



A multidisciplinary approach to the understanding of hydromedusan populations inhabiting Mediterranean submarine canyons

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Abstract

Studies carried out in four submarine canyons in the northwestern Mediterranean Sea have resulted in the discovery of a new fauna composed chiefly of hydromedusae. This finding has led us to postulate the existence of a singular planktonic community in these canyons that is probably maintained by the flux and deposit of organic material from the continental shelf. The specific composition and abundance of the populations differ from canyon to canyon and seem to be related to vertical fluxes, topography, and both the hydrographic and ecological features of each canyon. This hydromedusan fauna is characterized by meroplanktonic species that appear to live out their entire life cycles inside the canyons. Those cycles seem to be linked to seasonal production processes related to factors such as canyon topography, sedimentation, and circulation of water masses within the canyons. The present study indicates that submarine canyons could be a new key habitat to an understanding of the biodiversity of coastal and shelf zones. The origin of the deep-water Mediterranean fauna is reviewed, and the hypothesis of a Tethys origin for some of the deep-water hydromedusae endemic to the Mediterranean is entertained. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Submarine canyons incised in the continental slope may act as conduits for transport to the deep ocean basin. Organic matter originating in the water column and on the continental shelf flows along the canyon axis and sinks along with inorganic particulate matter. Sizeable accumulations of sediment and detritus that yield a steady supply of organic and inorganic debris have been observed on the floors of submarine canyons in different parts of the world (e.g., Rowe et al., 1982; McHugh et al., 1992; Vetter, 1995).

Sedimentation in submarine canyons is regulated mainly by currents flowing along the canyon axis. Current flow is predominantly vertical next to the bottom (Shepard et al., 1974; Shepard et al., 1979; Gardner, 1989; Hickey, 1995; Durrieu de Madron et al., 1996). Recent modelling of circulation patterns inside submarine canyons suggests that downwelling of shelf-slope water takes place along the upstream wall of the canyons and that upwelling typically occurs along the canyon axis and downstream wall (Klinck, 1995; Signorini et al., 1997). Upwelling and downwelling, sedimentation (organic and inorganic fluxes), and hydrodynamics all help to create a special habitat characterized by high local density and diversity of benthic and pelagic fauna greater than that in other habitats along the continental shelf and slope (Gage and Tyler, 1992; Greene et al., 1992; Vetter, 1995; Cartes, 1998).

Within the framework of the EUROMARGE NB Project, several moorings equipped with sediment traps were deployed inside and around the submarine canyons in the northwestern Mediterranean. The main object of the project was to study particle flux transfer from the continental shelf to the slope via submarine canyons. Preliminary results have shown that the canyons harbour a considerable accumulation of sediments and organic matter. Deposition processes are related to the transfer and fate of suspended particles in the water column along the Liguro–Catalan–Balearic Current (Palanques et al., 1994; Canals et al., 1995), and with a sedimentary depocentre between 700 and 1 000 depth. Besides sediment particles, a large assortment of gelatinous zooplankton was collected in the traps. Hydromedusae were the most abundant group of swimmers in the samples, most of them undescribed species (Gili et al., 1998,1999).

Hydromedusae are an important component of the deep-sea fauna; their diversity increases between 500 and 800 m (Kramp, 1968; Larson et al., 1992) and between 1000 and 1600 m (Pugh et al., 1997). Most deep-sea medusae are known from midwater levels, and few have been reported inhabiting the water layers near the sea bed, where conventional plankton sampling is difficult to carry out (Childress et al., 1989). However, observations made from manned submersibles (Mills, 1982; Mackie, 1985; Larson et al., 1992) have revealed concentrations of medusae near the sea floor. Observations made in the submarine canyon in Monterey Bay off California indicate that these topographic structures are probably an especially suitable habitat for medusae and other planktonic organisms (Matsumoto et al., 1997).

The principal object of this paper is to analyse the spatial and temporal distribution patterns of the hydromedusae inside certain Mediterranean submarine canyons in relation to different topographic features, sedimentation regimes, and hydrographic conditions. The hypothesis postulated is that the diversity and abundance of medusan

populations inhabiting submarine canyons are governed by geological and biological processes operating on two different time scales, namely, historical and present-day events.

Circulation in the northwestern Mediterranean is dominated by the Liguro-Provençal or Northern Current flowing along the continental slope. This current circulates through the Gulf of Lions, where it is sometimes influenced by a complex system of currents (Millot, 1990; Salat et al., 1990), and then penetrates into the Balearic Basin. Geostrophic circulation over the shelf and slope is controlled by a shelf-slope density front (Font et al., 1988) generated by the gradient between the low-salinity waters from the shelf and the more saline waters of the central basin. Associated with this frontal structure, the Northern Current flows along the continental side of the front as part of the northwestern Mediterranean cyclonic circulation pattern (Millot, 1987; Font et al., 1988).

2. Materials and methods

Mooring lines carrying sequential sediment traps and current meters were deployed at selected sites in the northwestern Mediterranean. The sediment traps were located 30 m above the bottom (mab), inside the Planier, Lacaze-Duthiers, and Foix canyons and on the continental slope in the Balearic Sea, at depths of approximately 1000 and 500 m at all locations. Inside each canyon, a sediment trap was deployed in intermediate waters (500 mab), that is, at midwater level, on the mooring lines deployed at the deeper sampling sites at 1000 m. Another sediment trap was also deployed at a depth of about 1000 m on the open slope outside each canyon. Location of the mooring lines is illustrated in Fig. 1.

Four sets of samples were studied: a complete annual sampling period from Foix Canyon (April 1993–April 1994) and from the Balearic site (May 1994–May 1995) and more irregular sampling (for logistical reasons) spanning two years in the Planier (October 1993–December 1995) and Lacaze-Duthiers (October 1993–December 1995) canyons. The sample collection interval was set for every 15 or 16 d, depending on the month, with six-month deployments at each site. Technicap model PPS3 sediment traps that included a carousel with 12 rotary collectors were employed (Heussner et al., 1990). *Aanderaa* model RCM 7-8 current meters with a sampling periodicity of 60 and 120 min were also tethered to the mooring lines.

Before the trap deployments, the sample tubes were rinsed and filled with a buffered solution of 5% formaldehyde in filtered sea water to prevent degradation of the organic matter in the trapped sediments. The samples collected were processed at the laboratory according to the method described by Heussner et al. (1990). The total sample was divided into several aliquots for the different analyses, and the biological components that were not part of the vertical flux, known as “swimmers” (Michaels et al., 1990) (the large living organisms that swim into the trap sample funnel and are preserved by the formaldehyde), were sorted under a dissecting microscope. The condition of the preserved gelatinous material was excellent, and it was examined for taxonomic study.

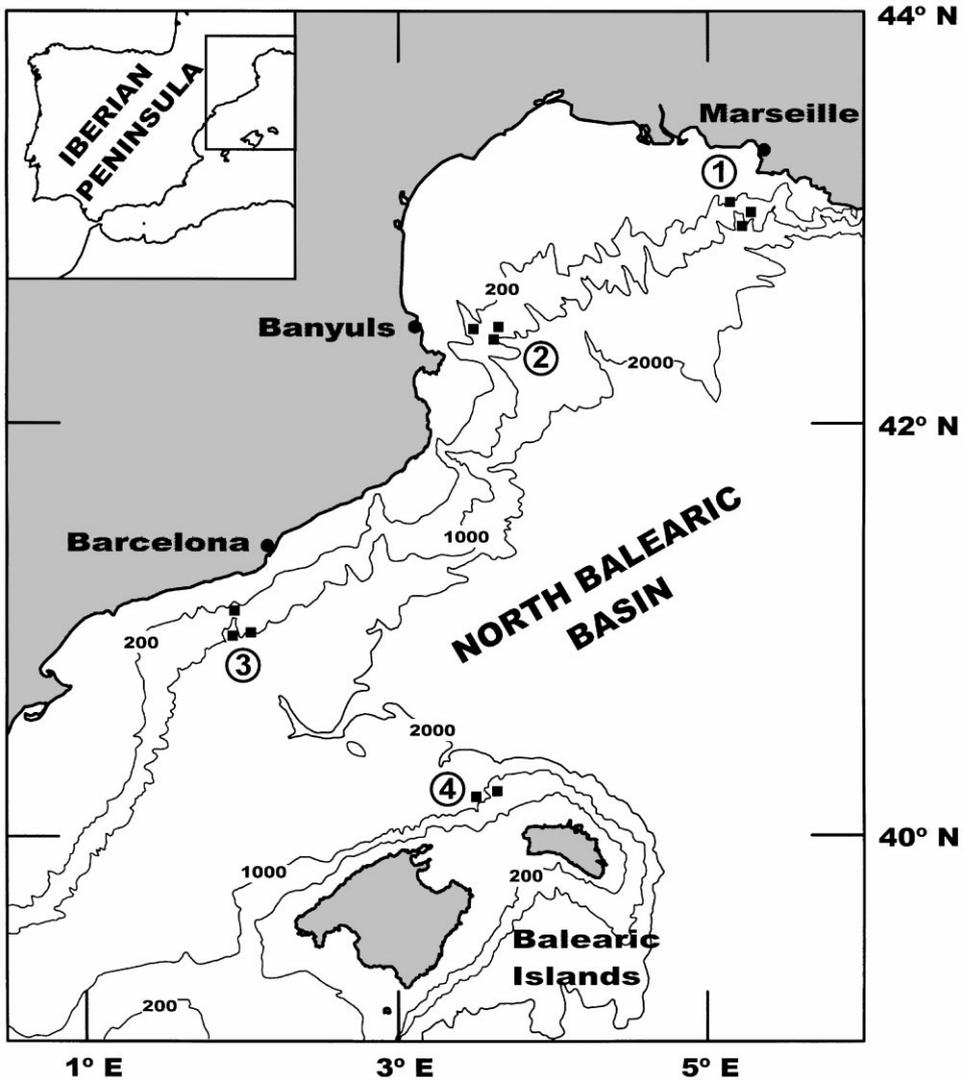


Fig. 1. Map of the area studied showing the location of the mooring line sites (black squares) during the EUROMARGE-NB experiment. Site1: Planier canyon; Site 2: Lacaze -Duthiers canyon; Site 3: Foix canyon and Site 4: Balearic slope. Sites 1 and 2 are in the Provençal margin region, Site 3 in the Catalan margin and Site 4 in the Balear margin.

Sample dry weight was determined from three subsamples of filtrates filtered through $0.45 \mu\text{m}$ Millipore filters, rinsed with distilled water, and dried at 40°C for 24 h. Total mass flux was calculated from the dry weight samples, collecting trap area, and sampling interval. Biogenic silica (opal) was analysed by wet-alkaline extraction with sodium carbonate according to the method described by Mortlock and Froelich (1989).

Morphology and seismic stratigraphy (see Discussion) were studied from seismic profiles. These profiles were recorded on two oceanographic cruises performed in the study area aboard the R/V *Cornide de Saavedra* in 1979 and 1982, using Sparkers systems and air guns. Seismic profiles were collected in analogue format.

3. Results

Twenty species of hydromedusae were collected by the sediment traps at the four mooring sites (Table 1). In Planier and Lacaze-Duthiers canyons most of the species were collected in the traps located at intermediate depths inside the canyons. At the Balearic Island site, which was in fact a bight rather than a canyon, no differences were observed between the populations in the traps “inside” and “outside” the sampling site. A very interesting finding is that no medusae were collected in the traps located outside Foix Canyon. Another interesting result was the differences in the numbers of individuals collected in the different canyons. In Planier Canyon most individuals were collected at intermediate depths, whereas in Foix and Lacaze-Duthiers canyons specimens were restricted almost exclusively to the traps located near the bottom along the canyon axis. All the new species were more common or exclusive to the deepest trap on the canyon axis, except the narcomedusan *Cunina simplex* (Gili, Bouillon, Pagès, Palanques, Puig, 1998) which was recorded at mid-water level.

The number of endemic species and individuals increased from Planier Canyon to Foix Canyon downstream of the Liguro-Provençal Current. At the Balearic site the bulk of the population was composed of common Mediterranean hydromedusae, mainly *Solmissus albescens* (Gegenbaur, 1856) (Table 1). In both Foix (Fig. 2) and Lacaze-Duthiers canyons medusae were captured between April and September 1993. In Planier Canyon and the Balearic (Fig. 3) site, some species (not endemic) were also found in autumn and winter. *Ptychogastria asteroides* (Haeckel, 1879), *Solmissus albescens*, and *Homoeonema platygonon* (Browne, 1903) were the only species common to all the canyons and were collected mainly in traps located in intermediate waters.

3.1. Topography

The general topographic characteristics of the sites studied were similar, with the exception of the Balearic site (Fig. 4). Planier, Lacaze-Duthiers, and Foix canyons are deeply incised in the continental margin, and their heads intersect with the continental shelf break. Their transverse profiles are mainly V-shaped. However, Foix Canyon is more confined than the others. The width of Planier and Lacaze-Duthiers canyons increases from 4–5 km at the head to 10–12 km where the axis attains 1500 m in depth. Foix Canyon is more sharply incised, and its width decreases from 4 km at the head to 2 km where the canyon axis descends to 1200 m in depth. The walls of these canyons are steep, with slopes ranging from a minimum of about 6° in all the canyons up to a maximum of 23° in Foix Canyon. The Balearic site is a 22-km-wide depression in the north Balearic slope. The maximum slope gradient of this depression is only about 3.7°.

Table 1
Species collected in the four submarine canyons studied

	FOIX			LACAZE-DUTHIERS			PLANIER			BALEARIC ISLANDS		
	Ind.	Depth (m)	Season	Ind.	Depth (m)	Season	Ind.	Depth (m)	Season	Ind.	Depth	Season
<i>Calyptopsis simplex</i>	-	-	-	1	500	Dec	-	-	-	-	-	-
<i>Amphinema rubra</i>	-	-	-	-	-	-	-	-	-	1	700	Jan
<i>Euphysa aurata</i>	-	-	-	1	500	Apr	-	-	-	2	700	Jan
* <i>Zanclaea</i> sp.	-	-	-	-	-	-	1	500	May	-	-	-
* <i>Foersteria antoniae</i>	-	-	-	-	500–1000	Apr–Jun	1	500	Jun	-	-	-
* <i>Foersteria aratae</i>	672	500–1000	May–Jul	-	-	-	-	-	-	-	-	-
* <i>Teclata recincolae</i>	81	500–1000	May–Jul	-	-	-	-	-	-	-	-	-
<i>Modeeria rotunda</i>	-	-	-	-	-	-	-	-	-	1	700	May
* <i>Barcino foixensis</i>	1	1000	May	-	-	-	-	-	-	-	-	-
<i>Cunina globosa</i>	-	-	-	-	-	-	-	-	-	1	700	Apr
* <i>Cunina simplex</i>	-	-	-	2	500	Apr	-	-	-	2	700	Apr
<i>Solmissus albescens</i>	3	1000	Jun–Jul	8	500	Apr–Nov	13	500	Jun–Nov	11	700	May–Dec
<i>Solmaris flavescens</i>	-	-	-	5	500	Jun–Jul	-	-	-	1	700	Jun
<i>Haliscera bigelowi</i>	-	-	-	-	-	-	-	-	-	2	700	Jan–May
<i>Haliscera racovitzae</i>	-	-	-	-	-	-	1	500	Sep	-	-	-
<i>Psychogastria asteroides</i>	26	500–1000	Apr–Sep	25	500–1000	Apr–Nov	4	500–1000	May–Jul	1	700	Jun
<i>Arctapodema australis</i>	-	-	-	-	-	-	1	500	Apr	-	-	-
<i>Homoeonema playgonon</i>	1	1000	May	2	500	Jun–Jul	12	500	Apr–Oct	5	700	May, Jul
<i>Persa incolorata</i>	-	-	-	1	500	Jul	1	500	Sep	-	-	-
<i>Sminthea eurygaster</i>	-	-	-	-	-	-	-	-	-	1	700	Dec
Σ individuals	784			50			34			27		
Σ species	6			9			8			11		
Σ species found only in the canyon axis	4			2			2			1		

*New species described in the study of the NW Mediterranean canyons (ind., total number of individuals sampled along a year cycle).

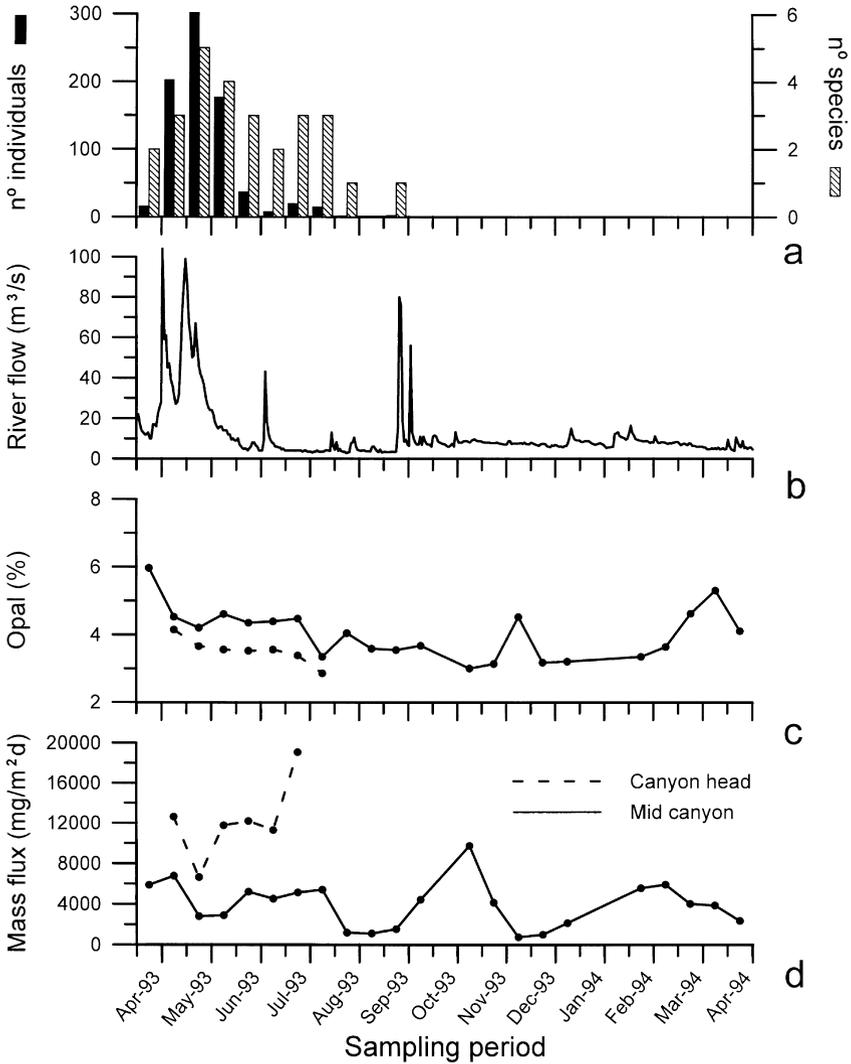


Fig. 2. (a) Temporal evolution of both the number of individuals and the species of medusae collected at 30 mab at 1180 m depth inside the Foix canyon in 1993; (b) daily water discharge, during the sampling period, of the Llobregat River, a local river near the Foix canyon site; (c) time series of biogenic opal contents and (d) total mass fluxes of settling particulate matter trapped at 30 mab at the Foix canyon head (600 m depth) and at the mid canyon (1180 m depth).

3.2. Mass flux

Temporal changes in mass flux involved both the number of individuals and the number of species of gelatinous zooplankton. The most complete annual series of swimmers was obtained from Foix Canyon. Total mass flux of settling particulate

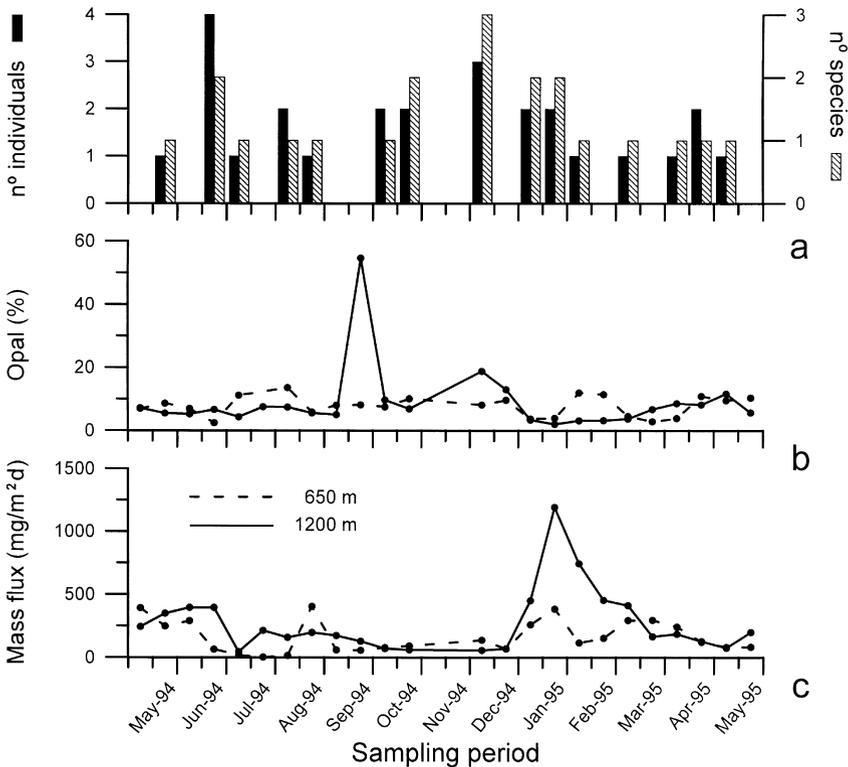


Fig. 3. (a) Temporal evolution of both the number of individuals and the species of medusae collected at the Balearic Islands site; (b) time series of biogenic opal contents and (c) total mass fluxes of settling particulate matter trapped at the Balearic Islands site (650 and 1200 m depth).

matter in Foix Canyon ranged from 6000 to 20 000 mg/m² d at the site at the head of the canyon and from 1000 to 11 000 mg/m² d at the mid-canyon site (Fig. 2d). The highest numbers of individuals and species were recorded in late spring, after a peak in biogenic opal and during and after the spring rise in river discharge volumes. Most canyon hydromedusan fauna was collected between May and July 1993 (Fig. 2a) during a period of slightly higher than average mass flux and opal content values.

The mean annual flux of organic constituents in the settling particulate matter was higher within the submarine canyons than on the open slope, except in the case of Planier Canyon. This correlated with the number of individuals and the number of species, which were also higher inside the canyons. The mean annual flux in the major organic constituents (organic carbon and biogenic opal) increased from Planier Canyon to Foix Canyon, where the flux values were highest (Fig. 5). This also correlated with the trend for the fauna considered, with higher numbers of individuals and species in the canyons with higher mean fluxes of organic constituents (Table 1). Conversely, the lowest number of individuals and new species were recorded at the Balearic site, where the flux of organic constituents was likewise lower (Fig. 5).

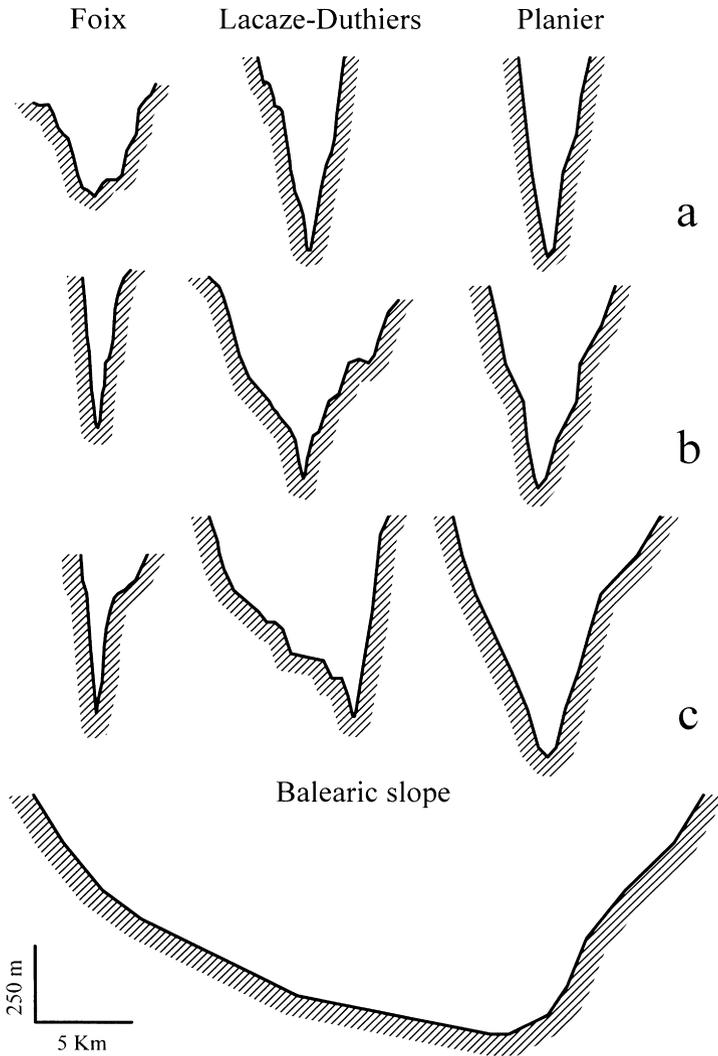


Fig. 4. Bathymetric profiles from the Foix, Lacaze-Duthiers and Planier canyons at approximately 500 m depth (a), 1000 m depth (b) and 1500 m depth (c), and from the Balearic slope at about 1000 m depth.

3.3. Bottom currents

The bottom current flow rates in the canyons studied ranged between 1.1 and 15 cm sec^{-1} (Fig. 6). Fluctuations in the bottom current flow did not exhibit any seasonal patterns, and the main current flow pattern did not change during the year. The main fluctuations were upcanyon–downcanyon current reversals that took place over time intervals of 6–10 d (Puig et al., 1999). The reversals were linked to forcing conditions affecting canyon circulation. If the deep current regime does not vary

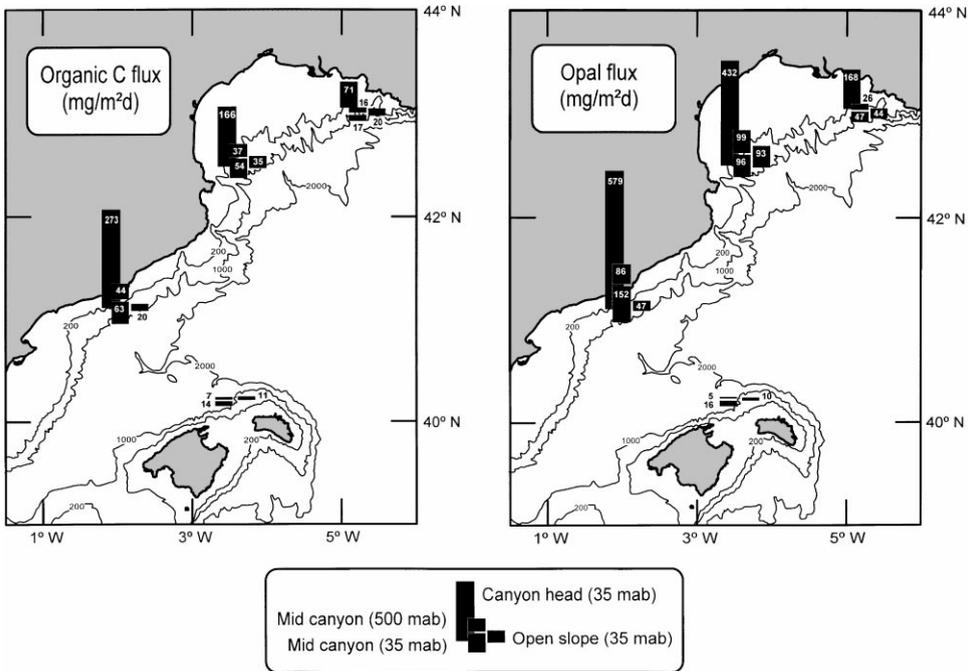


Fig. 5. Annual mean fluxes of organic carbon and biogenic opal of settling particles collected during the EUROMARGE-NB experiment, modified from Heussner et al. (1996).

during the year, abundance patterns for the gelatinous zooplankton cannot be related to variations in canyon flow patterns. However, deep canyon currents contribute to the development of that fauna, since flow rates are not strong enough to advect animals away.

3.4. Seismic stratigraphy

High-resolution seismic profiles have revealed the geological record in the areas of the canyons studied (Fig. 7). These profiles record the Pliocene and Quaternary deposits that lie above the Messinian reflector. Pliocene and Quaternary seismic units from the base to the top of the profile consist of transparent facies grading upwards to stratified facies incised by canyon floor units consisting of irregularly stratified facies. The canyon units suggest that these canyons have been active from the Messinian to the present time.

The Messinian reflector is a remnant of the Messinian unconformity formed during the drastic sea-level lowering that took place during Messinian times (Ryan and Cita, 1978). This reflector is incised by canyons that are the ancestors of the present ones (Palanques and Maldonado, 1983; Escutia, 1992). Within these paleocanyons fill deposits of irregularly stratified facies up to 100 m thick suggest submarine activity in those canyons during the Messinian. Thus, marine conditions have been constantly present in these canyons at least from Messinian times.

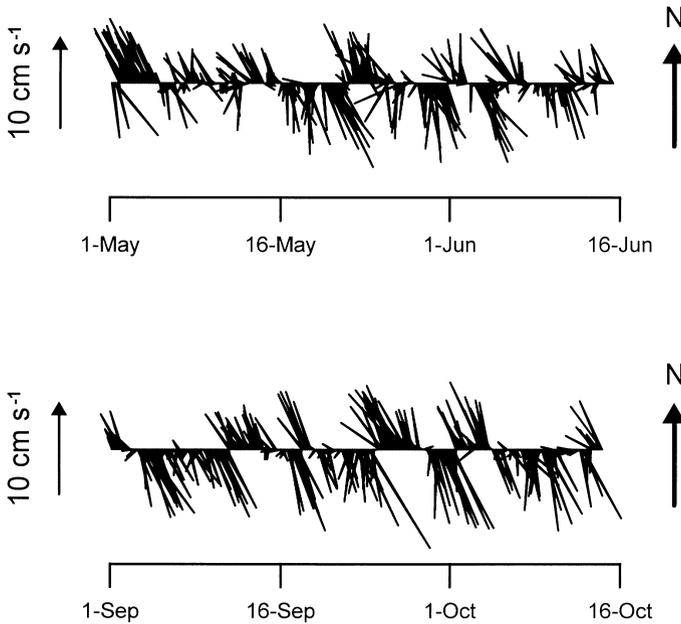


Fig. 6. Stick plots of currents from 30 mab at 1180 m depth in the Foix canyon axis, (a) May 1–June 16 th (b) September 1–October 16.

4. Discussion

4.1. Topographic effects on zooplankton aggregation

Submarine canyons have been shown to act as detritus traps and to accumulate substantial amounts of organic debris (Vetter, 1995). This phenomenon plays an important role in channelling plankton and benthos production (such as algae or macrophyte debris) to higher trophic levels, such as crustaceans and other macroplankton predators. High densities of demersal crustaceans and fish, as well as epibenthic crustaceans, have been observed inside submarine canyons, with densities at least one order of magnitude greater than in surrounding deep habitats (Greene et al., 1992; Stefanescu et al., 1994; Vetter, 1994). The aggregation phenomena observed within submarine canyons probably enhance species diversity. The geomorphological structure of each canyon can also be postulated to influence the fauna, acting to intensify or diminish the isolation of planktonic populations over time. Accordingly, the topographic differences observed within the four canyons studied (Fig. 4) may, perhaps, partially explain the qualitative and quantitative differences observed among them. Foix Canyon is much narrower than the others, and the samples collected within it presented the largest number of total species as well as the greatest number of endemic species (Table 1). It was followed in decreasing order of endemism but greater species number by Lacaze-Duthiers and Planier canyons, which are increasingly more open.

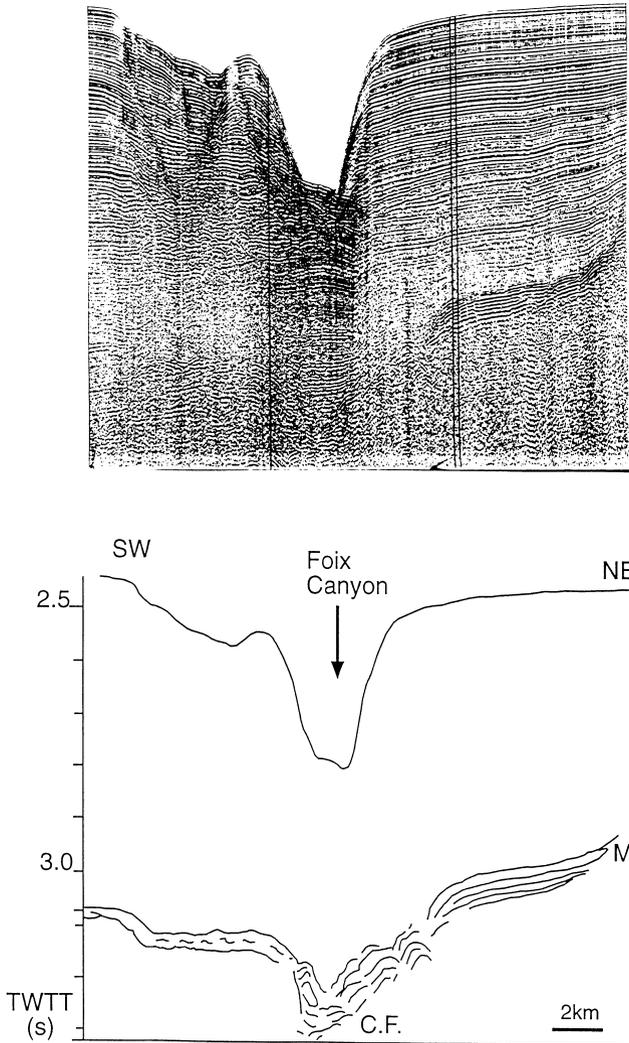


Fig. 7. Sparker seismic profile across the lower course of the Foix Canyon (top), with corresponding line drawings (bottom), TWTT, two-way travel time in seconds, M, Messinian reflectors; C.F. canyon fill deposits in the Messinian Foix Canyon, Messinian deposits below 3.0 s are interpreted to be marine sediments.

The samples from the Balearic site, which can actually be considered an open sea area, mostly consisted of common Mediterranean deep-water species (see Table 1).

4.2. Role of organic fluxes in spatio-temporal hydromedusan distribution patterns

The sea floor receives a rain of detritus, composed primarily of marine snow, faecal pellets, crustacean moults, and other fine particulate matter, and this has led to the

idea that deep-sea benthic communities are quite uniform (Rowe and Staresinic, 1979). In fact, not only do pulses of food tend to arrive sporadically, they also tend to accumulate in trenches that act as traps for coastal and shelf sediments (George and Higgins, 1979). These fluctuations in the available food supply generate a high level of heterogeneity in deep-sea communities located near the continental shelf and slope (Gage and Tyler, 1992).

Total mass flux values, as well as the fluxes of several constituents (mainly opal originating from biological activity in the surface waters on the shelf), increased progressively downstream from Marseille to Barcelona (from NE to SW) (Heussner et al., 1996) (Fig. 5). The Balearic site exhibited the lowest flux values for the entire system studied. The samples collected in the canyons showed that biogenic components varied with location and season and that variability in the vertical flux decreased downstream (that is, with increasing mass flux) (Heussner et al., 1996). Thus, differences in the number of individuals among the canyons considered may be linked to spatio-temporal differences in the vertical flux (food supply).

The total organic carbon flux supplied to the sea floor either remained constant or decreased with depth in Planier Canyon and at the Balearic Island site but increased with depth in Foix and Lacaze-Duthiers canyons. In consonance with these trends, the abundance of endemic species making up the hydromedusan populations increased in the deeper parts of the southernmost canyons. Abundance of canyon species may be linked to the supply and deposit of organic matter reaching the sea floor along the canyon walls (Greene et al., 1992; Vetter, 1995).

The most common species in the traps located inside Foix canyon displayed substantial fluctuations in abundance over the sampling period (Fig. 2). In comparison, the samples collected at the Balearic site (Fig. 3) revealed a fauna composition similar to that in the Mediterranean open-sea (Gili et al., 1987). Large numbers of specimens were collected on the Foix canyon axis in late spring and may be related to peak planktonic production in the Mediterranean in April (e.g., Margalef, 1985). This early spring planktonic bloom precedes the settling of organic detrital material on the continental shelf and its seaward transport as it is funnelled through the submarine canyons to the continental slope by some weeks. Maximum accumulation of organic matter on the canyon floors takes place in May and June (Buscail et al., 1990). This seems to favour an increase in the numbers of benthic-pelagic hydromedusae. Similar events were observed in a submarine canyon off La Jolla, California (Vetter, 1994) and canyons off the Georges Bank (e.g., Greene et al., 1992), where increases in macrophyte detritus enhanced the production of nearshore benthic species.

Most of the endemic species found in the bottom traps were meroplanktonic Leptomedusae with a sessile, benthic, modular, asexual stage, the hydroid, budding off a pelagic sexual stage, the hydromedusa. Hydroids generally undergo a growth period in which colony size increases prior to reproduction. In canyons such as Foix or Lacaze-Duthiers canyons, the life cycle of those hydromedusae can be speculated to be as follows. The large amount of opal and organic carbon observed at the end of winter and beginning of spring triggers hydroid colony growth. Hydroids are active benthic feeders on plankton and particulate organic matter (Gili and Hughes, 1995). Young medusan buds might form in April and use the accumulation of food from the

planktonic surface bloom to grow and develop, probably sexually, in June and July. Planular larvae are formed and develop immediately into new colonies or encyst and develop later on. If environmental conditions are adverse or food is in short supply, colonies may also undergo diapause, and then only the stolonate system survives and develops new colonies when conditions turn favourable again (Bouillon, 1968; Boero et al., 1996). The flux of sediments to the bottom layers thus becomes a key component regulating the occurrence of benthopelagic medusae by providing both an appropriate environment and substrate and potential food for medusan prey organisms. Etter and Grassle (1992) have demonstrated a correlation between species diversity in the deep-sea environment and diversity of organic particulate matter.

4.3. Hydrodynamic influences on zooplankton residence times

In general, interaction of fluctuating flows over the shelf and slope with abrupt topographies like those of submarine canyons, together with local circulation and mass balance, cause canyons to play an important role in coastal ecosystems, enhancing biological productivity and species richness (Hickey, 1995). In the northwestern Mediterranean, submarine canyons occupy nearly 50% of the continental slope overall. As already pointed out, there is a permanent shelf-slope front along the upper slope that separates coastal waters from the more saline waters of the open sea (Font et al., 1988), and the associated circulation pattern is dominated by a current flowing from NE to SW nearly parallel to the shelf edge. Different studies have recently shown that canyons in this area can strongly modify downstream circulation and shelf-slope exchanges of water and material (Durrieu de Madron, 1994). Hydrographic instabilities like filament offshoots from the main current have been observed to be associated with submarine canyons on the shelf in the Catalan Sea (Masó et al., 1990).

Planktonic species in submarine canyons display behavioural and biological traits adapted to sustaining their populations in these very singular habitats. Two different behavioural adaptations for escaping the effects of current flow have been observed in the species *Ptychogastria polaris* Allman, 1878 and *P. asteroides*. In the Pacific Ocean, *Ptychogastria polaris* specimens have been observed to spend most of their time attached to the substratum, where they probably feed and live (Larson et al., 1992). Those holoplanktonic medusae spend only a brief time in the water column, possibly to ensure that they will be less likely to be carried away by currents. *Ptychogastria asteroides* was more abundant in the traps located at intermediate depths and appears to display a slightly different behaviour, spending more time in the water column. This latter observation leads us to postulate that other endemic Mediterranean hydro-medusae may also have swimming periods when there are perturbations in the deep waters, with transport of large amounts of sediments and detritus. Water flow intensity and direction change continuously inside the canyon. Fig. 6 illustrates the data for two months, exemplifying two different hydrodynamic situations, one when medusae were common (a) and another when they were absent from the sediment trap samples (b). The medusae probably moved vertically near the bottom and along the canyon axis to elude significant downslope transport. It is also important to remember that the seasonal nature of the periods of major disturbance produced by current

flow in the canyons means that only the planktonic stages of hydromedusae are affected, the benthic stages (polyps) being unaffected. Polyps usually need a hard substratum for colony development, and this is probably located on the canyon walls, at a distance from sediment resuspension and from the strong currents that would make polyp settlement untenable. Sediment supply and removal are limiting factors for the survival of benthic hydrozoan stages (Gili and Hughes, 1995). The presence of both a benthic and a pelagic stages in the life cycles of most deep-dwelling canyon hydromedusae may contribute to survival of these organisms in submarine canyons.

Ptychogastria asteroides represents another example of the importance of hydrodynamic processes in submarine canyon communities. This species has previously been recorded at three sites in the Mediterranean: the Adriatic Sea, the Strait of Gibraltar, and off Villefranche-sur-Mer (Haeckel, 1879; Picard, 1955). Our results show it to be common in all northwestern Mediterranean submarine canyons. All previous specimens of *P. asteroides* were collected inshore from areas in the vicinity of the head of a submarine canyon near the coast, their presence there probably being indicative of intrusions by deep slope waters generated by up-canyon currents (Masó et al., 1990; Álvarez et al., 1996). Similar observations in the western Mediterranean have been reported for mesopelagic larval fishes (Sabatés and Masó, 1990).

4.4. *Is the submarine canyon fauna a Tethys relict?*

4.4.1. *Geological and historical framework*

Historical events have undoubtedly exerted a major influence on the recruitment of the Mediterranean hydromedusan fauna. In earlier geological eras the Mediterranean landscape was very different from that of the present time. The present Mediterranean Sea is a remnant of the ancient Tethys, an east-west seaway lying between the Eurasian and African crustal plates during the late Paleozoic Era and the Mesozoic Era, linking the present Indian Ocean and the proto-Atlantic Ocean. At the beginning of the Cretaceous, during the Cenomanian Age, about 95 Ma BP, the Mediterranean was connected to the North Sea through the Paris basin, to the tropical Atlantic through the Morocco Rif zone, and to the Indian Ocean through Mesopotamia.

In the early Miocene, during the Burdigalian Age (about 18 Ma BP), the junction of Eurasia and Africa closed off the eastern part of the Mediterranean, which remained connected only to the Atlantic. At around the same time, the Mediterranean was cut off from the Paratethys, and the climate turned drier and cooler (Hsü et al., 1978; Cita et al., 1978). In the late Miocene, during the Messinian, between 6 and 5 Ma BP, the strait between the Mediterranean and the Atlantic closed, and the Mediterranean was isolated and nearly dried up. Sea water was confined only to the deepest basins, which acted as potential areas of faunal refuge. The presence of foraminiferans, diatoms, and algal stromatolites in the Messinian bottom sediments (Montader et al., 1978) indicates the occurrence of marine environments where life was still possible during the Messinian crisis. In the late Miocene (late Messinian) the Paratethys (Lago Mare) inundated the eastern Mediterranean, possibly extending toward the western region. At the beginning of the Pliocene, around 5 Ma BP, the opening of the strait of Gibraltar (320 m in depth, Perés, 1985) restored the sea level and once again opened

up the possibility of faunal exchanges with the Atlantic. The strait has definitely acted as a barrier to penetration by the deep-water fauna.

4.4.2. Origin of canyon hydromedusan fauna

Some of the deep-water hydromedusan species may thus be relicts of the primitive Tethys fauna that survived the Messinian crisis. Their descended taxa could be responsible for the high level of endemism of deep-water Mediterranean hydromedusae (50% of the total Mediterranean endemics) observed from this series of studies of submarine canyon species (Gili et al., 1998,1999). The present distribution of the genus *Foersteria* can serve as an interesting example. *Foersteria purpurea* (Foerster, 1923) is known from British Columbia and Monterey Bay, California, in the Pacific (Wrobel and Mills, 1998); *F. bruuni* is found in the Indian Ocean (Navas, 1969); *F. antoniae* and *F. araiiae* have each been discovered in different canyons in the Western Mediterranean (Gili et al., 1998,1999). No members of this genus are known from the Atlantic. All are closely related and could have developed from a single ancestor present in the Indo-Pacific and the Mediterranean before the Burdigalian, by specific radiation and vicariance events, assuming, of course, that this Tethys fauna could have survived the subsequent dramatic geological events that affected this area. This could have happened because ancient paleocanyons corresponding to the present canyons studied have existed since Messinian times, although they then had different characteristics (Escutia, 1992; Palanques and Maldonado, 1983). Sediment deposits from the deeper parts of those Messinian paleocanyons indicate that conditions suitable for marine life continued to exist in the deeper portions of the north-western Mediterranean paleocanyons (Fig. 7).

Any eventual relict species would have had to survive heavy ecological stresses. This may have been possible mostly for species with resistant resting stages, such as cysts or chitinized stolonial systems (see Bouillon, 1968,1975; Marcus et al., 1994; Hairston et al., 1995; Boero et al., 1996). In this respect it is interesting to underline that most endemic Mediterranean canyon hydromedusae belong to the meroplanktonic Lep-tomedusae, which generally have strong, protected stolons.

The few holoplanktonic canyon species seem to have a different origin from that of the meroplanktonic species. *Solmissus albescens* is a eurybathic species that can be considered vicarious to, if not conspecific with, *S. marshalli* found in the Atlantic and the Indo-Pacific (see Gili et al., 1998), *Ptychogastris asteroides* is vicarious with *P. polaris*; *Solmaris leucostyla* (Will, 1844) is another epipelagic eurybathic species that Mayer (1910) considered to be merely a variant of the more common *S. flavescens* recorded in the Mediterranean, Atlantic, and Indo-Pacific. The endemic *Cunina simplex* has only been collected twice, both times in intermediate waters (Gili et al., 1998); it is a rather small narcomedusan that could easily escape identification. All these species could have entered the Mediterranean after the Messinian crisis. Of course, introduction of some other endemic deep-water species after the Messinian crises cannot be ruled out. Those species could later be restricted to particular canyon environments either as a result of ecological factors (salinity, water mass circulation), submarine geomorphology (crests, ridges, and canyons), or any other factor capable of preventing expansion and isolating them, thus increasing the likelihood of speciation.

The origin of the deep-water hydromedusan fauna would appear to be complex. Cenomanian links between the Mediterranean region and the tropical Atlantic and the Indo-Pacific could certainly have allowed faunal exchanges. After the Messinian crisis in the Pliocene, when the Strait of Gibraltar opened, many recent hydromedusae (not only deep-sea species) presenting Atlantic and Indo-Pacific affinities could have entered from the Atlantic and re-colonised the Mediterranean. Deep-sea Atlantic species could have been upwelled and advected to the Mediterranean, where they then adapted to the Mediterranean deep-water environment (see Boero and Bouillon, 1993). After the Pleistocene cooling, North Atlantic species also invaded the western Mediterranean, and they are probably responsible for the present-day boreal stock (Gili et al., 1998).

Overall, Mediterranean hydromedusae have an important endemic contingent (19.5%, see Boero and Bouillon, 1993), the endemic component also being significant for the deep-sea fauna (22%, see Gili et al., 1998). As discussed above, some of these might be Tethys relicts, while others might be “false endemics”, in that they have been observed only once, over a hundred years ago, and have not been found again despite intense research work in recent decades (Mills et al., 1996; Boero et al., 1997). Even though deep-sea speciation rates are largely unknown, it seems true that the deep-sea fauna is highly endemic (Wilson and Hessler, 1987). If environmental heterogeneity is one of the most widely accepted causes of speciation in deep-sea habitats (Jablonski and Bottjer, 1990; Grassle and Maciolek, 1992), submarine canyons may be one of the most specialized.

5. Conclusions

The relative richness and abundance of the hydromedusan fauna found in the submarine canyons off the coast of Catalonia provides a basis for suggesting that the gelatinous zooplankton, and particularly midwater and benthic-pelagic medusae, are important components of these environments. The hydromedusan fauna recorded in this study is a step towards broadening existing knowledge of deep-sea Mediterranean biodiversity.

A general overview of the biological and environmental features of the submarine canyons in the Mediterranean lends support to the view that canyon habitats shelter high diversity of species of hydromedusae, many of them new to science. That fauna appears to contain many species whose entire life cycle is confined to inside the canyons themselves. The life cycles of these species seem to be regulated by external factors such as transport of organic debris to the sea floor (related to river discharge, storms, etc.), circulation and interaction of water masses within the canyons, topography, and biological production in the water column. These findings suggest that submarine canyons are a key habitat for understanding biodiversity in the shelf and slope zones.

This and other studies of submarine canyon fauna have raised the rate of endemism of Mediterranean deep-water hydromedusae (50% of the total Mediterranean endemics), and historical and ecological features give reason to postulate that some of

the deep-water hydromedusan species may be relicts of the primitive Thetys fauna that survived the Messinian crisis.

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