Qatar Univ. Sci J. (1999), 19:

SPONGES (PORIFERA) IN SUBMARINE CAVES

By

Jean Vacelet

Centre d'Océanologie de Marseille (CNRS-Université de la Méditerranée, UMR 6540),
Station marine d'Endoume. 13007 Marseille, FRANCE

Keywords : *Porifera; Submarine cave; Deep-sea fauna; ancient reefs.*

ABSTRACT

Sponges (phylum Porifera) have the most simple and probably the most ancient body plan of the multicellular animals. They are, however, very successful in most benthic ecosystems. They are dominant in submarine caves, where their study has provided unexpected results.

Submarine caves share several ecological features with deep-sea habitats. The communities living in these habitats depend on allochthonous organic input, and some bathyal species are able to colonize the darkest parts of littoral caves. Some examples will be given, including calcified sponges,«living fossils» of ancient reef builders. Faunal and environmental similarities, however, are limited by the obvious differences in pressure, temperature, habitat size, and by the dispersal abilities of deep water organisms. A recently discovered Mediterranean cave more closely approximates deep-sea conditions, due to the entrapment of a cold water mass resulting in stable temperature conditions throughout the year. Easily accessible to scuba divers, this «bathyal island» in the littoral zone is a natural mesocosm of the deep Mediterranean which offers exceptional opportunities for deep-sea biology. Preliminary results have already provided unexpected insights, which are illustrated.

A large population of *Oopsacas minuta,* a representative of the bathyo-abyssal hexactinellid sponges, reproduces here year round - making possible the first observations of larval behaviour and ultrastructure to be carried out on this phylogenetically important group of invertebrates, and opening up the poorly known area of larval ecology of these deep-sea sponges. The presence of a species of the deepest known genus of sponges, *Asbestopluma* (8 840 m in the Central Pacific) is a fascinating opportunity to investigate the biology of the strange deep-sea cladorhizid sponges, which may live in the most oligotrophic abyssal basins. A highly unexpected result is that they are non-filter-feeding sponges with a carnivorous feeding habit. They capture and digest small crustaceans by means of filaments provided with minute hook-shaped spicules. The biology and peculiarities of this carnivorous sponge are illustrated by a video.

INTRODUCTION :

Submarine caves have often been considered as interesting natural candidates for mesocosms of the deep sea, whose access is difficult and expensive, Blind caves and deep-sea habitats closely resemble each other in terms of darkness and hydrodynamic conditions [1,2]. Both depend mainly on primary production elsewhere [3], resulting in some cases in a similar amount of trophic resources [4-6]. Similarities have also been described in faunal composition and structure of the assemblages of sessile invertebrates [1, 7], with several bathyal species living in the darkest parts of sublittoral caves. These data concern mainly sponges, which are on cave rocky surfaces the dominant group in number of species, biomass and surface covered. Sponges present a special interest in caves, due to the preservation of hypercalcified «living fossils» which are unexpected survivors of ancient reef builders, and to the presence of deep-sea species showing unexpected life strategies, including carnivory. Such caves have not yet been described in the Arabian Gulf.

THE SPONGE FAUNA OF SUBMARINE CAVES

The sponge fauna is remarkably rich and diverse near the apertures of submarine caves, in the semi-dark zone [1]. Dim light and a good water exchange with the productive area outside assure a low degree of competition with algae and abundant particulate food. Deeper in the cave, the benthic communities of the dark zones which depend on allochthonous inputs in the absence of local production by photosynthesis, display a dramatic decrease in biomass [5]. In such an environment some invertebrates from the bathyal zone find conditions nearly similar to those of the deep sea and have been able to colonize dark caves. Invertebrates normally living several hundred meters deep have been found at 3 m depth in littoral caves. These features have been described in various areas of the world ocean. A similar habitat is widespread in coral reefs, either in large tunnels from the outer reef front or in smaller cavities of the reef framework.

Among the bathyal invertebrates able to colonize shallow water caves, most remarkable are hypercalcified sponges, which have, in addition to the usual spicule skeleton, a solid non-spicular calcareous skeleton. This bears striking resemblances to that of various cnidarians, including the corals which build the modern coral reefs, and is able to fossilize. These «coralline sponges» are in fact survivors of enigmatic Palaeozoic and Mesozoic reef-builders, namely stromatoporoids, chaetetids «corals» and sphinctozoans, which were believed extinct.

The nature of these organisms has been long debated, and most were classified in the Cnidaria a few years ago. Four of these «living fossils» were first found in the bathyal zone at the beginning of the century, but their true existence has been disputed. The opinion that they were chimeras made of calcified organisms excavated by sponges, was commonly accepted. The discovery of a new main groups of deep-sea sponges, the class Hexactinellida and the family Cladorhizidae of class Demospongiae. 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.

SPONGE FAUNA OF THE CAVE

As usual in caves, the sponges are the dominant group on all the rocky surfaces, in number of species, biomass and surface covered. The percentage of cover, estimated on sampled rocky surfaces of the walls, decreases from the entrance area with varying temperature to the homeotherm zone. However the cover does not significantly decrease though the homeotherm zone up to the far end, contrary to what is observed for bryozoans [19]. This may be due to the utilisation by sponges of pulses of particles in certain hydrological circumstances.

HEXACTINELLID

Representatives of the class Hexactinellida (glass sponges) are predominantly bathyo-abyssal. Due to difficulties in preservation, these sponges remained mysterious for a long time. As early as the beginning of this century, their histological structure has been claimed to be very different from other sponges [20, 21]. Recent observations have confirmed that their tissues are mostly syncytial and that their choanocytes were 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 [22, 23] 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 poor, is unknown.

The Mediterranean cave in cold water has been colonized by *Oopsacas minuta,* an hexactinellid sponge which was previously known from only two minute specimens collected at 924m in depth at Mediterranean end of the Straits of Gibraltar [24]. Easy access to the cave population of *Oopsacas minuta,* with possibility of in *situ* processing has resulted in unusually good preservation of the delicate cytological structures [25]. Ultrastructural observations and experimental study of the particle uptake [26] by O. *minuta* show that the feeding strategy of hexactinellids differs notably from that of other sponges. Hexactinellids rely on the extensive 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). This is very different from a bathyal demospongs such as *Discodermia polydiscus* living in the same area of the cave, in which the aquiferous system is reduced, with small choanocyte chambers and an extremely dense mesohyl containing a huge number of symbiotic bacteria. In *situ* or laboratory experiments using latex beds, unicellular algae or bacteria have shown that the anucleate choanocytes of the hexactinellid are mostly used for the circulation of 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, by either its inhalant or exhalant side depending on the particle size.

The reproduction of hexactinellids was also poorly known, due to difficulty for access, and to the fact that deep-sea specimens rarely reproduce. Although many specimens from deep-sea hexactinellids have been studied, embryology and larvae have been correctly described only once [27], with the discovery of the presence of a unique larval skeleton of special siliceous spicules. Larval behaviour and ecology and dispersal ability are obviously unknown.

Contrary to deep-sea hexactinellids, the cave specimens of *O. minuta* sexually reproduce all year round, and stages of embryogenesis have been found in all examined specimens. This is obviously a good opportunity for both embryology and larval behaviour study, 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 called «trichimella» [25]. 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 surprising presence of multiflagellated cells, which are assumed to appear only in the triploblast and Protostomia/Spiralia lines [28] could indicate that hexactinellids have acquired multiflagellarity independently of other metazoans. The free larva is only 150-180 µm long and is rich in lipids and yolk. Data on the larva behaviour would be informative on the dispersal possibilities of deep-sea hexactinellids.

CLADORHIZID DEMOSPONGE

The second remarkable example of deep-sea sponge in the cave is a demosponge belonging to the exclusively deep-sea family Cladorhizidae. All the representatives of this family have a strange morphology, stalked with long, thin appendages. Cladorhizids include the deepest known sponges, with a species of the genus *Asbestopluma* found at 8 840 m depth in the Pacific [29]. They are able to live in the most food-poor basins under low surface productivity [30]. The adaptations and life history traits which allow them to withstand such extreme conditions were unknown.

The cave species, approximately 20 mm high, is a new species of *Asbestopluma, A. hypogea* [31], belonging to the genus which holds the depth record for sponges.

This is again an opportunity to study the life history traits of sponges which on average are deeper than the hexactinellids and even can 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 for the hexactinellid, it is likely that the cave species also lives under inaccessible overhangs in the nearby deep canyon and on rocky surfaces of the deep Mediterranean, whose biodiversity seems to be significantly under-evaluated.

We first investigated the aquiferous system of this deep-sea animal, because the organisation and fine structure of the canal system provide information on the feeding strategy of sponges. Contrary to the hexactinellid in which the aquiferous system is unusually highly developed, the cladorhizid appeared devoid of any aperture, canal and choanocyte. It is thus not a filter-feeder like other sponges. Subsequent studies demonstrated rather that it is carnivorous and feeds on small living prey, mostly crustaceans, a highly unexpected feeding habit in sponges [32, 33]. The long, thin filaments are covered by minute hook-shaped spicule disposed at right angle to the axis, which give the filaments a «Velcro»-like adhesiveness. Once trapped by their appendages, tiny swimming crustaceans are unable to free themselves, although there is apparently no toxic or paralysing secretion. After capture, cells of the sponge migrate towards the prey, which is engulfed in the sponge tissue within a few hours or days according to the prey size. Complete digestion of a 7 mm long crustacean is complete in 10 days. In the cave, prey are mostly tiny crustaceans, such as copepods, ostracods, mysids, but small polychaetes or pycnogonids may occasionally be caught. Specimens have been successfully raised in aquarium for several month, with a weekly change of sea water and feeding with either living nauplii of *Artemia salina* or commercially available deep-frozen *Artemia.* The characters and behaviour of this sponge have been illustrated by a video [33], a copy of which has been deposited in the Department of Marine Sciences of the University of Qatar.

This unusual mode of life is apparently shared by the other Cladorhizidae (approximately 90 species) in deep-sea habitats. The general absence of 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 has been suggested by the first author to describe a cladorhizid [34], although this unconventional hypothesis was considered highly unlikely by subsequent authors. However, the cladorhizids may have other nutrient sources as well. A *cladorhiza sp.* from a deep-sea methane venting, 4900 m deep near Barbados, is nutritionally reliant on methanotrophic symbiotic bacteria [35, 36], although also feeding on swimming prey. This dual source of carbon allows the sponge to constitute large aggregations of hundreds of individuals around the methane source, when deep-sea cladorhizids usually occur in low densities as discrete individuals.

The organization and biology of A. *hypogea,* and presumably of the other cladorhizid sponges differ widely from those 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. Although they are sponges by their poriferan spicules, the characteristics and mobility of their cells and the absence of organs, the representatives of Cladorhizidae do not match the classical definition of Porifera, which has to be reinterpreted.

CONCLUSIONS

The example of sponges shows that various general problems of deep-sea biology as well as of history of ancient reefs during geologic times could be successfully addressed in caves.

The unexpected life history traits which have been discovered in Porifera appear as secondary adaptations to the deep-sea conditions, and also address broad problems in biological evolution, such as the origin of deep-sea fauna, the apparition of multiflagellarity in animal cells, or the definition of the phylum Porifera. Significant advances in the knowledge of the poriferan adaptations to the deep sea have been made or may be foreseen, such as feeding strategies, seasonality of reproduction, dispersal ability and long-distance fertilization, and the place 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 that have been discovered here for sponges are likely the same as for their deep-sea populations.

Dark littoral caves also have an interest as refuge for invertebrates which had a major role in reef construction during the geologic times, and which were long believed extinct. A handful of these ancient reef builders survive in the precipitous slopes of the continental margin, which are difficult to access, and in littoral caves, where their study is easier. These «living fossils» provide direct knowledge of the fascinating world of ancient reefs which were previously known mostly by their fossil remains.

REFERENCES

1. **Harmelin, J.G., J. Vacelet and P. Vasseur 1985.** Les grottes sous-marines obscures : un milieu extrîme et un remarquable biotope refuge. Téthys 11(3-4): 214-29.
2. **Vacelet, J. 1996.** Deep-sea sponges in a Mediterranean cave. In: F. Uiblein, J. Ott and M. Stachowitsch (eds.) Deep-sea and extreme shallow-water habitats: affinities and adaptations. 11. pp. 299-312. Austrian Academy of Sciences, Vienna.
3. **Ott, J.A., A. Svoboda 1976.** Sea caves as model systems for energy flow studies in primard hard bottom communities. PSZN.1: Mar. Ecol. 40:478-85.
4. **Fichez, R. 1990.** Chloropigments as an oligotrophic index in the study of submarine caves. C. R. Acad. Sci. Paris 310:155-61.
5. **Fichez, R. 1990.** Decrease in allochtonous organic imputs in dark submarine caves, connection with lowering in bethic community richness. Hydropbiologia 207:61-69.
6. **Fichez, R. 1991.** Suspended particulate organic matter in Mediterranean submarine cave. Mar. Biol. 108 : 167-74.
7. **Riedl, R. 1966.** Biologie der Meereshöhlen. Verlag Paul Parey, Hamburg und Berlin.
8. **Vacelet, J., C. Lévi 1958.** Un cas de survivance, en Méditerrancée, du groupe d'éponges fossiles des Pharétronides. C. R. Acad. Sci. Paris 246:318-20.
9. **Hartman, W.D. T.F. Goreau 1970.** jamaican coralline sponges : their morphology, ecology and fossil relatives. In:W.G. Fry (ed). The Biolog of the Porifera. 25, pp. 205-43 Academic Press, London.
10. **Vacelet, J. 1985.** Coralline sponges and the evolution of the Porifera. In:S. Conway Morris, J.D. George, R. Gibson and H.M. Platt (eds.). The ofigins and relationships of lwoer invertebrates, 28, pp. 1-13 Clarendon Press, Oxford.
11. **Chombard, C., N. Boury-Esnault, A. Tillier and J. Vacelet 1997.** Polyphyly of «sclerosponges» (Porifera, Demospongiae) supported by 28S ribosomal sequences. Biol. Bull. 193 : 359-67.
12. **Vacelet, J. 1979.** Quelques stades de la reproduction sexuée d'une Eponge Sphinctozoaire actuelle. In : C. Lévi and N. Boury-Esnault (Eds.) Biologie des Spongiaires. 291, pp. 95-101. Editions de C.N.R.S., Paris.
13. **Wood, R., J. Reitner and R.R. West 1989.** Systematics and phylogenetic implications of the haplosclerid stromatoporid *Newellia mira* nov. gen. Lethaia. 22:85-93.
14. **Wood, R. 1998.** The ecological evolution of reefs. Annu. Rev. Ecol. Syst. 29:197-206.
15. **Anthony, K.R.N. 1999.** Coral suspension feeding on fine particulate matter. J. Exp. Mar. Biol. Ecol. 232 : 85-106.
16. **Vacelet, J. 1990.** Storage cells of calcified relict sponges. Cahp. 19. In: K. Ruetzler (ed.). New Perspectives in Sponge Biology, pp. 144-52. Smithsonian Institution Press, Washington.

17. **Schuhmacher, H., M. Plewka 1981.** Mechanical resistance of reefbuilders through time. Oecologia 49:279-82.

18. **Vacelet, J., N. Boury-Esnault and J.G. Harmelin 1994.** hexactinellid Cave, a unique deep-sea habitat in the scuba zone. Deep-Sea Res. 41:965-73.

19. **Harmelin, J.-G. 1997.** Diversity of bryozoans in a Mediterranean sublitoral cave with bathyal-like conditions : role of dispersal processes and local factors. Mar. Ecol. Prog. Ser. 153:139-52.

20 **Schulze, F. E. 1899.** Zur Histologie der Hexactinelliden. Sitz. Ber. K. Pr. Akad. Wiss Berlin 14:198-209.

21. **Ijima, I. 1901.** Studies on the Hexactinelida, Contribution I. (Euplectellidae). J. College Sci. imp. Univ. Tokyo 15:1-299.

22. **Rigby, J.K., H. Xian-Guang 1995.** Lower Cambrian demosponges and hexactinellid sponges from Yunnan, China. J. Paleontol. 69:1009-19.

23. **Steiner, M., D. Mehl, J. Reitner and B. D. Erdtmann 1993** Oldest entirely preserved sponges and other fossils from the Lowermost Cambrian and new facies reconstruction of the Yangtze paltform (china). Berliner geowiss. Abh 9:293-329.

24. **Topsent, E. 1927.** Diagnoses d'éponges nouvelles recuellies par le Prince Albert ler de Monaco. Bull, Inst. océanogr. Monaco 502:1-19.

25. **Boury-Esnault, N., J. Vacelet 1994.** Preliminary studies on the organization and development of a hexactinellid sponge from a Mediterranean cave, *Oopsacas minuta.* In : R. W. M. van Soest, ThM.G.van kempen and J.C. Braekman (eds.). Sponges in time and space; Biology, Chemisty, Paleontology, pp. 407-15. Balkema, Rotterdam.

26. **Perez, T. 1996.** La rétention de particules par une éponge hexactinellide, *oopsacas minuta* (Leucopsacasidae) : le rôle du réticulum. - Paticle uptake by a hexactinellid sponge, *Oopsacas minuta* (Leucopsacasidae): the role of the reticulum. C.R.Acad. Sci. Paris 319 : 385-91.

27. **Okada, Y. 1928.** On the development of a hexactinellid sponge, *Farrea sallasii.* J. Fac. Sci. imp. Univ. tokyo 2 (1) : 1-27.

28. **Nielsen, C. 1987.** Structure and function of metazoan ciliary bands and their phylogenetic significance. Acta Zool. 68:205-62.

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

30. **Gage, J.D., P.A. Tyler 1991.** Deep-sea Biology. Cambridge University Press, Cambridge.

31. **Vacelet, J., N. Boury-Esnault 1996.** A nwe species of carnivorous sponge (Demospongiae: Cladorhizidae) from a Mediterranean cave. Bull. Inst. roy. Sci. nat. Belgique 66 (suppl.) :109-15.

32. **Vacelet, J., N. Boury-Esnault 1995.** Carnivourous sponges. Nature 373: 333-35.

33. **Vacelet, J. 1998.** L'éponge carnivore. Film du CNRS Audiovisuel, 13 minutes.

34. **Sars, G.O. 1872.** On some remarkable forms animal life from the great deeps off the Norwegian coast. I. Partly from posthumous manuscripts of the late professor Dr. Michael Sars. Brøgger & Christie, Christiana, Norway.

35. **Vacelet, J., N. Boury-Esnault, A. Fiala-Médioni and C.R. Fisher 1995.** A methanotrophic carnivourous sponge. Nature 377:296.

36. **Vacelet, J., A. Fiala-Médioni, C.R. Fisher and N. Boury-Esnault 1996.** Symbiosis between methane-oxidizing bacteria and a deep-sea carnivorous cladorhizid sponge. mar. Ecol. Prog. Ser. 145:77-85.