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PLANKTONIC GRADIENTS ALONG A MEDITERRANEAN SEA CAVE

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SUMMARY

The existence of gradients in the composition of planktonic communities through a 50 m long submarine cave of the Medes Islands (NW Mediterranean) has been verified. In spite of an active water exchange (previously evaluated turnover ranges between 12 and 24 hours), strong gradients, persisting throughout all year, were found in both phyto- and zooplanktonic fractions. Numbers of both individuals and taxa of diatoms, dinoflagellates, copepods, and meroplanktonic stages of benthic invertebrates decrease steeply from the entrance of the cave to the inner parts, thus producing an almost total absence of plankton at the end of the cave. On the other hand, benthic diatoms, fungi and spirorbida - all benthic groups accidentally sampled - neither decrease nor even increase to the inner stations, which suggests a tolerance to the "cave effect". These results are so clear-cut that by themselves they can explain the puzzling decay of suspension-feeders among the benthic fauna from the inner parts of submarine caves in two ways : i) scarcity of benthic larvae for settlement, and ii) scarcity of phyto- and zooplankton for food.

KEY WORDS: Plankton, caves, gradients, W Mediterranean.

INTRODUCTION

Studies dealing with benthic fauna from worldwide submarine caves (see HARMELIN *et al.*, 1985, for references) point to the same general feature: a strong gradient in both benthic species richness and benthic biomass along the outside-inside axis; the deeper inside the cave the poorer the fauna. In spite of the universality of this pattern, which seems to suggest powerful and conspicuous causes, our knowledge of the subject has progressed very slowly.

Three kinds of causes have been advanced, all of them supported by very poor experimental evidence : 1) strong physical gradients inhibiting benthic survival; 2) trophic stress by food depletion, and 3) water stagnation or reduced water flow which will be at the origin of causes 1 and/or 2 (CINELLI *et al.*, 1977; BALDUZZI *et al.*, 1980, HARMELIN *et al.*, 1985; GILI *et al.*, 1986; FICHEZ, 1989, 1990, 1991b, d; ZABALA *et al.*, 1989).

Physical gradients (i.e. salinity, temperature, oxygen content), if present, are unlikely to be so strong as to prevent, by themselves, the survival of benthic biota (GILI, *et al.*, 1986). Light, the most conspicuous of these factors, can explain the disappearance of the benthic flora but not - or not at all- the decay of the benthic fauna (RIEDL, 1966; CINELLI *et al.*, 1977; BALDUZZI *et al.*, 1989).

Suspension-feeders and sediment-feeders do not seem to be very dependent on light if suspended materials are available to them.

The generally accepted explanation assumes caves to be permanent strong oligotrophic systems (FICHEZ, 1989, 1991a, b, c, d) where food supply is reduced by both planktonic and POM depletion.

Reduced water turnover may be the origin of oligotrophy either by reducing food inputs or by enhancing sedimentation (FICHEZ, 1989; 1991b, d).

Unfortunately, studies dealing with the models of water circulation inside caves are scarce. Persistent thermic gradients have been invoked as evidence of long water stagnation (POULIQUEN, 1971; PASSELAIGUE & BOURDILLON, 1985; FICHEZ, 1989). The persistence of benthic fauna throughout tunnels, where water movement is assumed to be important, was proposed as further indirect evidence of the importance of this parameter (HARMELIN, 1969). Nevertheless, flow measurements by means of plaster balls showed patterns of moderate (BALDUZZI *et al.*, 1989) or negligible decay of water movement inside caves relative to outer waters or to tunnels (ZABALA *et al.*, 1989).

All the hypotheses summarized above rest on the assumption that benthic life inside the caves is limited by adult mortality. But alternative hypotheses can be formulated on the basis of stresses for the survival of larval stages. There is evidences that settlement is severely reduced inside submarine caves (HARMELIN, 1980; GARCÍA & ZABALA, in prep.) but at present it is not known whether this phenomenon is due to: 1) larval scarcity inside caves due to larval behaviour, mortality, predation or sedimentation; 2) settlement failure even if larvae are

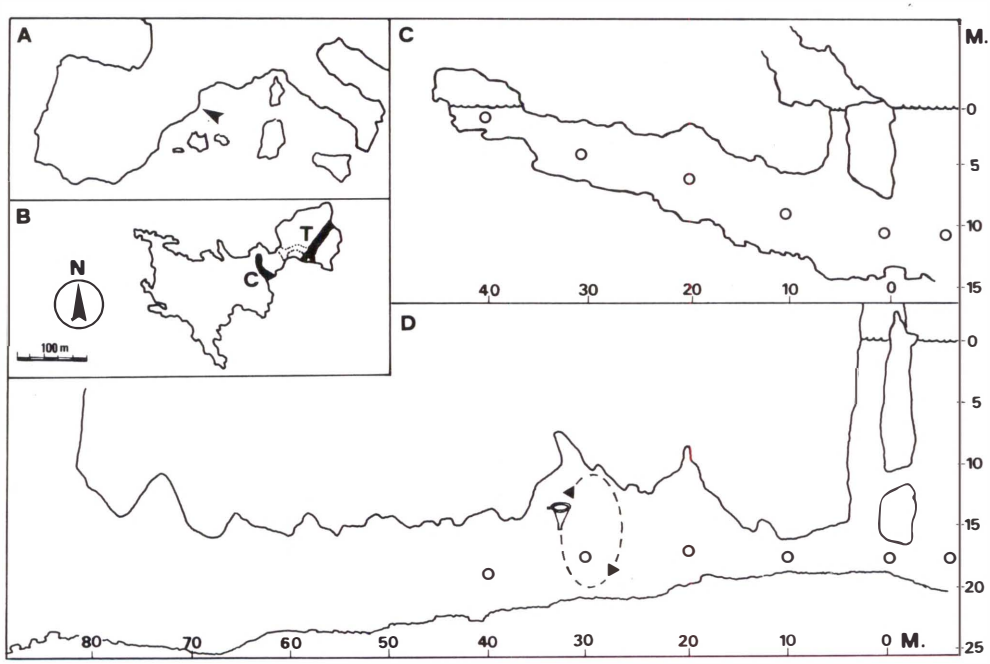

FIGURE 1. Sketch of study cave and tunnel. A) General location in the Western Mediterranean. B) Cave and tunnel situation in the Meda Petita island. C) Diagrammatic section of the cave showing sampling points (open circles). D) Diagrammatic section of the tunnel showing sampling points (open circles) and an example of the circular trajectories followed for zooplanktonic samples.

abundant, or 3) post-settlement mortality in the early stages of development.

To date, little attention has been paid to the study of planktonic communities living inside submarine caves. Only indirect estimates are available from values of chlorophyll and POM (FICHEZ, 1989, 1990; ZABALA *et al.*, 1989) or volume and size distribution of suspended particles as measured by Coulter counters (GILI *et al.*, 1986). But taxonomic details, based on direct microscopic examination, have rarely been reported. More precisely, the abundance of meroplanktonic larval stages of benthic fauna inside caves has not been evaluated.

The aim of this paper is to study the structure of planktonic communities along the axis of a cave, searching for the existence of a similar gradient to those previously reported for benthic communities (GILI *et al.*, 1986). As a part of the same project, an experiment on settlement on panels anchored outside and inside this cave was carried out simultaneously (GARCÍA & ZABALA, in prep.). The hypothesis invoked here assumes that a strong and persistent decay in phyto- and zooplanktonic communities inside the cave can explain, in itself, the equivalent decay in benthic fauna, in two ways: 1) food depletion, because phyto- and zooplanktonic organisms are the main trophic sources for the suspension-feeder dominant benthic biota, and 2) strongly reduced settlement of benthic organisms is due to the scarcity of meroplanktonic larvae.

MATERIAL AND METHODS

THE SITE

The study was carried out in a cave and a tunnel located in the Medes Islands (Catalonia, NW Mediterranean), where previous studies on benthic fauna, water flow and trophic-related parameters have been undertaken (GILI *et al.*, 1986; ZABALA *et al.*, 1989).

The cave is a karstic hole, roughly cylindrical in shape, less than 50 m long, 4 - 7 m in diameter, about 756 m^3 in volume (GILI *et al.*, 1986). It opens to the east side of the Meda Xica Island between 8 (upper) and 12 (lower) m depth. For 35 m after the entrance the "tube" runs straight E-W and rises slowly (the boulder-rocky bottom rises from a depth of 12 m to a depth of 6 m). The inner 10 m are characterized by a northward turn (45°) followed by a sudden increase in the bottom slope, which rises from a depth of 6 m to reach the sea level just at the end of the cave where an air-filled room develops (Fig. 1C). Light penetration in the cave displays a sharp gradient, 99 % of PAR disappearing within the first 10 m from the opening (GILI *et al.*, 1986).

One of the two mouths of the tunnel opens less than 50 m from the cave at similar orientation and depths (upper 16 m, lower 19 m; Fig. 1D). The tunnel is a roughly straight tube 83 m long, 8-12 m width, 4-9 m height, directed SW-NE and slowly descending to the northern mouth, which opens at 14 (upper) - 23 (lower) m depth (BIBILONI *et al.*, 1984; ZABALA *et al.*, 1989).

Macrobenthic fauna from the cave display the pattern of decay (GILI *et al.*, 1986) which characterizes submarine caves studied worldwide (see HARMELIN *et al.*, 1985 for references). Benthic assemblages of the tunnel do not show such a clear pattern of decay, at least from the point of view of biomass. Even if there is a conspicuous zonation with both species substitution and a decrease in species number, organic covering of the walls remains total (more than 100 %) throughout the tunnel (with the sole exception of the high vaults in the roof; BIBILONI *et al.*, 1984).

Water flow along the cave has been estimated as active enough to ensure the turnover of the whole mass of water

enclosed in the cave every 12-24 h (RIERA *et al.*, 1985; ZABALA *et al.*, 1989). Moreover, when samples of water of equivalent depths from outside and inside the cave were compared for hydrographic parameters such as temperature, salinity or oxygen content, a surprising equivalence was found throughout the year (GILI *et al.*, 1986). In this case the common annual cycle described for the neritic waters of this region (PALAU, 1988; MARGALEF, 1964; JACQUES, 1969), with a stratified season during summer and a mixed season during winter, should be applicable to the cave.

Although water flow through tunnels is assumed to be higher than flow through caves, the only empirical evidence reported to date from this tunnel relative to the cave does not support with this assumption (ZABALA *et al.*, 1989).

Phytoplanktonic communities from waters surrounding the Medes Islands were studied by PALAU (1988). Changes in the composition of zooplankton over two 24-h cycles were also reported from a station just above the entrance to the cave (BARANGÉ, 1988; BARANGÉ & GILI, 1988). Previous data on chlorophyllic pigment concentration seem to support the expectation that phytoplankton would decrease inside the cave (ZABALA *et al.*, 1989). But data provided by Coulter counter on suspended particles offered a much more homogeneous pattern (GILI *et al.*, 1986).

SAMPLING

Five sampling points were established at 10 m intervals along the sagital axis of the cave. An additional outer point, 10 m from the entrance, was chosen as a control. For practical purposes these points will be referred to by their distance from the mouth of the cave: -10 (outer), 0 (mouth), 10, 20, 30 and 40 (at 10, 20, 30 and 40 m from the entrance; Fig. 1). All six points were sampled with SCUBA-diving around midday, 5 times at different seasons between years 1987 and 1989 (6-VI-87 with two replicates, 29-VI-88, 6-VII-88, 13-X-88, 24-I-89). The same procedure was repeated inside the tunnel once on 29-VI-88. Scale differences between phyto- and zooplanktonic fractions led us to choose two separate procedures of sampling which were both handled by SCUBA-divers. Phytoplankton was sampled by aspiration of 125 cm^3 from the central point of the cave section at each sampling point with a polypropylene syringe. The sample was fixed with lugol solution at a final concentration of 1%. Zooplankton was sampled by swimming around the sampling point for 3 minutes with a 74 µm mesh, 314 cm^2 in section (sample volume around 3.14 m^3) following a circular trajectory only 30 cm away from the walls and roof (Fig. 1). Samples were immediately fixed with formaldehyde at a final concentration of 5%.

STUDY

A few weeks after sampling, phytoplankton was studied through a WILD M40 inverted microscope (UTERMÖHL, 1958) after a 48-h sedimentation procedure. All cells present in a count chamber (100 cm^3) were counted (x 125) for big and rare species; but only a half chamber was surveyed for ciliates and rare and small cells. For each sample, an aliquot (0.3 to 1.6 cm^3 in volume) was counted at a higher magnification (x 600) for commonest cells. Ocasionally, when the characteristics of samples seemed to demand it, larger (6.4 cm^3 volume; x 150 magnification) or smaller (0.016 cm^3; x 600) aliquots were additionally censused. As total counts per sample always ranged between 200 and 700 cells, a noticeable accuracy with error around ±10 % was reached, and confidence level was estimated to be 95 % (cf. LUND *et al.*, 1958).

Zooplankton was totally censused with a M4 WILD stereoscopic microscope (x4 -

x40) and organisms were sorted into large groups of heterogeneous taxonomic level (from family to class). In particular, Copepods account for the whole population (including copepodite and nauplii stages).

STATISTICAL PROCEDURES

Because of taxonomic inaccuracies, diversity estimations (SHANNON-WEAVER, 1963) and evenness estimations (PIELOU, 1966 a,b) were carried out on a fraction of the planktonic community (only the cells wholly classified at the species level) comprising diatoms, armoured dinoflagellates, chlorophyceans, cryptophyceans, cyanophyceans, euglenophyceans and silicoflagellates.

Multivariate analyses were carried out over Q mode matrix (LEGENDRE & LEGENDRE, 1979). Principal Component Analyses (PCA) were made over the correlation matrix of transformed [x=log (x+1)] abundance numbers. Only the commonest species, which were present in a large percent of samples, were used in order to avoid the bias produced by double zeros.

The statistical significance of differences between the slope of curves generated when abundance numbers are plotted against distance from the entrance of the cave, were determined by a *F*-Snedecor test (SOKAL & ROHLF, 1969).

RESULTS

PHYTOPLANKTON

183 taxa were identified, mainly at the species level, among all samples. Some species (Table I) are new additions to the regional catalogue (PALAU, 1988).

Cell density in "outer" waters (station -10) was always between 519 and 2753 cell cm^{-3}, a rank which agrees well with data previously recorded in this area in an annual cycle (PALAU, 1988). Nanoplanktonic flagellates and monads usually accounted for the main fraction (Fig. 2A). Diatoms and large dinoflagellates were always lower in number; among the former, opportunistic taxa such as *Chaetoceros* spp., *Leptocylindrus danicus* and *Nitzschia delicatissima* were strikingly dominant during periods of large proliferation (VI-87, VI-88, X-88). Only at these moments were diatoms more abundant than dinoflagellates. The reverse was observed among the poorest samples (VII-88, I-89). These proliferations agree well both in time and structure, but densities were up to 2 times higher than those reported for the north Catalonian coastal area (MARGALEF, 1964; JACQUES, 1969; PALAU, 1988). Cryptophyceans were minor components which reached their highest values in summer and winter (Fig. 2A). Planktonic ciliates showed densities very close to the annual regional mean, and also similar temporal patterns (PALAU, 1988).

Along the cave a clear gradient of phytoplankton cell numbers arises. From outside to inside, the same pattern of decimation persists throughout all year, both when planktonic assemblages are considered as a whole (Fig. 3A) and as separate taxocoenoses of diatoms, dinoflagellates and ciliates (Fig. 4 A-C). In association with decay of nanoplanktonic cell density, species richness drops overwhelmingly toward the inner end of the cave (Fig. 5 A, B).

No "cave-dwelling" phytoplankton (with cave preference) was found. Occasionally, the diatoms *Nitzschia closterium* and *Scrippsiella trochoidea* were found in higher densities in the medium cave zone than in outer waters. A moderate (0.36 cell cm^{-3}) proliferation of *Heterodinium* cf. *milneri*, a typical representative of dark deep plankton (SOURNIA, 1982), was also detected at this area during October 1988. Moreover, the existence of fungi, which were usually provided with conidiophora (maximum number 1755 spores cm^{-3}) in

TABLE I. Phytoplankters censused in this study. Species marked with an asterisk were not previously recorded in the Medes Islands area.

BACILLARIOPHYCEAE

Achnanthes sp.
Amphora spp. *
Amphiprora alata Kütz. *
A. gigantea (O'Meara) Cleve.
Amphiprora sp. *
Anaulus spp. *
Asterionella bleakeleyi W. Sm. *
Asterionella glacialis Castracane; syn. *A. japonica* Cleve.
Bacteriastrum delicatulum Cleve.
B. hyalinum Lauder.
Campylodiscus sp. *
Cerataulina pelagica (Cleve) Hendey; syn. *C. bergonii* (Peragallo) Schütt.
Chaetoceros danicus Cleve. *
C. peruvianum Brightwell.
Chaetoceros spp.
Cocconeis placentula Ehrenberg. *
Corethron criophilum Castracane; syn. *C. hystrix* Hensen.
Cyclotella spp.
Cymbella sp.
Denticula seminae nov. nom.; syn. *D. marina* Semina.*
Diatoma vulgare Bory.
Diploneis cf. *interrupta* (Kütz) Cleve.
Diploneis spp. *
Ditylum brightwellii (West) Grunow.
Fragillaria sp.
Gramatophora sp.
Guinardia flaccida (Castracane) Peragallo.
Hemiaulus hauckii Grunow.
Hemidiscus cuneiformis Wallich.
Leptocylindrus danicus Cleve.
L. mediterraneus (Peragallo) Hasle; syn. *Dactyliosolen mediterraneus* Peragallo.
Licmophora spp.
Melosira granulata (Ehrenberg) Ralfs.
M. sulcata (Ehrenberg) Kützing; syn. *Paralia sulcata.*
M. varians Agardh.
Navicula distans (W. Smith) Ralfs.
Navicula spp.
Nitzschia closterium (Ehrenberg) W. Smith.
N. longissima (Brébisson in Kützing) Ralfs in Pritchard.
N. paradoxa (Gmelin) Grunow; syn. *Bacillaria paradoxa* Gmelin.
N. pseudodelicatissima Hasle.
N. cf. *seriata* Cleve.
Odontella mobiliensis (Bailey) Grunow; syn. *Biddulphia mobiliensis* Bailey
Pleurosigma spp.
Rhizosolenia alata f. *genuina* Brightwell.
R. alata f. *gracillina* (Cleve) Grunow.
R. calcaravis Schultze
R. fragilissima Bergon.
R. hebetata F. *semispina* (Hensen) Gran; syn. *R. semispina* Hensen.
R. imbricata v. *shrubsolei* (Cleve) Schröder; syn. *R. shrubsolei* Cleve.
R. robusta Norman; syn. *R. sigma* Schütt.
R. setigera Brightwell; syn. *R. hensenii* Schütt.
R. stolterfothii Peragallo.
Schöderella delicatula (H. Peragallo) Pavillard.*
Skeletonema costatum (Greville) Cleve.*
Striatella unipunctata (Lyngbye) Agardh.
Synedra undulata (Bailey) Gregory.
Synedra sp.
Tabellaria sp.*
Thalassionema nitzschioides (Grunow) Van Heurk; syn. *Thalassiothrix nitzschioides* (Grunow) Grunow in Van Heurk.
Thalassiosira eccentrica (Ehrenberg) Cleve; syn. *Coscinodiscus eccentricus* Ehrenberg.
Thalassiosira spp.
Thalassiothrix frauenfeldii (Grunow).
Triceratium sp.
Trigonium alternans (Bailey) Mann; syn. *Triceratium alternans* Bailey.
Tropidoneis sp.

DINOPHYCEAE

Amphidinium crassum Lohmann.
A. operculatum Claparède & Lachman.
Amphidinium sp.
Amphidoma caudata Halldal; syn. *Oxytoxum tonollii* Rampi, *O. margalefi* Rampi.
Blepharocysta splendor-maris (Ehrenberg) Stein.
Brachydinium sp.
Ceratium azoricum Cleve.
C. candelabrum (Ehrenberg) Stein.
C. declinatum (Karsten) Jörgensen.
C. furca (Ehrenberg) Claparède & Lachmann.
C. fusus (Ehrenberg) Dujardin.
C. *hirundinella* (O. F. Müller) Schrank.*
C. macroceros (Ehrenberg) Vanhöffen.
C. massiliense (Gourret) Jörgensen.
C. pentagonum Gourret.
C. trichoceros (Ehrenberg) Kofoid.
C. tripos (Müller) Nitzsch.
Ceratium sp.
Cladopyxis sp.
Cochlodinium spp.
Dinophysis caudata Saville-Kent.
D. operculata (Stein) Balech.*
D. parva Schiller.
D. rotundata Claparède & Lachmann; syn. *P. rotundatum* (Claparède & Lachmann) Kofoid & Michener.
D. scoederi Pavillard.
Diplopsalis lenticula Bergh.
Dossodium asymmetricum (Mangin) Loeblich; syn. *Diplopsalis asymmetrica* Drebes & Elbrachter.

TABLE I. Cont.

Erythropsis sp.*
Gonyaulax ligustica Rampi.*
G. polygramma Stein.
Gonyaulax spp.
Gymnodinium sp.
Gyrodinium fusiforme Kofoid & Swezy
G. spirale (Bergh) Kofoid & Swezy
Gyrodinium spp.
Heterocapsa triquetra (Ehrenberg) Stein.*
Heterodinium cf. *milneri* (Murray & Whitting) Kofoid.*
Kofoidinium velleloides Pavillard.
Mesoporus perforatus (Gran) Lillick.
Micracanthodinium sp.
Noctiluca scintillans (Macartney) Ehrenberg; syn. *N. miliaris* Suriray ex Lamarck.
Oxytoxum brunelli Rampi.
O. gracile Schiller.
O. longiceps Schiller.
O. mediterraneum Schiller.*
O. scolopax Stein.
O. variabilis Schiller.*
Oxytoxum sp.
Palaeophalocroma sp.*
Podolampas palmipes Stein.
Polykrikos schwartzii Bütschli.
Pronoctiluca spinifera (Lohmann) Schiller.
Pronoctiluca sp.
Prorocentrum balticum (Lohmann) Loeblich; syn. *Exuviaella baltica* Lohmann.
P. compressum (Bailey) Abe ex Dodge; syn. *E. compressa* (Bailey) Ostenfeld.
P. dactylus (Stein) Dodge.*
P. micans Ehrenberg.
P. minimum (Pavillard) Schiller.*
P. triestinum Schiller
P. vaginulum (Ehrenberg) Dodge; syn. *P. adriaticum* Schiller.*
Prorocentrum spp.
Protoceratium aerolatum Kofoid.
Protoperidinium bipes (Paulsen) Balech; syn. *Minuscula bipes* (Paulsen) Lebour.
P. breve (Paulsen) Balech.
P. brochi (Kofoid & Swezy) Balech.
P. cerasus (Paulsen) Balech.
P. conicum (Gran) Balech.
P. depressum (Bailey) Balech.
P. diabolum (Cleve) Balech.
P. elegans Cleve.
P. leonis (Pavillard) Balech.
P. mite (Pavillard) Balech.
P. ovatum Pouchet.
P. ovum Schiller.
P. pallidum (Ostenfeld) Balech.
P. pedunculatum Shütt.
P. pyriforme (Paulsen) Balech.
P. quarnerense Schröeder.
P. steinii (Jörgensen) Balech.
Protoperidinium spp.
Pseliodinium vaubanii Sournia.
Ptychodiscus noctiluca Stein; syn. *P. inflatus* Pavillard.
Pyrocystis lunula (Schütt) Schütt.
Pyrophacus horlogium Stein.
Scaphodinium mirabile Margalef; syn. *Leptospathium navicula* Cachon & Cachon-Enjumet.
Scrippsiella trochoidea (Stein) Loeblich III; syn. *Peridinium trochoideum* (Stein) Lemmermann.
Torodinium robustum Kofoid & Swezy.
T. teredo (Pouchet) Kofoid & Swezy.
Torodinium sp.
Triadinium polyedricum (Pouchet) Dodge; syn. *Goniodoma polyedricum* (Pouchet) Jörgensen.

CLOROPHYCEAE

Halosphaera viridis Schmitz.
Monorhaphidium spp.; syn. *Ankistrodesmus* spp.
Pediastrum boryanum (Turpin) Meneghini.
P. simplex Meyen; syn. *P. clatratum* (Schöeter) Lemmermann.
Scenedesmus spp.

CRYPTOPHYCEAE

Cryptomonas spp.

CYANOPHYCEAE

Lingbya sp.
Merismopedia spp.
Oscillatoria thiebautii (Gommont ex Gommont) Geitler.

DESMIDIACEAE

Staurastrum sp.*

EUGLENOPHYCEAE

Eutreptiella marina da Cunha.*
Euglena sp.

HAPTOPHYCEAE

Coccolithus huxleyi (Lohmann) Kamptner.
Phaeocystis poucheti Lagerh.
Solenicola setigera Pavillard.

SILICOFLAGELLATOPHYCEAE

Dyctyocha fibula Ehrenberg.
D. speculum Ehrenberg; syn. *Distephanus speculum* (Ehrenberg) Haeck.

the inner half of the cave was signalled. Slightly different is the case of a group of benthic diatoms such as *Amphora* spp., *Diploneis* spp., and *Navicula* spp. which were strikingly dense in the inner stations of the cave during June 1987, so making a shift from the pattern of decay above described (Fig. 4A). Synchronically (June 1987), these taxa were abundant over experimental panels from the inner end of the cave (GARCÍA & ZABALA, in prep.)

ZOOPLANKTON

If number of individuals is the descriptor of abundance chosen, zooplankton from outer waters was clearly dominated by copepods (densities from 527 to 1639 individuals m^{-3}), followed by the sum of the whole meroplankton and, occasionally (June 1988), by appendicularians. The remainder of the true holoplankton represented a minimal fraction of the whole (Fig. 2B). These proportions agree with the structure of zooplanktonic populations reported from coastal waters in this area (VIVES, 1986). No marked oscillations in copepod frequency during the year cycle were observed (Fig. 2B) except in spring (June 1988), when copepod frequency (75

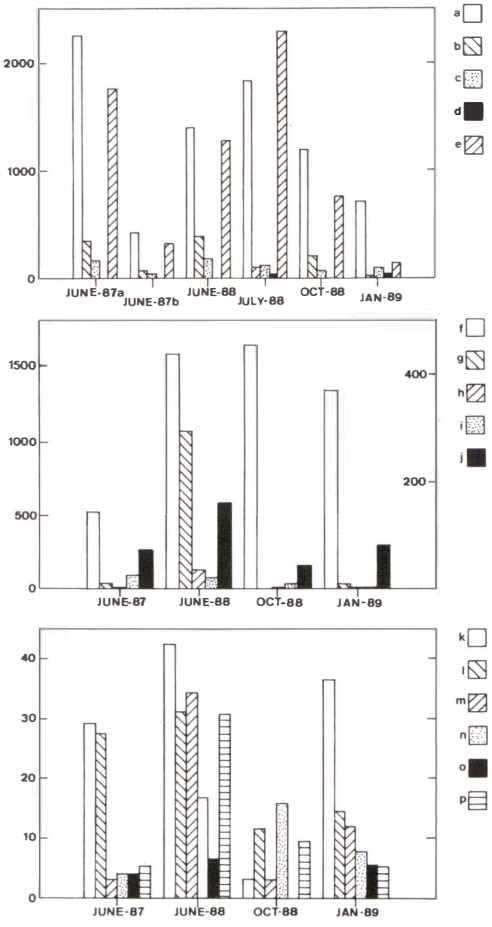

FIGURE 2. Density of planktonic groups in outer waters. A) Phytoplankton (cells cm^{-3}) and ciliates (cells dm^{-3}). B) Holoplankton (ind. m^{-3}) (scale at left, copepods; scale at right, other than copepods). C) meroplankton larvae (ind. m^{-3}). a) small flagellates; b) diatoms; c) dinoflagellates; d) cryptophyceans; e) ciliates; f) copepods; g) appendicularians; h) siphonophores; m) polychaetes; n) barnacles; o) echinoderms; p) others.

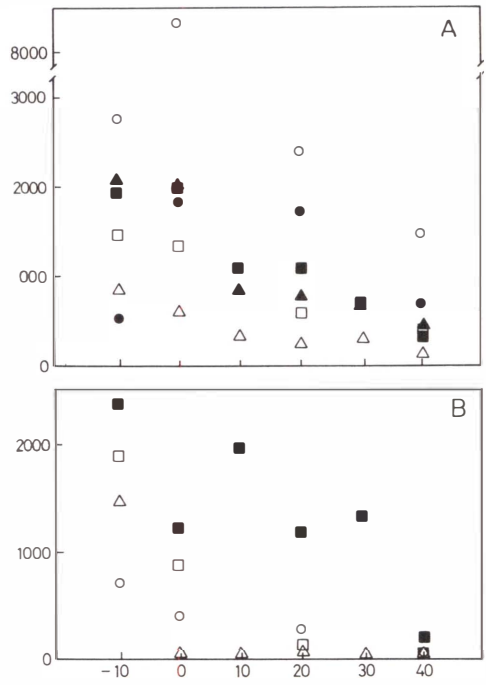

FIGURE 3. Densities of plankton along the cave for different seasons. A) Phytoplankton (cells cm^{-3}). B) Zooplankton (ind. m^{-3}) (open circles, June 87a; full circles, June 87b; full squares, June 88; full triangles, July 88; open squares, October 88; open triangles, January 89).

%) decreased to the benefit of appendicularians (14 %) and meroplankton (7.7 %).

11 high taxa were identified among the meroplanktonic fraction. Larvae of both bivalve and gastropod mollusks were the commonest organisms (Fig. 2C). Even if sampling was excessively reduced to assess the significance of seasonal differences, spring samples showed a peak in meroplanktonic density (162 ind. m^{-3}; 10 high taxa present). Bivalve and gastropod larvae, already provided with thin shells, and trocophora from polychaete worms were the dominant groups. Anthomedusae and barnacle larvae were also abundant but larvae of echinoderms were strikingly scarce; the rest of meroplankton was composed almost exclusively of cerianthid larvae. In contrast, the poorest samples were those from autumn (43 ind. m^{-3}; 9 taxa represented). In this season, all groups exhibit minimal densities with the only exception of barnacle larvae, which showed populations as dense as those from spring 1988; there are no echinoderm larvae. In

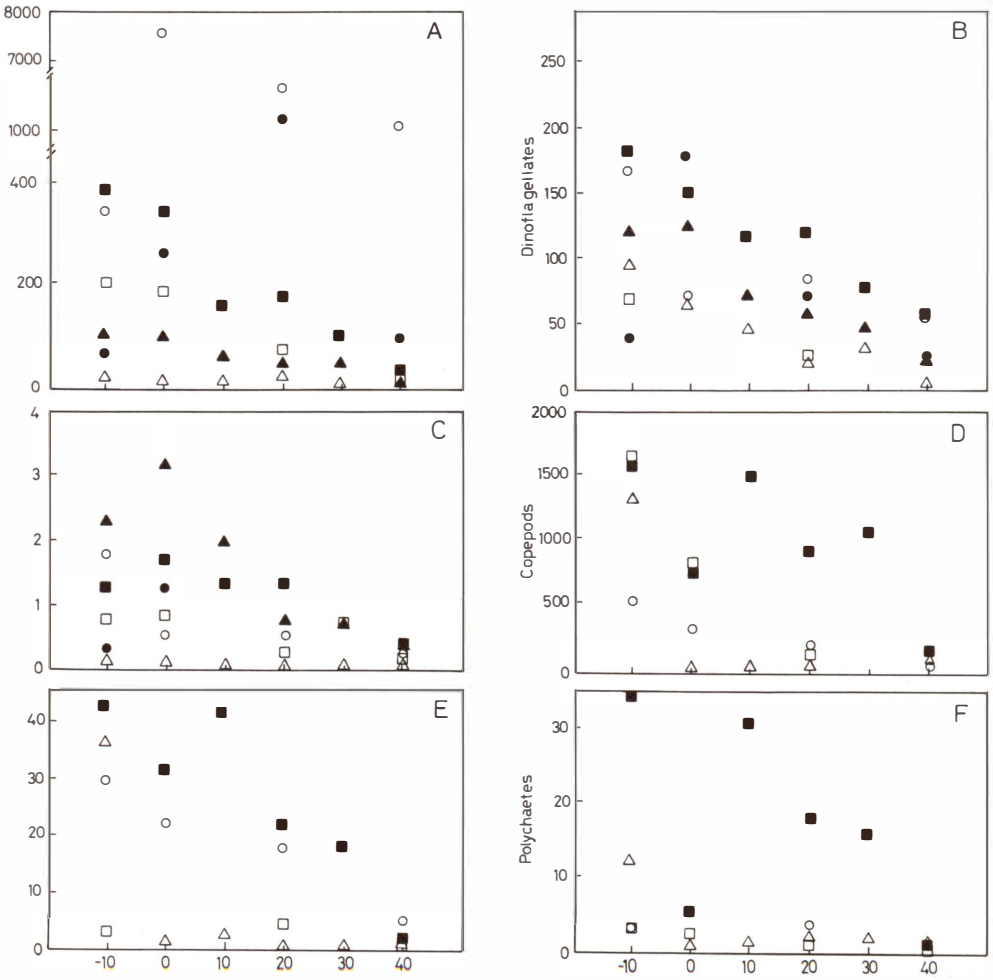

FIGURE 4. Densities of planktonic groups along the cave for different seasons. A) Diatoms (cells cm^{-3}). B) Dinoflagellates (cells cm^{-3}). C) Ciliates (cells cm^{-3}). D) copepods (ind. m^{-3}). E) Bivalves (ind. m^{-3}). F) Polychaetes (ind. m^{-3}). Symbols as in figure 3.

winter, meroplanktonic densities grew, partially due to the increase of polychaete worms, bivalve and echinoderm larvae. The latter reach densities similar to those from spring but gastropod larvae were as scarce as in autumn; barnacle larvae also showed their minimal annual density.

A strong gradient in zooplanktonic density was fairly clear along the cave throughout the year. Zooplanktonic density was higher in "outer" waters; it decreases progressively along the axis of the cave and reaches the minimal values at the inner end (Fig. 3B). Except in January 89, when there was a gentle increase in the medium part of the cave, richness (expressed as number of high taxa represented in each sample) also decays progressively from outer to inner waters (Fig. 5C). A similar pattern arises when each zooplanktonic group is represented separately (Fig. 4 D-F). Density of planktonic eggs of unidentified organisms showed the same general pattern of decay.

Larvae of clonal organisms such as sponges, bryozoans and ascidians were not found (inside or outside the cave) at any time during the annual cycle.

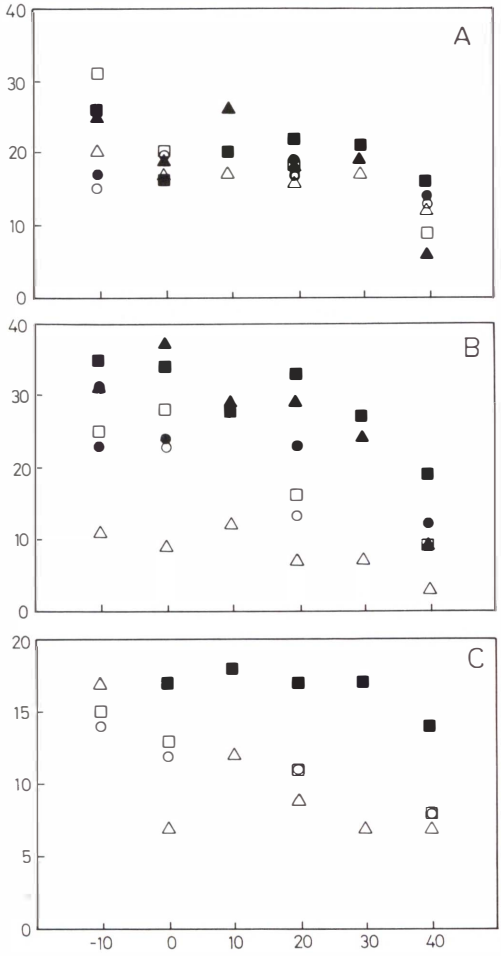

FIGURE 5. Taxonomic richness along the cave for different seasons. A) Diatoms (number of species per sample). B) Dinoflagellates (number of species per sample). C) Zooplankton (number of high taxa per sample). Symbols as in figure 3.

CAVE-TUNNEL COMPARISON

Samples from the tunnel also exhibit a pattern of decay in planktonic density, but the explanation of this pattern is unclear. When correlation between planktonic density *vs.* distance from the entrance is used as an estimator of the intensity of the planktonic gradient, samples coming from the cave always show good correlations between these two variables ($P<0.05$; Table II); in contrast, samples coming from the tunnel show far more erratic values. If diatoms, which are the only group to show a good correlation in both tunnel ($n=4$, $r=-0.96$, $P< 0.05$) and cave, are considered as reference, significant differences seem to arise between the slope of graphics representing the cave and the tunnel (Fig. 6; *F*-test, $P <0.01$). These results seem to suggest an agreement with the previous hypotheses about a higher water renewal in tunnels than in caves (HARMELIN, 1969), but contrasts with our previous results on dissolution of plaster balls (ZABALA *et al.*, 1989).

COMMUNITY STRUCTURE: FACTORS.

The structure of planktonic cave communities appears to be dependent on only a reduced number of factors as

TABLE II. Correlations between planktonic densities and the distances from the entrance of the cave and tunnel in June 1988. a) intercepts. b) Slopes (r, correlation coefficients; P, significance levels; N.S., non significative).

	Cave (n = 6)				Tunnel (n = 4)			
Planktonic taxa	a	b	r	P	a	b	r	P
Total phytoplankton	1713.40	-34.37	-0.960	0.01	1058.50	-29.83	0.898	N.S.
Diatoms	305.44	-7.12	-0.960	0.01	142.73	-3.41	-0.965	0.05
Dinoflagellates	152.65	-2.41	-0.980	0.001	95.24	-1.50	-0.888	N.S.
Ciliates	1.44	-0.02	-0.833	0.05	1.56	-0.02	-0.832	N.S.
Total zooplankton	1873.5	-32.48	-0.811	0.05	876.47	-9.52	-0.323	N.S.
Copepods	1290.16	-19.34	-0.690	N.S.	701.31	-7.24	-0.293	N.S.
Appendicularia	213.14	-5.51	-0.976	0.001	35.89	-0.47	-0.453	N.S.
Gastropods	28.94	-0.50	-0.855	0.05	7.74	0.04	0.136	N.S.

suggested by PCA applied to the group of the whole samples. PCA carried out on selected species of both phytoplanktonic (Table IIIa) and zooplanktonic fractions (Table IIIb) showed a very similar pattern. Phytoplankton analysis gives 3 eigenvalues higher than unity, these axes explaining 77.6 % of whole variance (47.6% for PC I; 18.5% for PC II; 11.5% for PC III). Zooplankton analysis gives only 2 eigenvalues higher than unity, both explaining 78.1% of whole variance (70.0% for PC I; 8.1% for PC II).

The highly significant correlation (n=20, r= 0.88, P< 0.001) between the component I of the two PCA also seems to suggest a similar interpretation for their significance (Fig. 7). Two facts facilitate this characterization:

1) With two highly significant exceptions (*Nitzschia closterium* and larvae of Spirorbidae, which are two "end cave" taxa), all species of both phyto- and zooplanktonic fractions load on positive values of the first component; then, a significant positive correlation between component I and planktonic density or biomass results.

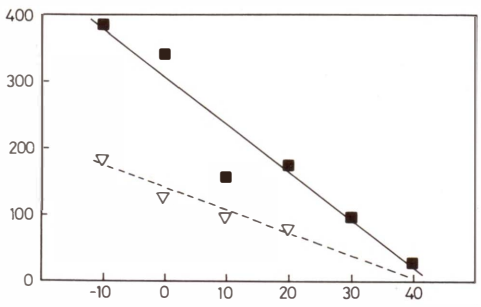

FIGURE 6. Comparison of densities of diatoms (cells cm^{-3}) from the cave (full squares) and the tunnel (inverted open triangles), in June 88, as a function of distance from the entrance. Differences between slopes are statistically significant (F-test; P< 0.01).

TABLE III. List of taxa used for Principal Component Analysis (PCA).

a) PHYTOPLANKTON

Chaetoceros spp.
Leptocylindrus danicus
Nitzschia closterium
Nitzschia pseudodelicatissima + N. seriata
Pleurosigma spp.
Rhizosolenia spp.
Thalassionema nitzschioides
Ceratium spp.
Diplopsalis lenticula + Dissodium asymmetricum
Gymnodinium spp.
Gyrodynium spp.
Prorocentrum spp.
Protoperidinium spp.
Scrippsiella trochoidea
Nanoplanktonic athecate dinoflagellates
Nanoplanktonic flagellates and monads
Planktonic cilliates

b) ZOOPLANKTON

Anthomedusae
Appendicularians
Bivalves
Cladocerans
Copepods
Echinoderms
Gastropods
Ostracods
Polychaetes
Siphonophorans
Spirorbidae
Unidentified eggs

2) There is a significant negative correlation between component I and the distance from the point where the sample was taken to the entrance of the cave. This is true for both phytoplankton (Fig. 8A; n=30, r=-0.57, P< 0.001) and zooplankton (Fig. 8B; n=20, r=-0.54, P< 0.001) analyses.

Thus we can confirm that the distance from the entrance of the cave is a prime factor in the structure of planktonic cave communities. This result reinforces the picture of a strong persistent planktonic gradient along the axis of the cave.

The second component of PCA on the phytoplanktonic fraction could be related to seasonality. This is fairly clear when factor scores of samples are plotted on the space defined by component I and component II (Fig. 9). Axis II separates samples from different seasons. Noticeably, the extreme high and low positions are occupied by samples from the outer station. Samples taken from the inner part of the cave tended to be closer together, pointing to the higher seasonal stability (or the lower seasonal variability) of planktonic communities in the cave. This trend is easily recognized when samples from each season are joined by straight segments following their relative position along the transect (Fig. 9). Irrespective of the position of the outer sample, they describe a convergent trajectory towards a restricted region of the space where all the inner samples overlap.

The higher seasonal heterogeneity of phytoplanktonic assemblages from the outer parts of the cave can be explained by the existence of largely dominant species which can exhibit strong seasonal fluctuations in density. With increasing distance from the entrance there is a reduction in the numbers of individuals of the commonest species, which is faster than the reduction of species numbers. This is suggested by comparing the evolution of both diversity and evenness indexes with increasing distance from the entrance (Fig. 10). Despite a net decrease in species richness, diversity (Fig. 10 A) rises because evenness (Fig. 10 B) rises quickly

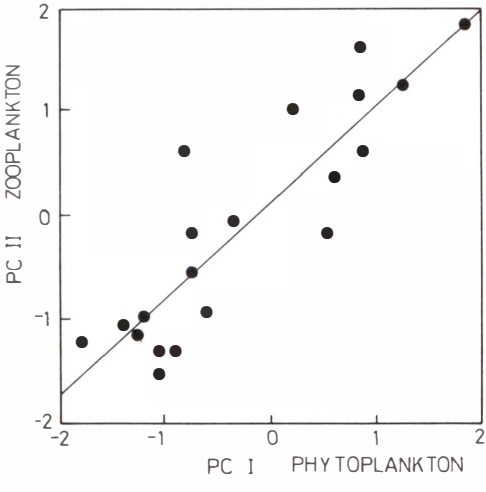

FIGURE 7. Relationship between the factor scores over the first component resulting from the PCAs carried out on the phytoplanktonic and the zooplanktonic samples (n=20; r=0.88; P< 0.01).

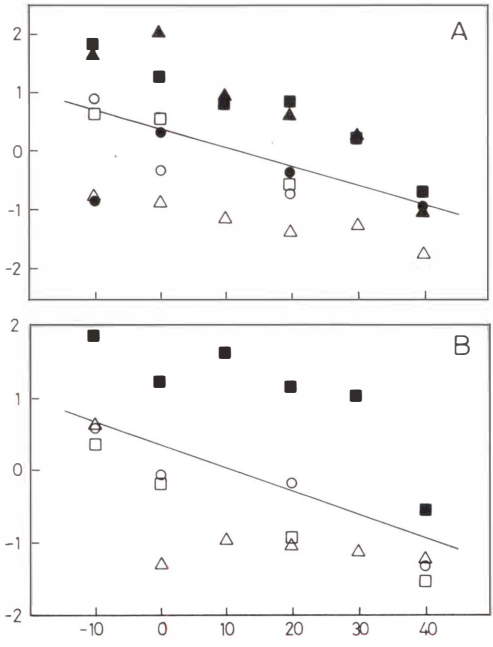

FIGURE 8. Relationship between the factor scores over the first components of PCAs and the distance from the entrance of the cave. A) Phytoplankton samples (n=20; r= -0.57; P< 0.001); B) Zooplankton samples (n=20; r=-0.54; P< 0.02). Symbols as in figure 3.

(only evenness shows a significant correlation with distance; n=30; r=0.40, P< 0.05).

DISCUSSION

STRONG PLANKTONIC GRADIENT

Although there is no clear taxonomic substitution within assemblages, both species number and density of planktonic communities show a strong gradient along the axis of the cave, the farther from the entrance the lower the values. This gradient is of special importance because it has rarely been reported (RIEDL, 1966).

The strength of this pattern relies on: i) its *magnitude*, ii) its *persistence* throughout an annual cycle, and iii) its *taxonomic catholicity*.

Magnitude. Decay values of the planktonic cells over a distance of only 50 m range between 60-100 % of the whole population. They range between 75-100 % for ciliates, copepodes, meroplanktonic larvae and diatoms (mean value 2 % ind. m^{-1}), or between 60-80 % for dinoflagellates and total phytoplanktonic cells. So high decay values are rarely reached on horizontal gradients from open waters. They have been reported from estuarine tidal fronts (MacALICE, 1970; INCZE & YENTSCH, 1981), or small-scale studies of neritic waters (WIEBE, 1970; FASHAM *et al.*, 1974; IBANEZ, 1976; ; PALAU, in prep.). Decay values are also several times higher than vertical gradients normally found in open waters as a result of productive, predatory, migratory and sedimentary processes (MARGALEF, 1969). Only gradients through summer thermoclines, estuarine pycnoclines (MacALICE, 1970) or deep chlorophyll maxima (ESTRADA, 1985; VENRICK, 1988) can equal such high values.

Persistence. Decay on planktonic communities along the axis of this cave is not a spureous event but a persistent

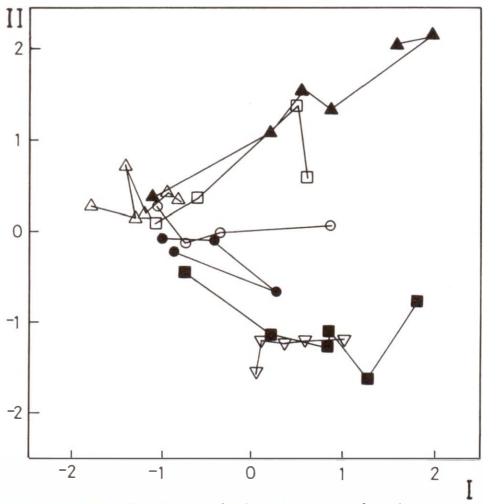

FIGURE 9. Position of the samples in the space defined by the first and second components resulting from the PCA carried out with the phytoplankton fraction. Trajectories join all contiguous samples from equal date with arrows pointing to inner samples. Symbols as in figures 3 and 6.

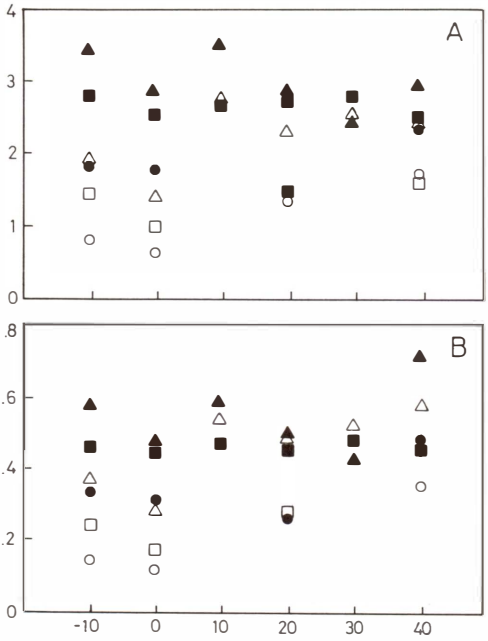

FIGURE 10. Relationship between the level of phytoplankton structure at different seasons and the distance from the entrance of the cave. A) H' diversity. B) Evenness. Symbols as in figure 3.

phenomenon which is reproduced accurately at each season and under very different environmental conditions. It also appears to be unrelated to absolute density of planktonic communities from surrounding outer waters which are representative of the neritic West Mediterranean planktonic communities. For example, results on the evolution of meroplanktonic organisms from outer samples during the annual cycle agree with those reported from neighbouring areas of Castellón (VIVES, 1966) and Banyuls-sur-Mer (THIRIOT- QUIÉVREUX, 1970).

The same pattern seems to be repeated in the tunnel, even if slightly smoother in its magnitude. As tunnels are assumed to be provided with higher water renewal (HARMELIN, 1969; HARMELIN *et al.*, 1985; but see ZABALA *et al.*, 1989) we are persuaded that this pattern will also be applicable to the submarine caves overall.

Taxonomic catholicity. Almost all taxonomic groups which have been identified show a similar pattern of decay. Only fungi, benthic diatoms and spirorbid larvae eventually display an inverted distribution, their density remaining stable or slightly increasing with increasing distance from the entrance. The taxonomic universality of this pattern strengthens our conviction that we are witness to a very general process which may equal the universality of the well documented pattern of decay in benthic assemblages from submarine caves (HARMELIN *et al.*, 1985).

THE "MOUTH BOUNDARY"

Station 0, just at the mouth of the cave, repeatedly breaks the general pattern of continuous decay in planktonic density by shifting to higher values than expected. This "anomaly" has been observed at different seasons, for the whole phytoplankton and also for the main taxa alone. The increase in phytoplanktonic density is coupled to a decrease in both diversity and evenness (Fig. 10). This suggests a proliferation of the commonest species more than the contribution of new taxa as the immediate cause of the increase in phytoplankton density. A similar "anomaly" emerges from an attentive examination of results on trophic-related parameters previously reported for the same cave (ZABALA *et al.*, 1989). This study reports an increase in chlorophyll concentrations, 665/665a ratios and oxygen concentration at this station; BOD_5 and ETS values also decrease, in agreement with expectations for a zone of phytoplanktonic proliferation. Nevertheless, the "anomaly" for the remaining parameters measured by these authors, e.g. POC, PON and bacterial activity ([^{3}H]-thymidine), consists in a conspicuous decrease at this station, which disagrees both with our data and with our expectations of it as a proliferative region.

But what are the causes of the persistence of this structure, if it is truly persistent? We suggest two untested clues which could overlap to produce a stronger effect. Dark caves seem to be zones where an active mineralization occurs, trapped organic matter being totally oxydized to inorganic dissolved compounds such as nitrate and phosphate nutrients, which are far more abundant inside than outside the cave (FICHEZ, 1989). When these nutrients, which cannot be used in photosynthesis because of the lack of light, reach the illuminated entrance to the cave, a minute process of enrichment should result. On the other hand, the entrance to the cave should be viewed as a kinetic boundary between two compartments provided with different degrees of freedom: an outer environment free in all three dimensions and an inner semi-restricted medium where advective processes should be limited by the proximity of walls. As a result, the existence of accumulative processes, which are characteristic of interphases, is not a remote possibility (MARGALEF, 1961; LEGENDRE, 1981).

A CAUSE FOR BENTHIC DECAY ?

The relevance of these results lies in the fact that the two gradients, the benthic and the planktonic, are probably not only parallel but also linked by a causal relationship. The planktonic impoverishment seems to be strong and persistent enough to account - by itself - for the decay of benthic macrofauna, which is dependent upon it, from the inner parts of the caves. There are two possible explanations :

1) **Low settlement.** Meroplanktonic larvae of the main benthic taxa were almost totally absent from samples of the inner parts of the cave even when larval density in outer waters was richer (in spring). The lack of larval stages of clonal organisms such as sponges, bryozoans and ascidians contrasts with the absolute dominance of these groups in benthic cave assemblages (GILI *et al.*, 1986). This paradox may be explained because these groups have mainly lecithotrophic larvae, which have a extremely short span of free life (JACKSON, 1986); but alternative explanations, such as those based on behavioural stresses (supposed), e.g. lack of light stimulus, cannot be rejected. This fact can easily explain the extremely low rates of benthic settlement on experimental panels reported by other authors (HARMELIN, 1980) and also detected by us (GARCÍA & ZABALA, in prep.). If not by itself, this low value of recruitment needs only the addition of a very weak factor of post-settlement or adult mortality to explain easily the entire paucity of benthic organisms in submarine caves.

2) **Trophic stress**. Planktonic paucity itself can be the cause of adult mortality of benthic organisms by enhancing trophic stresses. The relevance of meroplanktonic larvae - in addition to holoplanktonic biomass - in the food requirement of the dominant sessile benthic groups, which are mainly active filter-feeders, has recently been recognized (SEBENS & KOEHL, 1984).

Our present results strongly contrast with our previous results on the POM contents of water sampled in the same cave, which do not display a conspicuous gradient (GILI *et al.*, 1986; ZABALA *et al.*, 1989). The paradox has two possible explanations:

i) A high fraction of this POM could be tripton which has not been accounted for in this study. The decay of the planktonic fraction to the inner parts of the cave could be hidden by a reciprocal gradient of increasing triptonic fraction.

ii) Even if considerable amounts of POM reach the end of the cave, trophic quality is probably a constraint factor. At present, we believe that a large percentage of POM from the inner waters of the cave is due to the mineralization of faecal pellets egested by dense swarms of mysids inhabiting the cave (ZABALA *et al.*, in prep.) while planktonic POM seem to be genuinely lacking. Pellets should be inadequate as food for benthic filter-feeders settling over the walls and roofs of caves because of their high density, which also produces high sinking rates.

CAUSES OF PLANKTONIC DECAY

Thus the striking pattern of planktonic disappearance demands an explanation, but at present we are only able to forward and discuss several hypotheses. Two ways are possible :

1) Plankton enters the cave but it is unable to survive. Plankton death can arrive by: 1.1) predation; 1.2) sedimentation, or 1.3) physiological stress; or, alternatively,

2) The entrance of plankton to the cave is prevented, for example by behavioural constraints.

1.1. **Predation**. Predation by planktonic consumers is unlikely to be important because all planktonic groups, prey and predator, disappear at the same time. Predation by benthic suspension feeders from the entrance of the cave, where benthic biomass is very high, cannot be

completely rejected. Even if values of benthic biomass are known (GILI *et al.*, 1986), data on consumption rates from suspension-feeders of these communities - mainly sponges, scleractiniaria, hydroidea and bryozoa - are lacking. Nevertheless, such a strict planktonic depletion is unlikely to be at work all the time or, at least, it is unlikely to be effective during planktonic blooms.

1.2. **Physiological stresses**, such as those produced on photosynthetic pigments by large periods of darkness, have been reported to kill plankton quickly (SMETACEK, 1985). However, diatoms are physiologically adapted to maintain viability in dark waters as resting cells occurring as seeding populations at considerable depths in the ocean (SMAYDA & MITCHELL-INNES, 1974; PLATT *et al.*, 1983; SMETACEK, 1985). Resting, degradated or unpigmented photosynthetic cells should still be identifiable in samples if a cave-water turnover ranging over about 12-24 h is accepted (GILI *et al.*, 1986; ZABALA *et al.*, 1989). But this is not the case. Further, if light could explain the phytoplanktonic disappearance no environmental stress is known to operate inside this cave to kill zooplanktonic organisms.

1.3. **Sedimentation** is expected to be higher inside caves than in outer bottoms. But is it strong enough to provide a complete explanation for such a severe gradient? This is at present the unsolved question. Sedimentation rates inside submarine caves have recently been evaluated from a northwestern Mediterranean locality near Marseilles (FICHEZ, 1989). From this author's data, a function between sedimentation rates and the distance from the entrance of the cave can be described [sedimentated weight (g m^{-2} d^{-1}) = -50.60 distance (m) + 4096.16; r^2 = 0.90]. A similar function can be found which relates concentration of sestonic matter and the distance from the entrance of the cave [sestonic weight (mg m^{-3}) = -7.46 distance (m) + 1783.45; r^2 = 0.99). Note that the slope of the last function suggests a strong gradient very near to those describing the gradients of planktonic disappearance found in our study (Table II). As suggested by these numbers, sedimentation seems to be able to deplete seston from water at rates which are greater than or equal to those deduced from our results. Unfortunately we lack data about sedimentation rates in our cave.

Therefore, by exclusion of the other hypotheses, we think that sedimentation must be the effectively important factor in the process of decimation found on planktonic communities of submarine caves. Consequently, we suggest that further studies concentrate on the role of sedimentary input to the cave bottoms.

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