

THE PLEISTOCENE BATHYAL TELEOSTEAN FAUNA
OF ARCHI (SOUTHERN ITALY):
PALAEOECOLOGICAL AND PALAEOBIOGEOGRAPHIC IMPLICATIONS.

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Abstract. The early-middle Pleistocene teleostean fauna of the Archi section, cropping out along the Calabrian side of the Messina Straits was studied. The integrated approach, based on the palaeobathymetric method coupled with the palaeoecological approach, already used on deep circalittoral and epibathyal assemblages, was applied for the palaeoenvironmental reconstruction. The otolith benthic and bathypelagic associations, strongly bathyal in their composition, suggest a deep bathyal palaeoenvironment, 500 to 1000 m deep, which is in agreement with the invertebrate benthic faunas. Compositional, structural, and taxonomical features of the teleostean assemblages indicate clearly Atlantic or more generally oceanic affinities. The Archi teleostean fauna indicates a palaeoceanographic pattern with deep-water and near-bottom temperature lower than 8-10°C, quite different from the Recent Mediterranean.

Riassunto. È stata studiata la fauna a teleostei della sezione pleistocenica di Archi che affiora lungo il versante calabro dello Stretto di Messina. L'analisi delle associazioni ad otoliti è stata condotta applicando l'approccio integrato, già utilizzato per associazioni del circalitorale profondo e dell'epibatiale, basato sul metodo paleobatimetrico e l'approccio paleoecologico. Le associazioni bentoniche e bentonectoniche ad otoliti indicano un paleoambiente batiale presumibilmente compreso tra 500 e 1000 m.

Aspetti composizionali, strutturali e tassonomici di queste associazioni indicano la loro forte affinità con la fauna atlantica o genericamente oceanica. Tale affinità testimonia un regime paleoceanografico del tutto differente da quello del Mediterraneo attuale, con temperature al fondo inferiori agli 8-10° C.

Introduction

The Archi site is one of the best known deep-sea deposits cropping out in the Messina Straits area. It has been studied several times with particular attention to cnidarian faunas (Placella 1978; Guadagno et al. 1979) and molluscan faunas (Crovato & Taviani 1985; Taviani et al. 1990; Micali & Villari 1986; Rindone 1990). Placella (1978) and Guadagno et al. (1979) also addressed the deep-sea Atlantic character of the Archi corals. More

recently, Di Geronimo et al. (1997) carried out a new study of the benthic faunas (foraminifers, molluscs, bryozoans, and serpulids) in light of the modern knowledge regarding the deep-sea Pleistocene Mediterranean invertebrate faunas, bringing to attention the strong affinity of the benthic palaeocommunities with the present-day North Atlantic.

In the present work, the otolith assemblages from the Archi section were analysed to improve the knowledge of the Pleistocene deep-sea teleostean fauna, focusing mainly on their palaeoecology and palaeobiogeography. The integrated approach proposed by Girone (2000b), based on the palaeobathymetric method already well known in the literature (Nolf & Brzobohaty 1994) together with the palaeoecological approach, was applied for the palaeoenvironmental reconstruction. Indeed this integrated approach, already used on Pleistocene otolith assemblages (Girone 2000b), has provided a great improvement in the palaeoenvironmental reconstruction of deep circalittoral (*sensu* Pérès & Picard 1964; Pérès 1967) and epibathyal deposits. The deep-sea assemblages from the Archi site represent a good example to test the sensitiveness of the integrated approach in deeper settings.

The relationship between the teleostean fauna of the Archi section and the Atlantic fauna is discussed also in the context of an evolutionary model of the deep Mediterranean benthos based on the invertebrate faunas (Benson 1972; Di Geronimo et al. 1996; Di Geronimo & La Perna 1997; Corselli 2001).

Geological setting

The Archi section crops out on the Calabrian side of the Messina Straits. The Messina Straits zone is currently interpreted as a basin belonging to the Calabrian-

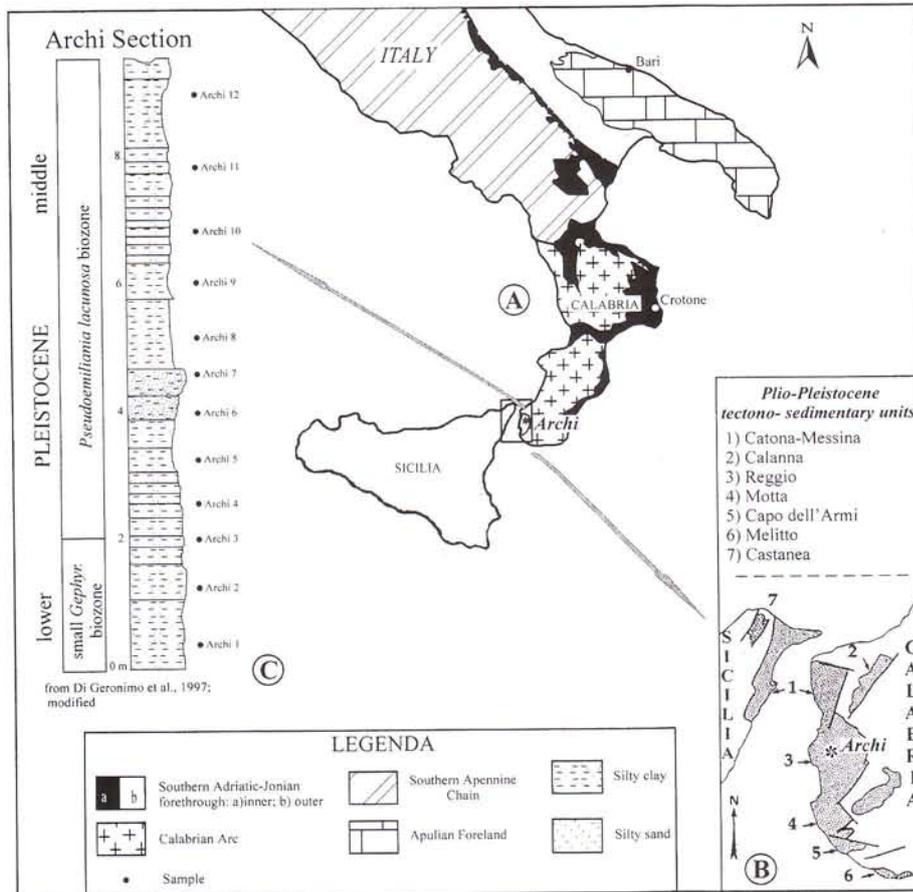


Fig. 1 - A: Location of the study area; B: The tectono-sedimentary framework of the Messina Straits area (from Di Geronimo et al., 1997, modified); C: The Archi section.

Peloritan Arc. It consists of tectonic crystalline-metamorphic units covered by the Capo d'Orlando Flysch (Late Aquitanian - Langhian) (Bonardi et al. 1980). This unit is tectonically overlain by the "argille varicolori", a chaotic *mélange* of pelitic matrix containing macrofossils as old as the Cenomanian and enclosing olistoliths of Palaeogene calciturbidites and Chatian-Early Miocene quartzarenitic turbidites. The *mélange* is overlain by an unnamed sequence of Serravallian-Tortonian turbiditic deposits and rare Messinian evaporites.

A subsequent discordant Plio-Pleistocene sequence was recently recognised (Barrier & Keraudren 1983; Barrier et al. 1985; Barrier 1987; Aifa et al. 1987; Montenat et al. 1987). It consists of diachronous facies whose age generally decreases from mainland to coastline and from north to south. They were deposited within small basins bounded by fault escarpments, which sometimes crop out showing remains of sessile faunas (Barrier et al. 1989, 1996). The Plio-Pleistocene fault systems split the Messina Straits area into several blocks that evolved as distinct basins corresponding to the "tectono-sedimentary entities" of Barrier (1984, 1987).

The Archi section, 9 m thick, belongs to the Reggio tectono-sedimentary entity (Fig. 1), which developed during the upper part of the Early Pliocene up to the middle-late Pleistocene. The sedimentary sequence begins with transgressive shallow-water deposits, evolves to bathyal units, and ends with the "Messina Gravel".

In particular, the section studied is located near

Reggio Calabria (southern Italy) (Fig. 1) and is well exposed along an N-S abandoned quarry front. It consists mainly of well-stratified pelitic sediments with beds generally faintly sloping westward (Di Geronimo et al. 1997). Two bed-sets were recognised along the quarry front: a lower one, whose beds are involved in a gentle flexure, and an upper one, showing parallel bedding. Within the markedly homogeneous pelitic sequence, two thicker and coarser (silty-sandy) beds stand out at the base of the upper bed-set (Di Geronimo et al. 1997).

According to the calcareous nannofossil assemblages, the section ranges from the early Pleistocene (small *Gephyrocapsa* nannofossil biozone) in its basal part (about the first three m), to the middle Pleistocene (*Pseudoemiliania lacunosa* nannofossil biozone) in the middle-upper part (Di Geronimo et al. 1997) (Fig. 1).

Previous studies of the benthic invertebrate fauna (foraminifers, molluscs, bryozoans and serpulids) indicate a bathyal palaeoenvironment, 500 to 1000 m deep. According to the planktonic foraminifera assemblages, the deposition occurred during a cold phase (Di Geronimo et al. 1997). Moreover, the compositional, structural and taxonomical features of the palaeocommunities indicate a strong affinity with the present-day North Atlantic or oceanic conditions involving a psychrosphaeric palaeoceanographic model with bottom temperatures lower than 8°-10° C, which is very different from the Recent Mediterranean model (Di Geronimo et al. 1997).

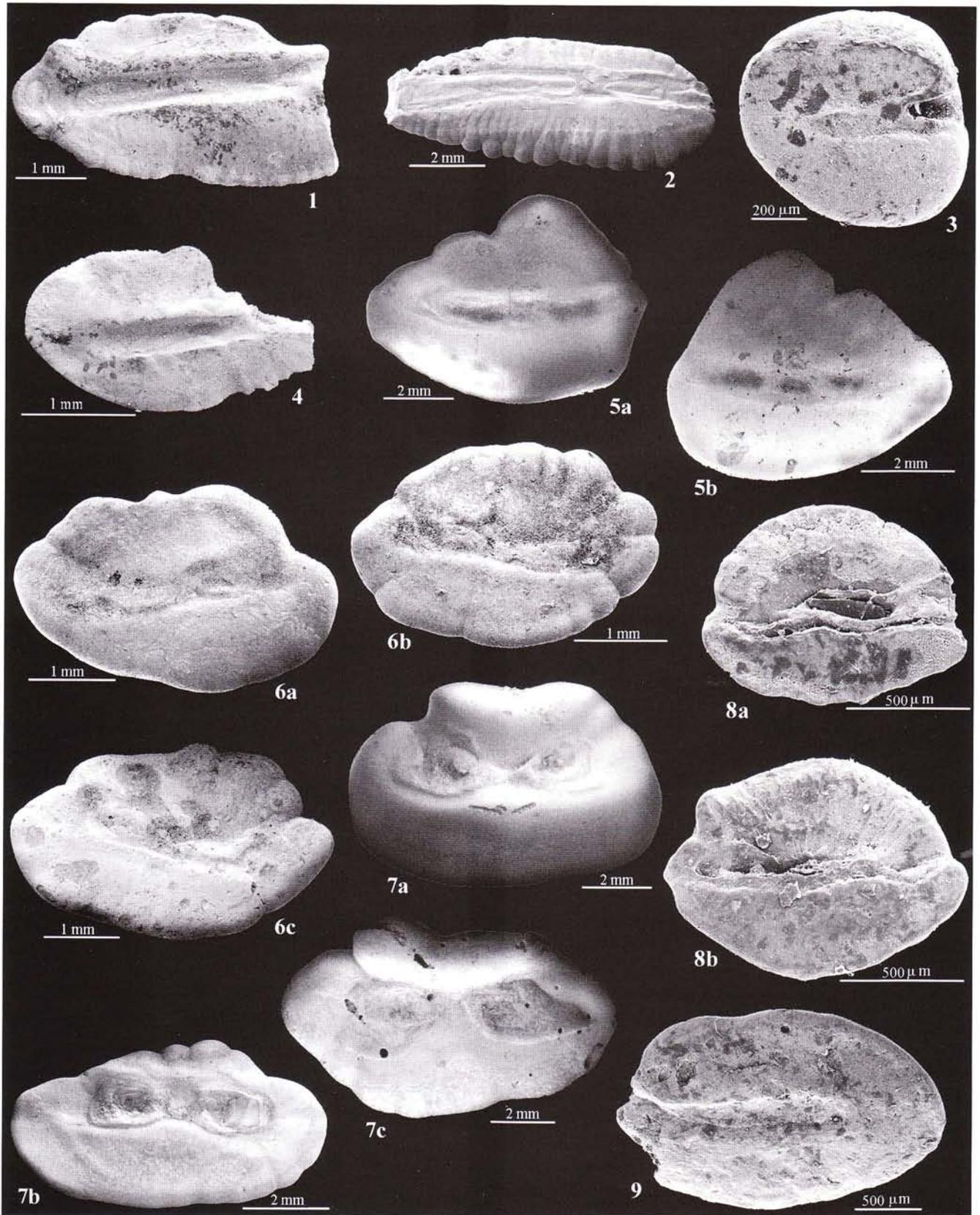


PLATE 1

All fossil otoliths are deposited in the collection of the Dipartimento di Geologia e Geofisica, University of Bari.

In the captions, the abbreviation L stands for left otolith and the abbreviation R for right otolith.

Fig. 1 - *Nansenia groenlandica* (Reinhardt, 1840) L; sample Archi 9. Fig. 2 - *Micromesistius pontassou* (Risso, 1826) L; sample Archi 8. Fig. 3 - *Chauliodus sloani* (Schneider, 1801) L; sample Archi 10. Fig. 4 - *Bathylagus euryops* (Goode & Bean, 1896) L; sample Archi 8. Fig. 5 - *Coelorrinchus stellaris* Nolf & Girone, 2000 a: L; b: R; sample Archi 7. Fig. 6 - *Coryphaenoides cf. guentheri* (Vaillant, 1888) - a: L; b-c: R; sample Archi 8. Fig. 7 - *Coryphaenoides rupestris* (Günner, 1765) R; a: sample Archi 8; b-c: Archi 9. Fig. 8 - Zoarcidae ind. L; a: sample Archi 7; b: Archi 4. Fig. 9 - *Bathypterois* sp. R; sample Archi 7.

SYSTEMATIC LIST OF THE TAXA FROM ARCHI SECTION		Archi 1	Archi 2	Archi 3	Archi 4	Archi 5	Archi 6	Archi 7	Archi 8	Archi 9	Archi 10	Archi 11	Archi 12
taxa in bold = Recent Atlantic taxa disappeared from Mediterranean		D%	D%	D%									
* = extinct species													
PELAGIC													
BATHYLAGIDAE	<i>Bathylagus euryops</i> Goode & Bean, 1896								5.3				
ARGENTINIDAE	<i>Nansenia groenlandica</i> (Reinhardt, 1840)									3.4			
	<i>Nansenia</i> ind.						0.3	0.3					
STERNOPTHYCHIDAE	<i>Maurolicus muelleri</i> (Gmelin, 1789)				3.2		0.6						
	<i>Polyipnus</i> aff. <i>pollii</i> Schultz, 1961										1.3	2.6	
GONOSTOMATIDAE	<i>Gonostoma</i> ind.										0.4		
PHOTICHTHYIDAE	<i>Vinciguerria attenuata</i> (Cocco, 1838)												1
	<i>Vinciguerria poweriae</i> (Cocco, 1838)										1.3		
CHAULIODONTIDAE	<i>Chauliodus sloani</i> Schneider, 1801										0.4		
MYCTOPHIDAE	<i>Bentosema glaciale</i> (Reinhardt, 1837)	9.6	8.9	22	6.4	54.5	20.6	17.7	53	45	2.1	20.6	9.5
	<i>Ceratocopelus maderensis</i> (Lowe, 1939)	36	20.3	38.5	35.4	18.2	38.2	29.6	21	10.3	36	40.5	15
	<i>Diaphus holti</i> Taaning, 1918										1.7	6	
	<i>Diaphus rafinesqui</i> (Cocco, 1838)			1			0.3	0.5			1.3	0.4	
	<i>Diaphus taaningi</i> Norman, 1930	7.2	18.8	9	9.6		5.6	16.2					
	<i>Electrona rissoi</i> (Cocco, 1829)						0.6						0.7
	<i>Hygophum benoitii</i> (Cocco, 1838)	23.2	18.3	19	22.5	18.2	11.4	11.6	5.2	6.9	26.1		63.2
	<i>Hygophum hygomi</i> (Lutken, 1892)	3.2	6.9				0.3	3			5.2	8.1	
	* <i>Hygophum</i> sp. 1	1.6		4			7.5	7			4.3	6.5	6.8
	* <i>Lampadena ionica</i> Girone & Nolf, 2002	0.8	4.9				0.3				1.7		
	<i>Lobianchia dofleini</i> (Zugmayer, 1911)		1		9.6	9.1					2.6	4.7	
	<i>Myctophum punctatum</i> Rafinesque, 1810	12	8.9	4	9.6		7.8	8	5.2	3.4	4.3	8.6	1.3
	<i>Notoscopelus elongatus</i> (Costa, 1844)	4	2.4	2	3.2		3.6	4	10.5	31	1.7	2	2.7
	* <i>Scopelopsis pliocenicus</i> Anf. & Mosna, 1976	1.6	8.4				1	0.7				8.7	
	<i>Symbolophorus veranyi</i> (Moreau, 1888)	0.8					1.3	1.5			1		
	total pelagic specimens	135	202	135	31	11	306	388	19	29	230	232	147
BENTHOPELAGIC													
ALEPOCEPHALIDAE	<i>Alepocephalus</i> sp.					27.2							
MYCTOPHIDAE	<i>Lampanyctus erocodilus</i> (Risso, 1810)	91.3	84.6	86	45.4	100	82.3	65.3			87.5	50	85.7
GADIDAE	<i>Gadiculus argenteus</i> Guichenot, 1850							8.2					
	<i>Micromesistius poulassou</i> (Risso, 1826)	4.3			18.2		11.7	8.1	20	25			
	<i>Phycis blienoides</i> (Brunnich, 1768)			14				2					
MACROURIDAE	<i>Coelorinchus coelorhincus</i> (Risso, 1810)	4.3					3						
	* <i>Coelorinchus stellaris</i> Nolf & Girone 2000							6.1				17	
	<i>Coryphaenoides rupestris</i> Gunners, 1765							2	20	75			
	<i>Coryphaenoides</i> cf. <i>guentheri</i> (Vaillant, 1888)								60				
CARANGIDAE	<i>Trachurus</i> sp.										12.5		
BENTHIC													
CHLOROPHTHALMIDAE	<i>Bathypterois</i> sp.							2					
BYTHIDAE	<i>Bellotia</i> cf. <i>apoda</i> Giglioli, 1883		7.6					4				33	
	<i>Bythitidae</i> sp. ind.		7.6					3	0.5				14.3
INCERTAE SEDIS													
ZOARCIDAE	<i>Zoarcidae</i> sp. ind.				9				2				
	total benthic and benthopelagic specimens	7	13	7	11	1	34	49	22	4	8	6	7

Tab. 1 - Systematic list of teleost taxa from Archi section. Relative abundance of each species and total amount of specimens per sample.

Results

The twelve bulk samples collected along the Archi section contain otoliths referable to thirty eight teleost taxa (Tab. 1), thirty four of which can be classified at specific level. The preservation of the otoliths is generally good. In some cases, though, the specimens of myctophids show solution effects (especially on the inner faces, and in particular in the sulcus area, whereas the outer faces are only slightly worn) or are encrusted by bryozoans or foraminifers indicating long exposure on the sea-bottom and a slow sedimentation rate. The difference in preservation of the inner and outer face of the otoliths may be due to the structure of the sulcus area. The surface of the sulcus of several fish is built of somewhat irregularly assembled carbonate particles which are loosely connected and

Material and methods

Twelve bulk-samples, each measuring about 10 dm³, were collected along the section (Fig.1). They were routinely processed for macrofaunal studies, and the residues sieved through a 250µm mesh. The coarser residues (>425µm) contained the greatest number of specimens while the finer portions (>250 µm) were sorted in order to detect small-sized pelagic species. The abundance and dominance of each taxon for each sample were calculated following the criterion proposed for the bivalve group by Di Geronimo & Robba (1976). The calculations were carried out separately for the pelagic and benthic - benthopelagic groups (Tab. 1).

In the palaeoecological approach, only the benthopelagic and benthic fishes were taken into account and, besides the taxonomic composition, other attributes of the associations were analysed (Girone 2000b). On the contrary, the entire assemblage (mesopelagic, benthopelagic, and benthic fishes) was analysed using the palaeobathymetric method proposed for this group by Nolf & Brzobohaty (1994).

show a meshwork structure, while areas outside the sulcus have a more compact structure (Martini 1974). Solution will affect the sulcus area much more than the other areas. The outer face of the sagittae will be more resistant to solution processes.

In sharp contrast to the other samples, samples Archi 6 and Archi 7 are rich, both in species and specimens. Sample Archi 5 contains the lowest number of specimens that are poorly significant palaeoecologically.

The otolith assemblages include 22 species that still live in the Mediterranean Sea with two of them, *Symbolophorus veranyi* and *Chauliodus sloani* (Pl. 1, fig. 3) identified as fossils for the first time. There are also five taxa, referable to Atlantic species, which have long disappeared from the Recent Mediterranean. Among these, the bathypelagic species *Bathylagus euryops* (Pl. 1, fig. 4), *Nansenia groenlandica* (Pl. 1, fig. 1) and the benthopelagic *Coryphaenoides rupestris* (Pl. 1, fig. 7) are, for the first time, reported as fossil species while *Polyipnus* cf. *pollii* and *Diaphus taaningi* were already known in the Mediterranean area. *P.* cf. *pollii* has been reported in the middle Pleistocene of the Montalbano Jonico section (Girone

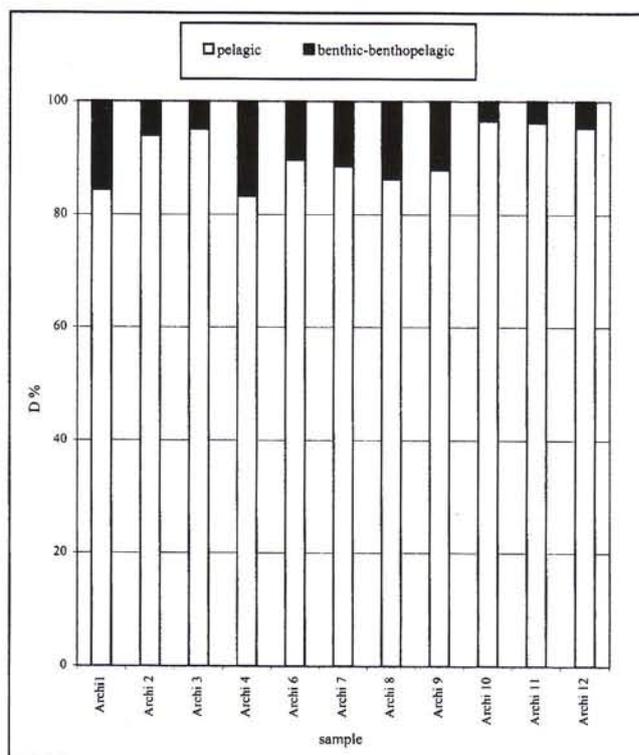


Fig. 2 - Benthopelagic-benthic-mesopelagic ratio in the otolith assemblages from the Archi section.

2000a; Girone & Varola 2001), and *D. taaningi* has been found from the Miocene (only Tortonian) to the middle Pleistocene (Brzobohaty & Nolf 2000; Girone 2000b).

Lampadena ionica, *Hygophum* sp. 1, *Scopelopsis*

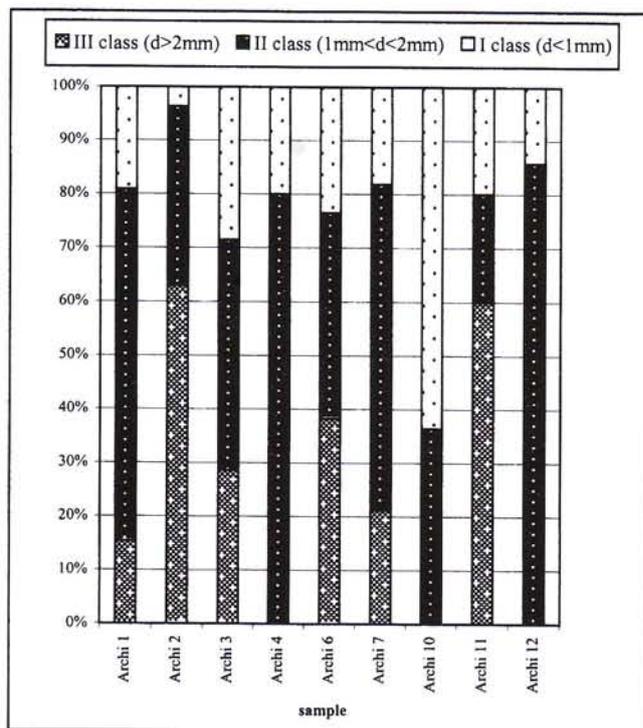


Fig. 3 - Size distribution of otoliths in *Lampanyctus crocodilus* populations from the Archi section.

pliocenicus and *Coelorrinchus stellaris* (Pl. 1, fig. 5) are fossil species; the first and the second are reported only in Pleistocene sediments of the Mediterranean (Girone & Nolf 2002; Girone & Varola 2001). *S. pliocenicus* is known as an endemic species of the Mediterranean area from the Miocene (Tortonian) to the Pleistocene, while *C. stellaris* has been reported in the late Oligocene sediments of Aquitaine and in the Late Pliocene (Gelasian) and early-middle Pleistocene of the Mediterranean (Nolf & Girone 2000).

The assemblages recognised are composed of low percentages of benthic and benthopelagic components that generally make up for less than 20% with respect to the pelagic group (Fig. 2), which is mostly represented by mesopelagic fishes (myctophids). Similar to the pelagic assemblages, the benthic and benthopelagic associations of Archi 6 and Archi 7 are the richest in specimens; the association of Archi 7 is also the richest in species (Tab. 1).

Therefore, in the benthic-benthopelagic group it is possible to distinguish bottom-related taxa that swim just above the sea bottom (benthopelagic) or that live in contact with it (benthic).

Benthic fishes (Tab. 1) are not common with only two species, *Bellotia* cf. *apoda* found in three samples (Archi 2, 7 and 11) and *Bathypterois* sp. (Pl. 1, fig. 9) detected only in sample Archi 7. The Recent vertical distribution of *B. apoda* is poorly documented because this species is known only from a few specimens found off Madeira and Portugal and in the Mediterranean. It has been caught in bottom trawls at depths from 30 to 500 m (Whitehead et al. 1986). On the contrary, the genus *Bathypterois* is circumglobal at tropical and temperate latitudes and is typical at bathyal to abyssal depths (Whitehead et al. 1989). In the Recent Mediterranean and in the Atlantic, five species belonging to this genus are reported. These, considered typical of deep bathyal environments, are generally found exclusively at depths greater than 700 m (Maurin 1968; Stefanescu et al. 1994).

The abundance of benthic fishes in the Archi section could increase if the specimens referred to *Bythitidae* sp. ind. and *Zoarcidae* sp. ind. (Pl. 1, fig. 8) were included. These families are represented mostly by benthic species living from a few meters to abyssal depths with only a few species being bathypelagic. In particular, the specimens referred to the *Bythitidae* are very small in size and are lacking diagnostic features for specific identification. Nevertheless, it is not to be excluded that they could belong to *B. apoda*.

The specific attribution of the specimens referred to the Family *Zoarcidae* was not possible due to the scarce Recent material available for comparison. The zoarcids are reported in cold and temperate waters of both hemispheres. Temperature and salinity are the main factors that influence their distribution. Several boreal species are linked to water temperatures lower than 0° C and a sali-

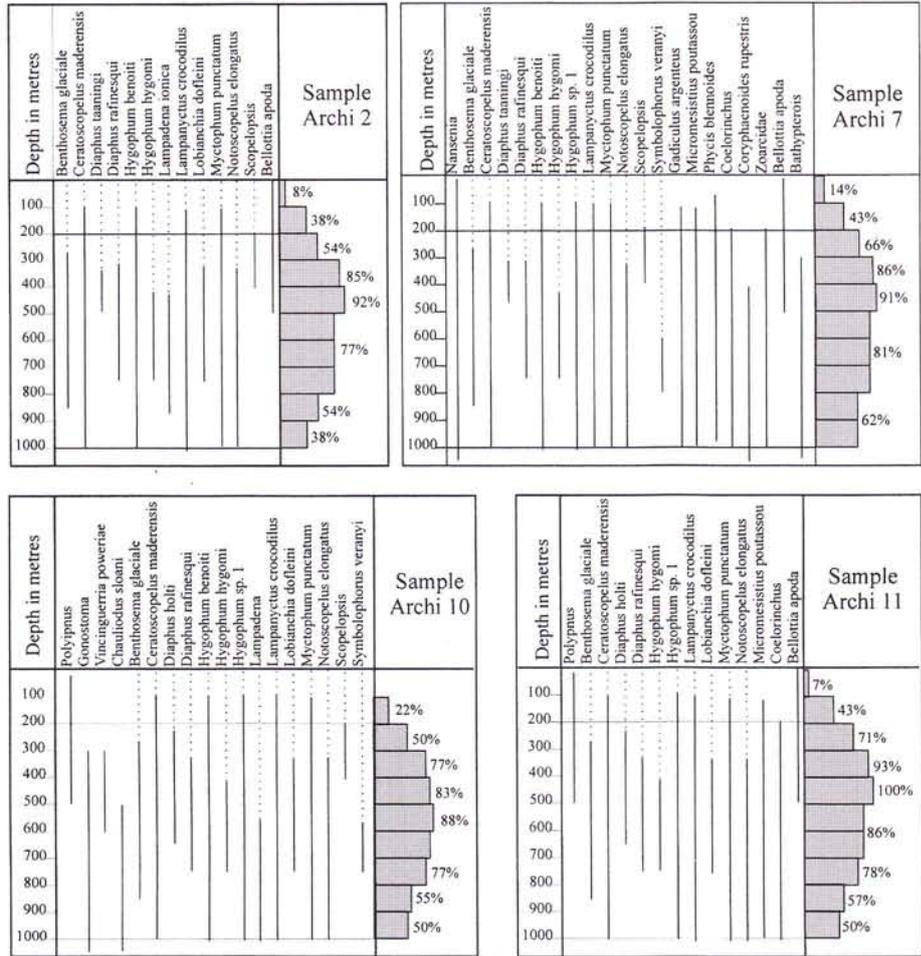


Fig. 4 - Recent bathymetric distribution of teleost taxa represented in Archi 2, Archi 7, Archi 10, and Archi 11 assemblages. For each 100 m bathymetric interval, the graph shows the potential presences, expressed as a percentage of the total number of taxa utilised in the analysis. The dotted lines indicate nightly presence of mesopelagic species at the surface; see Nolf & Brzobohaty (1994) for a more detailed discussion of the methodology.

nity of 34 ‰. *Melanostigma atlanticum* is the only species reported in the western Mediterranean. It is bathypelagic over the continental slope mostly at 400 - 1000 m depth.

The benthopelagic group includes mostly gadids and macrourids that represent the most abundant species. On the contrary, the myctophids, represented only by one species, are the most abundant in specimens and occur widely throughout the section. However, the myctophids show the highest diversity in the pelagic group (Tab. 1). Among the myctophids, *L. crocodilus* is a species that can change life habits during growth and consequently may be considered a pelagic or benthopelagic fish. In particular, the adults of this species dwell close to the bottom changing their life habit from mesopelagic in the juvenile stage to benthopelagic in later stages (Stefanescu & Cartes 1992). The distribution of the three class sizes recognised in the population of *L. crocodilus* from Archi (Fig. 3) suggests that the second and third classes are the most abundant. Observations performed on the sizes of recent populations (Girone 2000b) indicate that the second and third classes are made of adult specimens whereas the first is made of juveniles. Consequently, the populations of *L. crocodilus* were included in the benthopelagic associations.

Among the gadids, *Micromesistius poutassou* (Pl. 1, fig. 2) is the most common species while *Phycis*

blennoides and *Gadiculus argenteus* were found only occasionally. The gadid species are represented mostly by medium-large specimens, though very large specimens of *M. poutassou* and *P. blennoides* were found in samples Archi 6 and Archi 7. Among the macrourids, the North Atlantic *Coryphaenoides rupestris* is the most abundant. It was recognised in the samples from the middle-upper part of the section (samples Archi 7, Archi 8, and Archi 9) (Tab. 1) where it is represented by very large specimens. In the sample Archi 8, it is associated with the congeneric species *C. cf. guentheri* which represents 60% of the associations. *C. guentheri*, is the deepest species of this genus and, in particular, it has been found exclusively at depths greater than 800-1000 m (Stefanescu et al. 1994; Morales-Nin 1990).

The macrourid group includes also the Recent *Coelorinchus coelorincus* found in samples Archi 1 and Archi 6 and the fossil *C. stellaris* recognised in samples Archi 7 and Archi 11 (Tab. 1). The former species is represented mostly by medium-large individuals whereas the sizes of the specimens referable to *C. stellaris* range from medium-large in Archi 11 to very large in Archi 7.

Other species that occur occasionally include *Alepocephalus* sp. and *Trachurus* sp. whose taxonomic status is not well defined because of their poor preservation. The pelagic group includes mesopelagic and bathypelagic

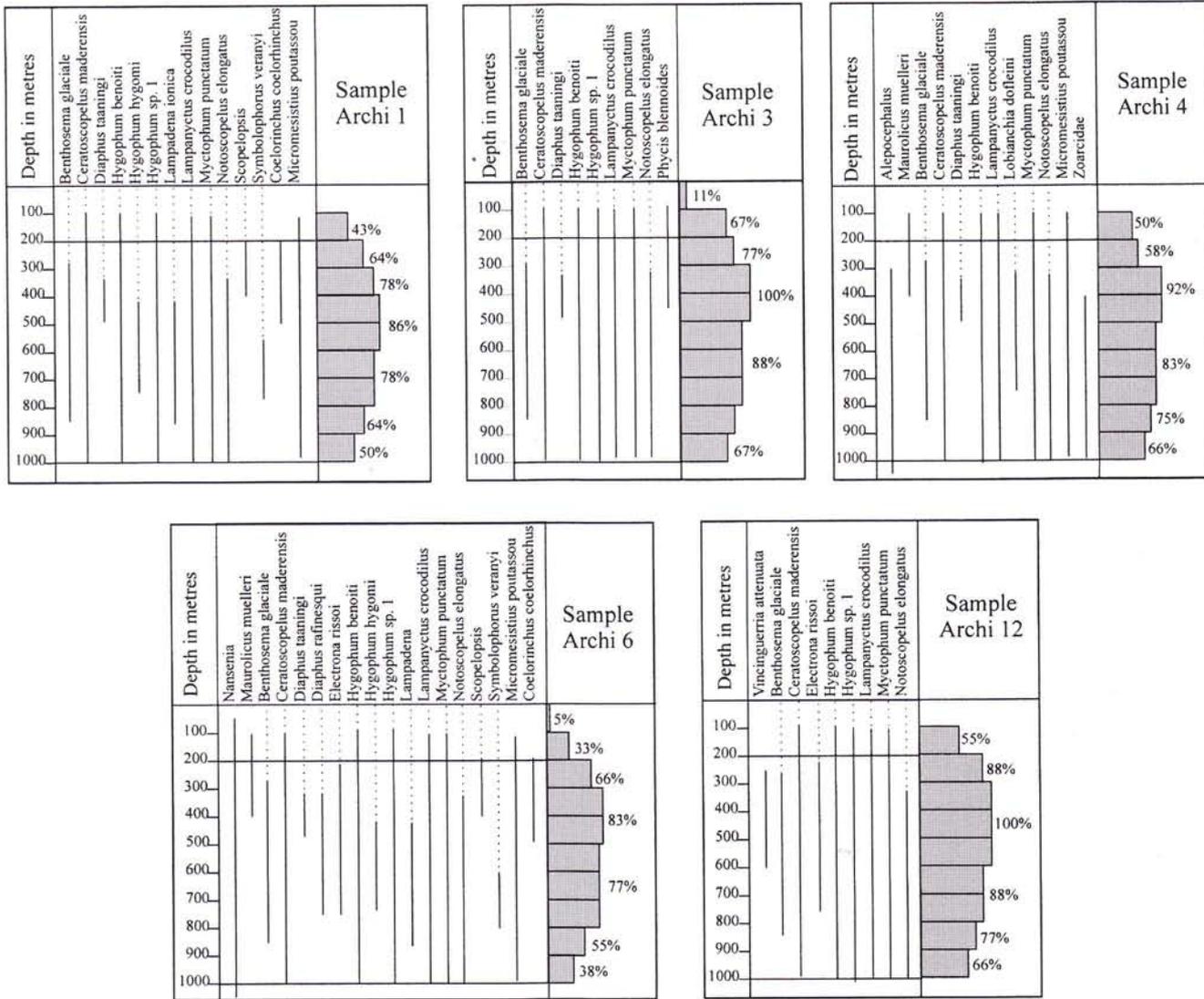


Fig. 5 - Recent bathymetric distribution of teleost taxa represented in Archi 1, Archi 3, Archi 4, Archi 6, and Archi 12 assemblages; see Fig. 4 for the explanation.

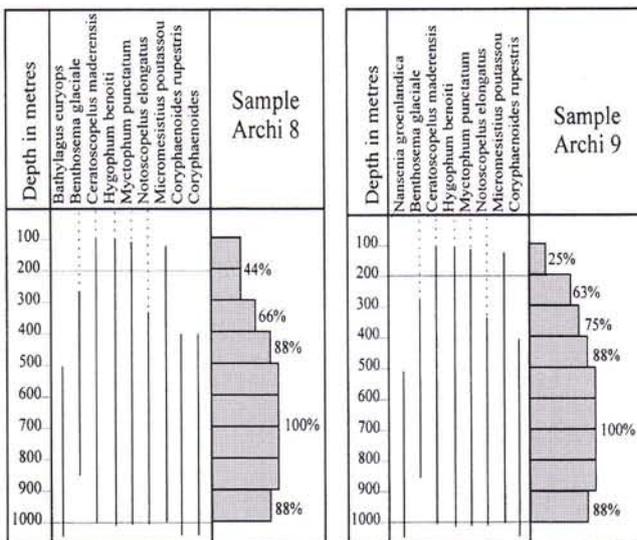


Fig. 6 - Recent bathymetric distribution of teleost taxa represented in Archi 8 and Archi 9 assemblages; see Fig. 4 for the explanation.

species. The mesopelagic species belong to the Family Myctophidae, to the sternoptychids *Maurolicus muelleri* and *Polyipnus cf. polli*, to the photichthyids *Vinciguerria attenuata* and *V. poweriae*, and to the stomiatoid *Chauliodus sloani*. *Bathylagus euryops* and *Nansenia groenlandica*, occurring respectively in Archi 8 and Archi 9, are bathypelagic fishes. The myctophids are notably dominant from 95% to 100%. *Benthoosema glaciale* and *Ceratoscopelus maderensis* occur in all samples whereas *Hygophum benoiti*, *Myctophum punctatum*, and *Notoscopelus elongatus* are distributed widely throughout the section. The occurrence and abundance of *Diaphus holti* and *Electrona rissoi* are occasional. The species recognised have a wide bathymetric distribution ranging from about 100-200 m to 1000 m. Other species of a more defined bathymetric range, from 400 to 700 m, include *Hygophum hygomi*, *Diaphus rafinesqui*, and *Symbolophorus veranyi*. Most of the myctophid species occurring in the assemblages undergo size stratification with generally juveniles at shallower depths of the bathymetric ranges and adults at

greater depths. The populations of the myctophid species from Archi are generally composed of individuals of heterogeneous size except for *Notoscopelus elongatus* and *Symbolophorus veranyi*, which are represented entirely by very large individuals.

According to the palaeobathymetric method, the graphs reconstructed for each assemblage indicate the highest peaks relative to bathymetric intervals at depths greater than 300-400 m and a rapid decline of percentages corresponding to the shallower depths.

The graphs of Archi 2, Archi 7, Archi 10 and Archi 11 clearly position the 100m-interval of maximum presence between 400 and 500 m for the assemblages Archi 2, Archi 7 and Archi 11 and between 500 and 600 m for Archi 10 (Fig. 4). In the other cases, the graphs show the 200 m and 300 m-intervals of maximum presence at depths between 400 m and 600 m (Archi 1), 300 m and 500 m (Archi 3, Archi 4, Archi 6) or 300 and 600 m (Archi 12) (Fig. 5). The graphs of the assemblages Archi 8 and Archi 9 show wide but clear maximum peak between 500 and 900 m with a rapid decline in the percentages above 500 m (Fig. 6).

Discussion

The otolith assemblages from the Archi section are characterised by the dominance of meso-bathypelagic species over the benthic-benthopelagic species. The dominance of meso-bathypelagic individuals may be related to their biological features and the heterogeneous nature of the genesis of fossil otolith assemblages (sensu Kidwell & Bosence 1991). Considering biological causes, it is worth noting that the pelagic species, in particular the myctophids, form large shoals. On the contrary, in the deep-sea environments, the benthic and benthopelagic fishes are rarely represented by dense populations. Moreover the mesopelagic fishes are the main preys of larger predators, which may introduce the mesopelagic otoliths into the sediment through their excrements (Nolf 1985).

However, this hypothesis does not exclude all the other factors that may have contributed to the origin of the fossil otolith assemblages. The pelagic assemblages contain otoliths from all fishes, distributed in the entire water column, that fall to the bottom. However, the otoliths of benthic and benthopelagic species belong only to fishes that lived on the sea-bottom. Consequently, populations of pelagic fishes recognised in the fossil assemblages are mixed populations, with specimens that lived in different strata of the water column and are not necessarily indicative of the bottom depth. The wide size range observed in the fossil pelagic populations reflects the size stratification that affects pelagic fishes during their life. The populations of benthic and benthopelagic fishes occurring in the fossil assemblages and showing generally a single or similar dominant size range, are the genuine populations that inhabited the investigated area

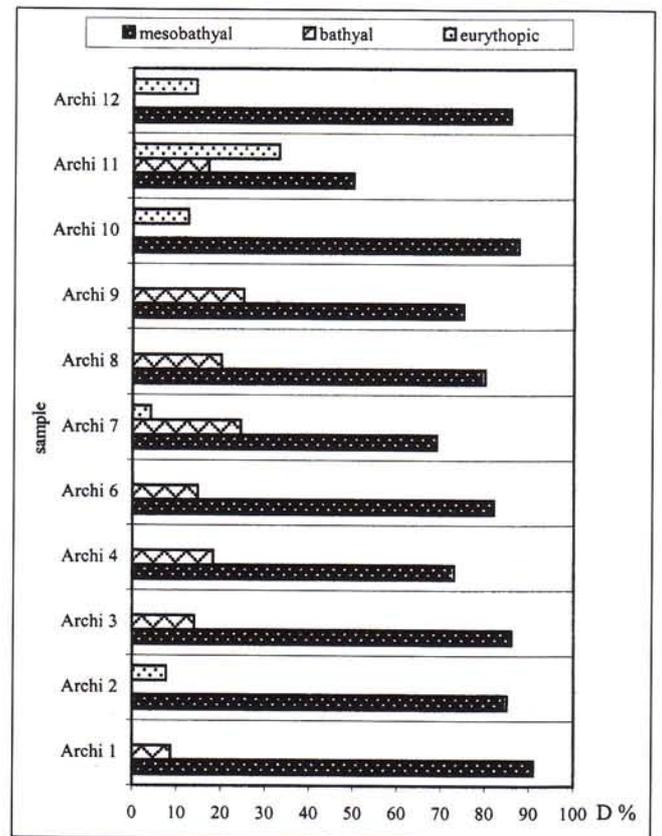


Fig. 7 - Distribution of benthic and benthopelagic fishes based on life environment in the Archi section.

and are really indicative of the bottom depth.

Similarly to benthic invertebrate associations (Di Geronimo et al. 1997), the increased richness of the teleostean benthic and benthopelagic associations in the middle part of the section (samples Archi 6 and Archi 7) can be related to a positive ecological response of the deep-sea communities to the hydrodynamically active phase. Field observations and sedimentological and palaeontological data suggest that the deposition of this stratigraphic interval was affected by hydrodynamic episodes, probably influenced by tectonics (Di Geronimo et al. 1997).

This kind of ecological response of the deep-sea communities and of demersal fish associations was already highlighted by Gooday & Turley (1990 and references) and Stefanescu et al. (1994) who showed the prominent role of near-bottom currents in increasing the organic inputs on the deep-sea bottom.

Palaeobathymetry

The otolith assemblages from the Archi section are clearly bathyal in their composition. In fact assemblages with macrourid otoliths, usually accompanied by great quantities of myctophid otoliths, are considered typical of continental slope sediments deposited at depths of at least 250 m (Nolf 1985; Nolf & Brozobohaty 1994). They

appear uncontaminated by reworked elements, except for the specimen of a gobiid which records an environment quite different from the deep-sea.

The benthic and benthopelagic associations include species typical of bathyal environments deeper than 400-500 m, such as the chlorophthalmid *Bathypterois*, the alepocephalid *Alepocephalus* and the deeper bathyal macrourids *C. rupestris* and *C. cf. guentheri*. The genera *Bathypterois* and *C. cf. guentheri* are generally reported as taxa closely associated with depths greater than 700-800 m (Stefanescu et al. 1994; Morales-Nin 1990). A similar ecologic setting is indicated by the genus *Alepocephalus*, even though the living Mediterranean *A. rostratus* has been found occasionally at shallower bathyal depths, showing a wider bathymetric distribution from 300 to 3600 m (Whitehead et al. 1989). However, according to Maurin (1968), *A. rostratus* is related to a sea bottom deeper than 500 m often associated with *L. crocodilus*.

C. rupestris shows a larger bathymetric distribution ranging from 400 m to over 1500 m even if it is more abundant at depths deeper than 600-700 m (Hareide & Garnes 2001; Lorance et al. 2001) where it is the dominant species in the fish communities. It has been found in Atlantic waters with temperatures of 8-10°C (Whitehead et al. 1986). This species undergoes seasonal vertical migrations, moving to deeper waters during the summer months and returning to shallower waters in the winter.

The common occurrence throughout the section of adult individuals of *L. crocodilus* should be also stressed. Maurin (1968) and Arena & Li Greci (1973) pointed out the frequent occurrence of the adult individuals of this myctophid at depths greater than 500 m on the sea floor of the central Mediterranean in association with the deep benthopelagic fishes. Therefore *L. crocodilus*, in its adult stage, takes on a notable meaning in the deep benthopelagic associations, in particular, in the Mediterranean Sea and is reported as a characteristic species on the middle slope 400-800 m deep (D'Onghia et al. 1998; Stefanescu et al. 1994).

In all benthic and benthopelagic associations from the Archi section, the dominance value of deep bathyal species is over 70% with the exception of the association from Archi 11 which represents only 50% (Fig. 7).

The group of epibathyal species, which are frequent along the section but with dominance value varying from 10% to 25% (Fig. 7), include the gadids *G. argenteus*, *M. poutassou* and *Phycis blennoides* and the shallower bathyal macrourids *C. coelorrinchus* and *C. stellaris*.

The gadids recognised, in subadult - adult stage, are considered as characteristic species of the upper continental slope in the bathymetric range between 200 and 400 m (Maurin 1968; Arena & Li Greci 1973; Cohen et al. 1990) where they show their maximum abundance. However, even if their abundance decreases sharply in the deeper setting, the presence of larger individuals is rather common.

In this framework, it is worth noting that the gadids found along the Archi section are mostly referable to large individuals. In particular the larger individuals of *M. poutassou* and *G. argenteus* were found in samples Archi 6 and Archi 7. Similarly, the living macrourid *C. coelorrinchus*, characteristic in about 200 to 500 m (Cohen et al. 1990), undergoes the larger-deeper phenomenon (Massutí et al. 1995; D'Onghia et al. 2000) and consequently the occurrence of large individuals in deeper setting is frequent. According to palaeontological evidence, the life habit of the fossil *C. stellaris* seems to be quite similar to the Recent congeneric and it also seems to have been subjected to the larger-deeper phenomenon. Observations carried out on the size of otoliths from different sites showed that the specimens of *C. stellaris* recognised in epibathyal associations are often smaller than the otoliths occurring in middle bathyal associations (Girone 2000b) in which the larger individuals are generally more common. The specimens of *C. stellaris* from the Archi section, in particular those found in the sample Archi 7, are comparable in size to the otoliths from middle bathyal associations. It is worth stressing again that in this sample the fossil species is associated with deep-sea taxa such as *C. rupestris*, *Bathypterois*, and *L. crocodilus*.

The benthic and benthopelagic associations, bathyal in their composition and structure, clearly indicate a deep bathyal environment located in the mesobathyal interval. A palaeodepth between 400-500 m and 1000 m can be tentatively inferred in agreement with the data from the analysis of the benthic invertebrate associations (Di Geronimo et al. 1997). No notable evidence of bathymetric changes can be identified even though the presence of deeper taxa such as *C. cf. guentheri* and *Bathypterois* in the middle part of the section could suggest a somewhat deeper setting.

The data obtained with the palaeobathymetric method are generally comparable with the data inferred by the palaeoecological approach based on benthic and benthopelagic associations. According to the palaeobathymetric method, the assemblages recognised clearly indicate a bathyal environment but the palaeodepths inferred are generally shallower than those calculated with the palaeoecological approach. The detailed analysis carried out on the benthic and benthopelagic associations suggests clearly that these are indicative of the mesobathyal environment and consequently the deeper parts of the bathymetric range, indicated by the graphs, may be more probable. In several cases, the shallower bathymetric ranges are influenced by the presence of mesopelagic fishes whose bathymetric distribution does not exceed 400 m in depth. It is obvious that their presence is not excluded in bottom assemblages deeper than 400 m but they are not representative of the real depth of the environment in which the assemblages were formed. On the other hand, the distribution of fish sizes and the larger-

deeper phenomenon must be taken into account for a more precise reconstruction of the deep-sea environment.

Palaeobiogeography and palaeoceanography

The Archi benthopelagic and pelagic teleostean fauna is characterised by a marked Atlantic affinity, already shown for the invertebrate benthic communities (Di Geronimo et al. 1997). Several deep-sea Atlantic species, no longer present in today's Mediterranean, were recognised and include the pelagic *Bathylagus euryops*, *Nansenia groenlandica*, *Polyipnus* cf. *polli*, and *Diaphus taaningi* and the benthopelagic *C. rupestris*.

B. euryops and *N. groenlandica* occur only in the North Atlantic from off southern Iceland to about 35° N and 45° N respectively (Whitehead et al. 1989). They are meso-bathypelagic fishes caught at depths ranging from 300 m to 1500 m in the northern areas and from 500 m to 1800 m in the southern areas. They are generally associated with water temperatures lower than 8–10°C; in different localities they were caught in water between 3°C and 4–5°C (Bigelow et al. 1964).

A similar meaning is shared also by the benthopelagic *C. rupestris*. This species, associated with bottom temperatures lower than 10°C, has been reported only in the North Atlantic from about 37°N to Baffin Island and Greenland, in the western Atlantic, and from 45° N to off Iceland and Norway in the eastern Atlantic. In the southern latitudes, *C. rupestris* has been captured off Africa in the Mauritania upwelling area.

Another faunal feature is represented by the occurrence of extinct species, closely related to deep-sea Atlantic or generally oceanic taxa, such as the pelagic *Lampadena ionica* and *Scopelopsis pliocenicus* and the benthopelagic *Coelorinchus stellaris*. Based on present knowledge, *Lampadena ionica* and *S. pliocenicus* can be considered as palaeoendemic Mediterranean species. The genera *Scopelopsis* and *Lampadena* have disappeared from the Recent Mediterranean; the living Atlantic species of *Scopelopsis* has been reported in the southern Atlantic while *Lampadena* is present in both North and South Atlantic (Nafpaktitis et al. 1977; Nafpaktitis & Paxton 1968; Nafpaktitis & Nafpaktitis 1969; Hulley 1981). A significant geographic distribution is shown by *S. multipunctatus*, the unique Recent species belonging to this genus that is found in the Atlantic ocean. This species has often been included in the south subtropical region according to the zoogeographic distribution proposed by Backus et al. (1970) (fide Nafpaktitis et al. 1977) in relation to physical boundaries. Recently, Hulley (1981) observed that in the south subtropical region *S. multipunctatus* is distributed only in the areas affected by the cold Benguela Current. Consequently, this geographic distribution suggests that this species cannot be considered only as a warm species.

Because of these faunistic, ecological, and biogeographical features, a marked oceanic scene arises from the fish associations which differ from those of the Recent Mediterranean as already highlighted for other vertebrate Pleistocene assemblages (Girone 2000b; Girone & Varola 2001). This is in agreement with results from the invertebrate communities in the examined site (Di Geronimo et al. 1997) and elsewhere (Benson 1972; Di Geronimo et al. 1996; Di Geronimo & La Perna 1996, 1997; Corselli 2001). A strongly different hydrological pattern is envisaged with near-bottom temperatures lower than 8–10°C as suggested by the North Atlantic living populations of benthopelagic fish *C. rupestris* and of serpulids *Neovermilia falcigera* and *Vitreotubus digeronimoi* (Di Geronimo et al. 1997). A different palaeoceanographic setting is suggested also by the presence of the northern Atlantic bathypelagic cold water dwellers *Bathylagus euryops* and *Nansenia groenlandica* and the presence of the eutrophic mesopelagic fishes *Diaphus taaningi* and *Polyipnus polli* (Girone & Varola 2001).

Conclusion

The analysis of the twelve bulk samples collected along the Archi section resulted in the recognition of thirty eight teleostean taxa, thirty four to the specific level. Among these, twenty two species still live in the Mediterranean Sea and include *Symbolophorus veranyi* and *Chauliodus sloani*, identified as a fossil for the first time, as well as *Vinciguerria* aff. *attenuata* and *Coryphaenoides* aff. *guentheri*, whose taxonomic status is not well defined. The Archi assemblages include the Atlantic bathypelagic species *Bathylagus euryops*, *Nansenia groenlandica*, and the benthopelagic *Coryphaenoides rupestris*, all reported for the first time as fossils and disappeared from the Recent Mediterranean. The Atlantic mesopelagic fishes *D. taaningi* and *P. cf. polli*, already reported in the Pliocene and Pleistocene sediments of the Mediterranean (Nolf et al. 1998; Girone 2000b; Girone & Varola 2001), also occur.

In this work, the palaeobathymetric method was integrated with the palaeoecological approach based on benthic and benthopelagic taxa providing more precise palaeoenvironment reconstructions. In particular, the analysis of the structure of fish populations, besides taxonomic composition, provided a good tool for the interpretation of Pleistocene deep-sea benthic and benthopelagic associations as already demonstrated for the deep-circalittoral and epibathyal associations (Girone 2000b).

The benthic and benthopelagic associations, strongly bathyal in their structure, are clearly indicative of a deep bathyal environment located in the middle bathyal interval. A palaeodepth comprising between 400–500 m and 1000 m can be inferred in agreement with the data from the ben-

thic invertebrate associations (Di Geronimo et al. 1997).

The present study contributes to the knowledge of the Mediterranean deep-sea teleostean faunas during the Pleistocene showing, once more, their marked Atlantic affinity. Because of the faunistic, ecologic, and biogeographic features, a marked oceanic scene arises from the studied teleostean fauna as it was highlighted by the study of the invertebrate communities. The presence of north-east Atlantic living populations of *B. euryops*, *N. groenlandica* and *C. rupestris* indicate a strongly different hydrological pattern with deep-water and near-bottom temperatures lower than 8-10°C, which are quite different from those of

the Recent Mediterranean.

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