Catalano-Balearic Basin, probably because it is channelled by the numerous canyons occurring in the continental part of this basin. The influence on the recruitment and incorporation of certain materials (e.g. tar) to the trophic webs is unknown.
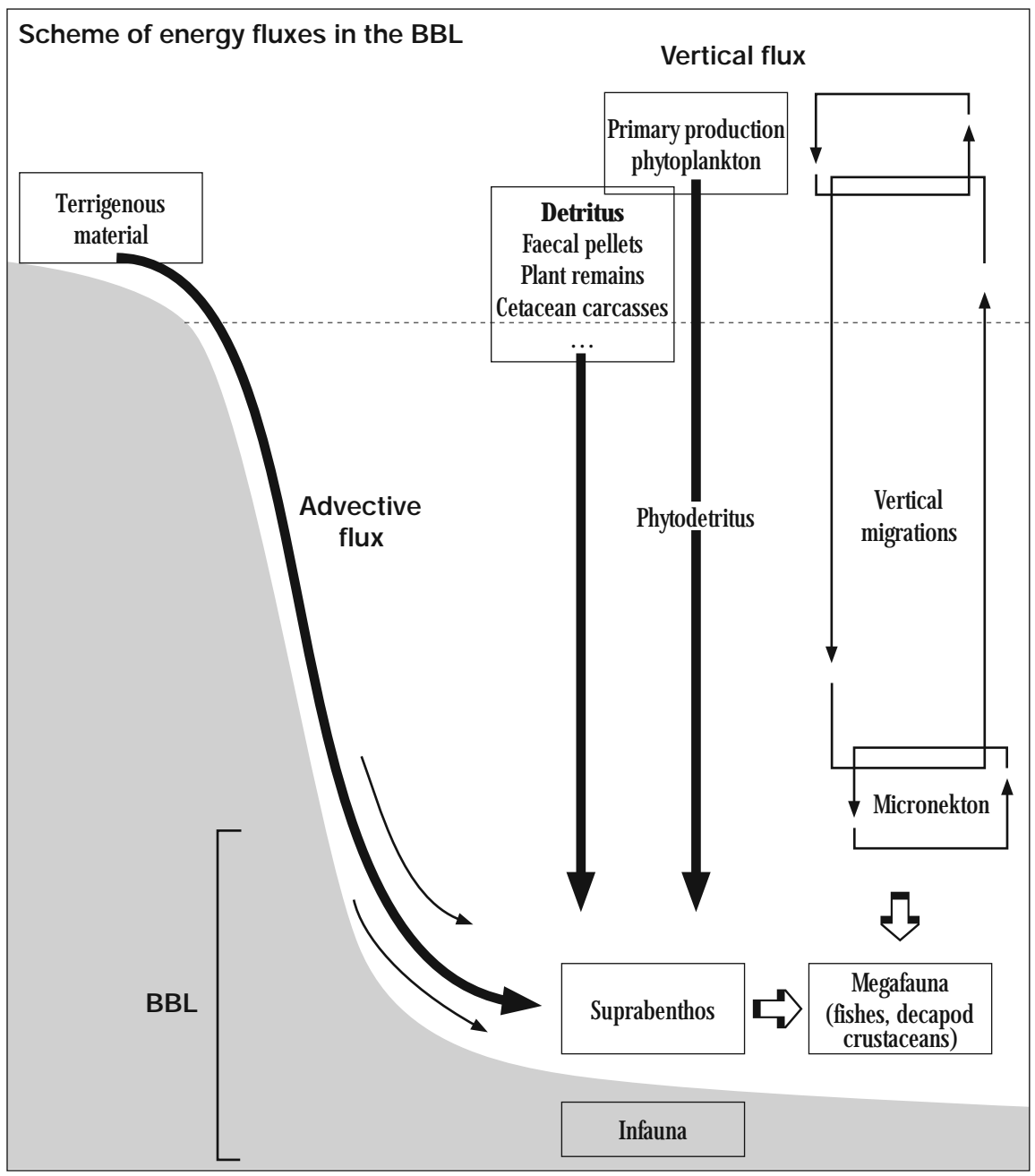
5. Finally, climate change induced by human activity influences the quantity and quality of food reaching the deep-sea Mediterranean ecosystems. Contrary to what might be expected, deep-sea ecosystems would respond quickly to climate change (Danovaro *et al.,* 2001).

- **The deep Mediterranean biological communities are adapted to a general oligotrophic environment, with local areas of higher productivity and biodiversity hotspots.**

- **These biological communities are very sensitive to human modification in the form of deep-sea trawling, waste disposal or chemical pollution.**

- **Human modification impacts directly on the communities by selectively affecting some of their components (e.g. removal of top predators by fishing, destruction of suspension feeders such as gorgonians or coral reefs), or indirectly by changing the structure of a complex trophic web, modifying secondary production patterns or the effect of climate change.**

Box 4. Mass fluxes in deep-water ecosystems

A theoretical scheme of mass fluxes through deep-water ecosystems inhabiting the Benthic Boundary Layer (the layer close to the sea floor where an important increase of living biomass is recorded). Two main pathways are involved (the advective flux of material of terrigenous origin and the vertical flux of material of pelagic origin). Fluxes of particulate organic matter (POM) are consumed primarily by benthos and suprabenthos close to the bottom, and by zooplankton-micronekton along the water column by means of chained vertical migrations. These organisms constitute the basis of the diet of benthopelagic megafauna (fish and large decapod crustaceans). The vertical and advective inputs vary depending on local productivity (river discharges, upwelling areas linked to eddies and oceanographic circulation), favouring the density of benthos-suprabenthos/zooplankton, and resulting in food webs where top predators prey on pelagic or benthic organisms.

Scheme of energy fluxes in the BBL

Vertical flux

Primary production phytoplankton

Terrigenous material

Detritus
Faecal pellets
Plant remains
Cetacean carcasses
…

Advective flux

Phytodetritus

Vertical migrations

BBL

Micronekton

Suprabenthos

Megafauna (fishes, decapod crustaceans)

Infauna

# 4. Unique environments of the Mediterranean deep-sea

4.1. Cold seeps

Upward seepage of cold fluids enriched in methane occurs worldwide along certain deep-sea tectonic features such as mud volcanoes (Henry *et al.,* 1996). These are the home of unique chemosynthesis-based communities (not relying on photosynthetic production) dominated by bacterial mats and particular species of bivalves and tubeworms, that are associated with endosymbiotic* chemo-autotrophic* bacteria. Specially evolved bacteria able to oxidize the methane are at the basis of this unique food web. Important cold seep areas hosting such unique benthic communities were first described in the Atlantic and in the Eastern and Western Pacific Oceans (Kennicut II *et al.,* 1985).

Initial evidence of benthic communities based on chemosynthesis in the Mediterranean referred to the Napoli mud volcano, on the top of the Napoli dome on the Mediterranean Ridge, at depths of 1900-m (Corselli and Basso, 1996). Cold seep biological communities relying on methane and associated to mud volcanoes and faults have recently been discovered in the southeastern Mediterranean Sea, south of Crete and Turkey (in the Olimpic field and Anaximander mountains, respectively; MEDINAUT/MEDINETH Shipboard Scientific Parties, 2000), at depths of between 1700-2000 m, as well as north of Egypt near the Nile delta. In the latter locality (near Egypt and the Gaza Strip), living communities of polychaetes and bivalves have been found at depths of 500-800 m (Coleman and Ballard, 2001).

The isolation of the Mediterranean deep-sea seeps and vent habitats from the Atlantic Ocean has resulted in the development of unique communities, as illustrated by the specific bivalve populations associated to Mediter-
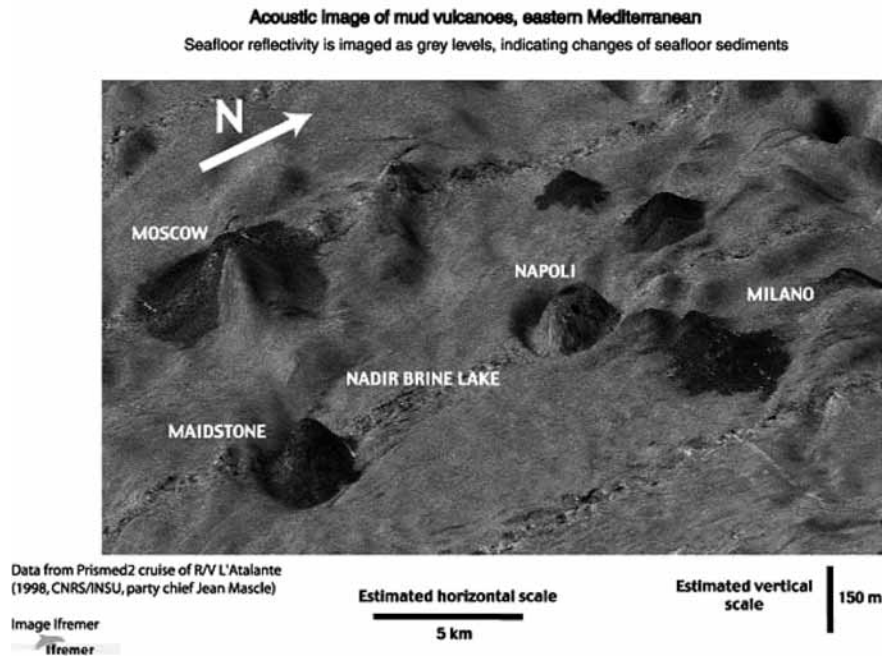

Credits: *GEBCO Digital Atlas, 2003,* Modified.
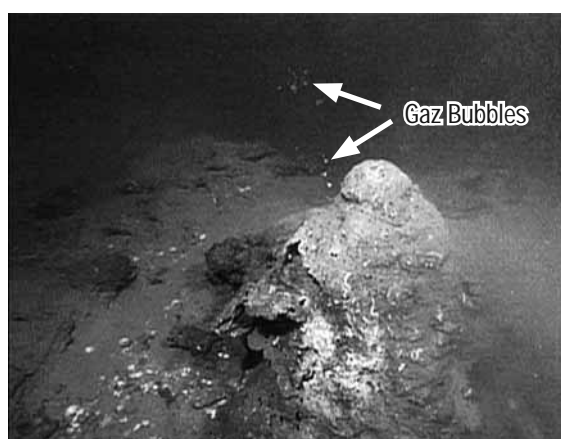
Credit: Coleman and Ballard (2001). © Springer.
See colour plate, p. 62.

ranean cold seeps, with species much smaller in size than those dominating in other seep sites. The biological community inhabiting the Anaximander mountains field, SW Turkey, is dominated by small bivalves belonging to 4 families (Lucinidae, Vesicomydae, Mytilidae and Thyasiridae) and tube worms (both pogonophoran and vestimentiferan species), all of which contain bacterial endosymbionts. Whereas worms, vesycomid and lucinid bivalves rely – through their sulfur-oxydizing-type symbionts – on the sulphide issued from microbial sulphate reduction processes in the superficial sediment, the mytilid symbionts are able to use either sulphides from the sediment or, directly, the methane expelled in the seeps (Fiala-Médioni, 2003).

Unlike cold seeps, which are well represented along the Mediterranean Ridge, active deep-sea hydrothermalism seems to be absent from the Mediterranean. Known hydrothermal vents in the region occur in shallow waters (< 100-m), associated to volcanic arcs – such as the Helenic Volcanic Arc. In these areas, trophic webs are mostly based on photosynthetic primary production and the associated macro-epibenthic biological assemblages are not distinct from the surrounding areas (Cocito *et al.,* 2000).

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Acoustic image of mud volcanoes, eastern Mediterranean
Seafloor reflectivity is imaged as grey levels, indicating changes of seafloor sediments

Data from Prismed2 cruise of R/V L'Atalante
(1998, CNRS/INSU, party chief Jean Mascle)

Image Ifremer

Ifremer

Estimated horizontal scale
5 km

Estimated vertical scale
150 m

Credit:
Loubrieu B., Satra C., 2001. Cartographie par sondeur multifaisceaux de la Ride Méditerranéenne et des domaines voisins. *Comité Français de Cartographie,* n°168, pp. 15-21.

Recent geological cruises involving multibeam mapping and use of the side scan sonar have uncovered the existence of numerous mud-volcanoes and anoxic basins in the Eastern Mediterranean (Desbruyères, 2003). Evidence of previously unknown mud-volcanoes in the Eastern Mediterranean opens the door to an increased occurrence of cold-seep type communities in the region. The recent discovery of pockmarks (geological structures consisting of shallow craters typically 30-40 m in diameter and 2-3 m deep) around the Balearic Islands (Acosta *et al.,* 2001) also points to the existence of these cold-seep type communities in the Western Mediterranean. In the majority of cases, the mechanism of pockmarks formation is attributable to gas discharges.

- **Cold-seeps harbour unique biocenoses based on the oxidation of methane as the primary carbon source (i.e., not based on photosynthetic production as in most marine environments), dominated by bacterial mats and communities of specialised bivalves and tubeworms.**

Box 5: Mud volcanoes

The term "mud-volcano" is generally applied to a more or less violent eruption or surface extrusion of watery mud or clay which is almost invariably accompanied by methane gas, and which commonly tends to build up a solid mud or clay deposit around its orifice which may have a conical or volcano-like shape. Mud volcanoes also commonly appear to be related to lines of fracture, faulting, or sharp folding.

In the Mediterranean, mud volcanoes are found along the Mediterranean Ridge, in the South Eastern Mediterranean (i.e. Napoli Dome, Olimpi mud volcano).

The motivating force responsible for a mud volcano is, in part, simply the weight of rock overburden borne by the fluid content of undercompacted shales. However, mud volcanoes all over the world are associated so invariably with quietly or explosively escaping methane gas, that it is reasonable to conclude that the presence of methane gas in the subsurface is also an essential feature of the phenomenon. The mud of the volcanoes is a mixture of clay and salt water which is kept in the state of a slurry by the boiling or churning activity of escaping methane gas. Some liquid oil is often, but not always, associated with the hydrocarbon gases of mud volcanoes.

Commonly, the activity of a mud volcano is simply a mild surface upwelling of muddy and usually saline water accompanied by gas bubbles.

Source: Geological Society of Trinidad and Tobago.

4.2. Brine pools

The eastern Mediterranean Sea hosts a unique environment that ranges among the more extreme ever described in relation to its compatibility with life. Five deep hypersaline anoxic basins (DHABs) were recently discovered on bottoms below 3300 m depth, i.e. in an environment with a complete absence of light and subject to high pressures (Lampadariou *et al.*, 2003). DHAB's are characterised by a salinity value higher than 30%, oxygen depletion and elevated methane and sulphide concentrations (De Lange *et al.*, 1990); the Urania basin presents the highest concentration of sulphide among the Earth aquatic environments. These unique environments have been isolated from the global ocean for millions of years. Surface of known DHAB's range from 5 to 20 km², and the strong difference in density between the brines and the surrounding seawater ensures a complete lack of mixing thereof. Newly described prokaryotic groups have been found in the interface area that harbours important populations of Bacteria and Archaea. First genetic evidence point to DHABs as harbouring a much higher diversity of unknown extremophilic bacteria than other hypersaline anoxic basins in the world. DHABs are toxic to megafauna and macrofauna, so they are only able to support protistan and meiofaunal communities that likely benefit from symbiotic associations with prokaryotes. Such meiofaunal assemblages (composed of nematodes, copepods, foraminifera, etc.) could even reach biomass values much higher than those found outside the brine pool, and many of the species involved are thought to be new for science (Lampadariou *et al.*, 2003).

- **Brine pools (or Deep Hypersaline Anoxic Basins, DHABS) harbour unique faunal assemblages, adapted to withstand high salinity levels (30 PSU), oxygen depletion and high concentration of methane and sulphide.**

4.3. Deep-sea coral mounds

Although most scleractinian reef-forming corals occur in tropical regions and in shallow water, there is a group of scleractinian corals which can exist in water between 4 and 12 °C, and at depths from *ca.* 50 m to over 2000 m where they typically settle escarpments, seamounts and overhangs in total darkness. These corals do not have symbiotic algae, but are still able to form a hard skeleton. They form colonies and can aggregate into patches and banks which may be described as reefs. The most common cold water coral is *Lophelia pertusa* which has a global distribution but is most common in the north-east Atlantic. It forms extensive buildups in the Atlantic Ocean between *ca.* 300-800 m, often in association with *Madrepora oculata* and *Desmophyllum cristagalli*. A study of *L. pertusa* coral reefs off the Faeroes indicated that the diversity of *L. pertusa* coral reefs is of a similar magnitude to that of some tropical, shallow water hermatypic corals. The overall faunal diversity and the number of species within many faunal groups (foraminifera, porifera, polychaetes, echinoderms and bryozoans) were found to be similar. The diversity of the taxa associated with the *L. pertusa* reefs is around three times as high as that of the surrounding soft sediment seabed, indicating that these reefs create biodiversity hotspots and increased densities of associated species (Tursi *et al.*, 2004).

Lophelia pertusa. Credit: Angelo Tursi. **See colour plate, p. 62.**

So-called cold-water coral reefs, which are currently the object of strong conservation efforts in the NE Atlantic (Gubbay, 2003), are also present in the Mediterranean. Though most of such occurrences are subfossil and date back to the last glacial age, witnessing cooler seawater and better food availability, some living relict reefs have been found (Mastrototaro *et al.*, 2002; Tursi *et al.*, 2004). During the coldest phases of the Pleistocene, these deep-sea coral banks were equally common in the Mediterranean basin, as proven by their recurrence within outcropping and submerged fossil assemblages found on the tops and flanks of submarine canyons, seamounts and banks of the whole Mediterranean at water depths in excess of *ca.* 300 m (Pérès, 1985). The postglacial onset of comparably warm, homothermic, nutrient-poor deep waters in the Mediterranean basin has been advocated as the major factor controlling the decline and almost total disappearance of these deep-sea cool water corals, although an indirect human impact cannot be ruled out. Pérès (1985) points

out that many subfossil white coral mounds are covered by a fine layer of sediment, possibly accumulated since historic times, due to progressive forest destruction by man. The most important frame-builder *Lophelia* has been identified as particularly vulnerable to the oceanographic changes linked to the glacial-postglacial transition, whilst viable *Madrepora* mounds still occur in some spotty areas of the Mediterranean basin. Deep-water corals are passive suspension feeders, and they are preferentially distributed on topographic irregularities (seamounts, promontories, canyons). Communities of white corals in the deep Mediterranean are dispersed elsewhere (e.g., Blanes canyon, Lacaze-Duthier canyon, Alboran Sea; Zibrowius, 1980; Zabala *et al.,* 1993). Considered as relict communities, they are mainly composed of dead branches, or with only a few terminal portions remaining alive. These *residual* colonies are often associated with sites receiving larger food inputs (e.g. in or near submarine canyons), and it has been postulated that the decline of these corals in the Mediterranean was linked with a decrease in trophic resources correlated with a water temperature increase (Delibrias and Taviani, 1984, for the Alboran sea). Recently, a healthy and well developed *Lophelia-Madrepora* deep-sea coral mound has been discovered in the Ionian Sea (North of Calabrian Arc), offshore from the Apulian platform, at between 300 and 1000 m depth (Giuliano *et al.,* 2003). As a general rule, it has been proposed that the last, relict, deep-water Mediterranean coral banks would settle areas characterized by local peculiar oceanographic conditions, enhancing nutrient availability which has so far prevented their total eradication from this basin, where present conditions are not adequate for them.

Though direct trawling (or other fishing methods) on coral reefs is the main obvious threat to the remaining Mediterranean deep-water coral reefs, trawling in the neighbouring bathyal mud bottoms could be equally deleterious on these suspension feeders, due to the ef-fects of sediment resuspension and related increased sedimentation, even at depths well beyond the ones trawled. A recent study showed evidence of how sediment resuspension from trawlers working at 600-800 m depth reached a depth of 1200 m (Palanques *et al.,* 2004).

- **Cold-water coral reefs formed by live colonies of the scleractinians *Lophelia pertusa* and *Madrepora oculata* are associated with highly productive environments, harbour high levels of diversity and are threatened (directly and indirectly) by fishing.**


4.4. Seamounts

Rising up from the sea floor, seamounts are steep-sided submerged mountains that provide unique habitats in oceans all over the world. Strictly speaking, seamounts are discrete areas of topographic elevation higher than 1000 m above the surrounding seafloor (International Hydrographic Bureau, 2001). The tops of seamounts can range from near the surface to several thousand metres below it.

While our knowledge of seamounts in the global oceans is far from complete, enough sampling has been done to show that seamounts support biologically unique and valuable habitats, being highly productive, and with high rates of biodiversity and endemisms (Richer de Forges *et al.,* 2000). They may act as refuges for relict populations or become centres of speciation (Galil and Zibrowius, 1998).

Though not comparable to certain Atlantic or Pacific areas, the Mediterranean sea harbours some impressive seamounts whose biodiversity values are still poorly known, in the Gulf of Lions, in the Alboran sea, in

Desmophyllum cristagalli.
Credit: Angelo Tursi. **See colour plate, p. 62.**

Eratosthene Seamount

Nile Fan
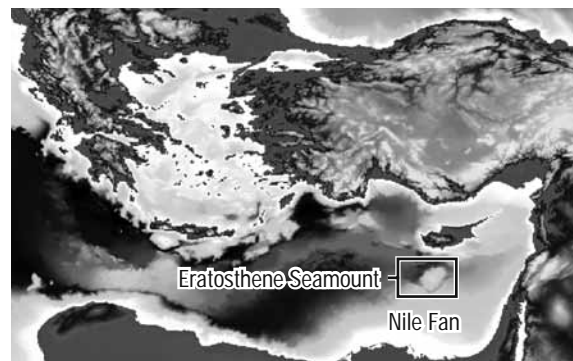
Credit: *GEBCO Digital Atlas, 2003,* Modified.

Box 6. The discovery of a deep-water coral reef in the Ionian Sea

In August 2000 a scientific cruise carried out by a team of the University of Bari rediscovered a living deep-sea coral reef 20-25 miles off Cape of Santa Maria di Leuca, southern Italy, in the Ionian Sea. The reef – already reported by Marenzeller in 1893 – is dominated by *Lophelia pertusa* and *Madrepora oculata*, though two further species of scleractinian corals were also found (*Desmophyllum cristagalli* and *Stenocyathus vermiformis*). The most important reef building species, *Lophelia* and *Madrepora*, occurred in samples taken from 425 to 1110 m depth.

A total 58 taxa (including 12 species of bone fish and 5 condrichthyans) were recovered and identified as characteristic species of the reef, associated species, accompanying species and co-occurring species, depending on their degree of reliance on the reef. Apparently, the vertical flux of organic matter in the area is remarkably high, which could result in a high availability of food to suspension feeders like *Lophelia* and *Madrepora*.

According to data recovered from the Ionian Sea reef, Tursi *et al.* (2004) postulate that the habitat provided by the biocoenosis of deep-water coral in the Mediterranean Sea acts as an 'oasis in the desert' (biodiversity hot-spot). It creates a three-dimensional structure that provides ecological niches to a diversity of species, including deep-sea characteristic species such as the Mediterranean orange roughy (*Hoplostethus mediterraneus*) and species of economic interest such as the rose shrimp (*Aristaeomorpha foliacea*) or the conger (*Conger conger*). These reefs, being a natural deterrent to trawling, are thought to produce a positive spill-over effect on the deep-water demersal resources intensively fished on the neighbouring muddy bottoms.

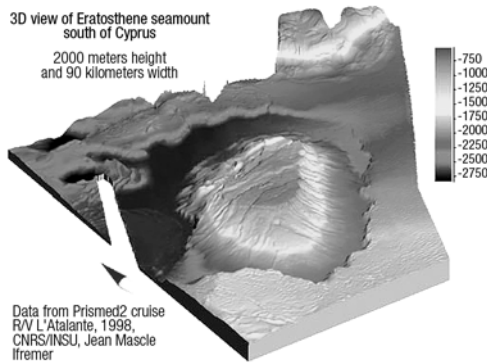Credit: *GEBCO Digital Atlas, 2003,* Modified.
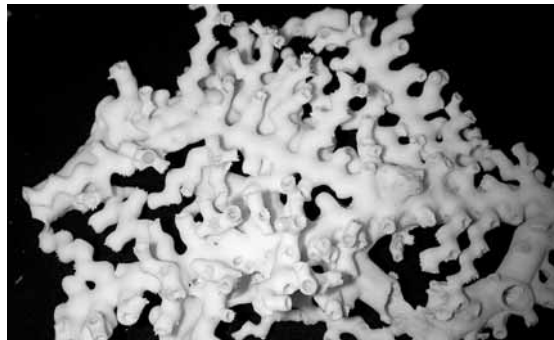
Madrepora oculata. Credit: Angelo Tursi.
See colour plate, p. 62.
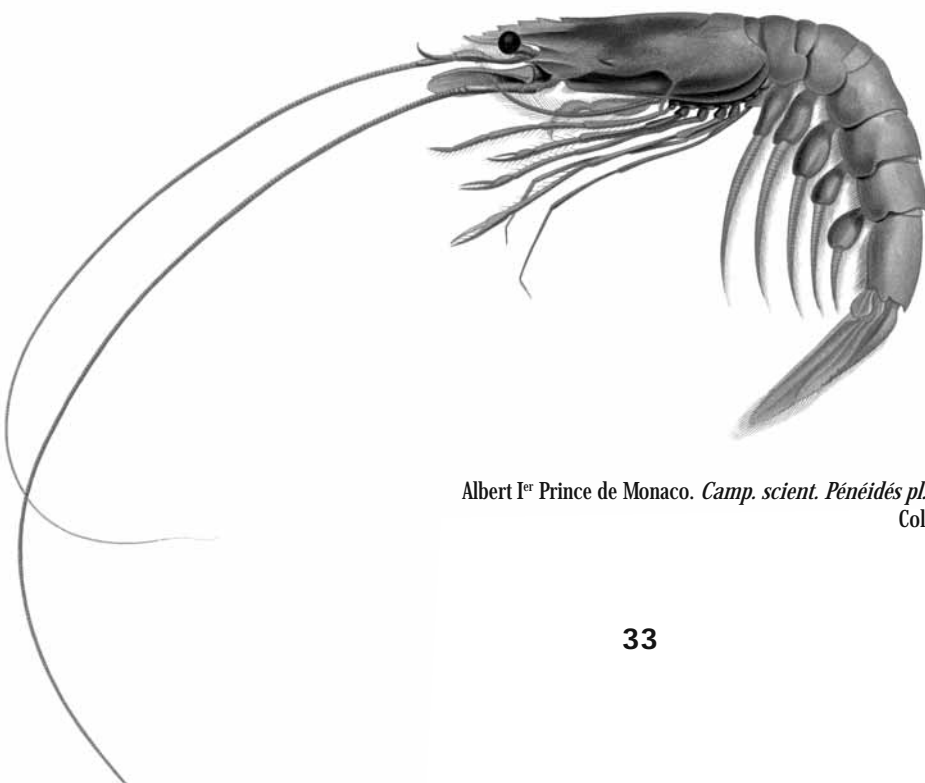
Aristeomorpha foliacea
Albert Ier Prince de Monaco. *Camp. scient. Pénéidés pl. III.* EL. Bouvier del, M. Borrel pinx.
Coll. Oceanographic Museum, Monaco.
See colour plate, p. 59.

the eastern Tyrrhenian basin, to the south of the Ionian abyssal plain and in the Levantine seas. Located off the south coast of Cyprus and west of Israel lies the massive Eratosthenes Seamount, 120 km in diameter at the base, and extending from the seafloor to within 800 m of the sea surface. Directly adjacent to the Eratosthenes Seamount is a deep (approximately 2750 m) depression, part of the Herodotus abyssal plain.

3D view of Eratosthene seamount south of Cyprus

2000 meters height and 90 kilometers width

Data from Prismed2 cruise R/V L'Atalante, 1998, CNRS/INSU, Jean Mascle Ifremer

Credits:

Sardou O. and Mascle J., 2003. Cartographie par sondeur multifaisceaux du Delta sous marin du Nil et des domaines voisins. Publication spéciale CIESM/Géosciences-Azur, série Carte et Atlas.

Loubrieu B. and Satra C., 2001. Cartographie par sondeur multifaisceaux de la Ride Méditerranéenne et des domaines voisins. *Comité Français de Cartographie,* n°168, pp. 15-21.
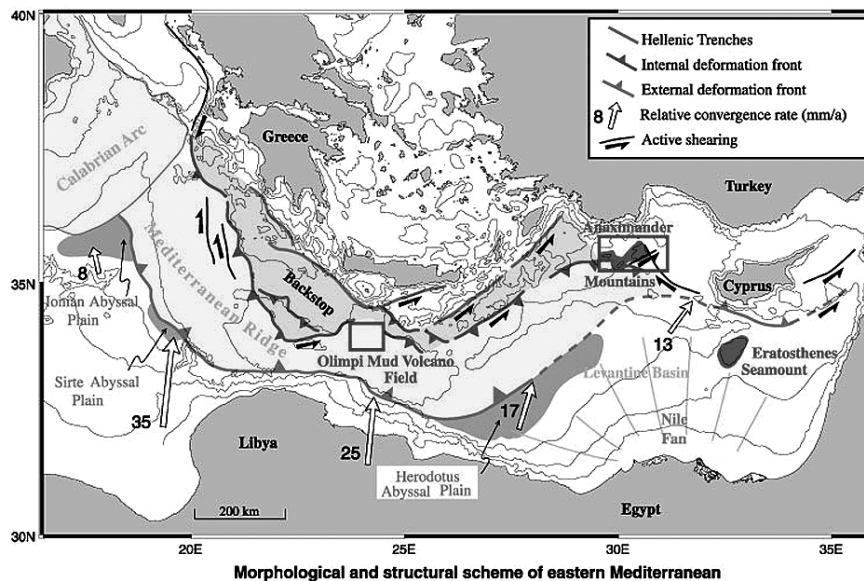
See colour plate, p. 63.

Galil and Zibrowius (1998) obtained benthos samples from the Eratosthenes Seamount and found that the fauna living on the seamount was rich and diverse, including two scleractinian corals (*Caryophyllia calveri*, *Desmophyllum cristagalli*), and a large array of other invertebrates in higher densities than sites of comparable depth in the Levantine basin. Red shrimps of commercial interest (*Aristaeomorpha foliacea*, *Aristeus antennatus* and *Plesionika martia*) were also caught by the beam trawl sampler.

Commercial trawling on seamounts, primarily targeting the orange roughy in the South Pacific, has considerable impact on the benthos of these communities (Koslow *et al.,* 2000).

- **Seamounts are submerged mountains that rise 1000 m or more above the surrounding seafloor and provide unique habitats with a wide array of invertebrates, including interesting corals (*Caryophyllia calveri*, *Desmophyllum cristagalli*). The biological communities of seamounts are threatened by fishing in some areas of the world (e.g. south Pacific seamounts) and these fragile communities require urgent protection.**

Box 7. The Mediterranean Ridge

The Mediterranean Ridge consists of a more than 1500 km long tecto-sedimentary-accretionary prism, which results from the offscraping and piling up of thick sedimentary sections, and which runs from the Ionan basin, to the west, to the Cyprus arc to the east. This complex was created by subduction of the African plate beneath the Eurasian plate to the north. It is an extensive fold-fault system corresponding to recent uplift and folding of past abyssal plains.

Credit:
Loubrieu B. and Satra C., 2001.

See colour plate, p. 63.

Morphological and structural scheme of eastern Mediterranean

5. Anthropogenic impact in the deep Mediterranean

5.1. Fisheries

Deep-sea fishing[1] is a relatively new phenomenon, and expanding in part of the world. In the Western Mediterranean it has become relatively important since the 1940-50's due to the high commercial value of deep sea Aristeid shrimps (mainly *Aristeus antennatus* and *Aristaeomorpha foliacea*).

Most oceanic fisheries have been concentrated in the upper regions of the oceans, either on the continental shelves for demersal fish, or the epipelagic regions for fish such as tuna, billfish or sharks (Haedrich, 1996). Now there is a pronounced shift of fisheries from shallow to much deeper regions (Hopper, 1995, Merrett and Haedrich, 1997), especially in the demersal fisheries, motivated by the growing number of collapsed fish stocks on the continental shelves, and in the Mediterranean, by the high value of deep-sea aristeid shrimps. Globally, large fish appear near the bottom in the deep sea; in the Mediterranean, fish are complemented by large shoals of aristeid shrimps that make a traditional (since the 1940's) deep-sea resource in many areas. Deep-sea fisheries now occur in parts of the world down to 1800 m depth (Haedrich, 1996). However, due to the slow growth of typical deep-sea fishes, it is unlikely that demersal deep-sea fisheries conducted by bottom trawl will ever be important in the long term because replacement rates are higher than current harvest rates (Haedrich, 1996). Once a deep-sea stock is depleted, it

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[1] There is no accepted definition of what constitutes a deep-sea fishery. The *Deep Sea 2003* conference considered deep-sea fisheries as those operating beyond the continental shelf break (i.e. deeper than 200 m, Lack et *al.,* 2003). The ICES (ICES, 2003) has defined deep-sea fisheries as those deeper than 400 m, while Koslow *et al.* (2000) consider deep-sea fisheries as those occurring deeper than 500 m. In this document, although we have generally reported information available from 200 m, we will focus on deep-water fisheries deeper than 400 m, i.e. following the ICES defintion.

will not return within a reasonable time span (Haedrich, 1996, Lack *et al.,* 2003; Koslow *et al.,* 2000). Several deep-water stocks are heavily exploited, or have collapsed, in the world's oceans: redfish (*Sebastes* spp.) and grenadier (*Coryphaenoides rupestris*) stocks in the North Atlantic; orange roughy (*Hoplostethus atlanticus*) in the South Pacific.

Currently, the Mediterranean fisheries below 200 m depth target decapod crustacean resources. In the upper slope (down to *ca.* 500 m), the "deep-water" shrimp *Parapenaeus longirostris* and the Norway lobster *Nephrops norvegicus* represent important fisheries in certain areas. These fisheries have important quantities of other commercial species, such as *Merluccius merluccius, Micromesistius poutassou, Conger conger, Phycis blennoides* and, to a lesser extent, monkfish (*Lophius* spp.) and the cephalopod *Todarodes sagittatus*. The by-catch of other decapod crustaceans is increasingly commercialised: glass shrimp *Pasipahea* spp., *Acanthephyra eximia, Plesionika* spp., *Geryon longipes, Paromola cuvieri.*

Deeper fisheries (approx. 400 m to 800 m) target almost exclusively aristeid shrimps (*Aristaeomorpha foliacea* and *Aristeus antennatus*), though some hake is also harvested by trawlers and bottom longliners. Other deep sea fisheries exist in the Mediterranean, but on a smaller scale: longliners targeting hake in the Gulf of Lions and the Italian Ionian sea, and longlines targeting the deep-sea shark *Hexanchus griseus* in the southern Aegean sea (600-1500 m, Sardà *et al.,* 2004a).

In the Greek Ionian sea, *A. foliacea* is more abundant than *A antennatus.* However, deep-water fisheries (> 500 m) are not yet well-developed in Greece (Mytilineou and Politou, 1997; Politou *et al.* 2003).

Even with a relatively short history of fishing, red shrimp stocks are already showing symptoms of overexploitation. Some *A. antennatus* stocks have collapsed in recent decades (late 1970's - early 1980's in Liguria, Orsi Relini and Relini, 1988), or show signs of overexploitation (Carbonell *et al.,* 1999), while some stocks (Demes-
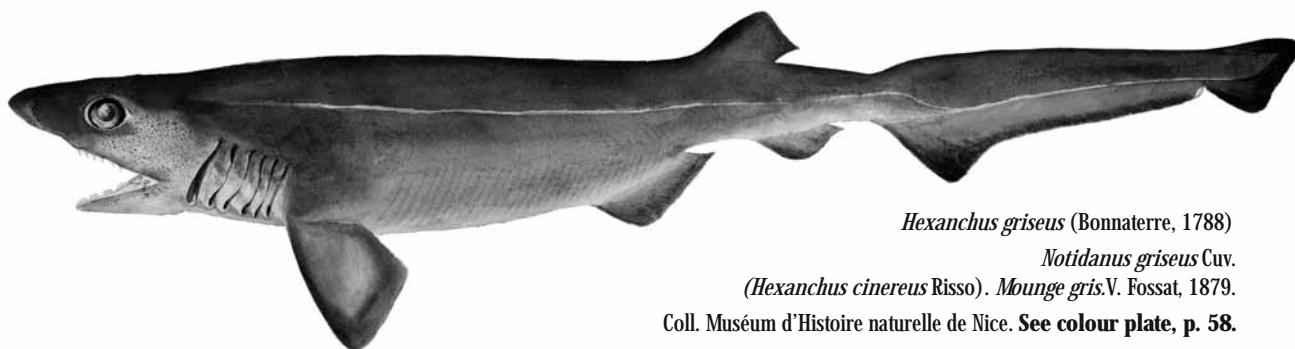
Hexanchus griseus (Bonnaterre, 1788)
Notidanus griseus Cuv.
(*Hexanchus cinereus* Risso). *Mounge gris.* V. Fossat, 1879.
Coll. Muséum d'Histoire naturelle de Nice. **See colour plate, p. 58.**

tre and Lleonart, 1993; Bianchini and Ragonese, 1994) seem to be underexploited to fully exploited. *A. foliacea* has decreased significantly from the commercial catches in many areas (Gulf of Lions: Campillo, 1994; Catalan sea: Bas *et al.,* 2003, Tyrrhenian sea: Fiorentino *et al.,* 1998) and is considered overexploited in Italian waters (Matarrese et al., 1997; D'Onghia *et al.,* 1998).

The potential fishing interest of the currently unexploited bottoms below 1000 m depth in the Western Mediterranean is very limited. This is so because the overall abundance of crustacean species is considerably lower, and fish communities are largely dominated by fish either of non-commercial interest (like the smooth head *Alepocephalus rostratus*) or of a small size (such as the Mediterranean grenadier *Coryphenoides guentheri*). If these species ever become of economic interest, the ecosystem effects of fishing could be very important. Given the importance of depths below 1000 m for the juveniles of red shrimp (**see Box 9**) and for the reproduction of many fish species, the exploitation of these bottoms would probably entail negative impacts on shallower ecosystems, beyond the rapid depletion of particularly vulnerable deep-sea megafauna communities.

In their review, Koslow *et al.* (2000) pointed out that deep sea fishes follow a highly conservative ecological strategy; the low fecundity and the low metabolic rates in a stable environment like the deep sea imply a high vulnerability for their populations.

- **Deep-water ecosystems are highly vulnerable to commercial exploitation due to the low turnover rates of the species adapted to these environments.**

- **Commercial exploitation based on deep-sea trawling has become increasingly important since the 1950's in the Mediterranean, targeting deep-water shrimp species (*Aristeus antennatus* and *Aristaeomorpha foliacea*) down to 1000 m depth.**

- **Trawling has an extremely important direct impact on sea-bottoms, as demonstrated in continental shelves throughout the world, or in the south Pacific orange roughy seamount fisheries.**

- **Given the state of shallow water fisheries, where most stocks are fully to over-exploited, and the high economic value of deep-water shrimps, increasing pressure to fish in deep water is to be expected in the near future.**

5.2. Other anthropogenic threats to the deep-sea Mediterranean

Anthropogenic threats are not limited to fishing. Grassle (1991) identified other sources of man-mediated impacts that may threaten the conservation of the diversity, structure and functioning of deep-water ecosystems. Among these, we can cite waste disposal (solid trash and other toxic compounds), pollution (Haedrich, 1996), oil exploration/pipelines, or, more indirectly, climate change (Danovaro *et al.,* 2001).

Kress *et al.,* (1993) reported the results of a monitoring study of the disposal of coal fly ash in the Eastern Mediterranean sea. The coal fly ash was dumped 70 km offshore from the coast of Israel, at 1400 m depth. A comparison of the benthic fauna at the centre of the disposal site with that of a control area indicated a severe impoverishment of the benthos in the affected area.

During a monthly cruise of the *Meteor* in the Eastern Mediterranean in 1993 between 194 and 4614 m depth, the litter retained in a beam trawl net included solid waste such as plastic and glass bottles, metal cans, nylon rope and plastic sheeting (Galil *et al.,* 1995). Although the disposal of all litter (except food waste) is prohibited in the Mediterranean, the study presented evidence that this regulation is routinely ignored: 70% of the trawl hauls contained litter (Galil *et al.,* 1995). Refuse generated by vessels is a major source of litter in the Mediterranean.

Toxicological studies have found that PCB levels in deep-water fishes (*Alepocephalus rostratus*, *Bathypterois mediterraneus*, *Coryphaenoides guentheri* and *Lepidion lepidion*) were lower than in coastal fishes, close to


Trash recovered from 2000 m depth in the Eastern Mediterranean.

the pollution sources, but much higher than in shelf to upper slope fishes (*Micromesistius poutassou*, *Phycis blennoides* and *Lepidorhombus boscii*) and within the same range as a top predator, such as *Thunnus thynnus* (Fig. 7, Porte *et al.,* 2000; Solé *et al.,* 2001). The levels of TPT (triphenyltin) were higher in two bathyal species (*Mora moro* and *Lepidion lepidion*) than in bivalves and fishes inhabiting harbours and the coastal area (Fig. 8, Borghi and Porte, 2002). These results point to a differential accumulation of PCBs and TPTs by deep-water fishes, suggesting that bathyal and abyssal food chains may already be affected by human activities on land.
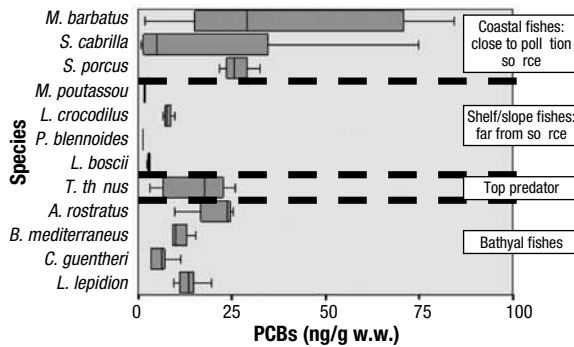
Mar. Ecol. Prog. Ser. 2000, 192: 259-266; *Deep-Sea Res.* 2001, 48(2): 495-513

Fig. 7. Concentration of PCB in fish tissue (from Porte *et al.,* 2000; Solé *et al.,* 2001).
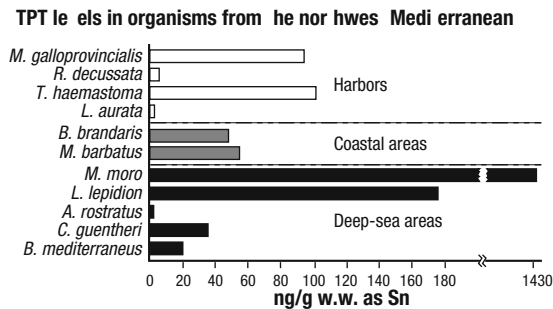
The deep-sea fish studied by the scientists at Spain's Institute of Chemical and Environmental Research show that TPT is persisting in the environment and subject to long-range transport. The levels of PCBs, dioxins, and TPT in these deep-see fish are lower than the levels of those contaminants found in organisms inhabiting harbors and coastal areas, but the TPT levels are much higher.

Fig 8. Triphenyltin concentration in Mediterranean fish (from Borghi and Porte 2002).

The effect of land-based human activity on deep-sea ecosystems has a long history in the Mediterranean, and dates to pre-industrial times – if we accept the suggestion by Pérès (1985) that one explanation for the often encountered sub-fossil white coral assemblages (covered by a fine layer of sediment) is the progressive forest destruction by man since the times of the early Mediterranean civilisations.

• **Human threats to the deep sea include waste disposal of chemical and solid waste, chemical pollution by land-based activities and the long-ranging effect of climate change.**

Box 8. Increasing catches, diminishing catch rates

The reported landings of aristeid shrimps in the Mediterranean have steadily increased over the last decade, with a maximum of 6,637 t in 2000 (GFCM capture production 1970-2002). However, a detailed analysis of the red shrimp (*Aristeus antennatus*) fishery, conducted by Bas *et al.* (2003) in the port of Blanes (Catalonia), showed that catch rates (in kg/HP) have decreased dramatically between the beginning of the fishery in the 1950's and the present (1997-2000): from around 0.4 kg/HP to around 0.04 kg/HP. The catches are increasing, but at a very high energetic cost: the engine power required to produce one unit of red shrimp is ten times what it was 50 years ago. The high prices fetched by red shrimps (typically above 30 €/kg on first sale) explain the increased effort towards this deep-water living resource, raising concern about its long-term sustainability.
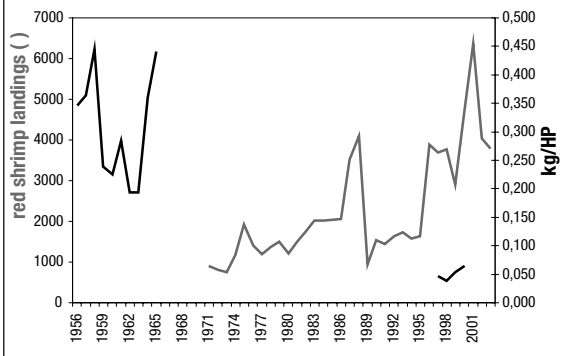
Box 9. An important deep-sea living resource in the Mediterranean, the red shrimp *Aristeus antennatus*

A. antennatus is present in the entire Mediterranean sea (except the Adriatic and the Black sea) and the Atlantic from the north Iberian peninsula to Angola. It is found, locally, from 100-200 m depth (Algeria, Italy, Egypt) to 3300 m (Sardà *et al.,* 2003a). However, its abundance is high only from 600 to 800 m, where the fishery takes place.

The growth rates of *A. antennatus* (k ranging from 0.25 to 0.3 yr^{-1}, Demestre and Martín, 1993) are much lower than those of other penaeids (k between 1.8-3.6 yr^{-1}). Estimates of natural mortality (M) are also much lower, around 0.5 yr^{-1} compared to M=1-4 yr^{-1} in other penaeids (Demestre and Martín, 1993). Hence, it is a typical deep-sea species of low productivity.

The population comprises a high proportion of adult females at depths shallower than 1000 m, with high density. Females form aggregations in spring and summer. Juveniles and males are abundant below 1000 m depth, with low population density. The smallest juveniles (CL < 15 mm) are recruited almost exclusively below 1000 m, probably after *ca.* 1 year of larval / post-larval development (Cartes and Demestre, 2003). Juveniles are present, seasonally, in submarine canyons.

Sardà *et al.* (1994) reported that the stock of *Aristeus antennatus* in the NW Mediterranean appears to remain constant at approximately optimum levels of exploitation because part of it is unexploited below 1000 m depth. The study provided a rationale for interpreting the seasonal catch fluctuations observed in the red shrimp fishery. Females contribute to most of the catches shallower than 1000 m throughout the year, and the catch levels vary seasonally. Catch of males varied seasonally and by depth. Juveniles were present in catches from autumn to spring, and varied significantly by depth and season. The role of local topographic features, *viz.* submarine canyons, in the recruitment of this species was important.

The fishery shows important fluctuations over the short and mid-term (cycles of minimum catches every 8-10 years, Carbonell *et al.,* 1999) and seasonal fluctuations (summer fishing occurs usually in deeper waters and in autumn-winter around 400 m). Additionally, a general decrease in catches in the Spanish Mediterranean since the early 1950's is noted: from a peak of ~900 t in 1953 to 200-400 t in the 1980s (350 t in Demestre and Martín, 1993). This decreasing trend in the catches has been accompanied by *i)* an important increase in the engine power of the trawlers involved in the fishery; and *ii)* an important increase in the economic value of this species.

The evolution of exploitation in the Balearic Islands shows an overall increasing trend (Carbonell *et al.,* 1999), with a period of very low catches at the beginning of the 1980's. This decrease in catches coincided with that observed in other shrimp fishing grounds in the western Mediterranean (Ligurian Sea, Gulf of Lions). From 1983 a recovery in catches began, and in recent years the annual catch has stabilised at a level similar to that attained during the 1970's.

Landings of this resource showed high fluctuations in all Italian Seas. In the Ligurian Sea, *A. antennatus* was an important resource until 1979. In the period 1976-1980 the population decreased progressively until commercial fishing in the area was suspended. As of 1987 the catches increased and, at present, the quantities are of commercial interest, although very variable from year to year (Relini and Orsi Relini, 1987; Orsi Relini and Relini, 1994). Orsi Relini and Relini (1985) formulated some hypotheses to explain this variability, such as environmental decay, overfishing, pathologic causes, hydrological changes, and failure of recruitment due to predation upon juveniles. In the Ionian Sea, absence of *A. antennatus* was frequently observed in concomitance with high catches of *Micromesistius poutassou* and *Phycis blennoides* (Matarrese *et al.,* 1997).

Many authors coincide in stressing that the absence of fishing below 1000 m helps explain the high levels of exploitation sustained by the species. Most of the population fished are adult females, while the males and juvenile fraction of the population, living deeper than 1000 m, may help replenish the exploited stock. However, an increase in the exploitation rates of adult females might undermine the reproductive capabilities of the stock. Additionally, exploiting the juvenile fraction (deeper than 1000 m) might lead to recruitment overfishing in the future.