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CLUES TO DEEP-SEA BIODIVERSITY IN A NEARSHORE CAVE

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MEDITERRANEAN
BATHYAL
SUBLITTORAL CAVES
VERTICAL DISPERSAL
PORIFERA
BRYOZOA

MÉDITERRANÉE
BATHYAL
GROTTES SOUS-MARINES
DISPERSION VERTICALE
PORIFERA
BRYOZOA

ABSTRACT. – Populations of unexpected bathyo-abyssal invertebrates (mainly sponges) established in a large sublittoral Mediterranean cave attest that biodiversity of the deep-sea rocky bottoms is outstandingly underestimated. Stability of temperatures around bathyal values in the water body trapped below a within-cave thermocline is the key factor allowing propagules upwelled from a nearby canyon to colonize this habitat. Easy access to these deep-sea animals allows to investigate more thoroughly their reproductive and dispersal strategies, and to evaluate the between-clade differences in cross-shelf transfer aptitudes.

RÉSUMÉ. – Des populations d'invertébrés bathyo-abyssaux inconnus (principalement Eponges) établies dans une grotte sous-marine méditerranéenne attestent que la biodiversité des fonds rocheux profonds est notablement sous-estimée. La stabilité des températures à des valeurs proches de celles du bathyal dans la plus grande partie de la grotte sous une thermocline est le facteur clé qui a permis à des propagules importées depuis un canyon voisin par des upwellings de coloniser cet habitat. L'accès facile à ces animaux des grandes profondeurs permet d'étudier plus en détail leurs stratégies de reproduction et de dispersion, et d'évaluer les différences d'aptitude des divers groupes à franchir le plateau continental.

The deep-sea benthos is no more considered as a low-diversity environment, as it was some decades ago. However, the actual species richness of this huge habitat is still in discussion (Grassle 1989, Gray 1994). The origin of the diversity, the maintenance of the diversity through equilibrium or disequilibrium explanations, the colonization processes, and the relationships between diversity and food resources are still poorly known in the deep sea (Gage & Tyler 1991).

Knowledge of diversity and functioning of the deep Mediterranean communities is notoriously incomplete, especially on rocky substrates due to sampling difficulties and habitat fragmentation that enhances the diversity of local situations. The reputation of poorness of the Mediterranean bathyal fauna is essentially based on soft bottom communities and has never been proved for rocky bottoms.

We address some of these problems in submarine aphotic caves, considered as mesocosms of deep-sea conditions. Although direct comparisons of species richness and assemblage composition and structure between bathyal rocky substrates and littoral aphotic habitats are difficult, cave studies may give some general insights into the patterns of the Mediterranean slope biodiversity.

The studies are conducted mainly in a large cave (3PP Cave, French Mediterranean coast, La Ciotat : 43°09.47' N, 05°35.01' E), whose topography induces stable temperature conditions similar to those occurring below the summer thermocline in the Mediterranean (Fig. 1). This littoral cave shelters several invertebrates that are unexpected representatives of the stenothermic deep-sea fauna, whose source populations are hypothesized to be located in a nearby canyon (Boury-Esnault *et al.* 1993, Vacelet *et al.* 1994, Vacelet 1996, Harmelin 1997). Temperature records performed year-round attest that water uplifted from intermediate depths during upwelling events episodically flows down into the cave, and suggest that these water bodies may advect propagules produced in the deep-sea (Vacelet 1996, Harmelin 1997) (Fig. 2).

Species census in 3PP Cave revealed a combination of eurythermic cavernicolous species (many of them being eurybathic) and bathyal or bathyo-abyssal invertebrates previously unrecorded from other caves. Moreover, these cave-dwelling deep-sea representatives belong to taxa which were unrecorded from the deep Mediterranean : the cladorhizid sponge *Asbestopluma hypogea* (Vacelet & Boury-Esnault 1995, 1996), the hexac-

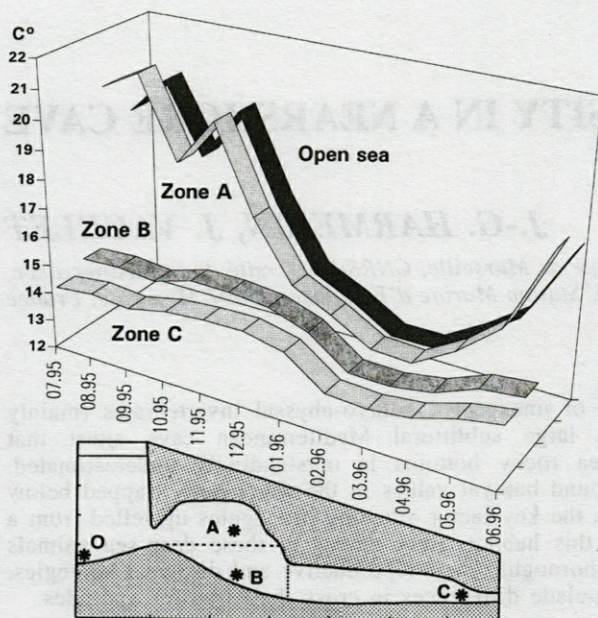


Fig. 1. – Year-round fluctuations of monthly means of water temperature (from ca. 300 measurements per month) in the open sea (O : - 18 m) and into 3PP Cave, above (A : - 13 m) and below (B : - 20 m, C : - 24 m) the within-cave thermocline.

tinellid sponge *Oopsacas minuta* (Boury-Esnault & Vacelet 1994, Vacelet *et al.* 1994), two new genera and species of sponges without skeleton (Vacelet and Perez in press), new genera of Tardigrada and Polychaeta from the meiofauna (Villora-Moreno 1995, 1996), new species of Chaetognatha (Casanova 1992). Most obviously, these taxa did not differentiate in the cave, that was submerged relatively recently (7-8 000 years) during the last Holocene rise, and the most plausible hypothesis is that they colonized the cave through propagules from deep-sea populations of nearby Cassidaigne canyon (7 km off).

The unexpected occurrence of these bathy-abyssal invertebrates indicates that diversity in Mediterranean deep rocky habitats is markedly richer than previously estimated from dredging or sampling by submersibles. However, these indications are unequally shared among clades and are given mainly by sponges. Among bryozoans, another group commonly distributed in both cryptic nearshore and slope hard-substrate habitats, only one species normally restricted to the slope, *Puelina setiformis*, colonized the cave (Harmelin 1997).

Easy access to the cave-dwelling specimens of these bathyal species allows to investigate more thoroughly their reproductive and dispersal strategies. The discovery that *Oopsacas minuta* reproduces very actively year round in the cave (Boury-Esnault & Vacelet 1994) gives new insight into

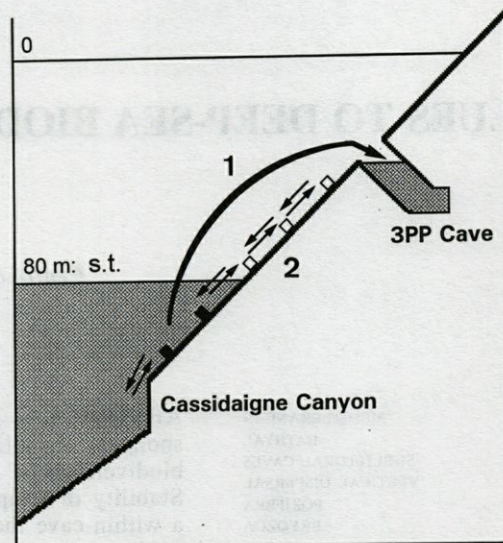


Fig. 2. – Patterns of faunal exchanges between deep-water habitats and 3PP Cave. 1, direct transfer of advected propagules from habitats located below the summer thermocline (s.t.) towards the cave thanks to strong upwelling events : the only dispersal route possible for deep-water homothermic species. 2, stepping-stone dispersal through scattered habitats and several generations : concerns only eurythermic species.

the reproductive potential of hexactinellids, a typical deep-sea group in which sexual reproduction is very rarely observed. This stronger reproductive activity is presumed to be induced by the amount of food supply into the cave, higher than usually in the deep Mediterranean, and suggests that sexual reproduction in deep-sea sponges is strongly dependent on intermittent food pulses. The cladorhizid sponge *Asbestopluma hypogea* constitutes another model of the distribution patterns occurring in the deep-sea hard bottom communities. The local distribution of this tiny species in numerous small patches (Vacelet & Boury-Esnault 1996) suggests that it can disperse according to both short- and long-distance mechanisms : the first providing the aggregative settlement on the cave walls, the second being responsible of the founding event from the deep sea. This species spawns specialized spermatocysts instead of the free spermatozoa usual in sponges, probably an unusual adaptation for long-distance cross fertilization.

Investigation in progress, both on the genetic structure of populations and on bioclast remains in the cave sediment will seek informations on the history of the cave biodiversity, e.g. on the number of founding events from the deep-sea. First results of a colonization experiment indicate that propagule transportation towards the homothermic cave habitat by the water bodies downwelling into the cave is not a common phenomenon : panels deployed during 14 months in diverse

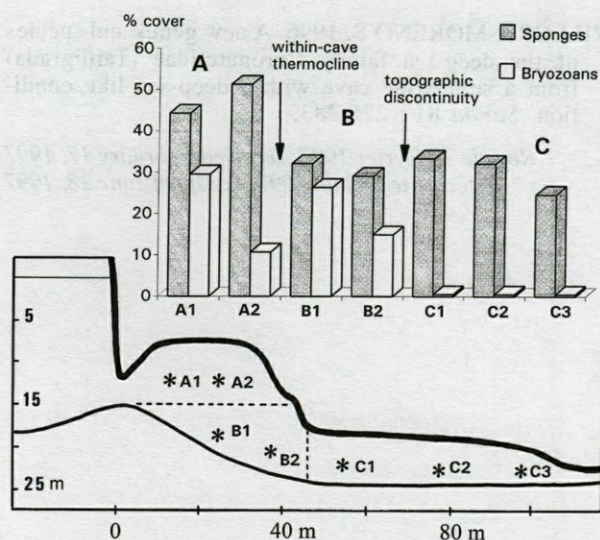


Fig. 3. – Modifications of percent cover of sponges and bryozoans on the walls of 3PP Cave at increasing distances from entrance and according to two thermic regimes (A, eurythermy, B-C, homothermy). The topographic discontinuity corresponds to a 30° change in the cave orientation.

cave locations revealed that the settlement rate was strikingly low in the homothermic part even at short distance from entrance (25 m). In contrast, panels located just above in the eurythermal layer were richly fouled. This lack of settlement success below the thermal front, even for the most common sciaphilous species, suggests the existence of strong physical barriers. The chance of repeated founding events from the deep sea is thus likely to be very weak. The past and present patterns of the topography-induced small-scale circulation within the cave are likely to be of major importance in the success of transfer of allochthonous propagules within the wall's boundary layer.

The problem of the relationships between diversity and trophic resources in the bathyal zone are also addressed in the cave as mesocosm. Preliminary results indicate that the relatively high level of particulate organic matter, as compared with most Mediterranean deep-sea habitats, may determine the dominance of sponges, both in number of species and in surface covered along the cave gradient. The occurrence among 3PP Cave sponges of examples of the various feeding adaptations to oligotrophic deep-sea adaptations allowed significant advances in this poorly investigated topic. Evidence was brought that hexactinellids and cladorhizids have developed opposite strategies, the former relying on overdevelopment of their aquiferous system (Perez 1996) and the latter on carnivory (Vacelet & Boury-Esnault 1995), a unique example in sponges. In contrast to sponges (Fig. 3), bryozoans present a

strong clinal decrease in both species richness and abundance (size and number of colonies) along the cave gradient (Harmelin 1997), indicating that sponges and bryozoans are not equally successful in utilizing the trophic resources available within the boundary layer of the cave walls.

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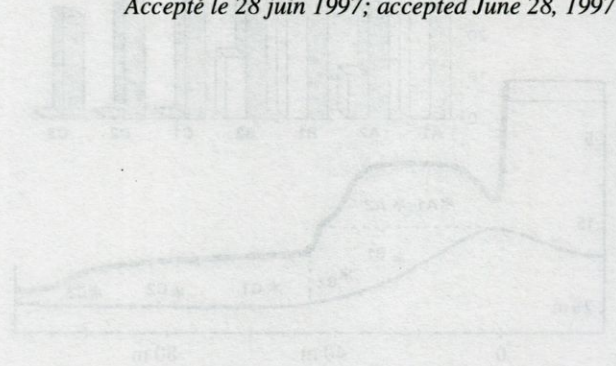


Fig. 2. Mediterranean water level (m) over the 1997 season. The x-axis represents the day of the year (from 0 to 30) and the y-axis represents the water level (m). The water level increases from 2 m on day 0 to 8 m on day 25, then drops sharply to 4 m on day 28, and finally rises to 6 m on day 30.

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data locations revealed that the settlement rate was strikingly low in the homogeneous part even at short distance from entrance (25 m). In contrast, genetic diversity was high in the cave. These results were highly linked. The lack of settlement success below the threshold even for the most common siphonous species suggests the existence of strong physical barriers. The chance of repeated founding events from the deep sea is thus likely to be very weak. The genetic present patterns of the topography-induced small-scale circulation within the cave are likely to be of major importance in the success of dispersal of allochthonous propagules within the water boundary layer.

The problem of the relationships between diversity and trophic resources in the bathyal zone is also addressed in the cave as mesobenthic primary results indicate that the relatively high level of particulate organic matter, as compared with most Mediterranean deep-sea habitats, may determine the dominance of sponges both in abundance and in surface covered along the cave system. The coexistence among 31P Cave suggests the availability of the various feeding strategies to maintain the deep-sea sponges. This was significant evidence in this poorly investigated and little evidence was brought that siphonous and colonial sponges have developed opposite strategies: the former relying on overabundance of their siphonous system (Perez 1997) and the latter on canopy (Vacelet & Boury-Sanait 1997) a unique example in sponges. In contrast to sponges (Fig. 2), siphonous present a