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Tatjana Bakran-Petricioli[1], Jean Vacelet[2], Helmut Zibrowius[2], Donat Petricioli[3], Pierre Chevaldonné[2] & Tonći Rađa[4]

1 Division of Biology, Faculty of Science, University of Zagreb, Zagreb, Croatia
2 DIMAR, Centre d’Océanologie de Marseille, Station Marine d’Endoume, Rue de la Batterie des Lions, Marseille, France
3 D.I.I.V. Ltd for Marine, Freshwater and Underground Ecology, Sali, Croatia
4 Speleological Society Špiljar, Split, Croatia

The sponges *Oopsacas minuta* (Hexactinellida) and *Asbestopluma hypogea* (Demospongiae, Cladorhizidae) belong to groups that are typical of deep water, but both species have already been recorded from the shallow water Trois Pe´pe´s cave at La Ciotat (Marseille area). We here report on subsequent findings of *A. hypogea* in two other littoral caves: one at Garmenjak Island in the Mid-dle Adriatic (Croatia), the other at Jarre Island (Marseille, France). The maxi-mum temperatures experienced *in situ* by these populations are not only significantly higher than those from the deep Mediterranean Sea, but they are also up to 6 °C higher than those reported for the Trois Pe´pe´s cave population, up to 23.1 °C in July 2002 for the Garmenjak population and 22.8 °C i n August 2004 for the Jarre population (exposures from a few hours to a few days). The average summer temperature inside both caves remains several degrees lower than the outside temperature at the same depth. Long-term sur-vival of *A. hypogea* populations at the relatively high summer/autumn tempera-tures in both Jarre cave (4 years monitoring) and Garmenjak cave (5 years monitoring) indicates that the species can successfully colonise such shallow habitats in spite of its presumed deep-water origin. We also report additional cave records of *O. minuta* in the Adriatic (Croatia): from the marine part of the ˇZiva Voda anchialine cave at Hvar Island, from the marine caves at Isˇki Mrtovnjak, Lastovo and Frasˇkeric´ Islands. The wide distribution of this species in the deep Mediterranean is substantiated by a record on Santa Lucia Bank north of Corsica (303 m) and photographs taken by the submersible Cyana in the Central Tyrrhenian Sea (2912 m, 2845 m) and the Ionian Sea (2447 m). All the findings of these two species in the Mediterranean are reviewed and possible patterns of their colonisation of littoral caves are discussed.

Problem

Sponge species belonging to groups otherwise typical of deep water, *Oopsacas minuta* Topsent 1927 (Hexactinell-ida) and *Asbestopluma hypogea* Vacelet & Boury-Esnault 1996 (Demospongiae, Cladorhizidae), have previously been recorded from the permanently cold part of a very special littoral cave (Trois Pépés cave at La Ciotat) near Marseille in the French Mediterranean (Vacelet *et al.* 1994; Fig. 1, Table 1). Their discovery in shallow waters

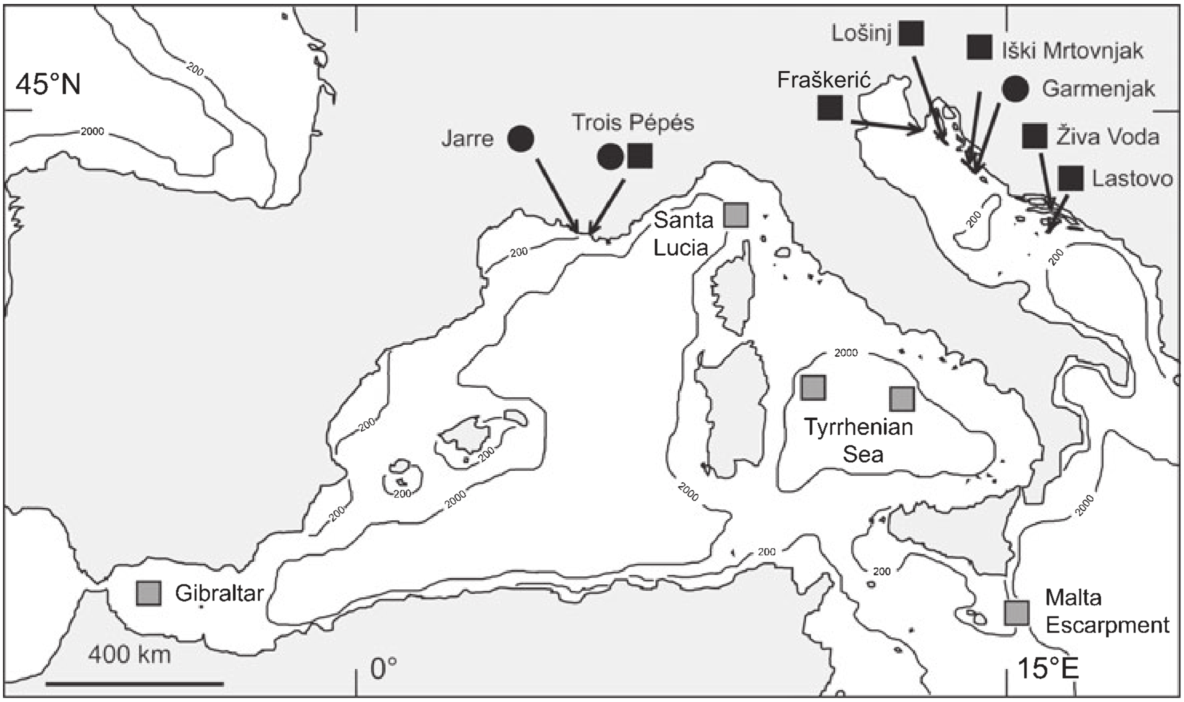

Fig. 1. Distribution of the currently known populations of the hexactinellid sponge *Oopsacas minuta* (squares) and of the cladorhizid sponge *Asbestopluma hypogea* (circles), all located in the Mediterranean. Grey squares represent deep water occurrences of *O. minuta* whereas black squares are cave occurrences.

made these unusual forms easily accessible for biological studies.

Sloping inwards from 15 to 24 m behind an entrance sill, the Trois Pépés cave traps a dense, cold-water mass in winter that keeps a temperature close to that characteristic of the great depths of the Mediterranean Sea (13 °C) year round. Winter homothermy of the water column above a nearby deep canyon and reduced temperature variation inside the cave enabled various deep-water organisms to colonise that particular shallow habitat (Boury-Esnault *et al.* 1993; Vacelet *et al.* 1994; Vacelet 1996; Harmelin & Vacelet 1997). Based both on its hydrographic characteristics and its faunal composition, Trois Pépés cave qualifies as a 'bathyal island' at shallow depth.

Originally, *O. minuta* was only known from two minute specimens collected in 1894 from deep water on the Mediterranean slope in the Straits of Gibraltar (Fig. 1, Table 1). A century later, it was rediscovered at some 20 m depth in the Trois Pépés cave in France (Vacelet *et al.* 1994). Remarkably, *O. minuta* does not occur in the many other, generally ascending caves of the Marseille area that do not have that particular homothermic low temperature regime. Given the first two widely disjunctive records (Straits of Gibraltar and Marseille area), it was concluded that *O. minuta* must be more widely distributed in the Mediterranean bathyal zone where it had previously been overlooked because of its localisation on inaccessible deep hard ground.

The discovery of a cladorhizid sponge of the genus *Asbestopluma* at 17 m depth in the same Trois Pépés cave provided the opportunity to investigate a member of this group devoid of an aquiferous system and choanocytes (Vacelet *et al.* 1994); these investigations were carried out both *in situ* and by simple aquarium experiments. It soon became evident that this sponge is macrophagous and 'carnivorous' (Vacelet & Boury-Esnault 1995). It passively captures prey such as small crustaceans (up to 8 mm long) on its filaments provided with raised, hook-shaped spicules. Capture is followed by intense sponge cell migration, extracellular digestion, phagocytosis and intracellular digestion by archaeocytes and bacteriocytes, the whole process taking up to 10 days (Vacelet & Duport 2004). The strange sponge from Trois Pépés cave was then described as a new species, *Asbestopluma hypogea* Vacelet & Boury-Esnault 1996.

The geographically nearest congeneric species is *Asbestopluma hydra* from the Arctic (1847 and 2394 m). With a record from 8840 m in the Pacific, *Asbestopluma* is so far the deepest known genus of sponges. Given this general 'deep-sea connection' (cladorhizids are typically deep-water organisms) it was assumed that *A. hypogea*

Table 1. Summary of all findings of 'deep-sea' sponge species *Asbestopluma hypogea* Vacelet & Boury-Esnault 1996 (Demospongiae, Cladorhizidae), and *Oopsacas minuta* Topsent 1927 (Hexactinellida).

species	known sites	depth	collection dates	habitat description	reference
Asbestopluma hypogea	Trois Pépés cave, La Ciotat, South of France; 43°10.2′ N, 5°36′ E	17–22 m	1992	Rock surfaces of a descending cave, from the entrance to 50 m into the cave, the highest density of sponges 15–20 m from cave entrance (dim light)	Vacelet *et al.* 1994; Vacelet & Boury-Esnault 1996
	Cave on Veli Garmenjak Island, Telašćica Nature Park (SE of Dugi Otok), Croatia; 43°52.0′ N, 15°10.9′ E	24–26 m	25.8.2000 & 31.8.2000	Rock walls and detached stones in the narrow entrance passage of a descending cave (dim light)	this paper
	Cave on Jarre Island, Riou Archipelago, Marseille, South of France; 43°11.8′ N, 5°22.1′ E	15–17 m	3.7.2001	Rocky outcrops and small boulders in a small depression 70 m from the cave entrance (total darkness)	this paper
Oopsacas minuta bathyal occurrences	Mediterranean slope in the Straits of Gibraltar (Prince of Monaco stat. 406); 35°59.5′ N, 5°24′ W	924 m	21.6.1894–22.6.1894		Topsent 1927, 1928
	Malta Escarpment, Ionian Sea (cruise ESCARMED-2; French submersible Cyana dive 80–26); 36°34′ N, 15°33′ E	2447 m	14.6.1980; not collected, only photographed	Vertical to overhanging rock surfaces	this paper
	Central Tyrrhenian Fault, central Tyrrhenian Sea (cruise CYRRHENE; French submersible Cyana dive 84–75); 40°13.7′ N, 11°49.3′ E	2911–2913 m	16.8.1984; not collected, only photographed	Vertical to overhanging rock surfaces	this paper
	Flavio-Gioia Escarpment, central Tyrrhenian Sea (cruise CYRRHENE; French submersible Cyana dive 84–87); 40°01.9′ N, 13°01.2′ E	2845 m	2.9.1984; not collected, only photographed	Vertical to overhanging rock surfaces	this paper
	Santa Lucia Bank, Ligurian Sea (cruise LM99-47; R/V Urania); 43°31.56′ N, 9°16.55′ E	303 m	3.1.2000	No information as the specimens were on a piece of rock taken by grab	this paper
Oopsacas minuta cave occurrences	Trois Pépés cave, La Ciotat, South of France; 43°10.2′ N, 5°36′ E	18–24 m	1992	Vertical and overhanging rock walls, 50–120 m from cave entrance (total darkness); the highest density of sponges 60–80 m from the cave entrance	Vacelet *et al.* 1994
	Živa Voda anchialine cave, Hvar Island, Croatia; 43°07.0′ N, 17°03.0′ E	15–30 m	15.9.1998; 26.9.2000	In marine part of the cave, on rock walls and vertical sides of big boulders on the cave bottom (total darkness)	this paper
	Medvjeđa Špilja anchialine cave, Lošinj Island, Croatia, North Adriatic	8–16 m	2004	In marine part of the cave, on rock walls and ceiling of the cave channels (total darkness)	Jalžić *et al.* 2005; Jalžić (personal communication)

Table 1. Continued.

species	known sites	depth	collection dates	habitat description	reference
	Cave on Iški Mrtovnjak Island, SE of Iž Island, Croatia, Central Adriatic; 44°00.6′ N, 15°10.6′ E	10–23 m	1.9.2005	Vertical and overhanging rock walls in the inner part of the cave (total darkness)	this paper
	Usidrena Jama cave near Pasadur strait, Ubli, Lastovo Island, Croatia, South Adriatic; 42°45.9′ N, 16°49.3′ E	18–22 m	15.10.2005	Overhanging rock walls in the deeper part of the cave (total darkness)	this paper
	Cave on Fraškerić Island, Zabranjeni Kanal, Pula, Croatia, North Adriatic; 44°49.4′ N, 13°50.5′ E	6 m	29.9.2006	Vertical rock walls in dark side channel (total darkness)	this paper

also occurs in deep Mediterranean habitats, but records are so far still missing. This is easily explained by the small size and fragile structure of *A. hypogea* which, on a dredged deep rock sample, would be too inconspicuous for collectors other than sponge experts to note. In the Trois Pépés cave, both *O. minuta* and the even smaller *A. hypogea* inhabit vertical to overhanging rock surfaces and are easily overlooked.

The aim of this study was to review all the published findings of these two intriguing 'deep sea' sponge species in the Mediterranean and to report on new discoveries, especially with reference to the temperature and light characteristics of some of their littoral habitats and to discuss possible colonisation patterns of littoral caves by the two species.

Material and Methods

Study areas

Four of the eight new sites for *Oopsacas minuta* are bathyal and located in the western basin (Ligurian and Tyrrhenian Seas) and in the Ionian Sea. Four new littoral sites are located in the Adriatic Sea (Fig. 1, details in Table 1).

In the Ligurian Sea, *O. minuta* has been sampled on Santa Lucia Bank (between the northern tip of Corsica and the Ligurian coast) during cruise LM99 of the Italian research vessel 'Urania'.

During geological cruises in the Mediterranean Sea, many dives have been conducted on deep rocky bottoms with the manned submersible 'Cyana' of IFREMER. The resulting large series of photographs were examined for benthic life (H.Z.). Some show small, whitish, epifaunal organisms recognisable as *O. minuta*. The respective dive sites are listed here:

— cruise CYRRHENE (17 dives) in the Central Tyrrhenian Sea (Gennesseaux *et al.* 1986): 'Cyana' dive 84–75 in the Central Tyrrhenian Fault, photos no. 55 (time 12/34/04) and no. 56 (time 12/34/12), both showing the same group of specimens; 'Cyana' dive 84–87, in the Flavio-Gioia Escarpment, photos no. 179 (time 13/02/12) and no. 180 (time 13/02/32), both showing the same group of specimens.

— cruise ESCARMED-2 (25 dives) on deep escarpments in the Ionian Sea (Biju-Duval *et al.* 1982; Charrier *et al.* 1987): 'Cyana' dive 80–26 in the Malta escarpment, photo no. 147 (time 13/11/17), showing a group of specimens.

In the middle Adriatic Sea, a population of *O. minuta* has been discovered in the marine part of Živa Voda anchialine cave on Hvar Island, Croatia (near Zaglav village, Kozja Cove). The cave is located in karstic limestone on the steep south-eastern side of the island. The entrance is inland, *ca.* 100 m away from the sea and *ca.* 30 m above sea level.

Another littoral population of *O. minuta* has been found recently in the descending marine cave off the small Iški Mrtovnjak Island (also known as Maćin Školj), located SE of Iž Island, Croatia, in the Middle Adriatic. The cave entrance is at 6 m depth on the eastern side of the island, exposed to south-eastern winds from the open sea.

In the South Adriatic, the littoral finding of *O. minuta* is located in the Usidrena Jama marine cave on the western part of Lastovo Island, Croatia. The entrance to this descending cave is at 6 m depth and it is located near the Pasadur strait in the enclosed bay of Ubli village.

The most recent littoral finding of *O. minuta* is located in a shallow marine cave (entrance at 4 m depth) on Fraškerić Island in Pula, Croatia, North Adriatic. This is the shallowest and northernmost finding of this species.

The Adriatic *Asbestopluma hypogea* population has been discovered in a cave at Veli Garmenjak Island in Telašćica Nature Park (SE of Dugi Otok, Croatia; Fig. 1, Table 1). This vertical cave has its entrance at 23 m depth on the rocky bottom (karstic limestone) of an overhang formed along the western side of a vertical fault (orientation 130°) on the SE side of the island. In front of the overhang a sandy bottom slopes down from 24 to almost 90 m. This side of the island is exposed to southern and south-eastern winds from the open sea.

We also investigated two other descending, cold-water trapping caves in the same area, a cave in Kravljačica Cove on Kornat Island (43°49.5′ N, 15°16.6′ E) and Sket's cave on Levrnaka Island (43°49.6′ N, 15°15.4′ E), but we were unsuccessful in finding these two sponge species.

The Jarre cave population of *A. hypogea* occupies a very small area in a large, long cave (length *ca.* 130 m, depth 15–17 m) having its entrance (15–17 m) in a cliff on the south coast of Jarre Island, Riou Archipelago, near Marseille, France (Fig. 1, Table 1).

Sponge sampling

Specimens of *Oopsacas minuta* were collected by diving and deep-water sampling or were detected with reasonable confidence on underwater photographs taken by a manned submersible. Specimens were available from five new sites, four littoral and one bathyal (Fig. 1, Table 1). For the first time, *in situ* photographs were available from three bathyal sites.

In the Ligurian Sea six specimens of *O. minuta* were obtained (H.Z.) from a grab sample on Santa Lucia Bank (303 m) between the northern tip of Corsica and the Ligurian coast.

In the Adriatic Sea, populations of *O. minuta* were observed and sampled by diving:

— In Živa Voda cave, Hvar Island; T.R., 25.10.1997 and 15.9.1998, 15 m; Branko Jalžić, 26.9.2000, 20–30 m, three additional specimens.

— In the cave off the Iški Mrtovnjak Island; D.P. and Hrvoje Čižmek, 1.9.2005, 10 m; three specimens.

— In Usidrena Jama cave, Lastovo Island; D.P. and Hrvoje Čižmek, 15.10.2005, 18 m; one specimen.

— In the cave on Fraškerić Island, Pula; P.C. and D.P., 29.9.2006, 6 m; 1 specimen.

Likewise, the Adriatic specimens of *Asbestopluma hypogea* were observed and collected by diving in the cave at Veli Garmenjak Island; D.P. and T.B.-P., 25.8.2000, 24 m; D.P., J.V. and P.C., 31.8.2000, 24 m (Fig. 1, Table 1).

Since its discovery (P.C., 3.7.2001, 17 m; Fig. 1, Table 1), the Jarre cave *A. hypogea* population has been inspected at least every 2 months, but due to its small size, only limited sampling was done.

DNA analyses

DNA was extracted from both French and Croatian *Asbestopluma* samples for comparative purposes. Although satisfactory molecular markers easily applicable to all sponge species still remain to be found (Wörheide *et al.* 2005), a 710-bp fragment of the mitochondrial gene coding for subunit I of the cytochrome oxidase (mtCOI) was amplified by PCR (Folmer *et al.* 1994). Sequences were obtained after cloning PCR products.

Temperature measurements

Long-term water temperature measurements at the *Asbestopluma* site at Veli Garmenjak Island have been taken since 2000 using small stow away temperature data loggers (Onset Computer, USA, ±0.2 °C accuracy) at a 16-min sampling interval. Some interruptions of the series were caused by the loss of data loggers. Data loggers were put in three positions: under the overhang but outside the cave entrance, depth 26 m; inside the cave where *Asbestopluma* lives, depth 24 m; and in the lower chamber of the cave below the *Asbestopluma* level, depth 30 m.

Three temperature data loggers (Seamon mini, Hugrún, Iceland; ±0.05 °C accuracy) have been deployed continuously in Jarre cave since 11 July 2001, and recorded at 3-h intervals. One is placed within the *Asbestopluma* at 17 m depth, another still in the cave but *ca.* 10 m away from the *Asbestopluma* zone, at 15 m and one at 17 m immediately outside the cave.

Light intensity measurements

Light intensity in Garmenjak cave was measured using stow away light intensity data loggers (Onset Computer), from 28 to 30 April 2001, at 1.3 min intervals, in three positions: under the overhang but outside the cave entrance, depth 26 m; inside the cave where *Asbestopluma* lives, depth 24 m; and in the lower chamber of the cave below the *Asbestopluma* level, depth 27 m.

Results

Sponge occurrence

Živa Voda, Usidrena Jama and Iški Mrtovnjak caves in the Adriatic and Trois Pépés cave in the Marseille area, all inhabited by *Oopsacas*, have in common that they are descending, cold water trapping caves, but their configuration otherwise differs considerably.

The marine part of Živa Voda cave can only be entered from land (*i.e.,* from the sub-aerial part of the cave). The first 20 m of the cave consists of a descending shaft which then bifurcates. The ESE corridor contains a fresh/brackish water pool terminating in a siphon (depth *ca.* 30 m). This submerged part has yielded archaeological remains. In fact, it had been used as a permanent freshwater source (probably since the Bronze Age) – hence the name Živa Voda (=live water). It contains freshwater fauna (three species of hydrobiid gastropods found by T.R.). The SE corridor (seaward corridor) widens into a small chamber (4 × 7 m) with a small pool, 1.5 m in diameter. The water is brackish only at the surface. The upper 4 m of the pool is narrow, but deeper down, the cave is more spacious (5–10 m wide, *ca.* 40 m long, sloping down in SE direction to 38 m depth) and contains 'limpid' seawater. Here, in the totally dark area, the population of *Oopsacas minuta* occurs at a depth of 15–30 m. No connection with the open sea has yet been found, but it surely exists via long, narrow and impenetrable crevices in the karstic rock. The distance to the open sea is difficult to estimate. The *Oopsacas* population inhabits the rock walls and vertical sides of big boulders on the bottom. Its distribution in the cave is uneven, with a population density of *ca.* 5–10 individuals 0.25 m^{-2}. The species was identified based on skeletal characters, which are in agreement with the holotype. Specimens collected on 26.9.2000 were 2, 2.4 and 3.2 cm long. Specimens collected on 25.10.1997 and 15.9.1998 were not sexually reproducing.

The remaining marine fauna in Živa Voda cave is still poorly known. Serpulid polychaetes of the genus *Protula* (their tubes at least) are present. Only one other sponge species (collector Branko Jalžić, 26.9.2000) has so far been examined but not yet identified (its appearance is haplosclerid but its spicules look halichondrid: oxea 450–500 × 20 μm and thin microxea 70 μm).

The entrance to Iški Mrtovnjak cave is funnel-shaped, about 1 m in diameter. At 9 m depth, it narrows to only 0.6 m and widens again into the main cave chamber which is 15 m long, 5 m wide and 29 m deep. The lower portion of the cave steeply slopes towards NW. The slope and bottom of the cave are covered with a thick layer of sediment (mostly shell fragments). The cave contains various types of speleothems: stalactites, 'curtains', stalagmites, stalks – all covered with serpulid tubes. The *O. minuta* population was observed on the vertical and overhanging rock walls in the inner, completely dark part of the cave, between 10 and 23 m. Macroscopic determination of species was confirmed with the skeletal characteristics. Sponges are unevenly distributed throughout the cave: there are 1–10 specimens m^{-2}. The largest sponges are up to 5 cm long. Specimens collected on 1.9.2005 for species determination were 0.9, 1 and 1.5 cm long. Sea temperature outside the cave at the time of sampling was 23.5 °C, inside, where *Oopsacas* lives, only 15 °C.

The Usidrena Jama marine cave on Lastovo Island also has a funnel-shaped entrance, 2 × 1 m wide. The first part of the cave consists of two connected descending vertical shafts bent at 12 m depth. At 18 m, the vertical shafts widen into a 3 × 6 m chamber, ending with the sediment-covered bottom at 24 m. A scarce population of *O. minuta* (species confirmed by skeletal characteristics) inhabits overhanging rock walls between 18 and 22 m in total darkness. The animals are much smaller than those in the other caves we studied, the biggest being 1.5 cm long.

The Fraškerić cave is located on the W bank of the island. It has two entrances: south at 6 m depth, 3 × 2 m wide, and north, 2 × 2 m wide. The main chamber of the cave is 30 × 6 m, 3 m high with an air pocket on the ceiling. On the SE wall of the chamber is the entrance to the dark channel (Zabranjeni Kanal) in which *O. minuta* was found. The channel is horizontal, tunnel-shaped, 2.5–3 m wide, mostly 2 m high (30 m from entrance it is only 0.5 m high), with very fine sediment on the bottom. It winds towards SE, regularly changing direction *ca.* 30° from left to right. At the time of research a 0.5-m thick pocket of freshwater was present along the ceiling from 10 to 50 m from entrance of the channel. Seawater temperature at the end of September 2006 was 23 °C at the entrance but gradually decreased inside the channel, reaching 17 °C some 60 m from the entrance. There, on the rock walls, three individuals of *O. minuta* (up to 2 cm long) were recorded. The rest of the channel, which continues further, was not investigated.

The small population of six specimens of *O. minuta* (4 mm in length) obtained on Santa Lucia Bank in the Ligurian Sea were all attached to a piece of rock bearing various other epifaunal organisms. These comprised many specimens of a white, solidly attached, conical foraminiferan, a tiny stalked sponge *Stylocordyla* sp. and various encrusting sponges, the actinian *Kadophellia bathyalis*, attached valves of the bivalve *Spondylus gussoni* and of the brachiopod *Novocrania anomala*, incrusting bryozoan colonies and tubes of the serpulid polychaete *Semivermilia agglutinata*. The recovery of the small population of *O. minuta* from this bathyal site was due to particular circumstances: the grab had taken no mud and the piece of rock was its only contents. Washing off mud to examine the sample would most certainly have damaged or destroyed these highly fragile small sponges. Collected in the winter season (3.1.2000), the deep-water specimens from Santa Lucia Bank were not sexually reproducing. Their skeletal characters agree closely with those of the holotype.

In the great depths of the Ionian and Tyrrhenian Seas (Table 1), specimens of *O. minuta* are recognisable on *in situ* photographs in spite of a rather poor definition (Fig. 2). These are not close-up shots, but have been taken for geological purposes. At all three sites, several specimens are visible hanging down from subvertical to slightly overhanging rock surfaces blackened by the manganese coating typical of these depths. They are recognisable as whitish, apparently not massive but hollow tubular, cylindrical to slightly bell-shaped individuals with the typical distal orifice, exactly as we see them *in situ* in the littoral caves. At the Ionian site, they are attached to a vertical wall covered by dead solitary scleractinians, most probably *Desmophyllum cristagalli* of late Pleistocene age. At the two Tyrrhenian sites the specimens are attached to barren rock, with no other epifauna, either ancient or recent, being visible. When initially examined for benthic life, the series of photographs from cruise ESCARMED-2 provided information on a population of large live hexactinellids of a different type (Zibrowius 1985). The small *O. minuta* went unnoticed at the time, long before its rediscovery in the littoral cave near Marseille. We recognised it only after having first seen it in the cave environment. It is difficult to extrapolate the size of the specimens photographed at these deep sites. They appear to be a few centimetres in size, of the same order as the largest cave specimens observed (up to 7 cm in Trois Pépés cave).

The vertical cave entrance on Garmenjak Island in Adriatic is funnel-shaped with a diameter of *ca.* 2 m at 23 m

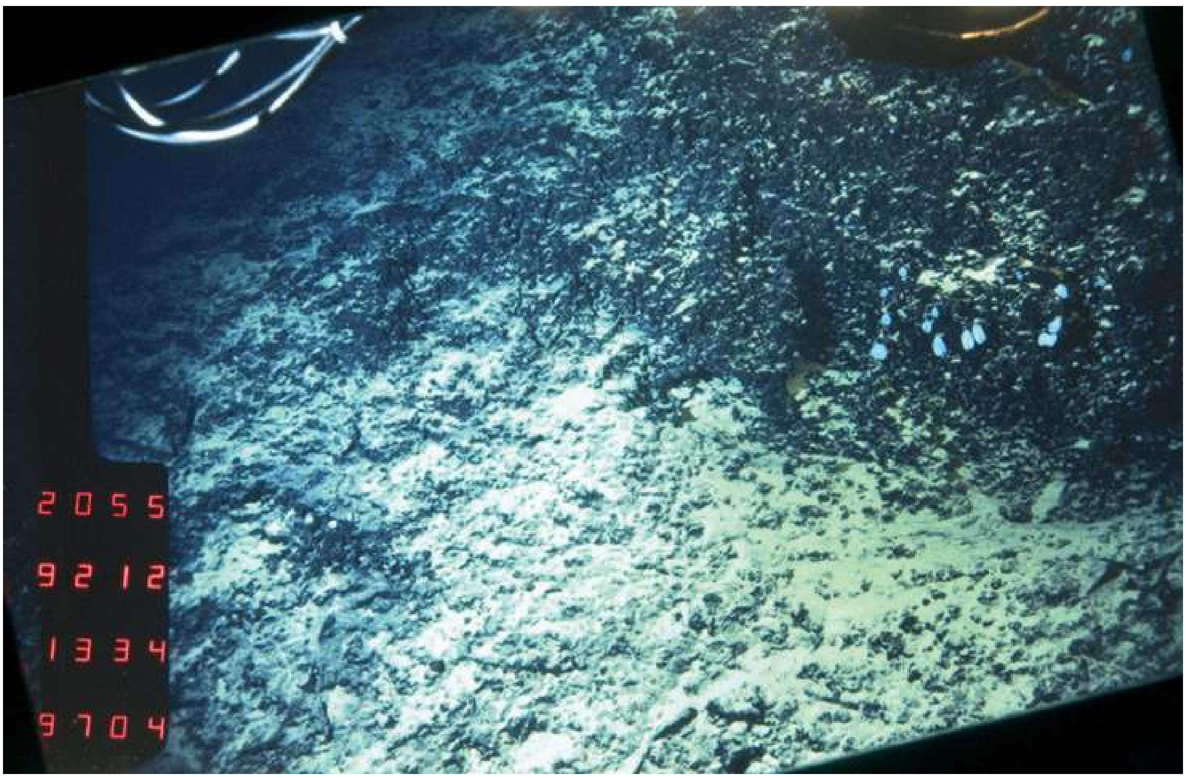

Fig. 2. *Oopsacas minuta*, group of specimens photographed *in situ* in the deep Tyrrhenian Sea: cruise CYRRHENE, CYANA dive 84–75 photo no. 55 (time 12/34/04), 16.8.1984, 2911–2913 m, Central Tyrrhenian Fault.

depth, narrowing to only 0.6 m at 24 m. At 26 m, it widens into a small chamber, with the bottom at 32 m covered by sediment. The population of *A. hypogea* inhabits both solid rock (wall of the narrow entrance passage) and detached, fallen down, flat stones lying in the funnel next to the narrow passage from 24 to 26 m (Fig. 3). No dive was conducted in the lower chamber to protect the *Asbestopluma* population in the passage. Thus, the fauna of the lower chamber presently remains unknown. This is also a descending cave, trapping colder and denser water. The longest sampled specimen of *Asbestopluma* was 15 mm. The density of the not evenly distributed population was estimated to be *ca.* 100 individuals per m^2. Identification of this population is based on skeletal characters (which did not differ from the population of Trois Pépés cave). The DNA sequence of the amplified mtCOI fragment revealed no difference between the Garmenjak *Asbestopluma* and the Jarre and Trois Pépés samples.

The Jarre cave in France, known to marine scientists since 1977, is one of the most explored in the area, but *A. hypogea* was only discovered there in 2001. The reason is that the population occupies a very limited area, *ca.* 70 m from the cave entrance, in total darkness, just where the bottom gently slopes from 15 down to 17 m before going up again. While Jarre cave is not a descending cave, this small depression in an area where the general direction of the cave suddenly changes is apparently sufficient to provide a suitable habitat for the sponges. The depression traps a small lens of colder water, although only over an area of *ca.* 3 m × 1 m on the cave bottom, where *Asbestopluma* is attached to rocky outcrops or small boulders. The presence of boulders and gravel (not silt or mud) in this unique area of the cave suggests the occasional occurrence of significant currents. This population is not very large and is very inconspicuous. It is located 15 km away from the other known population of the area in Trois Pépés cave.

Fig. 3. *Asbestopluma hypogea*, in the entrance passage of the littoral cave on Garmenjak Veli Island (Nature Park Telašćica, Croatia), depth 24 m, the largest sponge is 10 mm high, 13.10.2003 (photo: D. Petricioli).

Temperature and light measurements

Although temperature measurements at the Garmenjak site have been taken since October 2000, the only complete series with data from all three positions was from August 2002 to June 2003 (Fig. 4). During this period, water exchange in the upper part of the cave (documented *Asbestopluma* habitat) seems to have occurred during October and November 2002, while exchange with the deeper part of the cave probably occurred between December 2002 and April 2003. Most of the year, *Asbestopluma* lives at temperatures close to and below 16 °C, whereas during autumn it is often exposed to higher temperatures. In October 2002, it was 19–20 °C (highest value on 17.10.2002; Fig. 4); in late October and early November 2001, temperature rose to 19 °C (not shown); in late October and early November 2000, temperatures were 19.1–20.2 °C (highest value on 28.10.2000; not shown). The only exceptional event in this 3-year period occurred at the beginning of July 2002 (1.7.2002) when, after a period of no or very low water mixing, an abrupt levelling of temperature in both positions caused a sudden mixing in the *Asbestopluma* habitat (Fig. 5). Such unstable conditions lasted for almost 2 months (from 1.7.2002 to 24.8.2002), stopped only by an intrusion of cold water. In that period, *Asbestopluma* was periodically subjected to temperatures above 19 °C (19–21 °C), with a

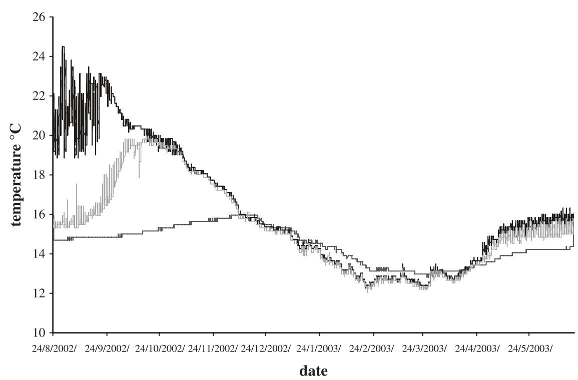

Fig. 4. Sea-water temperature in Garmenjak cave measured with temperature data loggers, 24 August 2002 to 18 June 2003. Water exchange in the upper part (*Asbestopluma* habitat) seems to have occurred during October and November 2002, exchange with the lower chamber between December 2002 and April 2003. Black: under the overhang but outside the cave entrance, depth 26 m. Light grey: next to *Asbestopluma* inside the funnel-shaped entrance, depth 24 m. Dark grey: in the lower chamber, depth 30 m.

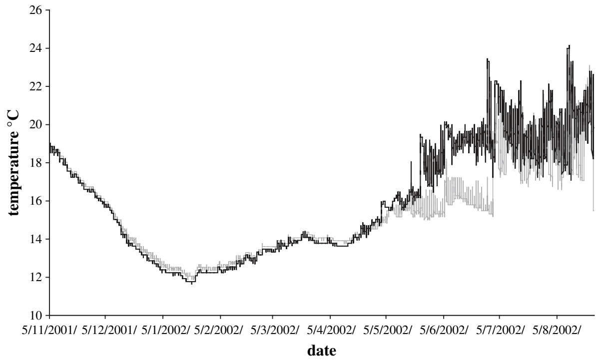

Fig. 5. Sea-water temperature in Garmenjak cave measured with temperature data loggers, 5 November 2001 to 24 August 2002. From May to early July almost no water mixing occurred in the upper part. This period was followed by a temperature levelling, which caused a sudden mixing. In the *Asbestopluma* habitat unstable conditions lasted for almost two months (1 July to 24 August 2002), ending with a sudden intrusion of cold water. Black: under the overhang but outside the cave entrance, depth 26 m. Light grey: next to *Asbestopluma* inside the funnel-shaped entrance, depth 24 m.

very short (1 h) extreme of very warm water, 23.1 °C, on 22.8.2002 (Fig. 5).

The other particular feature of the *Asbestopluma* habitat on Garmenjak Island is that it receives a certain amount of dim light (Fig. 6).

In the Jarre cave from late November to late April, the temperature is homogeneous between the *Asbestopluma* zone, the other parts of the cave (not shown), and the outside (Fig. 7). Winter temperature can occasionally drop to 12.4 °C (see 8.2.2003, Fig. 7). In late spring, summer and early autumn, temperature in the *Asbestopluma* zone is always significantly lower than that outside the cave. The difference peaked at 5.8 °C on 27.8.2002 (Fig. 7). In summer and early autumn, the strong northern wind (Mistral) regularly induces an upwelling and a mixing of the water column; whereas temperature quickly returns to elevated values in the open water, fluctuations in the *Asbestopluma* zone are buffered considerably and do not rise easily. During this period, the mean temperature remains at 16.7 °C with an occasional peak at 19 °C, compared with an average of 18.8 °C outside the cave with peaks at 23 °C for that particular series (Fig. 7). The maximum temperature ever recorded in the *Asbestopluma* zone was 22.8 °C in August 2004, a month during which outside temperatures almost reached 25 °C and the difference between the two zones reached 6.9 °C (not shown).

Discussion

The collection of *Oopsacas minuta* from a deep site in the Ligurian Sea strengthens our confidence that this is indeed the species we identified on the photographs taken by the submersible Cyana. Altogether, the new findings reported here confirm that *O. minuta* is widely distributed in the Western Mediterranean bathyal zone, especially on vertical to overhanging rock surfaces that are not easily accessible to collecting gear (Fig. 1, Table 1).

The colonisation of littoral caves by *O. minuta* and *Asbestopluma hypogea* has occurred in at least two distant areas (NW Mediterranean and Adriatic Sea) where two main requirements are met. First, a special thermal regime in the cave based on low temperature homothermy year round, similar to that of the deep Mediterranean. This homothermy is mostly achieved through a descending cave profile enabling density trapping of a cold water mass in winter. Secondly, the capability of propagules to travel all the way from a deep population reservoir up to the caves during seasonal (winter) homothermy.

All the caves where *Oopsacas* and *Asbestopluma* have been found are descending or have a special topography

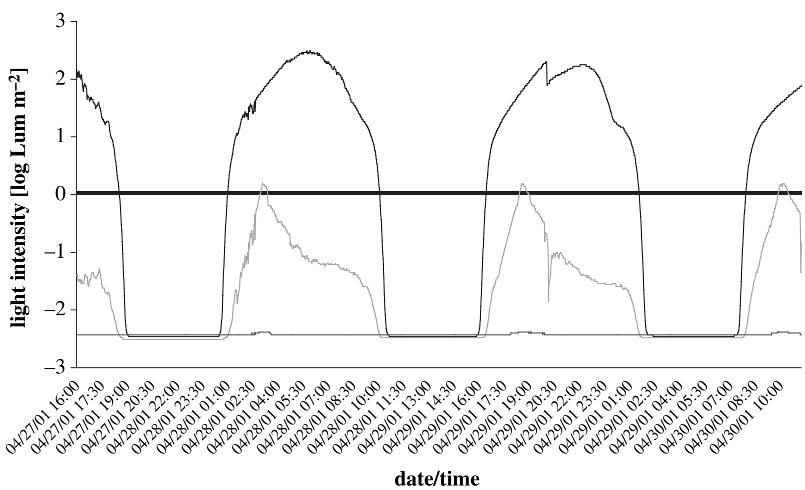

Fig. 6. Light intensity in Garrnenjak cave measured with stow away light intensity data loggers, at 1.3 min intervals, 28 to 30 April 2001. Black: under the overhang but outside the cave entrance, depth 24 m. Light grey: next to *Asbestopluma* inside the funnel-shaped entrance, depth 24 m. Dark grey: in the lower chamber, depth 27 m.

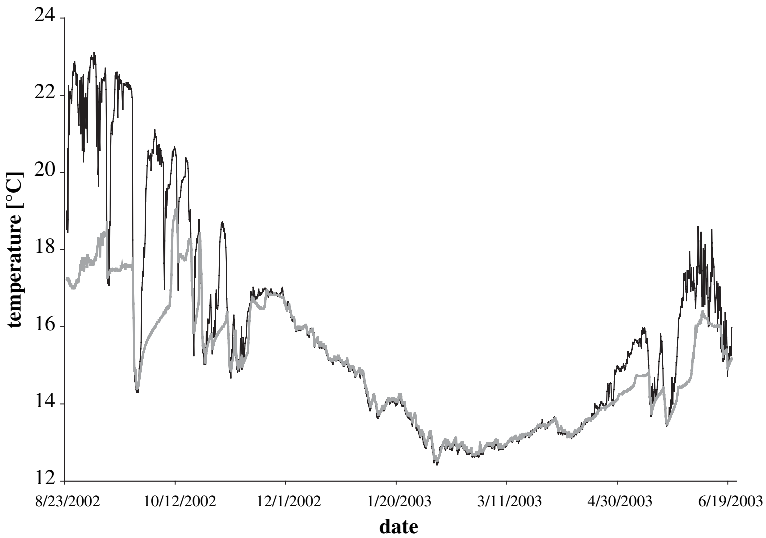

Fig. 7. Sea-water temperature in Jarre cave measured with temperature data loggers, 24 August 2002 to 18 June 2003. Black: outside the cave, depth 17 m. Light grey: within the *Asbestopluma* habitat, 17 m depth.

that traps cold water (Fig. 1, Table 1). In the particular case of the very shallow Fraškerić cave, the cave profile is horizontal but the numerous narrow passages and turns allow cold water to be trapped year round. Homothermy in Trois Pépés is confirmed by the temperature time-series measurements (Harmelin & Vacelet 1997). In Živa Voda marine cave, temperature oscillations are strongly damped (14.6 °C in winter to 17.9 °C in summer), so the annual range is notably reduced compared with that at similar depth in the nearby open sea (Novosel *et al.* 2005).

Outside the *Asbestopluma* habitat in Garmenjak cave (Figs 4 and 5), short-term temperature oscillations in the warm season are superimposed on the seasonal variations. This previously observed feature (Gačić & Vučak 1982; Orlić 1987; Novosel *et al.* 2004) coincides with a periodic cycle in the water column stratification, which has been related to internal wave motions inducing displacements of the thermocline. These temperature oscillations sometimes homogenise the temperature (therefore water mixing) between the *Asbestopluma* habitat and the outside of the cave (Fig. 5).

Although most of the year, in both caves, *A. hypogea* lives in temperatures near and below 16 °C, it can periodically – in summer to late autumn – withstand temperatures above 19 °C, usually 19–21 °C (Figs 4, 5 and 7); brief extremes were 23 °C for Garmenjak cave in August 2002 (Fig. 5) and 22.8 °C for Jarre cave in August 2004 (not shown). That is *ca.* 6 °C higher than the upper temperatures originally reported for the Trois Pépés cave population.

The observations that water exchanges between the *Asbestopluma* habitat and the open sea are more the rule than the exception, along with the fact that this 'deep-sea' organism periodically withstands rather high temperatures, indicates that this organism – as several other documented deep-sea species (Vacelet *et al.* 1994) – has greater adaptative capabilities than previously thought. It can therefore colonise such microhabitats when certain conditions are met.

Many marine caves are present along the eastern coast of the Adriatic Sea, resulting from typical subaerial karstic features that were submerged after the last glaciation, during sea level rise. Preserved speleothems now encrusted by marine organisms can be found deep below the sea level, so far noted down to 60 m in the Adriatic Sea (Bakran-Petricioli 2004). Descending, cold water trapping caves are a well-known feature on the subsided Croatian coast. For example, we (D.P., J.V. & P.C.) also explored a cave (maximum depth 20 m) at Levrnaka Island in the Kornati Archipelago. It had previously been reported as containing water with a temperature 'remarkably lower than outside it, probably the same as under the thermocline' (Boris Sket's observation cited by Fransen 1991).

In the case of Trois Pépés cave near Marseille, the likely source of propagules is the Cassidaigne canyon only 7 km away (Harmelin & Vacelet 1997). The well-known strong upwellings induced by north-western winds (locally known as Mistral) there probably facilitate propagule dispersal from the deep canyon population.

Concerning Živa Voda cave, the nearest deep-water areas are: (i) the South Adriatic depression (maximum depth 1233 m) *ca.* 80 km away (the 200 m isobath line approaching the southernmost islands of Palagruža and Mljet by only 20–25 km); (ii) the Mid Adriatic Jabuka depression (maximum depth 275 m) at a distance of *ca.* 130 km (the 200 m isobath line approaching the Kornati archipelago by only 10 km). The Garmenjak and Iški Mrtovnjak caves are *ca.* 40–60 km away from the Jabuka depression and 220 km from the South Adriatic depression, while Usidrena Jama on Lastovo is about 40 km away from the South Adriatic depression. The cave on Fraškerić Island in the North Adriatic is the furthest away.

A typical deep-water fauna has been found in the Jabuka depression, including the colonial scleractinians (both recorded dead only) *Madrepora oculata* and *Lophelia pertusa* (Županović 1969); deep populations of *O. minuta* and *A. hypogea* can be expected here. In fact, the presence here of another cladorhizid sponge had been documented by Babić (1922): *Cladorhiza abyssicola* Sars, 1872 was obtained from a depth of 200 m at location 43°9.6′ N and 15°28.5′ E, *ca.* 80 km from Garmenjak cave and 127 km from Živa Voda cave.

The dense cold water in Jabuka depression originates from the North Adriatic and spills over, forming the bottom water layer of the South Adriatic depression. This water eventually exits through the Otranto Strait, subsequently becoming the bottom water layer of the entire Eastern Mediterranean (Gačić *et al.* 2001).

On the other hand, a northwestward flow prevails in the intermediate layer of the South Adriatic (between 20–40 m and 200–400 m depth), a water mass flowing in from the Levantine Basin. Its flow intensity varies considerably from year to year. Accordingly, the colonisation of the cave straight from a distant deep reservoir may not be the most likely scenario.

The distance, both spatial and temporal, between putative deep Adriatic *Oopsacas* populations and Živa Voda, Usidrena Jama, Iški Mrtovnjak and Fraškerić cave populations is much greater than the distance between the presumed deep reservoir and the cave populations in the Marseille area. Assuming that propagules of *A. hypogea* and *O. minuta* have a short planktonic life-span (as usual in sponges), we may hypothesise that suitable 'stepping-stone' hard bottom habitats (still to be located) exist between the deep areas and the distant colonised island caves. Our findings of *Oopsacas* in Hvar, Lastovo, Iški Mrtovnjak and Fraškerić caves, far from each other, provide evidence that other littoral descending caves must have been colonised by such deep-sea species, stepwise and progressing along the Croatian coast. That is also supported by the recent report of *Oopsacas* in another littoral cave on the island Lošinj in the North Adriatic (Jalžić *et al.* 2005), far away from the Adriatic deep areas (Fig. 1, Table 1).

Extrapolating the colonisation process should also consider the Pleistocene/Holocene history of the Adriatic Sea. During the lowest stand of the sea in the Late Pleistocene, the deeply cut Cassidaigne canyon near Marseille, not far from the shore, always remained a deep-water body. When in the early Holocene the rising sea level immersed Trois Pépés cave, a deep population reservoir of *O. minuta* was probably within close reach (a few km only). In contrast, much of the present Adriatic Sea was emerged land in the Late Pleistocene, with a bottleneck connection between the southern Adriatic deep basin and the Jabuka depression, than a much shallower water body (depth *ca.* 150 m) strongly influenced by freshwater inflow (Correggiari *et al.* 1996). In the early Holocene, large surfaces over large distances were flooded before Živa Voda, Garmenjak, Iški Mrtovnjak or Fraškerić caves were reached.

The behaviour and dispersal ability of hexactinellid and cladorhizid larvae remain unknown. The larvae of *O. minuta* are small and most probably have a limited swimming ability, as common in Porifera. However, they have multiflagellated cells and contain abundant reserve products (Boury-Esnault & Vacelet 1994; Boury-Esnault *et al.* 1999a). These unusual features in Porifera may point to a relatively long-lived free-larval stage and thereby to greater dispersal ability than typical for demosponge larvae. Observations made in Trois Pépés cave indicate that sexual reproduction of *O. minuta* is common there and that the species is one of the most successful short-distance colonisers of new substrates. Experimental stakes, strings and panels placed in the cave have been colonised by many small specimens of *O. minuta* within a few months (Fig. 8). On the other hand, there are only a few descriptions of embryos in Cladorhizidae, all suggesting that their larvae are relatively large. Free-swimming larvae, however, have never been observed, and the aggregative distribution of *A. hypogea* in Trois Pépés cave (Vacelet & Boury-Esnault 1996) does not indicate particularly great dispersal ability. This species does appear to be more tolerant to a certain amount of light and apparently lives in significant (for caves) currents. Such characteristics may somehow improve its dispersal capabilities and its tolerance to habitats at intermediate depths.

In Trois Pépés cave, the largest specimens of the natural population of *Oopsacas* are rather loosely attached to the cave wall and are easily detached by air bubbles released by divers (Vacelet *et al.* 1994). Once free, the individuals, with their low tissue and skeleton density, may float for a while before settling onto the cave floor. This suggests that individuals accidentally detached from deep hard ground may be drifted into shallow waters by upwellings induced by north-western storms in the Marseille area. Such a passive transport of whole individuals towards a cave or intermediate habitats could be coupled with a subsequent release of larvae. Such a dispersal mechanism, including fragmentation and sexual reproduction, has been suggested in littoral demosponges (Maldonado & Uriz 1999).

In each cave, colonisation may have occurred just once by a single founding event or repeatedly, either via

Fig. 8. Successful short-distance colonising of new substrata by *Oopsacas minuta* in Trois Pépés cave (France): young sponges on the stake 90 m from entrance. 22 m depth, 24.9.1996 (stake is 18 mm in diameter; photo: J.-G. Harmelin).

swimming larvae of sexual origin or via drifted adults. For *O. minuta*, considering the high success of sexual reproduction in Trois Pépés cave, it is possible, but not necessarily the case, that colonisation took place only once after the immersion of the cave during the Holocene period, some 7000 years ago. Indications obtained from spicule characters are too imprecise and appropriate molecular markers not yet developed to determine genetic homogeneity or heterogeneity.

Further genetic investigations of the geographically and bathymetrically distant populations of both *O. minuta* and *A. hypogaea* can be expected to shed a new light on the sequence of colonisation events and on the degree of conspecificity. Indeed, the often-cited 'cosmopolitanism' in sponges often reflects over-conservative systematics rather than genetic homogeneity (Boury-Esnault *et al.* 1999b; Klautau *et al.* 1999; Lazoski *et al.* 2001; Plotkin & Boury-Esnault 2004).

In Trois Pépés cave, where both *Asbestopluma* and *Oopsacas* are present, the two species inhabit different parts of the cave. *Asbestopluma* is present only in the zone near the entrance, whereas *Oopsacas* is confined to the inner and larger, totally obscure zone where the temperature is more stable.

Finally, the location of the *Asbestopluma* habitat in all three caves (Garmenjak, Jarre and Trois Pépés) may be connected to a critical point of cave mysid circadian migrations. Mysid swarms were recorded in all three caves (Chevaldonné & Lejeusne 2003), and mysids are known to be suitable prey for this 'sit and wait' predator (Vacelet & Duport 2004).

Summary

We report here the findings of *Oopsacas minuta* in four littoral caves of the Adriatic Sea and in the bathyal zone of the Ligurian, Tyrrhenian and Ionian Seas. We confirm its previously presumed wider distribution in the Mediterranean Sea and provide an insight into the colonisation ability of this 'bathyal' hexactinellid. We also report the finding of *Asbestopluma hypogea* in two other littoral caves: one near the type locality (NW Mediterranean, France), the other in the Adriatic Sea. We further show that these newly discovered shallow-water populations withstand at least short-term exposure to relatively high summer/autumn seawater temperatures compared with those in the deep Mediterranean.

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