

Deep-water Hydromedusae from the Lacaze-Duthiers submarine canyon (Banyuls, northwestern Mediterranean) and description of two new genera, *Guillea* and *Parateclaia**

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SUMMARY: Several species of hydromedusae are reported from material collected by sediment traps placed in the Lacaze-Duthiers submarine canyon, off Banyuls (north-western Mediterranean). Two new taxa *Guillea canyonicolae* gen. nov. et sp. nov. and *Parateclaia euromarge* fam. nov., gen. nov. et sp. nov., are described. The existence of highly-specific hydromedusa populations in other Mediterranean canyons which appear to be related via geological history, topography, hydrographic and ecological features peculiar to each canyon, is discussed in relation to these new records.

Key words: Hydromedusae, submarine canyons, western Mediterranean, swimmers, deep-sea fauna, biodiversity, *Guillea canyonicolae*, *Parateclaia euromarge*.

INTRODUCTION

Interactions between the fluctuating continental runoff flows over the shelf and slope areas with abrupt topographies, together with local circulation and mass balance, give nearshore submarine canyons a key role in some coastal ecosystems, enhancing species richness and biological productivity (Hickey, 1995). The channeling of organic matter from the shelf to deep water through submarine canyons gives rise to high biomass levels and production rates in the plankton and benthos in such

canyons (Greene *et al.*, 1992; Vetter, 1994, 1995; Vetter and Dayton, 1998) resulting in biological communities in submarine canyons that are more productive and diverse than was thought only a short time ago (Gage and Tyler, 1992; Gage *et al.*, 1995).

In the north-western Mediterranean, submarine canyons occupy nearly 50 % of the total continental slope. Recent investigations carried out in some of them have revealed a deep-water fauna composed mainly of meroplanktonic hydromedusae (see Gili *et al.* 1998, 1999, 2000). Spatio-temporal trends in the organic (carbon and biogenic silica) content of vertical fluxes of particulate matter have yielded a good match with the number of individuals and

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species of hydromedusae collected in these canyons (Gili *et al.*, 2000). These observations led us to postulate the presence of unique plankton populations in these canyons, which are probably supported by the flux and storage of organic material coming from the continental shelf.

Previous studies carried out in three canyons (Fig. 1), Foix (near Barcelona), Lacaze-Duthiers (near Banyuls) and Planier (near Marseille) have shown that the specific composition and abundance of the medusa populations appear to be different between canyons (Gili *et al.* 1998, 1999, 2000). These studies covered an entire year in the Foix canyon while in other canyons, temporal trends had to be inferred from less sampling. The present study represents results derived from a second survey in the Lacaze-Duthiers canyon, carried out from December 1995 to January 1997. During that period, sediment traps collected several species of hydromedusae including the two new ones described here. Their occurrence is analysed, taking into account the previously proposed hypotheses (Gili *et al.*, 1998,

1999, 2000), suggesting the existence of specific hydromedusa populations in each canyon investigated; such specificity seems closely related to the geological history, topography, and both hydrographic and ecological features of each of the studied canyons.

MATERIAL AND METHODS

A mooring line equipped with sequential sediment traps was deployed at a single station in the Lacaze-Duthiers canyon. One sediment trap was located at 1000 m depth, 30 mab (metres above the bottom) and another in intermediate waters 500 mab during a full-year sampling period (December 1995-January 1997). The sediment traps were Technicap model PPS3, which incorporates a carousel with 12 rotary collectors (Heussner *et al.*, 1990). The sample collecting interval was set at 15 or 16 days, depending on the month. Before trap deployments, the sample tubes were rinsed and filled with a neutralized

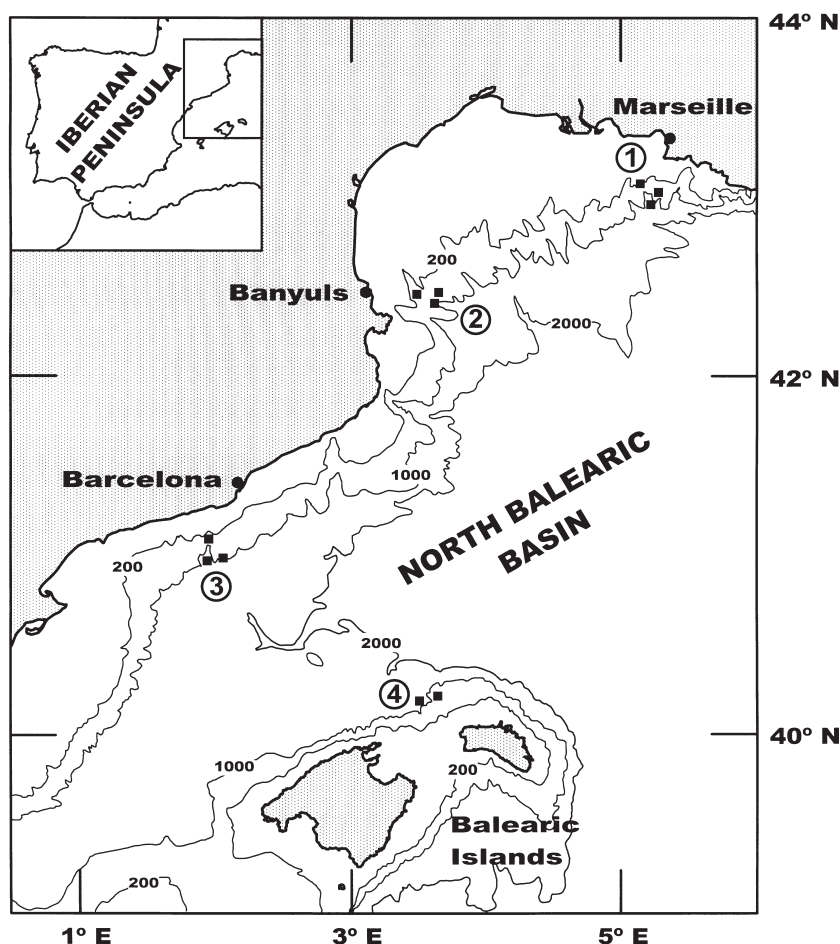


FIG. 1. – Map of the study-area, showing the location of the mooring sites (black squares) during the EUROMARGE-NB experiments. Site 1: Planier canyon; site 2: Lacaze-Duthiers canyon; site 3: Foix canyon; site 4: Balearic slope.

5% formaldehyde solution in filtered seawater to prevent degradation of organic matter between collection and the time that the traps were taken up. The samples were processed in the laboratory and swimmers were removed by hand-picking under a dissecting microscope. Gelatinous swimmers had been preserved in excellent condition, which facilitated taxonomic investigations of the hydromedusae.

RESULTS

Material collected and species descriptions

ANTHOMEDUSAE

FILIFERA

Family PANDEIDAE Haeckel, 1879

Leuckartiara brownei Larson and Harbison, 1990 (Fig. 2)

Material examined: 1 specimen, 7.0 mm high, 15-31 October 1996, 500 m depth.

This is the first record of this species in the Mediterranean. It was previously recorded only in the Southern Ocean, in surface waters of the Ross Sea (Larson and Harbison, 1990) and in the Weddell Sea where several specimens were collected from the surface down to the 720-450 m depth range (Pagès and Schnack-Schiel 1996; Pagès unpublished data).

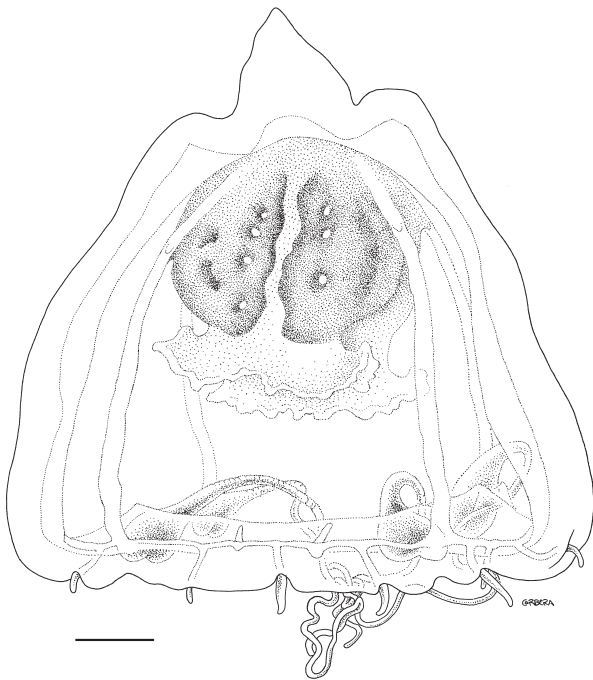


FIG. 2. – *Leuckartiara brownei*. Scale: 1 mm.

CAPITATA

Family EUPHYSIDAE Haeckel, 1879

Euphysa aurata Forbes, 1848

Material examined: 1 specimen, 3.3 mm high, 16 March-1 April 1996, 500 m depth.

Family ZANCLEIDAE Russell, 1953

Zanclea sp.

Material examined: 1 specimen, colour deep red, 3.6 mm high, 1-15 May 1996, 500 m depth.

LEPTOMEDUSAE

Family LAODICEIDAE Agassiz, 1862

Diagnosis: Leptomedusae with marginal cordyli with or without cnidocysts; with 4, 8, or more simple or branched radial canals; gonads on radial canals, on radial canals and lobes of manubrium or in manubrial pouches; marginal tentacles hollow; with or without marginal cirri; with or without adaxial ocelli; without statocysts.

Guillea gen. nov.

Etymology: This genus is dedicated to Prof. Alain Guille for his outstanding activities as Director of the Observatoire Océanologique de Banyuls (Laboratoire Arago) and for his relevant contribution to the knowledge of the Mediterranean marine fauna. Prof. Alain Guille is one of the founders of the *Laboratoire Européen des Sciences de la Mer* (LEA), within whose framework this and previous works related to medusae in submarine canyons have been carried out.

Diagnosis: Laodiceidae with club-shaped cordyli; with marginal cirri; with adaxial ocelli; with 4 simple radial canals; manubrium with perradial pouches, with gonads developing in numerous dorso-lateral lamellar folds (gonadal diverticulae) extending from the proximal part of manubrium into the manubrial pouches and out onto the proximal portions of the radial canals.

Remarks: This new genus has the basic characters of the family Laodiceidae. It is close to the genus *Laodicea* by virtue of its club-shaped cordyli, marginal cirri and ocelli; it also shows affinities with the genus *Ptychogena* by the presence of manubrial pouches and gonadal diverticulae. However, the genus *Ptychogena* has been classically defined as deprived of cirri and ocelli; therefore the new genus *Guillea* is here proposed. This new genus appears to have characters intermediate between the genera *Laodicea* and *Ptychogena*.

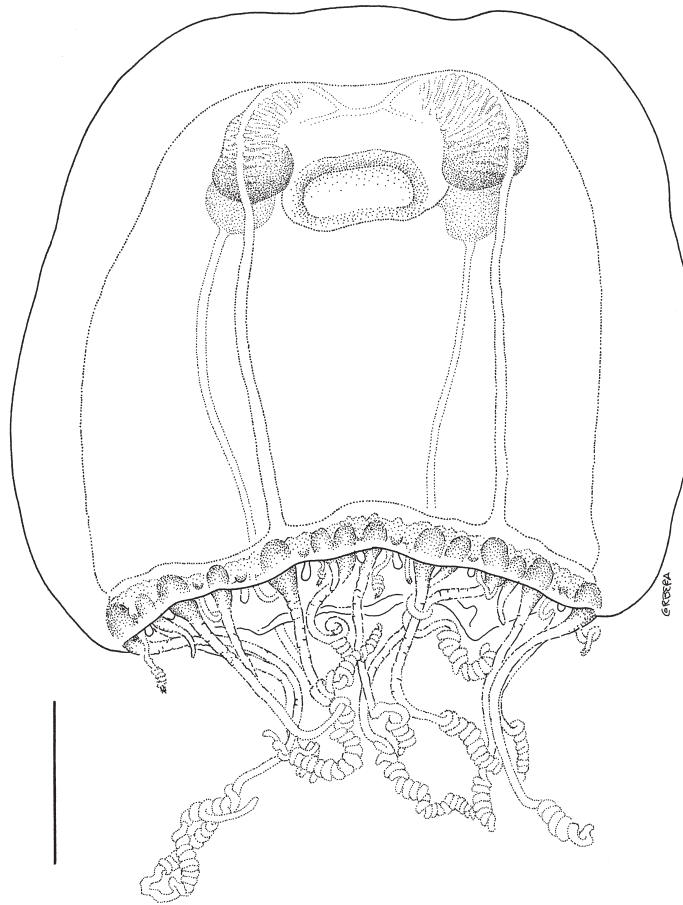


FIG. 3. – *Guillea canyonicolae*. Scale: 1 mm

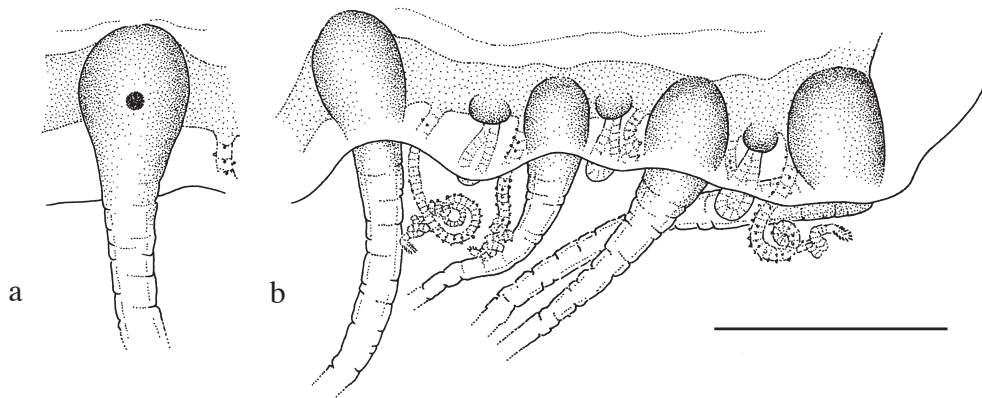


FIG. 4. – *Guillea canyonicolae*, detail of the umbrella margin; (a) adaxial view of the tentacle, showing ocellus; (b) abaxial view, showing club-shaped cordyli and spiral cirri. Scale: 0.5 mm.

***Guillea canyonicolae* sp. nov.**
(Figs. 3 and 4)

Type locality: Lacaze-Duthiers canyon, off Banyuls (France), north-western Mediterranean.

Material examined: one specimen collected at 500 m depth on 1-16 March 1996 and deposited at the Institut de Ciències del Mar, Barcelona, Spain.

Etymology: *canyonicolae*, inhabitant of canyons.

Description: Umbrella higher than a hemisphere, dome-shaped, 4.5 mm wide, 4.0 mm high; with vertical walls and flatly rounded apex, mesoglea uniformly thick; velum narrow; manubrium quadrangular, short, with four perradial gastric pouches; mouth large, almost circular, without distinct lips but with swollen margin, faintly folded; four simple narrow radial canals not meeting exactly in the center of

manubrial roof; circular canal narrow; four perradial gonads, differentiating into numerous dorso-lateral lamellar folds (gonadal diverticulae), extending from proximal part of manubrium into the gastric pouches to proximal parts of the radial canals; up to 24 marginal tentacles with coiled extremities; marginal bulbs broad, rounded; one club-shaped cordylus without cnidocysts and one to two spiral cirri between successive tentacles; one ocellus on the adaxial side of each marginal bulb.

Diagnosis: Umbrella higher than a hemisphere, dome-shaped, 4.5 mm wide, 4.0 mm high; with rounded apex, mesoglea uniformly thick; manubrium quadrangular, short, with four perradial pouches; mouth large, without distinct lips; four simple narrow radial canals; circular canal narrow; 4 perradial gonads differentiating into dorso-lateral lamellar folds (gonadal diverticulae) from proximal part of manubrium into the gastric pouches to the proximal parts of the radial canals; up to 24 marginal tentacles; marginal bulbs broad, rounded, each with one adaxial ocellus; one cordylus and one to two spiral cirri between successive tentacles.

Family MITROCOMIDAE Torrey, 1909

Foersteria antoniae Gili, Bouillon, Pagès, Palanques, Puig and Heussner 1998

Material examined: All specimens were collected at 500 m depth; 2 specimens, 16 February-1 March 1996; 2 specimens, 1-16 March 1996; 3 specimens, 16 March-1 April 1996; 3 specimens, 1-16 April

1996; 3 specimens, 16 April-1 May 1996; 3 specimens, 1-16 May 1996; 2 specimens, 16 July-1 August 1996; 3 specimens, 1 August-1 September 1996; 3 specimens, 5-6 mm wide, 1-16 September 1996. Size: 4.1-6.2 mm wide.

Family TECLAIDAE fam. nov.

Diagnosis: Leptomedusae with 4 simple radial canals; with hollow tentacles; with 4 simple lips; with gonads elongated forming linear sacs on radial canals, separated from manubrium; with one to three cordyliform structures between successive tentacles; without ocelli; without cirri; with or without open statocysts.

Parateclaia gen. nov.

Diagnosis: Teclaiidae with open statocysts.

Parateclaia euromarge sp. nov.

(Figs. 5 and 6)

Type locality: Lacaze-Duthiers canyon, off Banyuls (France), north-western Mediterranean.

Material examined: 3 specimens, 16 July 1996; 2 specimens, 1-16 August 1996; 2 specimens, 1-16 September 1996. All specimens were collected at 1000 m depth. Holotype and paratypes deposited at the Institut de Ciències del Mar, Barcelona, Spain.

Etymology: *euromarge* in acknowledgement of the European Community research program EUROMARGE which made possible the study of the medusan fauna in submarine canyons.

Description: Umbrella to 6.0 mm wide, 4.5 mm high; somewhat flatter than a hemisphere; mesoglea

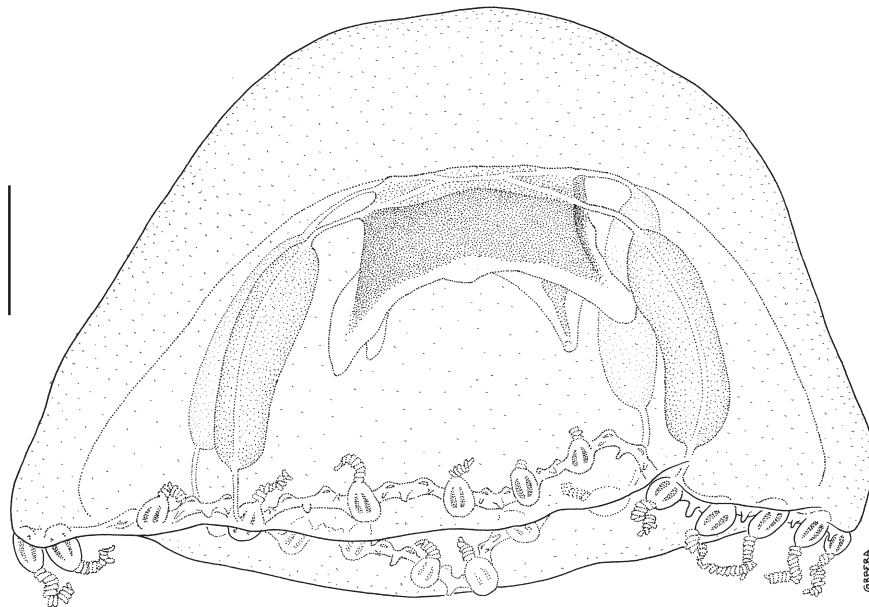


FIG. 5. – *Parateclaia euromarge*. Scale: 1 mm

fairly thick at the apex, thinning towards umbrella margin; exumbrella sprinkled with cnidocysts; velum narrow; manubrium short, square, with large base, about 1/4 of subumbrella cavity height and 1/3 of subumbrella cavity width, without gastric peduncle, colour light brown; mouth with 4 simple groove-like lips, white in colour; as long as manubrium height; with 4 simple radial canals not meeting in the centre of the manubrial roof, circular canal narrow; up to 24 hollow marginal tentacles; with elongated conical marginal bulbs each with two large brown bands; up to three cordyliform conical structures, each with central brown pigment spots and terminal cnidocysts; one to two open statocysts between successive marginal tentacles; gonads elongated, cylindrical, extending along the middle 2/3 of the radial canals and leaving both ends free.

Remarks: *Teclaia recincolae* Gili, Bouillon, Pagès, Palanques and Puig 1999 was tentatively referred to the Laodiceidae by Gili *et al.*, (1999). The discovery of this new species, which is nearly completely identical to *T. recincolae* except for the presence of open statocysts, questions the family position of this genus which is taken out from the Laodiceidae. Only two previously described families of Leptomedusae have open statocysts, the Mitrocomidae and the Tiaropsidae (Bouillon, 1985). The latter exhibits very special compound sense organs formed by the association of ocelli and an open statocyst which excludes it from the present discussion. The Mitrocomidae constitutes a uniform family mainly characterised by the possession of open statocysts and without cordyli. The inclusion of species without statocysts and with cordyliform structures would greatly disturb the definition of this family. We prefer to create a new family for these two very unusual deep-water species. *Teclaia recincolae* has been found in the Foix canyon, Catalán Sea at 1210-1180 m depth (see Table 1). None of the specimens observed (81) had open statocysts. All the specimens of *Parateclaia euromarge* have been found in the Lacaze-Duthiers canyon off Banyuls at 500 m depth and had open statocysts. As stated above these two genera are almost indistinguishable except for the presence/absence of sense organs. They presumably differentiated from a common ancestor, having been isolated by geological events in the above-mentioned canyons. Whether the original species did or did not have open statocysts is an insoluble question, but open statocysts are a character found in many deep-water medusae (see Gili *et al.*, 1998).

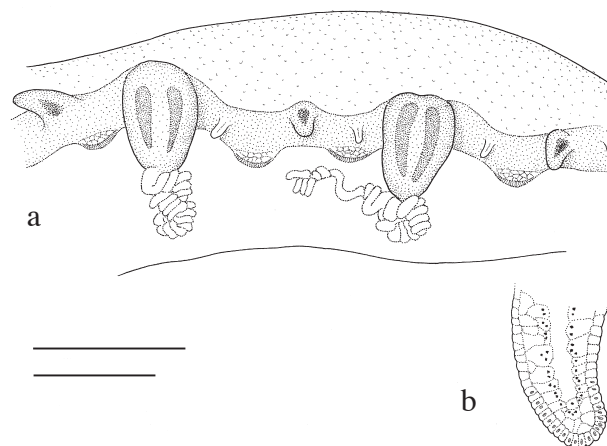


FIG. 6. – *Parateclaia euromarge*, detail of the umbrella margin: (a) abaxial view showing the elongated conical marginal bulbs, each with two large brown bands, the cordyliform conical structures, and the open statocysts between successive marginal tentacles. Scale: 0.5 mm ; (b) microscopic view of the cordyliform structures with terminal cnidocysts. Scale: 0.05 mm.

NARCOMEDUSAE

Family CUNINIDAE Bigelow, 1913

Cunina simplex Gili, Bouillon, Pagès, Palanques, Puig and Heussner, 1998

Material examined: 1 specimen, 1 August-1 September 1996; 1 specimen, 1-16 September 1996; 1 specimen, 1-16 October 1996. Size: 3.7-4.0 mm wide.

Solmissus albescens (Gegenbaur, 1857)

Material examined: 3 specimens, 1-16 January 1996; 1 specimen, 1-16 February 1996; 1 specimen, 16 April-1 May 1996; 1 specimen, 1-16 May 1996; 1 specimen, 1-16 December 1996; all these specimens were collected at 500 m depth. In addition one specimen collected at 1000 m depth on 1-15 December 1995. Size: 2.1-2.8 cm wide.

TRACHYMEDUSAE

Family PTYCHOGASTRIIDAE Mayer, 1910

Ptychogastria asteroides (Haeckel, 1879)

Material examined: 1 specimen, 16 March-1 April 1996; 1 specimen, 1-16 April 1996; 2 specimens, 16 April-1 May 1996; 4 specimens, 16 May-1 June 1996; 3 specimens, 1-16 June 1996; all these specimens were collected at 500 m depth. In addition one specimen collected at 1000 m depth on 1-16 October 1996. Size: 1-4 mm high.

Family RHOPALONEMATIDAE Russell, 1953

Homoeonema platygonon Browne, 1903

Material examined: 1 specimen, 1.4 mm high, 15-31 October 1996, 500 m depth.

Persa incolorata McCrady, 1859

Material examined: 2 specimens, 1.8-2.1 mm high, 1-16 June 1996, 500 m depth.

TABLE 1. – Species collected in the three submarine canyons investigated in the western Mediterranean. New species described are in bold. The species collected at stations located outside the canyons and cited in previous studies (Gili et al., 1998, 1999, 2000) are also listed.

	Foix	Lacaze-Duthiers	Planier	Stations outside of canyons
<i>Foersteria araiæ</i> Gili, Bouillon, Pagès, Palanques and Puig, 1999	•			
<i>Teclaia recincolae</i> Gili, Bouillon, Pagès, Palanques and Puig, 1999	•			
<i>Barcino foixensis</i> Gili, Bouillon, Pagès, Palanques and Puig, 1999	•			
<i>Solmissus albescens</i> (Gegenbaur, 1857)	•	•	•	
<i>Ptychogastria asteroides</i> (Haeckel, 1879)	•	•	•	
<i>Homoeonema platygonon</i> Browne, 1903	•	•	•	
<i>Calycopsis simplex</i> Kramp and Damas, 1925		•		
<i>Euphysa aurata</i> Forbes, 1848		•		
<i>Cunina simplex</i> Gili, Bouillon, Pagès, Palanques, Puig and Heussner, 1998		•		
<i>Solmaris flavescens</i> (Kölliker, 1853)		•		
<i>Leuckartiara brownei</i> Larson and Harbison, 1990		•		
<i>Guillea canyonicolæ</i> gen. nov., sp. nov.		•		
<i>Parateclaia euromarge</i> gen. nov., sp. nov.		•		
<i>Foersteria antoniae</i> Gili, Bouillon, Pagès, Palanques, Puig and Heussner, 1998		•	•	
<i>Persa incolorata</i> McCrady, 1859		•	•	
<i>Zanclæa</i> spp.			•	
<i>Haliscera racovitzæ</i> (Maas, 1906)			•	
<i>Arctapodema australis</i> (Vanhöffen, 1902)			•	
<i>Sminthea eurygaster</i> Gegenbaur, 1857				•
<i>Amphinema rubra</i> (Kramp, 1957)				•
<i>Modeeria rotunda</i> (Quoy and Gaimard, 1827)				•
<i>Cunina globosa</i> Eschscholtz, 1829				•
<i>Haliscera bigelowi</i> Kramp, 1947				•

GENERAL REMARKS

Recent investigations carried out in four western Mediterranean submarine canyons have shown that the specific composition and abundance of the hydromedusa populations differ between each canyon (see Table 1). These differences may be related to environmental factors which are summarized as follows:

1) The seasonal fluxes observed inside submarine canyons possibly enhance species abundance and the geomorphological structure of each canyon appears to have a great influence on its faunal composition. For instance, the narrowest canyons (such as Foix), having less communication with the open sea, appear to favour species isolation and so seemingly have induced greater speciation over evolutionary times.

2) Flux of biogenic components varies according to location and period of the year and it increases downstream (from Planier to Foix canyons), following the Northern Current. The number and abundance of endemic species also appears to increase from Planier to Foix canyons.

3) Seasonal distribution of the most abundant common hydromedusae, all of which are meroplanktonic, reflects the probable existence of a polyp or other resting stages, and a life-cycle adapted to the environmental fluctuations inside the canyons.

The highest number of species and individuals have been collected from March to mid-June in the traps located nearest the sea floor. However, the global number of medusae in Mediterranean canyons appears to remain quite constant, because some specimens have also been collected during summer in the intermediate-depth traps (Fig. 7). *Foersteria antoniae*, a species only reported from the Lacaze-Duthiers and Planier canyons (Gili et al. 1998) was present in the bottom trap during spring and early summer, while *Parateclaia euromarge* was present only during summer in the intermediate-depth traps of Lacaze-Duthiers canyon. The medusae collected during autumn and winter were common species like *Solmissus albescens* and *Ptychogastria asteroides* that have been recorded in all the Mediterranean canyons investigated (Gili et al. 1998, 1999, 2000).

In order to study relationships between environmental factors and species occurrence, temporal evolution of total mass fluxes inside the Lacaze-Duthiers canyon during 1996 was studied (Heussner unpublished data) (Fig. 7). The total mass fluxes (Fig. 7a) and the opal (biogenic silica) percentage (Fig. 7b) (derived from biological activity from the surface waters on the shelf) are higher in the spring when the number of both species and individuals of hydromedusae increased in the trap samples. The spring total flux peak (potential food supply to the

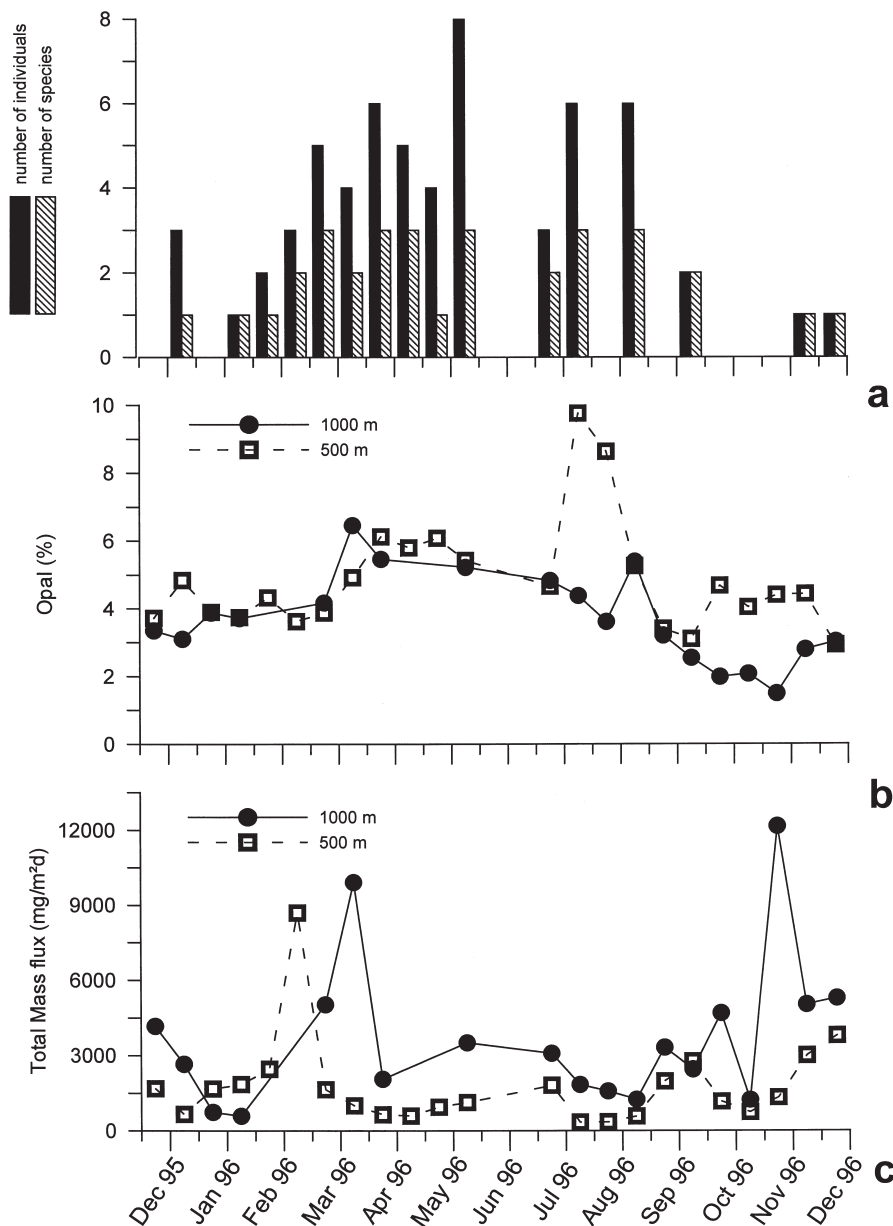


FIG. 7. – Lacaze-Duthiers canyon, 1996: (a) temporal evolution of both the number of individuals and the species of hydromedusae collected during the year; (b) time series of biogenic opal contents; (c) total mass fluxes of settling particulate matter trapped 30 mab and 500 mab at the Lacaze-Duthiers canyon on 1000 m bottom depth.

canyon bed) appears to serve as a threshold episode which triggers medusa population growth. After the spring, medusan populations remain quite constant until early autumn, when both medusa abundance and opal flux decrease. The rather small increase of fluxes during the summer at the intermediate level coincides with the occurrence of *Parateclia euro-marge* in the traps. These general trends agree with previous observations in the Foix canyon (Gili *et al.* 2000), where the higher number of individuals and species appears after a peak of biogenic opal caused by the spring discharge of rivers. The observations

at the Lacaze-Duthiers canyon seem thus to support the previously mentioned hypotheses concerning environmental control of the biodiversity of medusae inhabiting canyons

In general, the biological and environmental features of the submarine canyons in the north-western Mediterranean lead to the postulation that these habitats shelter a high and perhaps novel faunal diversity, known so far mostly by new species of hydromedusae. The endemic hydromedusan species of the Planier, Lacaze-Duthiers, and Foix canyons are closely related (see Table 1). For instance, *Foersteria antoniae* occurs

in low numbers in two canyons, Planier (with very few individuals) and Lacaze-Duthiers canyon, which could mean that both canyons are and/or were connected by currents. Both of those canyons are quite isolated from the southernmost canyon (Foix) where *F. araiæ* is the endemic dominant species. More investigations in additional, and still-unstudied canyons located between Foix and Lacaze-Duthiers (near Blanes and Palamós) are needed to define possible biogeographical borders and whether their existence could be related with environmental constraints. The isolation of species could be related to the hypothesis mentioned in previous papers that this fauna appears to be characterised mostly by species that develop their entire life-cycle inside a canyon. These life-cycles seem to be governed by external factors such as transport of organic debris to the sea floor (related to river inputs, storms, etc.), interaction and circulation of water masses along with the canyon's topography, and biological production throughout the water column. These observations have led us to consider submarine canyons as key habitats for the understanding of biodiversity in the shelf and slope zones.

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