Deep-sea sponges in a Mediterranean cave

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Abstract: Submarine caves share several ecological features with deep-sea habitats and could be considered as a natural mesocosm of the bathyo-abyssal zone, despite differences in temperature. A unique Mediterranean cave which entraps a cold water mass, resulting in stable temperature conditions throughout the year, is a specially interesting 'bathyal island' in the littoral zone. It has been colonized by deep-sea invertebrates, whose likely source of propagules is a nearby canyon, 100 to 3000 m deep. The example of sponges shows that various general problems of deep-sea biology could be successfully addressed in the cave. A representative of the deep-sea hexactinellid sponges reproduces here year round - enabling the first observations of larval behaviour and ultrastructure to be carried out on this phylogenetically important group of invertebrates, and opening the unknown field of larval ecology of deep-sea sponges. The presence of a species of the deepest known genus of sponges, *Asbestopluma* (at 8840 m depth in the Central Pacific), is a fascinating opportunity to investigate the biology of the strange deep-sea cladorhizid sponges, which can live in the most oligotrophic abyssal basins. A highly unexpected result is that cladorhizids are non-filter-feeding "sponges" with a carnivorous feeding habit.

Introduction

The interest of mesocosms is obvious in such an extreme environment as the deep sea, whose access is difficult and expensive. However, laboratory approximations of deep-sea habitats are difficult to design. Submarine caves have often been considered as interesting natural candidates for such mesocosms. Blind caves and deep-sea habitats closely resemble each other in terms of darkness and hydrodynamic conditions. Both depend mainly on primary production elsewhere (OTT and SVOBODA 1976), resulting in some cases in a similar amount of trophic resources (FICHEZ 1990a, b, 1991). Similarities have also been described in faunal composition and in the structure of sessile invertebrate assemblages (RIEDL 1966, HARMELIN et al. 1985), with several bathyal species living in the darkest parts of sublittoral caves. The resemblance, however, is limited by the obvious differences in pressure, temperature, and habitat size. Furthermore, natural colonization of caves by deep-sea organisms, a relatively recent event after the Holocene sea-level rise, is limited by their dispersal ability, and, until recently, high-rank taxa of sessile animals specific of the deep sea have not been found in caves.

A recently discovered Mediterranean cave more closely approximates the deep-sea environment, above all in the stable temperature conditions similar to those of the deep Mediterranean (VACELET et al. 1994). The cave contains many examples of deep-sea organisms that have never been found in "normal" caves, including a typically bathyo-abyssal subphylum of Porifera. This "bathyal island" in the littoral zone offers opportunities to address significant problems both in the biology of deep-sea taxa and in the functioning of deep-sea communities. In this paper, I will illustrate how this unique environment already has notably contributed to the knowledge of deep-sea sponges and of invertebrate adaptations to the deep-sea environment.

The cave habitat

The "3 PP cave", a 120-m-long tunnel, is located near La Ciotat on the French Mediterranean coast (VACELET et al. 1994). This area is the site of the strongest upwelling along the north Mediterranean coast (MILLOT 1979), and a deep canyon ("Cassidaigne Canyon"), 100 to 3000 m in depth, is located only 7 km from the cave. Unlike most Mediterranean caves, which are inwardly ascendant due to their karstic origins, this cave slopes downward (Fig. 1), with its floor extending from 15 m at the entrance to a depth of 25 m at the far end. Because of this descending profile, the cave is filled with a density-trapped cold body of water. The interior water temperature shows only very small seasonal fluctuations compared to exterior water at the same depth (13.0-14.7 °C versus 13.0-24.7 °C in 1991; see records in Fig. 1 for 1995). These temperature conditions, which imply a water residence time of several months during the warm season, approximate the 13 °C homothermy of the deep Mediterranean. Darkness is complete after a bend in the tunnel at 50 m from the entrance. The floor is covered by several meters of muddy sediment with traces of biogenic activity.

A more complete study of the cave environment, which appears to be complex, is in progress. A slowly entering current, approximately 1 cm s^{-1}, has been recorded near the floor in summer conditions and has also been observed by divers. This current within the trapped water mass is of unknown origin. Preliminary nutrient, microbial, and particle analysis (J.-C. ROMANO, E. VACELET, pers. comm.) indicates that pulses of nutritional inputs occur up to 110 m from the cave opening, possibly transported by this slow current. Mucus aggregates have been observed in some circumstances on the walls and ceiling, and the cave environment appears to be more food-rich than both ascending caves and deep Mediterranean habitats (FICHEZ 1990b). The past environmental conditions and fauna of the cave are presently being studied from their records in the sediment and bioclasts.
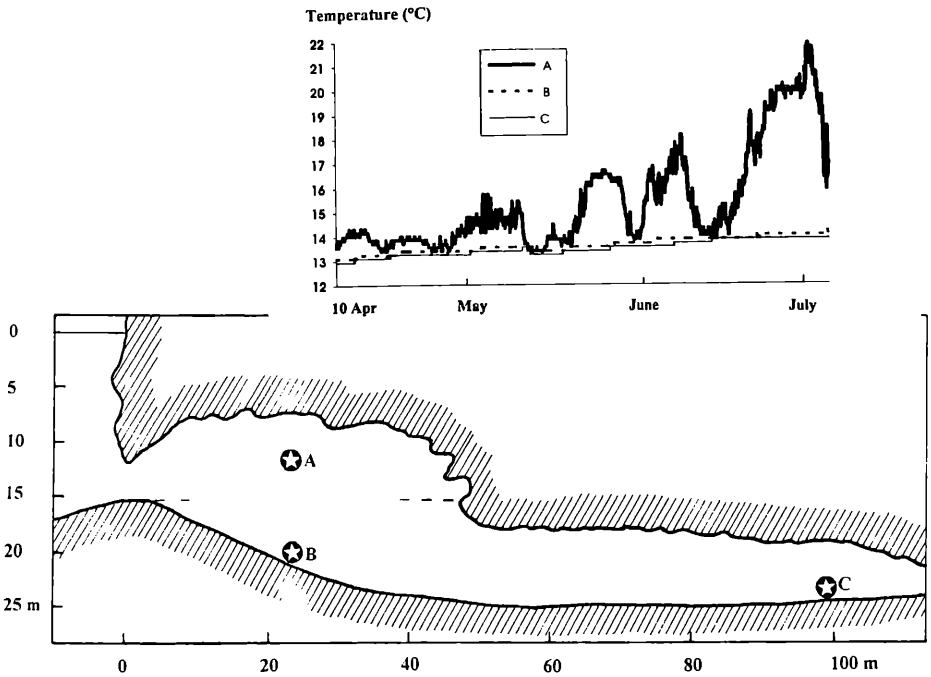
Fig. 1: Profile view of the "3 PP cave", with temperature records from 10 April to 5 July 1995 in three zones. In A, the temperature displays the same variations as in the external zone. In B and C, the cold water mass trapped within the cave has a stable temperature year round, approximating that of the deep Mediterranean (13 °C).

Sponge fauna of the cave

As usual in caves, sponges are the dominant group on all rocky surfaces, both in number of species, biomass, and surface covered. According to a study now in progress (J. G. HARMELIN, pers. comm.), the percentage of cover, estimated on collected rocky surfaces of the walls, decreases from the entrance area (with varying temperature) to the homeothermic zone. However, the cover does not significantly decrease along the homeothermic zone up to the far end, contrary to the situation observed for bryozoans. This may be due to the utilisation of particle pulses by sponges under certain hydrological circumstances.

In addition to the usual sponge fauna of dark caves (POULIQUEN 1971), the homeothermic zone contains several deep-sea sponges that have never been found in shallow water, including caves with a normal temperature regime. The sponge assemblage includes representatives of the main groups of deep-

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sea sponges, with significant examples of their presumed adaptations to deep-sea conditions. This allows a direct study of the various feeding and reproductive strategies of these deep-sea animals, which are poorly known due to difficult access.

Hexactinellids

A first species is the hexactinellid *Oopsacas minuta* TOPSENT, 1927 (Fig. 2 A). Representatives of the class Hexactinellida (glass sponges), sometimes considered as a subphylum of Porifera (REISWIG and MACKIE 1983), or even a phylum of its own (BERGQUIST 1985), are predominantly bathyo-abyssal, although a few species have been recorded from the continental shelf in cold-water regions (KOLTUN 1970b, MACKIE and SINGLA 1983). These sponges are difficult to preserve adequately for cytological studies. As early as the beginning of the 20th century, their histological structure was described as being very different from other sponges (SCHULZE 1899, IJIMA 1901). Recent observations have confirmed that their tissues are mostly syncytial and that their choanocytes are anucleate cells wrapped in a special tissue, the reticulum. These peculiarities are of special interest in the problem of early metazoan evolution. Such a structure in animals which might be the oldest known metazoans (STEINER et al. 1993) is not consistent with the hypothesis that sponges are the first step in metazoan organisation, deriving from unicellular choanoflagellates. To what extent these peculiarities may represent a relatively recent adaptation to filter-feeding in the deep sea, where particulate food is scarce, is unknown.

Fig. 2: A: Evaluation of the population density of the hexactinellid *Oopsacas minuta* (white, urn-like sponges) on a wall in the "3 PP cave", 20.5 m depth and 80 m from the cave opening. The species was previously known from two small specimens from 924 m in the Gibraltar Straits (from KELLY-BORGES 1995). B: Population of the carnivorous cladorhizid sponge, *Asbestopluma hypogea*, in the "3 PP cave", 18 m depth and 15 m from the cave opening. Maximum length of these specimens is 15 mm.

Easy access to the cave population of *Oopsacas minuta*, with the possibility of *in situ* processing, has resulted in unusually good preservation of the delicate cytological structures (Fig. 3A, B). The observations may challenge the interpretation of the hexactinellids as a giant syncytium (BOURY-ESNAULT and VACELET 1994). Both ultrastructural observations and experimental study of the particle uptake (PEREZ unpubl.) by *O. minuta* show that the feeding strategy of hexactinellids differs notably from that of other sponges, as already suggested (REISWIG 1990). These sponges rely on a great development of the aquiferous cavities, concurrently with an extreme thinness of the living tissue (less than 10 μm in most areas of the chamber wall, including the anucleate choanocytes, reticulum, and mesohyl with a few symbiotic bacteria). This is very different from a bathyal demosponge such as *Discodermia polydiscus* living in the same area of the cave: its aquiferous system is reduced, the choanocyte chambers are small and the extremely dense mesohyl contains a huge number of symbiotic bacteria. *In situ* or laboratory experiments using latex beads, unicellular algae, or bacteria have shown that the anucleate choanocytes of the hexactinellid are mostly used to circulate water and do not trap and digest particles, unlike in other classes of sponges, Demospongiae and Calcarea. Phagocytosis and digestion are performed by the special structure in which the anucleate choanocytes are wrapped, the reticulum, either by its inhalant or exhalant side depending on particle size (Fig. 3A, B). Besides their role in circulating the water, the anucleate choanocytes may also participate in a possible absorption of dissolved organic matter; this remains to be investigated. Such a role may be fulfilled by the microvilli of the choanocytes, which remarkably contain thread-like symbiotic bacteria inside the collar, thus in direct contact with the circulating water. Pumping activity appears to be intermittent, possibly stopping when the sponge is overfed after a heavy input of particulate food. During the study, which was conducted in the cold season when water exchange with the outside is possible, many specimens were found without any pumping activity, especially when mucus aggregates were observed on the cave walls and ceiling.

The reproduction of hexactinellids is poorly known due to difficulty of access and also to the fact that deep-sea specimens, as well as those from cold-water shelves reproduce only infrequently. Although many specimens of deep-sea hexactinellids have been studied, their embryology and larvae have been correctly described only once (OKADA 1928), with the discovery of the presence of a unique larval skeleton of special siliceous spicules. Larval behaviour and ecology, as well as dispersal ability, are unknown.

Contrary to deep-sea hexactinellids, the cave specimens of *O. minuta* sexually reproduce year round, and stages of embryogenesis have been found in all examined specimens. This is obviously a good opportunity to study both embryology and larval behaviour, but also addresses the problem of seasonality of reproduction in deep-sea species. This constant and active reproduction may be related to a higher food input in the cave than in the deep sea. The larva is similar in gross morphology to that previously described by OKADA in another species, but reveals interesting ultrastructural characteristics of the hexactinellid larva, which has been termed a "trichimella" (BOURY-ESNAULT and VACELET 1994). The flagellated equatorial zone is made up of multiflagellated mononucleate cells, with up to 50 flagella per cell. The flagellated cells are covered by a thin epithelium pierced by the flagella, which is a unique structure in invertebrates. The presence of multiflagellated cells, which are assumed to appear only in the triploblast and Protostomia/Spiralia lines (RIEGER 1976, BARNES 1985, NIELSEN 1987), is highly surprising. It could indicate that hexactinellids have acquired multiflagellarity independently of other metazoans. Upon ist release, the trichimella has well developed choanocyte chambers, although they are devoid of both a reticulum and intracollar symbiotic bacteria, indicating that they have no role in nutrition at this stage. The free larva is only 150-180 µm long and is rich in lipids and yolk. It swims with the round, lipid-rich pole forward, contrary to OKADA's interpretation. Data on larval behaviour would be informative on the dispersal possibilities of deep-sea hexactinellids.

These dispersal abilities allowed *Oopsacas minuta* to colonise the cave. The species was previously known from only two minute specimens collected at 924 m at the Mediterranean end of the Straits of Gibraltar (TOPSENT 1927). It most probably it has a wider distribution in the bathyal zone of the Mediterranean, where it may live under overhangs as in the cave, with few possibilities to be sampled. Although no specimen has been collected, the species has been identified with reasonable accuracy on *in situ* photographs from the manned submersible "Cyana" in the Tyrrhenian Sea, 2913 m depth, and near Malta, 2447 m depth (H. ZIBROWIUS, pers. comm.). The probable source of propagules for the cave is the nearby "Cassidaigne" canyon. The population probably reproduces in the cave after an initial colonisation event, which might have been either by larvae or by drifting specimens. In the cave, large individuals are easily detached by water movement and fall slowly towards the cave floor, indicating a possible transport of whole individuals from the bathyal canyon through upwellings.

Cladorhizid demosponge

The second remarkable example of a deep-sea sponge in the cave is a demosponge belonging to the exclusively deep-sea family Cladorhizidae. All representatives of this family have an unusual morphology - stalked with long, thin appendages. Cladorhizids include the deepest known sponges, with a species of the genus *Asbestopluma* found at 8840 m depth in the Pacific (KOLTUN 1970a). They are able to inhabit the most food-poor basins under low surface productivity (GAGE and TYLER 1991). The adaptations and life history traits which allow them to withstand such conditions are unknown.

The cave species, approximately 20 mm high, is a new species, *Asbestopluma hypogea* (VACELET and BOURY-ESNAULT in press), belonging to the genus which holds the depth record for sponges (Fig. 2 B). This is again an opportunity to study the life history traits of sponges which typically live

Fig. 3: A: Scanning electron microscope view of a chamber wall of the hexactinellid *Oopsacas minuta*, after experimental feeding with phototrophic bacteria (*). The anucleate choanocytes ("collar bodies", C) are wrapped inside the reticulum (R), which entraps and digests the food particles. Several stages in the capture and digestion of the bacteria are shown (*). Note the presence of symbiotic, rod-like bacteria within the collar (>). Scale bar = 1.85 µm. Photo T. PEREZ

B: Transmission electron microscope view of the chamber wall of *Oopsacas minuta*, after experimental feeding with latex beads, 1 µm in diameter, 2 h after incubation. A latex bead (*) is entrapped in the reticulum (R). Note the extreme thinness of the chamber wall. R...reticulum. F...flagellum. C...choanocyte (collar body). Arrows: symbiotic bacteria in the mesohyl or in the collar. Scale bar = 1.2 µm. (From PEREZ unpublished).

C: Scanning electron microscope view of the filaments of the carnivorous sponge *Asbestopluma hypogea*. Their "Velcro-like" appearance is due to raised, hooked spicules (anisochelae) which entrap the appendages of tiny crustaceans that serve as prey. The swellings are sperm cysts, which migrate along the filaments during maturation. Scale bar = 26 µm.

D: Scanning electron microscope view of the carnivorous cladorhizid sponge *Asbestopluma hypogea*, 16 h after capture of mysid crustaceans. The filaments are disorganised, and the prey are partly or completely engulfed by the sponge tissue. Scale bar = 380 µm.
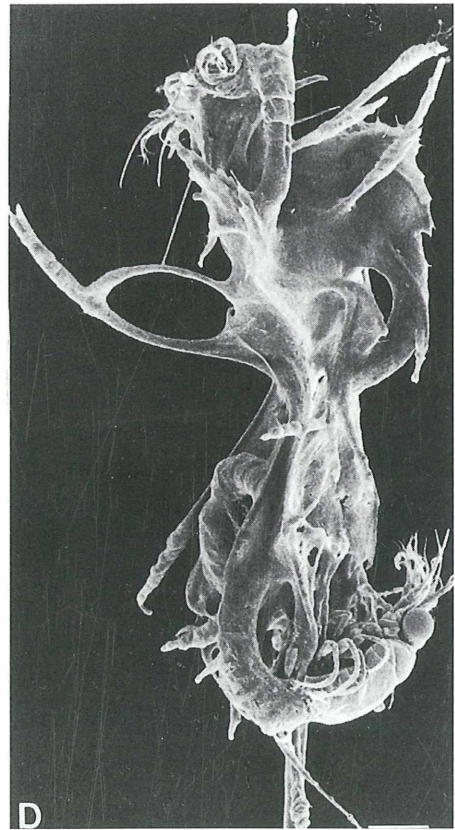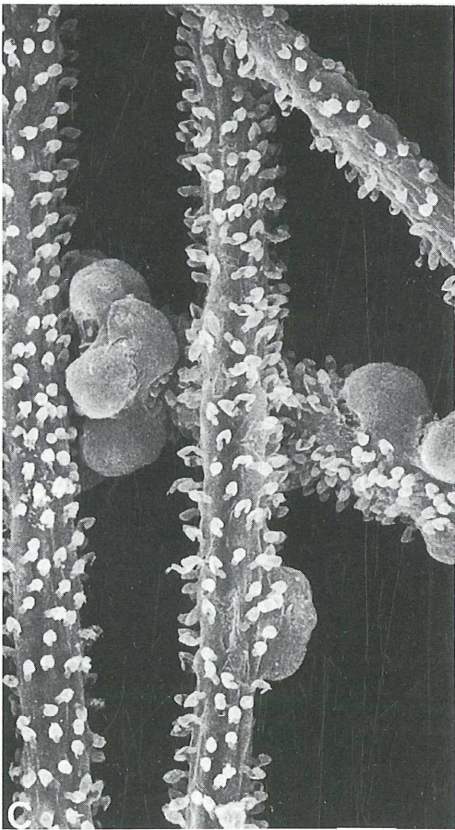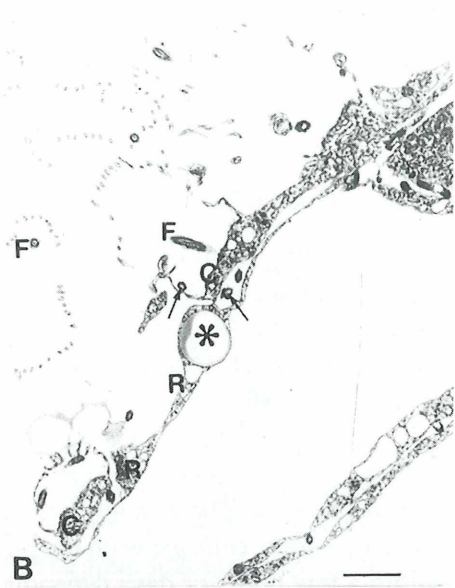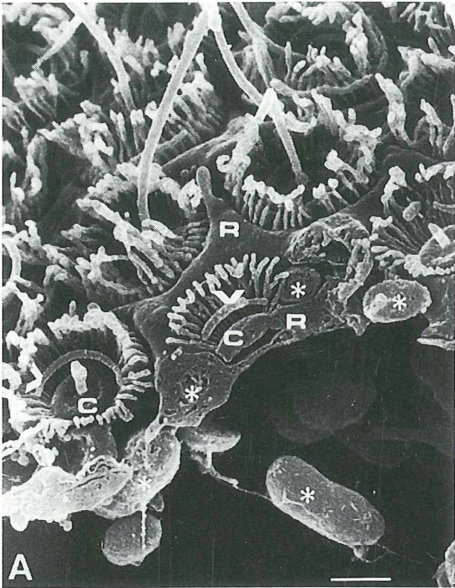
deeper than the hexactinellids and can even reach the hadal zone. Only one species of Cladorhizidae was known in the deep Mediterranean, in which the genus *Asbestopluma* has never been recorded. As in the hexactinellid, the cave species most likely also lives under inaccessible overhangs in the adjoining deep canyon and on rocky surfaces of the deep Mediterranean, whose biodiversity seems to be significantly underevaluated.

The feeding habit of *A. hypogea* is most unexpected. It is devoid of any aperture, canals or choanocytes, and thus is not a filter feeder. Rather, it is carnivorous and feeds on small, living prey, mostly crustaceans (VACELET and BOURY-ESNAULT 1995a, b). The long, thin filaments are covered by minute, hook-shaped spicules (anisochelae) disposed at right angles to the axis, which give the filaments a "Velcro"-like adhesiveness (Fig. 3 C). Once their appendages become trapped, tiny swimming crustaceans are unable to free themselves. There is apparently no toxic or paralysing secretion. After capture, surface cells grow on the prey, which is engulfed in the sponge tissue within a few hours or days depending on the prey size (Fig. 3 D). Complete digestion of a several-mm-long crustacean takes 10 days. In the cave, prey consist mostly of crustaceans up to 7 mm long, such as copepods, ostracods, and mysids, although small polychaetes may occasionally be caught. Specimens have been successfully raised in aquarium for several months, with a weekly change of seawater and feeding with either living nauplii of *Artemia salina* or commercially available, deep-frozen *Artemia*.

This unusual mode of life is apparently shared by the other Cladorhizidae (approximately 90 species) in deep-sea habitats. The general absence of an aquiferous system, that intrigued early observers, could not be due to poor preservation. Small animals are often found trapped in the filaments or appendages of specimens collected by trawls. The hypothesis that the sponge could feed on the particles collected by the appendages was suggested by the first author to describe a cladorhizid (SARS 1872), although it was considered highly unlikely by subsequent authors (RIDLEY and DENDY 1887, LUND-BECK 1905). However, the cladorhizids may have other nutrient sources as well. A *Cladorhiza* sp. from a deep-sea methane vent, at 4900 m near Barbados is nutritionally reliant on methanotrophic symbiotic bacteria (VACELET et al. 1995), although it also feeds on swimming prey. This dual source of carbon allows the sponge to form large aggregations of hundreds of individuals around the methane source, where deep-sea cladorhizids usually occur in low densities as discrete individuals.

Deep-sea cladorhizids incubate large embryos. These have rarely been observed in *A. hypogea*, and their structure cannot be described yet. The specimens often occur in aggregates of 5 to 10 individuals in large areas devoid

of other individuals, indicating that a very short distance mechanism of reproduction occurs. In contrast to oocytes and embryos, spermatogenesis has frequently been observed in specimens collected year round. In sponges, sperm cells usually originate from choanocytes and choanocyte chambers, and are spawned by the canals. In the absence of both choanocyte chambers and a canal system, highly unusual mechanisms of spermatogenesis have been developed. Spermatocysts appear first in the body, then migrate during maturation towards the end of the filaments, where they appear as small swellings (Fig. 3 C). In the mature sperm cyst, the sperm cells, with an elongated nucleus, form a central mass surrounded by two envelopes, the outer one made up of closely intertwined cells. The cyst then acquires two tufts of small pin-hair spicules and becomes free. Its subsequent fate is unknown, but a working hypothesis is that it drifts towards another individual, on whose Velcro-like filaments it would be trapped by its pin-hair spicules and releases the sperm cells. This would be a unique strategy to face the general problem of fertilization in the deep sea, where there is a great spatial separation between individuals in low density populations.

The organization and biology of *A. hypogea*, and presumably of the other cladorhizid sponges, differ widely from that known in other sponges. These organisms lack all the basic sponge attributes, although their spicules are similar to those of three different lines of evolution in the order Poecilosclerida of the Demospongiae. The most likely interpretation is that in deep-sea habitats, where active filter feeding has a low yield, these sponges have deviated from the filtering organization typical of Porifera and have developed a new body plan that resembles no other anatomical design. This may be compared to the emergence of macrophagy in abyssal tunicates, but with a more extreme result as the main Porifera attributes have disappeared.

Conclusions

The example of sponges shows that various general problems of deep-sea biology can be successfully addressed in the cave. The unexpected life history traits discovered in these Porifera appear as secondary adaptations to the deep-sea conditions, and also provide insights into broad problems in biological evolution, such as the origin of deep-sea fauna or the appearance of multiflagellarity in animal cells. Significant advances in the knowledge of poriferan adaptations to the deep sea have been made or may be foreseen, including feeding strategies, seasonality of reproduction, dispersal ability, and long-distance fertilization; the position of sponges in the deep-sea food web has to be reconsidered. Although the conditions in the cave only approximate the true deep-sea conditions, the life strategies discovered here for sponges

are most likely the same as for their deep-sea populations, and the differences, if any, are informative. For instance, the food supply for sponges, which is higher in the cave than in most deep environments of the Mediterranean, results in the same feeding strategies and also in a more continuous reproduction. Such an environment is very promising for other fields in deep-sea biology and ecology.

Acknowledgements

References

BARNES, R. D., 1985: Current perspectives on the origins and relationships of lower invertebrates. - In MORRIS, S. C., GEORGE, J. D., GIBSON, R., PLATT, H. M., (Eds): The origins and relationships of lower invertebrates, pp. 360-367. - Oxford: Clarendon Pr.

BERGQUIST, P. R., 1985: Poriferan relationships. - In: MORRIS, S. C., GEORGE, J. D., GIBSON, R., PLATT, H. M., (Eds): The origins and relationships of lower invertebrates, pp. 14-27. - Oxford: Clarendon Pr.

BOURY-ESNAULT, N., VACELET, J., 1994. Preliminary studies on the organization and development of a hexactinellid sponge from a Mediterranean cave, Oopsacas minuta. In VAN SOEST, R. W. M., VAN KEMPEN, T. M. G., BRAEKMAN, J. C., (Eds): Sponges in time and space; Biology, Chemistry, Paleontology, pp. 407-415. - Rotterdam: Balkema.

FICHEZ, R., 1990a: Chloropigments as an oligotrophic index in the study of submarine caves.- C. R. Acad. Sci. Paris 310: 155-161.

FICHEZ, R., 1990b: Decrease in allochthonous organic inputs in dark submarine caves, connection with lowering in benthic community richness. - Hydrobiologia 207: 61-69.

FICHEZ, R., 1991: Composition and fate of organic matter in submarine cave sediments; implications for the biogeochemical cycle of organic carbon.- Oceanol. Acta 14: 369-377.

GAGE, J.D., TYLER, P.A. 1991: Deep-sea biology. - Cambridge: Univ. Pr.

HARMELIN, J. G., VACELET, J., VASSEUR, P., 1985: Les grottes sous-marines obscures : un milieu extréme et un remarquable biotope refuge.- Téthys 11: 214-229.

IJIMA, I., 1901: Studies on the Hexactinelida, Contribution I. (Euplectellidae). - J. Coll. Sci. Imp. Univ. Tokyo **15**: 1-299.

KELLY-BORGES, M., 1995: Sponges out of their depth. - Nature **673**: 284.

KOLTUN, V. M., 1970a: Sponge fauna of the north-western Pacific from the shallows to the ultra-abyssal depths. - Inst. Oceanol. Acad. Sci. U.S.S.R. **86**: 165-221.

KOLTUN, V. M., 1970b. Sponges of the Arctic and Antarctic; a faunistic review. - In FRY, W. G., (Ed.): The biology of the Porifera, pp. 285-297. - London: Acad. Pr.

LUNDBECK, W., 1905: Porifera. Pars II: Desmacidonidae (pars). - The Danish Ingolf-Expedition **6**: 1-219.

MACKIE, G. O., SINGLA, C. L., 1983: Studies on hexactinellid sponges. I. Histology of *Rhabdocalyptus dawsoni* (LAMBE, 1873). - Philos. Trans. R. Soc. London **301**: 365-400.

MILLOT, C., 1979: Wind induced upwellings in the Gulf of Lions. - Oceanol. Acta **2**: 261-274.

NIELSEN, C., 1987: Structure and function of metazoan ciliary bands and their phylogenetic significance. - Acta Zool. **68**: 205-262.

OKADA, Y., 1928: On the development of a hexactinellid sponge, *Farrea sollasii*. - J. Fac. Sci. Imp. Univ. Tokyo **2**: 1-27.

OTT, J. A., SVOBODA, A., 1976: Sea caves as model systems for energy flow studies in primary hard bottom communities. - Pubblicazioni della Stazione Zoologica di Napoli **40**: 478-485.

PEREZ, T., in press: La rétention des particules par une éponge hexactinellide, *Oopsacas minuta* (Leucopsacacidae): le rôle du reticulum. - Particle uptake by a hexactinellid sponge, *Oopsacas minuta* (Leucopsacacidae): the role of the reticulum. - C. R. Acad. Sci. Paris.

POULIQUEN, L., 1971: Les spongiaires des grottes sous marines de la région de Marseille: écologie et systématique.- Téthys **3**: 717-758.

REISWIG, H. M., 1990. In situ feeding in two shallow water hexactinellid sponges. - In RÜTZLER, K., (Ed.): New perspectives in sponge biology, pp. 504-510. - Washington, DC: Smithsonian Inst. Pr.

REISWIG, H. M., MACKIE, G. O., 1983: Studies on hexactinellid sponges. III. The taxonomic status of Hexactinellida within the Porifera.- Philos. Trans. R. Soc. London **301**: 419-428.

RIDLEY, O. S., DENDY, A., 1887: Report on the Monaxonida collected by H.M.S. Challenger during the years 1873-1876, Vol. 20. Report on the Scientific

Results of the voyage of H.M.S. Challenger. - London: Majesty's Stationery Office.

RIEDL, R., 1966: Biologie der Meereshöhlen. - Hamburg und Berlin: Verlag Paul Parey.

RIEGER, R. M., 1976: Monociliated epidermal cells in Gastrotricha: Significance for concepts of early metazoan evolution.- Z. zool. Syst. Evolutionsforsch. **14**: 198-226.

SARS, G. O., 1872: On some remarkable forms of animal life from the great deeps off the Norwegian coast. I. Partly from posthumous manuscripts of the late professor Dr. Michael SARS. - Christiana: Brígger & Christie.

SCHULZE, F.E., 1899: Zur Histologie der Hexactinelliden. - Sitzungsber. Kaiserl. Preuss. Akad. Wiss. **14**: 198-209.

STEINER, M., MEHL, D., REITNER, J., ERDTMANN, B. D., 1993: Oldest entirely preserved sponges and other fossils from the Lowermost Cambrian and new facies reconstruction of the Yangtze platform (China).- Berl. geowiss. Abh. **9**: 293-329.

TOPSENT, E., 1927: Diagnoses d'éponges nouvelles recueillies par le Prince Albert 1er de Monaco. - Bull. Inst. Océanogr. **502**: 1-19.

VACELET, J., BOURY-ESNAULT, N., 1995a: Carnivorous sponges. - Nature **373**: 333-335.

VACELET, J., BOURY-ESNAULT, N., 1995b: Quand les éponges ont des dents.- La Recherche **26**: 458-459.

VACELET, J., BOURY-ESNAULT, N., in press: A new species of carnivorous sponge (Demospongiae: Cladorhizidae) from a Mediterranean cave.- Bull. Inst. R. Sci. Nat. Belg.

VACELET, J., BOURY-ESNAULT, N., HARMELIN, J. G., 1994: Hexactinellid Cave, a unique deep-sea habitat in the scuba zone.- Deep-Sea Res. **41**: 965-973.

VACELET, J., BOURY-ESNAULT, N., FIALA-MÉDIONI, A., FISHER, C. R., 1995: A methanotrophic carnivorous sponge.- Nature **377**: 296.

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