

# Transfers of bryozoan species between the Atlantic Ocean and the Mediterranean Sea via the Strait of Gibraltar

Mediterranean Sea  
Gibraltar area  
Biogeography  
Bathyal  
Bryozoa

Méditerranée  
Région de Gibraltar  
Biogéographie  
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## ABSTRACT

The deep-water benthos (115-2100 m) was sampled in the Atlantic-Mediterranean exchange area (*Balgim* cruise, N.O. *Cryos*: Iberian-Moroccan Gulf, Strait of Gibraltar, Alboran Sea). The species richness of the bryozoan fauna (146 spp.) showed a marked between-site variability. Peaks of species richness occurred on both sides and in the Strait of Gibraltar under various conditions of temperature and salinity. The common features of the corresponding sites were the abundance of suitable substrates and the presence of currents facilitating supply of food and propagules. In the Alboran Sea, the species richness decreased with depth more rapidly than in the Atlantic and the depth distribution of several deep-water species showed an upward shift. There is an eastward decrease in the stock of Atlantic species: 15 % of them are not found beyond the Strait sill and only 79 % of the remaining species extend to the whole Mediterranean. Several endemic Atlantic species or morphotypes can live in conditions of typical Mediterranean water (high temperature and salinity), but do not spread beyond the eastern limits of either the Gibraltar Strait or the Alboran Sea. These occurrences are hypothesized to be signatures of local increases of the trophic resources, which could mask the barrier effect of the Mediterranean oligotrophy. The organic sedimentation originating from the high-productivity area localized in the north-west of the Alboran Sea appears to create this distribution pattern.

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## RÉSUMÉ

Transferts d'espèces de bryozoaires entre l'Atlantique et la Méditerranée par le détroit de Gibraltar

Le benthos profond (115-2100 m) a été échantillonné dans la zone d'échanges Atlantique-Méditerranée (campagne *Balgim*, N.O. *Cryos* : golfe ibéro-marocain, détroit de Gibraltar, mer d'Alboran). Le nombre d'espèces de bryozoaires (146 spp.) montre une grande variabilité inter-sites. Des pics de richesse sont rencontrés de part et d'autre et dans le détroit. Les sites correspondants diffèrent hydrologiquement, mais sont tous caractérisés par une abondance en substrats colonisables et la présence de courants (= apports de nourriture et de propagules). La diminution du nombre d'espèces en profondeur est plus rapide en mer d'Alboran

qu'en Atlantique et la distribution verticale de certaines espèces est décalée vers le haut. Il y a un net appauvrissement vers l'est du stock des espèces atlantiques : 15 % des espèces ne franchissent pas le seuil du détroit et seulement 79 % des espèces restantes sont distribuées dans l'ensemble de la Méditerranée. Plusieurs espèces ou morphotypes endémiques de l'Atlantique peuvent vivre dans une eau typiquement méditerranéenne (température et salinité élevée) alors qu'elles ne dépassent pas les limites du détroit ou du bassin d'Alboran. Cette distribution pourrait être conditionnée par un accroissement local des ressources trophiques, qui masquerait l'effet barrière de l'oligotrophie méditerranéenne ; ce rôle est attribué à la sédimentation organique produite par la zone à très forte productivité du NW du bassin d'Alboran.

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## INTRODUCTION

The present-day major pathway between the Mediterranean Sea and the world's oceans is the region which includes the Gulf of Cadiz, Gibraltar Strait and Alboran Sea. This area of intense hydrological transfer significantly marks the physical and biological dynamics of the whole Mediterranean (Minas *et al.*, 1984; Lacombe, 1988). The Mediterranean is a concentration basin with a water deficit estimated at 0.8-1 m per year (Béthoux, 1984), compensated by an Atlantic flux penetrating at the surface through the Gibraltar Strait. A deep Mediterranean outflow is fed by Levantine intermediate water and by deep Mediterranean water formed in the north of the Western basin (Gascard and Richez, 1985; Minas *et al.*, 1991; Fig. 1). The depth of the interface between the two flows in the strait is marked by a strong vertical salinity gradient from 37.0 to 37.5 and varies between 40 and 200 m depth depending on location and tides (Gascard and Richez, 1985; Fig. 15-16, 46). The Mediterranean outflow is characterized by high temperature and salinity and is nutrient-poor. After crossing over the Strait, it flows into the Atlantic towards the west and north (Faugères *et al.*, 1985; Fig. 1) and progressively reaches its equilibrium density depth (1 200-1 300 m).

The Strait's physiography is marked by a sill at its Atlantic outlet at about 280 m. This topographic barrier prevents deep Atlantic water from entering the Mediterranean and thus determines a "warm" homother-

my at approximately 13°C below 200-300 m depth. This relatively high temperature and a salinity greater than 38.0 clearly distinguish the Mediterranean bathyal environment from that found in the Atlantic.

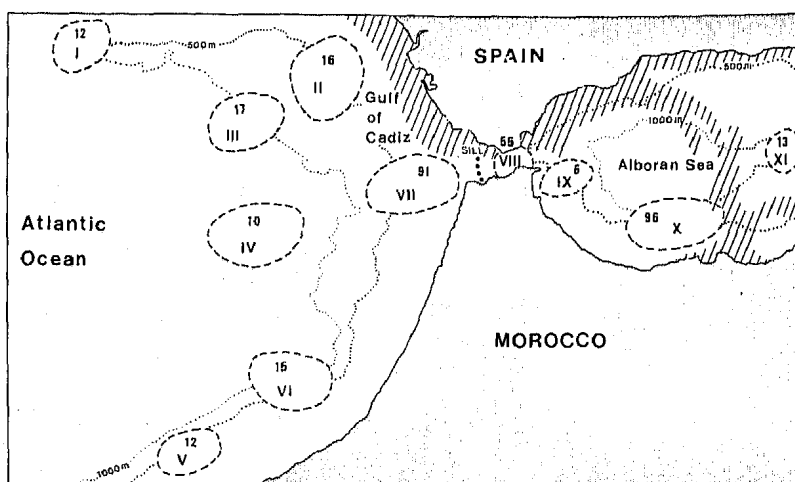
Within the strait and the north-western part of the Alboran Sea, the rapid flow of water masses in the opposite direction over a rough topography causes high ascendent transfers to occur. The nutrients upwelling into the photic layer are taken up in the double anticyclonic vortex which drive the Atlantic waters in the northwest Alboran basin (Fig. 1), resulting in an exceptionally high primary production compared to other parts of the Mediterranean (reviews in Minas *et al.*, 1991; Vergnaud-Grazzini and Pierre, 1991).

The present-day pattern of hydrological exchanges in the Gibraltar region does not appear to have undergone any significant changes during the past 18,000 years (Béthoux, 1984; Vergnaud-Grazzini *et al.*, 1989). However, the preceding geological and climatic events which marked the period from the closing of the Indian Ocean (20 MY) to the last glacial time (Würm) considerably affected these exchanges and led to a series of extinctions, renewals and alternations in "cold" and "warm" Mediterranean fauna (*see* Pérès, 1967; 1985 for the benthos). The permanency of a paleo-Mediterranean stock in the Mediterranean, contested by proponents of a total drying out of the basin during the Messinian period, only involved a small number of species, most likely of littoral distribution. Most groups in the current deep-water

Figure 1

Balgim sampling stations distributed in eleven groups (Roman numeral: group number; Arab numeral: number of collected bryozoan species). Hachured zone: high chlorophyll concentration in surficial waters (from Jacques and Tréguer, 1986, in Minas *et al.*, 1991).

Stations de récolte de la campagne Balgim réparties en onze groupes (chiffre romain : numéro du groupe; chiffre arabe : nombre d'espèces de bryozoaires récoltées). Zone hachurée : forte concentration de chlorophylle dans les eaux de surface (tiré de Jacques et Tréguer, 1986, dans Minas *et al.*, 1991).



Mediterranean benthos are characterized by a low number of species and individuals and a low proportion of endemic taxa, which indicate the relatively recent colonization of the bathyal zone (Fredj and Laubier, 1985).

The existence of viable deep stenobathic populations in the Mediterranean has been questioned by Bouchet and Taviani (1992). Fossil records (Barrier *et al.*, 1989; Rosso, 1990) demonstrate that a richer bathyal fauna, more similar to that found in the Atlantic, existed in the Mediterranean during the Plio-Pleistocene period, most probably due to different hydrological conditions.

During the *Balgim* oceanographic cruise (N.O. Cryos, 25 May-22 June 1984) the benthos was sampled on both sides of the strait (115-2 100 m). The programme's goals were centred on the following questions: 1) Is it possible to discern patterns in the benthos distribution in the Gibraltar region which could explain the present-day low species richness of the Mediterranean bathyal compared to the Atlantic? 2) Does this paucity of species involves a physical barrier (sill and counter current) or a physiological barrier (*i. e.*, effects of properties of Mediterranean deep water)? 3) Particularly, does the Mediterranean outflow modify the benthos along its path through the Gulf of Cadiz?

The present study is a synthesis of data on the distribution of bryozoans sampled during this programme.

## MATERIAL

Bryozoans (152 taxa: Harmelin and d'Hondt, 1992 *a* and *b*) were present in sixty eight sampling stations distributed on both sides of Gibraltar Strait and divided into eleven geographical groups (Tab. 1, Fig. 1). The Atlanto-Mediterranean region was subdivided in four zones (NE Atlantic Ocean, Strait of Gibraltar, Alboran Sea, other parts of the Mediterranean) in order to distinguish distributional trends in 146 collected species (data from the present study and literature).

## RESULTS

### Variability of species richness

The spatial distribution of species richness has a high heterogeneity, even for sampling stations located in the same geographic and bathymetric zone. This phenomenon affected all sampled depths. Thus, among the forty sampling stations located between 115 and 580 m depth, eleven stations contained only one species, while ten other stations were particularly rich, each having 15 to 55 species. The latter were located in the Gulf of Cadiz, Gibraltar Strait and Alboran Sea, either in typically Atlantic water (DR42, DW43: group VII), or in Mediterranean flow into the Atlantic (DR40, DR49, DW50: group VII) or in typically Mediterranean water (DR130, DW132, DR133, DW134: group X, DR153:

Table 1

Characters of the station groups: number, mean depth and depth range of sampled stations, mean per station and global number of species collected in each group.

Caractères des groupes de stations : nombre, profondeur moyenne et profondeurs extrêmes des stations échantillonnées, nombres moyen et global d'espèces collectées dans chaque groupe.

Group	N stations	Depth (m) mean (range)	N species mean (global)
IBERO-MOROCCAN GULF			
I	7	1246 (681-1523)	3.0 (12)
II	9	586 (370-990)	2.1 (16)
III	6	1336 (903-1917)	2.3 (17)
IV	5	1509 (1222-2035)	3.0 (10)
V	6	212 (147-355)	3.5 (12)
VI	8	1141 (500-1691)	2.4 (15)
VII	13	345 (135-826)	12.8 (91)
STRAIT OF GIBRALTAR			
VIII	3	415 (115-580)	21.3 (55)
ALBORAN SEA			
IX	2	321 (290-352)	3.0 (6)
X	7	270 (145-480)	24.1 (96)
XI	2	363 (170-555)	6.5 (13)

group VIII). These stations shared the characteristic of being rich in substrates for bryozoans: coarse-grained sands containing large-sized shells (sometimes making up a thanatocenosis), large corals (*Madrepora*, *Lophelia*, *etc.*) or rocks.

The number of species recorded in the eleven groups of stations also varied considerably (Tab. 1). Three groups show high overall richness (55 to 96 species). These species concentrations were found in the Gulf of Cadiz, west of the mouth of Gibraltar Strait (group VII), in Gibraltar Strait (group VIII) and in the south of the Alboran Sea (group X). The other groups of stations had far fewer species (6 to 17 species).

This initial approach thus revealed a large heterogeneity in the geographic distribution of species richness in the Gibraltar region, with richness peaks located both in the Atlantic and the Mediterranean.

A drastic drop in species richness was observed in all samples below the continental shelf (Tab. 2). This diversity decrease was most marked below 600 m in the Atlantic and was also apparent in the Alboran Sea: none of the seven samples at a depth greater than 600 m yielded any bryozoan. In addition, the values for species richness in the Alboran Sea between 290 and 555 m were very similar to those in the Iberian-Moroccan Gulf between 680 and 2 035 m, both in terms of average number and maximum number of species per sample.

This upward shift of species richness also appears to affect the vertical distribution of some species. This is particularly apparent for *Euginoma reticulata* and *Kinetoskias smitti* (Tab. 3), which were found in the Alboran Sea at a much lower depth than in the Atlantic.

Table 2

Depth distribution of species richness. St.N: number of sampling stations; Sp.n: mean species number per sample; Sp.N: maximum species number per sample.

Distribution verticale de la richesse spécifique. St.N : nombre de stations de récolte; Sp.n : nombre moyen d'espèces par prélèvement. Sp.N : nombre maximal d'espèces par prélèvement.

	St. N	Sp. n	Sp. N
Lower continental shelf (whole studied area, 115-205 m)	14	23	55
Continental slope (whole studied area, 252-2 035 m)	54	4,0	22
Upper continental slope (Atlantic, 252-556 m)	18	5,5	22
Upper continental slope (Mediterranean, 290-555 m)	6	2,8	7
Lower continental slope (Atlantic, 681-2 035 m)	28	3,2	7
Lower continental slope (Mediterranean, 720-1 405 m)	7	0	0

Table 3

Atlantic versus Mediterranean depth distribution (m) of some species (data from literature or from personal sources). \*: maximum depth observed in the Alboran Sea.

Distribution verticale (en m) de quelques espèces en Atlantique et en Méditerranée (données de la littérature ou personnelles non publiées). \*: profondeur maximale observée en mer d'Alboran.

	Atlantic	Mediterranean
<i>Euginoma reticulata</i>	1 427-5 000	352*
<i>Kinestokias smitti</i>	2 195-5 223	480*
<i>Puellina scripta</i>	360-990	205*
<i>Crisia calyptostoma</i>	170-850	170*
<i>Crisia pyrula</i>	135-511	3-80
<i>Crisia tenella</i>	150-900	70-480*
<i>Plagioecia inoedificata</i>	310-1 070	10-300
<i>Eurystrotes compacta</i>	10-500	5-130

## Dispersal of Atlantic species towards the east

### The different stages

Of the 146 species considered, 136 are known from the NE Atlantic and 102 from the Mediterranean (Fig. 2). The Atlantic stock thus decreases towards the east in successive stages: nearly 85 % of the species cross over the Gibraltar Strait sill, and 79 % reach the Alboran Sea. Another decrease occurs in other parts of the Mediterranean where only 68 % of the initial Atlantic stock (92 species) occurs.

The 44 Atlantic species which are not distributed throughout the Mediterranean can be classified into three sets (Fig. 2). The first set (A: 20 species) includes species not present east of the sill. Most of these species are bathyal. For half of them (A\*: 9 species), sampling corresponded in whole or part to sites affected by the Mediterranean outflow.

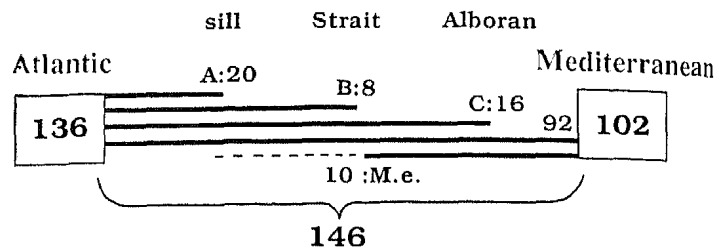


Figure 2

Geographic distribution of 146 species collected in the Gibraltar area (136 distributed in the Atlantic, 102 in the Mediterranean). A: 20 species absent east of the sill. B: 8 species absent east of the Strait. C: 16 species absent beyond Alboran Sea's limits. M.e.: 10 Mediterranean endemics. \*: presence in Mediterranean water (A-B: MOW, C: LIW).

Distribution géographique de 146 espèces récoltées dans la région de Gibraltar (136 distribuées en Atlantique, 102 distribuées en Méditerranée). A : 20 espèces absentes à l'est du seuil. B : 8 espèces absentes à l'est du détroit. C : 16 espèces absentes au delà des limites de la mer d'Alboran. M.e.: endémiques méditerranéennes. \*: présence dans de l'eau méditerranéenne (A-B: MOW, C: LIW).

A: *Ascorhiza mawatari*, *Arachnoidea thalassae*, *Aethozoon pellucidum*, *Clavodesia biradiculata*, *Bugulella elegans*, *Nordgaardia cornucopioidea*, *Cleidochasma strangulatum*, *Jaculina tessellata*, *Sertella atlantica*, *Adeonellopsis multiporosa*, *Fedora edwardsi*, *Pseudoalcyonidium bobinae*\*, *Hincksina longispinosa*\*, *Euginoma vermiformis*\*, *Puellina bifida*\*, *Phylactella labrosa*\*, *Schizomavella linearis profunda*\*, *Sertulipora guttata*\*, *Gemellipora eburnea*\*, *Ascosia pandora*.

B: *Calyptotheca obscura*, *Reptadeonella insidiosa*, *Bicrisia gibraltarensis*, *Crepis longipes*\*, *Cribrilina alcornis*\*, *Teuchopora edwardsi*\*, *Escharella longicollis*\*, *Idmidronea flexuosa*\*, *Crisia calyptostoma*, *Metalcyonidium gautieri*\*, *Copidozoum macilentia*\*, *Setosellina roulei*\*, *Kinetoskias smitti*\*, *Euginoma reticulata*\*, *Puellina scripta*\*, *P. orientalis lusitanica*\*, *Escharina johnstoni*\*, *Schizotheca tuberigera*\*, *Reteporella sparteli*\*, *Entalophoroecia elegans*\*, *Crisia aculeata*\*.



Figure 3

Endemic species from the upperbathyal NE Atlantic living in Gibraltar Strait in MOW water: "*Cribrilina*" *alcicornis* (x 80). Balgim DR152 (group VIII, 550 m).

Espèce endémique du bathyal supérieur de l'Atlantique NE vivant dans le flux méditerranéen sortant du détroit: "*Cribrilina*" *alcicornis* (x 80). Balgim DR152 (groupe VIII), 550 m.

The second set (B) includes 8 species not found in the Mediterranean, but present in the strait (group VIII). Three of them were found at station DR 151 (115 m), which is washed by the Atlantic current entering the Mediterranean: these are circalittoral species whose overall distribution is still poorly understood. The five other species in the set (B\*) were abundant in the two deep-water stations (DR152, DR153: 550-580 m), which are drained by the outflowing Mediterranean current. They are typical of hard substrates of the bathyal zone, living in these stations on deep-sea coral skeletons and tests of the large barnacle *Trachilisma gigas*.

The third set (C) includes 16 species which reach the Alboran Sea but are not spread throughout other parts of the Mediterranean. According to the stratification of water masses at these localities (Guibout, 1987), the shallowest sampling stations of groups X-XI (145-170 m) are washed by water whose salinity is approximately 37.5 and are thus located near the interface between modified Atlantic water and Levantine intermediate water (LIW,  $S > 38.0$ ). The other sites (195-480 m), inhabited by most of this set's species (C\*: 11 species), are washed by the LIW. For ten of these species, only one or a very small number of specimens were sampled at a single site. However, some of these species were also known in the Atlantic through a very small number of samples.

#### Biogeographical models

The set of Atlantic bathyal species occurring in deep-water sites of the Gibraltar Strait washed by the Mediterranean outflow (B\*) is well-characterized by *Cribilina alcicornis* Jullien. This cribrimorph ranges geographically from the western approaches of the English Channel to Gibraltar Strait and is a typical component of the upper bathyal community (16 of the 19 available records are from 450-760 m depth), often encrusting skeletons of deep-sea corals. In the strait, *C. alcicornis* occupies the same habitat, except for the hydrological parameters, which are typically Mediterranean. Presence of ovicells (Fig. 3) indicates that this relatively large population can be self-maintained without exogenous recruitment.

Three species from set C (Atlantic species colonizing the Alboran Sea) are well-represented in the *Balgim* material (3 to 5 stations): *Puellina orientalis lusitanica*, *Schizotheca tuberigera* and *Escharina johnstoni*. They are all distributed above 200 m, but represent three distinct biogeographic models.

The geographic domain of *P. orientalis lusitanica* Harmelin (Fig. 4) as currently known includes southern Portugal, Gulf of Cadiz and the Gibraltar area, while the nominative subspecies is known only in the southern Mediterranean, east of the Sicilian strait. A third subspecies, *P.o. azorensis* appears to be distributed only in the Azores (Harmelin, 1988 a). This subspecies radiation might originate in a putative paleo-Mediterranean ancestor related to the Mediterranean endemic *Puellina pedunculata*.

Although rarely recorded, *Schizotheca tuberigera* (Jullien) has a relatively broad distribution in the Atlantic (Harmelin

and d'Hondt, 1992 a), from southern Spain to the Gulf of Guinea. However, its Mediterranean distribution does not appear to extend beyond the Alboran Sea. This Ascophorina is probably a representative of the southern Atlantic fauna ("Senegalian") whose expansion toward the north and into the Mediterranean occurred during climatic fluctuations in the Pliocene and the Quaternary periods (Mars, 1963).

*Escharina johnstoni* (Quelch) is widely found in the Alboran Sea up to its upper northern limit (Boronat Tormo, 1987; Saguar and Boronat, 1987; Lopez de la Cuadra and Garcia-Gomez, 1988). This easily identified species represents a pool of northern colonizers. It was previously known only in the NE Atlantic, from north of the British Isles to the Canary Islands (Aristegui and Cruz, 1986). As evidenced by many inventories, it is absent from the rest of the Mediterranean.

The vast distribution of *P. scripta* in the present-day upper bathyal of warm-temperate and tropical seas (Gulf of Cadiz, Caribbean Sea, Indian Ocean, Pacific Ocean) is considered to be a relict from a Tethyan distribution (Harmelin and Aristegui, 1988). The sampling of *Puellina scripta* (Reuss) in the Alboran Sea (DW134, 205 m: group X) represents the only record of this deep-water cribrimorph in the Mediterranean. *Puellina scripta* was known in middle Miocene deposits of the Paratethys basin of Vienna (Bishop and Househam, 1987). It also lived in the upper Mediterranean bathyal zone during the pre-Messinian period (Tortonian of Carboneras, Spain SE, Barrier *et al.*, 1992). In five out of the eight *Balgim* stations (groups II, VII, VIII, X) containing this species, the colonies encrusted skeletons of deep-sea corals (*Madrepora oculata*, *Lophelia pertusa*, *Caryophyllia cyathus*). Tortonian specimens from

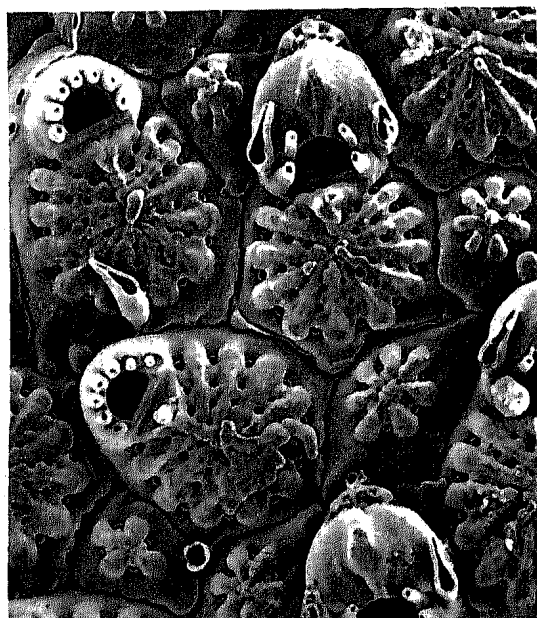


Figure 4

An Atlantic species established in the Alboran Sea: *Puellina orientalis lusitanica* (x 80). *Balgim* DW134 (group X), 205 m.

Une espèce atlantique établie en mer d'Alboran : *Puellina orientalis lusitanica* (x 80). *Balgim* DW134 (groupe X), 205 m.

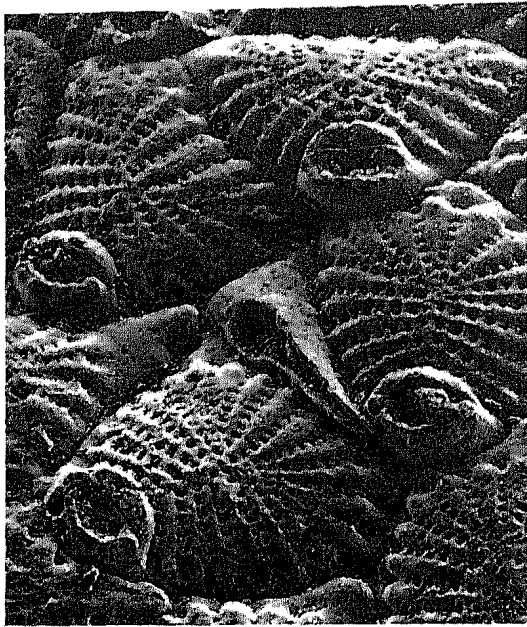


Figure 5

A paleo-Mediterranean species: *Puellina scripta* (x 64). This fossil specimen is from the pre-Messinian upper-bathyal Mediterranean (Tortonian of Carboneras, SE Spain; encrusts *Labyrinthocyathus* sp.).

Une espèce paléoméditerranéenne : *Puellina scripta* (x 64). Spécimen fossile du bathyal supérieur de la Méditerranée pré-messinienne (Tortonien de Carboneras, Espagne SE, sur *Labyrinthocyathus* sp.).

Carboneras (Fig. 5) also incrust calices of another bathyal scleractinian, *Labyrinthocyathus* sp.

Two cheilostomes, *Puellina venusta* Canu and Bassler and *Crassimarginatella crassimarginata* (Hincks), which are well-distributed throughout the Mediterranean, are present in the Alboran Sea with Atlantic phenotypes. The Mediterranean population of *Puellina venusta* differs from the Atlantic population (Harmelin, 1978) by a very pronounced crenulation of the proximal edge of the orifice (= *Cribrilaria crenulata* Harmelin, 1970; Fig. 6 C). The uncrenulated Atlantic morphotype (Fig. 6 A) was found in the Gulf of Cadiz, as well as in the south of the Alboran Sea. In addition, an intermediate morphotype (orifice slightly crenulated, with high within-colony variability, Fig. 6 B) was found on the Andalusian coast at the eastern outlet of Gibraltar Strait (Lopez de la Cuadra and Garcia Gomez, 1988).

The Mediterranean population of *Crassimarginatella crassimarginata* differs from the Atlantic population in the form of its avicularium (Harmelin, 1973): in the Mediterranean morphotype (Fig. 8) the mandible bears a distal denticle whereas in the Atlantic morphotype it is rounded. In the *Balgim* material, the two colonies collected on either side of the Gibraltar Strait had Atlantic-type avicularia (Fig. 7), although the sampling site in the Alboran Sea (DW132, 170 m: group X) had rather typical Mediterranean hydrologic characteristics.

#### Dispersal of Mediterranean species towards the west

The Mediterranean outflow is most likely to be responsible for the transfer of propagules from the upper-bathyal zone

of the Alboran Sea towards the Gulf of Cadiz. However, the reality of this phenomenon can only be tested through the occurrence of endemic Mediterranean species. The number of these species is nevertheless very small: only ten Mediterranean endemics were found in the *Balgim* material.

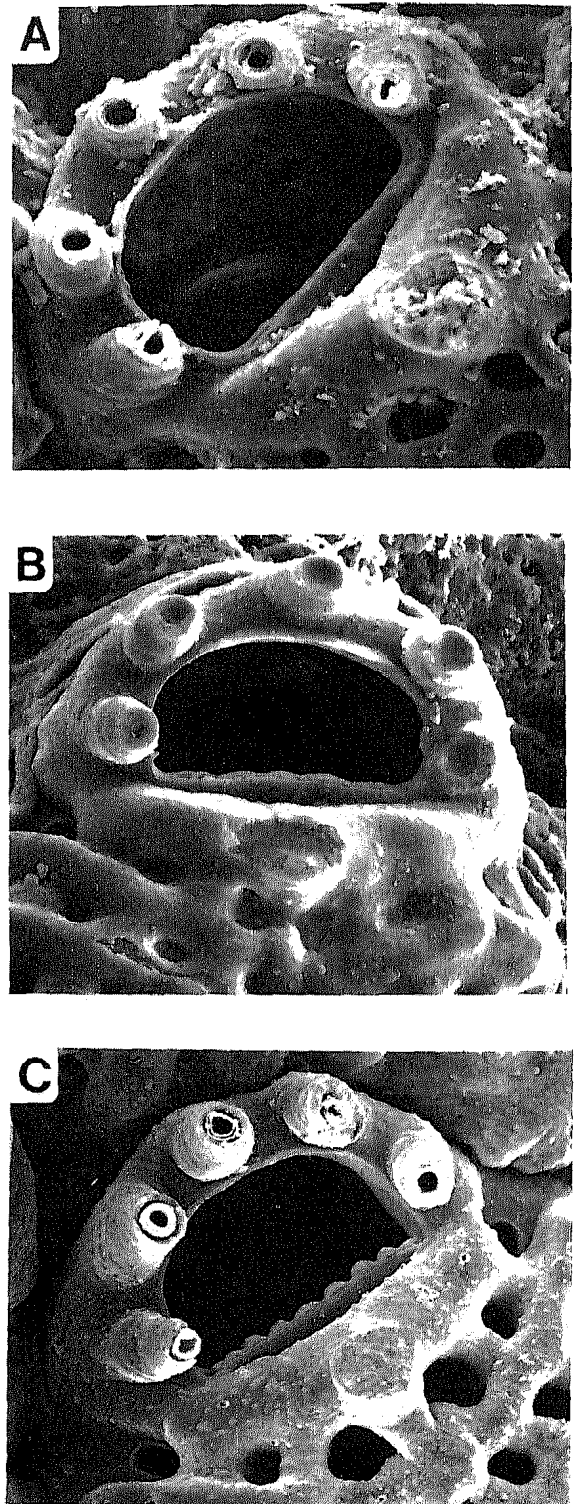


Figure 6

Orifice of *Puellina venusta* (x 290). A: Atlantic form, Balgim DR130 (group X), Alboran Sea, 145 m. B: intermediate form, La Atunara (6-10 km north of Gibraltar), 145 m. C: Mediterranean form, Provence, 150 m.

Orifice de *Puellina venusta* (x 290). A : forme atlantique, Balgim DR130 (groupe X), mer d'Alboran, 145 m. B : forme intermédiaire, La Atunara (6-10 km nord de Gibraltar), 40-60 m. C : forme méditerranéenne; Provence, 150 m.





Figures 7-8

*Avicularium of Crassimarginatella crassimarginata* (x 100). 7: *Atlantic form*, Balgim DR49 (group VII), 521 m. 8: *Mediterranean form*, Provence, cave, 6 m.

*Aviculaire de Crassimarginatella crassimarginata* (x 100). 7 : forme atlantique, Balgim DR49 (groupe VII), 521 m. 8 : forme méditerranéenne; Provence, grotte, 6 m.



Figure 9

A Mediterranean endemic species which can cross over the Strait of Gibraltar: *Puellina pedunculata* (x 120). Balgim DR42 (group VII), Gulf of Cadiz, 135 m.

Une espèce endémique de Méditerranée pouvant franchir le détroit de Gibraltar : *Puellina pedunculata* (x 120). Balgim DR42 (groupe VII), golfe de Cadiz, 135 m.

Two eurybathic cribrimorphs (depth range: 3 to 700 m) endemic to the Mediterranean, collected near the western outlet of Gibraltar Strait, demonstrate effectively that transfer of Mediterranean elements towards the Atlantic can occur. *Puellina radiata* (Moll) was found only in the Alboran Sea

and on the eastern slope of the Gibraltar Strait during the Balgim programme. However, one specimen was collected west of the sill (Spartel Bank) during another cruise (*Calypso*, SME 1282, 110 m, 30 August 1958; Harmelin, unpublished data). Three colonies of *Puellina pedunculata* Gautier were collected in the Gulf of Cadiz (Fig. 9) near the outlet of Gibraltar Strait (DR42, 135 m; DW43, 150 m: group VII) above the Mediterranean water layer. These are the first verified records of these two species outside the Mediterranean.

## DISCUSSION

High between-site variability in species richness is a common phenomenon in deep-sea environments (Rex, 1983), already noticed for bryozoans (Cook, 1981; Gordon, 1987). The localization of species-rich sites shows no clear relationship with the hydrological characteristics in the Iberian-Moroccan Gulf. The essential factor would appear to be the presence of coarse-grain sands and small substrates, which is in turn determined by the action of currents, that also supplies nutrients and propagules. Monniot and Monniot (1988) also suggested the important role of currents in the species richness of certain stations for ascidians from the same programme.

The  $\theta$ -S properties of the Mediterranean outflow are sufficiently distinctive to be identified all along its course in the Atlantic Ocean. However, they do not induce any notable decrease in bryozoan species richness in the Gulf of Cadiz. The rapid east to west decrease of salinity (Ambar and Howe, 1979) may be partly responsible for this lack of biological response.

The decline in species richness noted in the bathyal zone corresponds to a general phenomenon for bryozoans (Ryland, 1970; Hayward and Ryland, 1978; Harmelin, 1988 *b*). The highly marked accentuation of this trend in the Mediterranean may be due to environmental deficiencies as well as to lack of recruitment of propagules. The homothermy at 13°C below 200 m in the Mediterranean can be an insurmountable obstacle for cold stenothermal bathyal species. Similarly, it is likely that the high salinity of the Mediterranean deep water ( $S > 38.4$ ) will be another exclusion factor for many Atlantic species.

The upward shift of the depth distribution for some bryozoans observed in the Mediterranean has also been noted for brachiopods and mollusks (Barrier *et al.*, 1989), Turridae gastropods (Bouchet and Taviani, 1992) and for planktonic organisms (Casanova, 1977). This phenomenon could be the result of a high oligotrophy coupled with high temperature, as observed in the deep Mediterranean environment. According to van der Spoel and Schalk (1988), the distribution of deep-water species at an abnormally shallow depth in basins where the temperature of the deep layers is high could be explained by an increase in metabolic activity, which would lead to increased food requirements. If trophic resources are too limited at greater depths, the regional persistence of a species is only possible when it transfers its habitat to more nutrient rich layers. This hypothesis suggested for planktonic forms, could also apply to certain benthic organisms.

The trophic factor could be responsible for the exclusion of bathyal Atlantic species from the Mediterranean and also explain why some of these species can survive in the Alboran Sea. If the hypothesis of a relationship between primary productivity of upper layers and richness of the deep benthos is accepted (Gage and Tyler, 1991), the strong oligotrophy in the Mediterranean could be a limiting factor for deep-water benthic species whose trophic requirements are too high. In the Alboran Sea, the organic rain from the exceptionally productive chlorophyll "field" located in its western portion (Minas *et al.*, 1984; Fig. 1) generates conditions contrasting markedly with the other parts of the Mediterranean. A part of this descending flux of organic matter undergoes bacterial degradation in the water column, and this results in a very marked oxygen minimum (Packard *et al.*, 1988; Minas *et al.*, 1991). It is probable that an undegraded portion of this sedimentation reaches the bottom when depth is not too great and increases the benthos food resources. Such trophic supply could favour survival of Atlantic species which have crossed through the physical barrier of the Gibraltar Strait. This organic sedimentation is shifted from the superficial production zone towards the east and southeast (Minas *et al.*, 1984) and thus provides nutrients for the sampling stations (group X) with high species number. These sites shelter several typically Atlantic species, despite Mediterranean hydrological conditions.

In addition, the strong dynamics of deep Mediterranean water at the bottom of the Gibraltar Strait probably compensates for the low density of nutrient elements, and could thus partially explain some distributions (set B\*, *see below*).

A lack of larval recruitment is obviously a major factor in the absence from the Mediterranean of many deep-water species whose dispersal is not maintained by planktotrophic

larvae. A direct transfer of bryozoan larvae from the bathyal Atlantic into the Alboran Sea implies: 1) the capacity of larvae to reach upper layers ( $< 200$  m) to be carried by the Atlantic flux entering the Mediterranean; 2) larval tolerance to a period at a relatively shallow depth; 3) a duration of larval life compatible with the time of vertical and horizontal transfer; 4) resistance to stress by penetration into deep Mediterranean water with high temperature and salinity.

This type of direct transfer has few chances of occurring. In fact, no species with planktotrophic larvae, whose survival time is equal to or greater than 12 hours before metamorphosis, was found in the studied stock. A step-by-step transfer, which would involve several generations and entail not only larval dispersal, but also colony movement, is more compatible with the short lifespan of these larvae (McKinney and Jackson, 1989). Colony transportation on its substrate, when this is sufficiently light and mobile ("rafting"), or after zoarial fragmentation for erect forms, is possible considering the turbulence which exists in the strait. However, deep west-to-east transfer is limited by physical obstacles. Firstly, deep circulation (MOW) occurs from east to west, and, secondly, due to the high hydrologic dynamics of this flux, some biotopes of deep-water species, such as mud bottoms, are not found in the strait (Heezen and Johnson, 1969).

The presence of populations of endemic species from the NE Atlantic upper bathyal (set B\*) in deep sites in the strait is enigmatic. In fact, these species appear to be excluded from the Mediterranean, including from the Alboran Sea, although they tolerate deep-water Mediterranean hydrologic conditions. The particular sites (DR152, DR153) are drained by water masses whose characteristics at the bottom of this zone (Coste *et al.*, 1988: Tab. 1, station 8) are the same as those of eastern sill water with a salinity greater than 38.4. Two alternate hypotheses can be suggested to explain this abnormal distribution: 1) these populations were founded by recruits from the Gulf of Cadiz, which were transported towards the east through a complex turbulent system with lateral and vertical currents which characterizes this zone (Heezen and Johnson, 1969); 2) these populations are relicts established when the Strait's hydrology was different from today and they survive by self-recruitment.

The physical barrier of the deep east-west current may have been less efficient or even removed during certain periods of time during the Gibraltar Strait's history. During the Pliocene, according to Thunell *et al.* (1987), the water exchange through the strait was made by a deep Atlantic inflow and a shallow less dense Mediterranean outflow while a reversal of this stratification occurred during the Quaternary. The existence of other phases of reversal in the strait's currents during the Quaternary is controversial. This would have occurred at the end of the Würm (*ca.* 10,000 yr B.P.) according to Huang and Stanley (1974). But, according to Diester-Haas (1973) and Vergnaud-Grazzini *et al.* (1989), the present-day stratification was established since at least 18,000 yr B.P. However, several indications suggest that a decrease in deep water circulation in the Alboran basin occurred *ca.* 8-9,000 yr B.P. along with an increase in the thickness of the Atlantic flow entering the Mediterranean (Vergnaud-Grazzini and Pierre, 1991), which might have favoured transfer of Atlantic species to



the upper bathyal. Some elements based on alternations in benthic macrofauna, as shown by Mars (1963) and accepted by Ruggieri (1967) and Pérès (1967; 1985), favour the theory of a reverse in exchanges through the Gibraltar Strait during the Pliocene and Quaternary. The same hypothesis is suggested by Barrier *et al.* (1989) to explain the presence in Plio-Pleistocene deposits of the Messina Strait of bathyal Atlantic forms no longer existing in the present-day Mediterranean, such as pedunculated crinoids, which lack a planktonic larval stage. Whatever their origin, these populations of bathyal Atlantic species in the strait do not appear to be a source of propagules for the Mediterranean, whether due to problems of dispersal or physiological compatibility.

The occurrence of Atlantic endemics in the Alboran Sea presents a similar problem, although all the representatives are not bathyal species. Do the colonies sampled correspond to current, occasional recruitment with no basis in viable populations ("pseudopopulations", Bouchet and Taviani, 1992) or to a real colonization, of more or less ancient origin, of the basin? In the latter case, does the present-day state correspond to an expansion phase or, inversely, to a contraction of a domain which was much larger in the recent geological past, when the conditions in the deep Mediterranean were more similar to those in the Atlantic? For Atlantic species whose confinement within the Alboran Sea could be conditioned by trophic resources, increasing eutrophization of the neritic zone in the Mediterranean could favour their further expansion. All these possibilities may be represented. The current distribution of *Escharina johnstoni* in the circalittoral benthos of the Alboran Sea is possibly a signature of the inflowing Atlantic water ( $S < 37.0$ ; Gascard and Richez, 1985), but it could also possibly correspond to an initial phase of an expansion in the whole Mediterranean.

Some regions acted as refuges during the main biotic crises (Vermeij, 1986). According to Ruggieri (1967), the Iberian-Moroccan Gulf could have played this role during the Messinian crisis. The cribrimorph *Puellina scripta* appears to be a good example of a deep-water paleo-Mediterranean species excluded from the Mediterranean basin during the Messinian and whose reinstallation in the Mediterranean could have been due to this reservoir.

Are the different morphotypes of *P. venusta* found in the Alboran Sea environmentally induced or genetically determined? In the first hypothesis, the water surrounding the colonies would have sufficiently pronounced Atlantic characters to induce the Atlantic morphotype. However, the hydrology of the corresponding sampling sites (145-205 m, off the Moroccan coast) is more Mediterranean than Atlantic ( $37.5 < S < 38.0$ ; Guibout, 1987). The second

hypothesis implies that the Mediterranean environment has no influence on the Atlantic phenotype: colonies in the Alboran Sea could form a deme of the Atlantic population which would be maintained through self-recruitment and/or be maintained by propagules transferred by the Atlantic current. The intermediate morphotype from the Andalusian coast could thus correspond to a hybridization between elements from the Atlantic and Mediterranean populations.

## CONCLUSION

The bathyal bryozoan fauna is clearly poorer in species number in the Mediterranean than in the Atlantic. This feature is less evident for the stock of species which can live above 200 m.

The area north of the Iberian-Moroccan Gulf affected by the Mediterranean outflow is not poorer in species than the south, which is typically Atlantic.

The sill and the rapidly flowing subjacent Mediterranean water layer appear to create a physical barrier for propagation of deep-water Atlantic species in the Mediterranean.

The  $\theta$ -S particularities of Mediterranean water do not appear to be a factor in exclusion of several Atlantic bathyal species which are not distributed throughout the Mediterranean.

The trophic factor is presumed to be the defining factor for survival of populations of deep-water Atlantic species in the Mediterranean water of Gibraltar Strait and the Alboran Sea.

The exceptional primary productivity of the north-west Alboran basin could induce this distribution pattern, through an increase in trophic resources for the benthos, which would compensate the Mediterranean oligotrophy.

The Atlantic endemics found in deep-water localities of Gibraltar Strait and the Alboran Sea may be : 1) relicts, established when the water circulation allowed a better transfer from the bathyal Atlantic; 2) more recently established population thanks to the random success of series of slight vertical and lateral transfers dependant on the Strait's highly complex dynamics.

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## REFERENCES

- Ambar I. and M.R. Howe (1979). Observations of the Mediterranean outflow. I: Mixing in the Mediterranean outflow. *Deep-Sea Res.*, 26A, 535-554.
- Aristegui J. and T. Cruz (1986). Consideraciones biogeográficas sobre el orden Cheilostomata (Ectoprocta) en Canarias. *Vieraea*, 16, 161-171.
- Barrier P., I. Di Geronimo, C. Monténat, M. Roux and H. Zibrowius (1989). Présence de faunes bathyales atlantiques dans le Pliocène et le Pléistocène de Méditerranée (déroit de Messine, Italie). *Bull. Soc. géol. Fr.*, 8, 5, 787-796.
- Barrier P., H. Zibrowius, P. Lozouet, C. Monténat, P. Ott d'Estevou, F. Serrano and H.J. Soudet (1992). Une faune de fond

- dur du bathyal supérieur dans le Miocène terminal des Cordillères Bétiques (Carboneras, SE Espagne). *Mésogée*, **51**, 3-13.
- Béthoux J.-P. (1984). Paléo-hydrologie de la Méditerranée au cours des derniers 20 000 ans. *Oceanologica Acta*, **7**, 1, 43-48.
- Bishop J.D.D. and B.C. Househam (1987). *Puellina* (Bryozoa, Cheilostomata; Cribriliniidae) from British and adjacent waters. *Bull. Br. Mus. nat. Hist. (Zool.)*, **53**, 1, 1-63.
- Boronat Tormo J. (1987). Briozoos de los fondos coralíferos del litoral Sureste Iberico del mar de Alboran. *Tesis Licenciatura, Universidad de Valencia, España*, 184 pp.
- Bouchet P. and M. Taviani (1992). The Mediterranean deep-sea fauna: pseudopopulations of Atlantic species? *Deep-Sea Res.*, **39**, 169-184.
- Casanova J.-P. (1977). La faune pélagique profonde (zooplancton et micronecton) de la province atlanto-méditerranéenne. *Thèse de Doctorat ès-Sciences, Université d'Aix-Marseille I, France*, 255 pp.
- Cook P.L. (1981). The potential of minute bryozoan colonies in the analysis of deep-sea sediments. *Cah. Biol. mar.*, **22**, 89-106.
- Coste B., Le Corre P. and H.J. Minas (1988). Re-evaluation of the nutrient exchanges in the Strait of Gibraltar. *Deep-Sea Res.*, **35**, 767-775.
- Diester-Haas L. (1973). No current reversal at 10,000 years BP at the Strait of Gibraltar. *Mar. Geol.*, **15**, M1-M9.
- Faugères J.-C., M. Frappa, E. Gonthier and F. Grousset (1985). Impact de la veine d'eau méditerranéenne sur la sédimentation de la marge sud et ouest ibérique au Quaternaire récent. *Bull. Inst. Géol. Bassin Aquitaine*, **37**, 259-287.
- Fredj G. and L. Laubier (1985). The deep Mediterranean benthos. in: *Mediterranean marine ecosystems*, M. Moraitou-Apostoulou and V. Kiortsis, editors. Nato Conference series. Plenum Press Publications, 107-145.
- Gage J.D. and P.A. Tyler (1991). *Deep-sea biology*. Cambridge University Press, Cambridge, 504 pp.
- Gascard J.-C. and C. Richez (1985). Water masses and circulation in the western Alboran Sea and in the Straits of Gibraltar. *Prog. Oceanogr.*, **15**, 157-216.
- Gordon D.P. (1987). The deep-sea Bryozoa of the New-Zealand region. in: *Bryozoa: present and past*, J.R.P. Ross, editor. Western Washington University, Bellingham, USA, 97-104.
- Guibout P. (1987). Atlas hydrologique de la Méditerranée. IFREMER et SHOM, Paris, 150 pp.
- Harmelin J.-G. (1973). Les bryozoaires des peuplements sciaphiles de Méditerranée: le genre *Crassimarginatella* Canu (Cheilostomes Anasca). *Cah. Biol. mar.*, **14**, 471-492.
- Harmelin J.-G. (1978). Sur quelques cribrimorphes (Bryozoa Cheilostomata) de l'Atlantique orientale. *Téthys*, **8**, 173-192.
- Harmelin J.-G. (1988 a). Espèces affines microsypatriques chez *Puellina* (Bryozoa, Cheilostomata) et description d'espèces nouvelles. *Zoologica Scr.*, **17**, 25-38.
- Harmelin J.-G. (1988 b). Les bryozoaires, de bons indicateurs bathymétriques en paléocéologie? *Géol. Médit.*, **15**, 49-63.
- Harmelin J.-G. and J. Aristegui (1988). New Cribriliniidae (Bryozoa, Cheilostomata) from the upper bathyal of the Atlanto-Mediterranean region. *J. nat. Hist.*, **22**, 507-535.
- Harmelin J.-G. and J.-L. d'Hondt (1992 a). Bryozoaires des parages de Gibraltar (campagne océanographique *Balgim*, 1984). 1: Cheilostomes. *Bull. Mus. natn. Hist. nat., Paris, sect. A (1)*, **4**, 14, 23-67.
- Harmelin J.-G. and J.-L. d'Hondt (1992 b). Bryozoaires des parages de Gibraltar (campagne océanographique *Balgim*, 1984). 2: Cténostomes et cyclostomes. *Bull. Mus. natn. Hist. nat., Paris*, in press.
- Hayward P.J. and J.S. Ryland (1978). Bryozoa from the Bay of Biscay and Western approaches. *J. mar. biol. Ass. U.K.*, **58**, 143-159.
- Heezen B.C. and G.L. Johnson (1969). Mediterranean undercurrent and microphysiography west of Gibraltar. *Bull. Inst. océanogr., Monaco*, **67**, 1382, 1-95.
- Huang T.C. and D.J. Stanley (1974). Current reversal at 10,000 years at the Strait of Gibraltar, a discussion. *Mar. Geol.*, **17**, M1-M7.
- Lacombe H. (1988). Considérations générales sur l'océanographie physique méditerranéenne. *Océanographie pélagique méditerranéenne*, H.J. Minas et P. Nival, editors. *Oceanologica Acta*, vol. sp. No.9, 7-12.
- Lopez de la Cuadra C.M. and J.C. Garcia Gomez (1988). Briozoos queilostomados del Estrecho de Gibraltar y areas proximas. *Cah. Biol. mar.*, **29**, 21-36.
- Mars P. (1963). Les faunes et la stratigraphie du Quaternaire méditerranéen. *Recl Trav. Stn mar. Endoume*, **28**, 43, 61-97.
- McKinney F.K. and J.B. Jackson (1989). *Bryozoan evolution*. Unwin Hyman Ltd, London, UK, 238 pp.
- Minas H.J., B. Coste and M. Minas (1984). Océanographie du détroit de Gibraltar et des parages annexes. *Courrier CNRS*, **57**, 10-17.
- Minas H.J., B. Coste, P. Le Corre, M. Minas and P. Raimbault (1991). Biological and geochemical signatures associated with the water circulation through the Strait of Gibraltar and the western Alboran Sea. *J. geophys. Res.*, **96**, C5, 8755-8771.
- Monniot C. and F. Monniot (1988). Ascides profondes de chaque côté du seuil de Gibraltar (Campagne *Balgim*). *Bull. Mus. natn. Hist. nat., Paris, sect. A (3)*, **4**, 10, 415-428.
- Packard T.T., H.J. Minas, B. Coste, R. Martinez, M.-C. Bonin, J. Gostan, P. Garfield, J. Christensen, Q. Dortch, M. Minas, G. Copin-Montegut and C. Copin-Montegut (1988). Formation of the Alboran oxygen minimum zone. *Deep-Sea Res.*, **35**, 1111-1118.
- Pérès J.-M. (1967). The Mediterranean benthos. *Oceanogr. mar. Biol. a. Rev.*, **5**, 449-533.
- Pérès J.-M. (1985). History of the Mediterranean biota and the colonization of the depths. in: *Key Environments. Western Mediterranean*, R. Margalef, editor. Pergamon Press, Oxford, UK, 198-232.
- Rex M.A. (1983). Geographic patterns of species diversity in the deep-sea benthos. in: *Deep Sea Biology*, G.T. Rowe, editor. John Wiley and Sons, New York, USA, 453-472.
- Rosso A. (1990). Thanatocoenose würmienne à bryozoaires bathyaux en mer Tyrrhénienne. *Rapp. P.-v. Réun. Commn int. Explor. scient. Mer médit.*, **32**, 1, 23.
- Ruggieri G. (1967). The Miocene and later evolution of the Mediterranean Sea. in: *Aspect of Tethyan Biogeography*, C.G. Adams and D.V. Ager, editors. *Syst. Ass. Publ.*, **37**, 283-290.
- Ryland J.S. (1970). *Bryozoans*. Hutchinson University Library, London, UK, 175 pp.
- Saguar J. and J. Boronat (1987). Briozoos de las islas Columbretes. in: *Islas Columbretes. Contribucion al estudio de su medio natural*, L.A. Alonso Matilla, J.L. Carretero and A.M. Garcia Carrascosa, editors. General. Valenc., Valencia, España, 391-415.
- van der Spoel S. and P.H. Schalk (1988). Unique deviations in depth distribution of the deep-sea fauna. *Deep-Sea Res.*, **35**, 1185-1193.
- Thunnel R.C., D.F. Williams and M. Howell (1987). Atlantic-Mediterranean water exchanges during the late Neogene. *Paleoceanography*, **2**, 661-678.
- Vergnaud-Grazzini C. and C. Pierre (1991). High fertility in the Alboran Sea since the last glacial maximum. *Paleoceanography*, **6**, 519-536.
- Vergnaud-Grazzini C., M. Caralp, J.-C. Faugères, E. Gonthier, C. Pujol and J.-F. Saliège (1989). Mediterranean outflow through the Strait of Gibraltar since 18 000 years BP. *Oceanologica Acta*, **12**, 4, 305-324.
- Vermeij G.J. (1986). Survival during biotic crises: the properties and evolutionary significance of refuges. in: *Dynamics of extinction*, D.K. Elliott, editor. John Wiley and sons, New York, USA, 231-246.