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Biotic affinities in a transitional zone between the Atlantic and the Mediterranean: a biogeographical approach based on sponges

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Abstract. This study characterizes the demosponge assemblages established on the continental shelf of Alboran Island, a site where the faunistic influences of three biogeographical regions overlap (i.e. Mauritanian, Lusitanian and western Mediterranean regions). The patterns of species composition and abundance of Alboranian fauna are compared with those of five other Atlantic–Mediterranean islands. This comparison provides a general idea about the faunistic affinities of the Alboranian assemblages, as well as an estimate of the general faunistic heterogeneity in the biogeographical province.

An important biogeographical regionalism was found in both the quality and quantity of the demosponges. The general pattern of biotic affinity is determined predominantly by horizontal distances (geographical distances) and marine currents. The role of vertical distance (bathymetry) was much less significant. However, it is an important determinant for Alboranian assemblages. The infralittoral assemblages of this island are strongly affected by Lusitanian fauna. Circalittoral

assemblages, however, harbour fauna with a peculiar species composition, lacking affinities with all other communities considered in this study. This fact suggests strongly that the circalittoral level of the Alboranian shelf is an ecotone established in the boundary layer between the Atlantic and Mediterranean water masses.

The pattern of present-day biotic affinities among all the archipelagos was also used to test, by parsimony analysis, various hypotheses on the historical origin of the Mediterranean benthos. Results suggest that sublittoral Mediterranean fauna have a major Lusitanian–Mauritanian origin, although a few Tethyan or Paleomediterranean elements still persist in some circalittoral communities of the Alboranian shelf.

Key words. Alboran Sea, Atlantic–Mediterranean region, biogeographical parsimony analysis, demosponge bathymetric distribution, demosponge biogeography, Paleomediterranean fauna.

Resumen. Este estudio es una caracterización de las poblaciones de demosponjas establecidas en la plataforma continental de la isla de Alborán, un enclave localizado en una zona donde se solapan las influencias faunísticas de tres regiones biogeográficas (región Mauritánica, Lusitánica y Mediterráneo Occidental). La composición y abundancia de especie de la fauna alboraniense se han comparado con las de otros cinco archipiélagos atlántico–mediterráneos para obtener una idea general de las afinidades faunísticas de Alborán, así como una estimación de la heterogeneidad faunística de la provincia biogeográfica.

Hay un regionalismo biogeográfico importante tanto en la calidad como en la cantidad de la fauna de demosponjas. El patrón general de afinidades bióticas está determinado principalmente por las distancias horizontales (distancias geográficas) y las corrientes marinas. El papel de las distancias verticales (batimetría) es mucho menos significativo. Sin embargo, es un determinante importante en el caso de los asentamientos bentónicos de la plataforma de Alborán. Las comunidades del nivel infralitoral de esta isla están fuerte-

mente influenciadas por la fauna lusitánica. Los asentamientos circalitorales, sin embargo, albergan una fauna con una particular composición específica, que carece de afinidad con cualquiera de las restantes comunidades consideradas en este estudio. Este hecho sugiere que el nivel circalitoral de la plataforma de Alborán es un ecotono establecido en la interfase que separa las masas de aguas noratlántica y mediterránea.

El patrón actual de afinidades bióticas entre los archipiélagos se ha utilizado también para testar, mediante análisis de parsimonia, varias hipótesis sobre el origen del bentos mediterráneo. Los resultados sugieren que la fauna mediterránea sublitoral tiene un origen mayoritariamente Lusitano–Mauritánico, aunque algunos elementos del Tethys o del Paleomediterráneo todavía persisten en comunidades circalitorales de Alborán.

Palabras clave. Análisis de parsimonia biogeográfico, biogeografía de demosponjas, distribución batimétrica de demosponjas, fauna Paleomediterránea, Mar de Alborán, región atlántico–mediterránea.

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INTRODUCTION

Alboran Island is a Mediterranean site located in an area where the faunistic influences of three Atlantic–Mediterranean biogeographical regions (Mauritanian, western Mediterranean and Lusitanian region) intersect. Consequently, the benthic assemblages of the continental shelf of Alboran Island are envisaged to be especially useful settings for supplying information on the recent, and perhaps past, faunistic interchange between the Atlantic and the Mediterranean through the Straits of Gibraltar. However, despite such interest these benthic assemblages have been virtually ignored by taxonomists until recent Spanish, French and Italian extensive surveys began in the 1980s with the aim of gaining a global and integrated faunistic understanding. The material collected during some of these surveys has thus allowed us to carry out a first representative census for the sublittoral demosponge assemblage from Alboran Island. Comparison of this sponge fauna with that described in five other islands scattered throughout three Atlantic–Mediterranean biogeographical regions (Mauritanian, Lusitanian and western Mediterranean) has been used to assess the scope of faunistic heterogeneity in the Atlantic–Mediterranean province, as well as in the area where these three regions intersect. Moreover, the pattern of present-day biotic affinities in such natural scenery has also been used tentatively to test various hypothetical assumptions about the historical origin of the Mediterranean benthos.

Environmental background

Besides its interest from the point of view of its biogeographical position, i.e. point of intersection, Alboran Island is considered to be a singular Atlantic–Mediterranean site for the particular circulation of the surrounding water masses (Lacombe, 1971; Lanoix, 1974). A current of surface water coming from the North Atlantic (NAS) occurs approximately between 0 and 70 m depth (e.g. Cano, 1977, 1978a, b; Parilla, 1984). The NAS water bathes the infralittoral level of the continental shelf of Alboran Island (abbreviated as ALB-NAS), with a salinity of 36–36.6 p.p.t. around the island and a temperature of 19–23°C (Cano, 1977, 1978a). Beneath the Atlantic surface water, a mass of Mediterranean intermediate water moves in the opposite direction. The intermediate water actually consists of two types of waters: one coming from the eastern Mediterranean, through the Straits of Sicily (EMI) and the other of a local origin in the West Mediterranean basins (WMI). The EMI water is characterized near Alboran Island by a salinity of 38.5 p.p.t. and a temperature of 13°C (Cano, 1977, 1978a). The EMI water resides on the WMI, between the NAS and up to 200 m in depth. A 70–80 m thick zone of water mixing (interface) occurs between the Atlantic (NAS) and the Mediterranean (WMI) waters. The interface is described conventionally in the salinity maps by the isohaline of 37.5 p.p.t. Near Alboran Island the upper limit of this interface is commonly located at

55–70 m depth, while the lower limit is at 100–120 m depth, depending on both the sporadic presence of geostrophic gyres and atmospheric pressure (e.g. Cano, 1977, 1978a,b; Cano & Gil, 1984; Parrilla, 1984; Hopkins, 1989). This interface water layer, therefore, bathes the upper circalittoral level of the continental shelf of Alboran Island (abbreviated as ALB-INT). The peculiar T/S diagrams of this interface, along with the sporadic vertical movement of its limits, are characteristic features which make this water notably distinctive from other north eastern Atlantic and Mediterranean water masses. However, even though water circulation has been relatively well studied little is known about the eventual correlation between the faunistic composition of the sublittoral benthos and the three water masses described above.

Historical background

To tackle interpretation of the present-day Atlantic–Mediterranean relationships of the Alboranian benthos, it would be necessary to go back to the Upper Miocene (± 6 million years ago), when it is postulated by most geologists that the Mediterranean (Paleomediterranean) was isolated from the Atlantic as a probable result of the northward movement of the African block against Europe. The concept of a totally desiccated Mediterranean basin during the short Messinian period was quite prevalent among scientists as recently as 20 years ago (e.g. Hsü, Cita & Ryan, 1973). However, such a concept is not universally accepted now. Nowadays, the debate is focused mainly on demonstrating whether the residual local environments were so extreme (i.e. *sebka* or *playa* type) as to lead to a complete extinction of the Miocene fauna (e.g. Ruggieri, 1967) or, conversely, if a shallow, briny sea remained allowing some dynamic process to take place (e.g. Benson, 1976; Sonnenfeld & Finetti, 1985; Stanley, 1990) and the survival of a Paleomediterranean biotic stock that could have led to the repopulation of the Mediterranean during the Pliocene. At the beginning of the Pliocene waters cascaded into the Mediterranean through two straits reopened between the Atlantic and the Mediterranean (Betic and Rif Straits) and at that time the Mediterranean was mainly repopulated with marine fauna from the Ibero–Moroccan Bay and the West African coast (Ruggieri, 1967; Klausewitz, 1973; Pérès, 1989).

Quaternary macro-events are relatively well known, since the western Mediterranean is a region in which the universal chronology of the Marine Pleistocene has been established (e.g. Zeuner, 1959; Fairbridge, 1961). It is commonly accepted that during the interglacial periods the global climatic conditions afforded a warm Mediterranean with a deficient water balance. Under such conditions there was an important penetration of Atlantic surface water into the Mediterranean, favoured by westerlies, incorporating Senegalian elements. Conversely, during the glacial periods the water balance was positive in the Mediterranean and therefore the pattern of currents at Gibraltar was reversed: there was an outflow of Mediterranean surface water and an

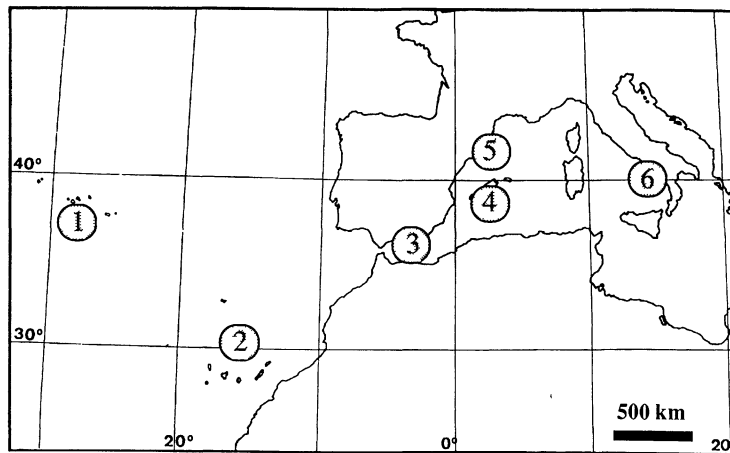


FIG. 1. Geographical location of the archipelagos considered in the present study. 1 = Azores, 2 = Canary Islands, 3 = Alboran Island, 4 = Cabrera Island, 5 = Medas Island, 6 = Island of Ischia.

inflow of deep Atlantic water over the sill, thereby carrying cold-water fauna. Such inversion of currents might be responsible for the alternating appearance/disappearance of cold-water (Celtic) and warm-water (Senegalian) species. However, a restricted number of species of both types might have co-existed in zones where hydrographic conditions were not too extreme, as was postulated to occur in the Gibraltar area (Mars, 1963). The Celtic species seem, therefore, to be characteristic of deep water conditions whereas Senegalian elements would consist mainly of shallow water species. It is also postulated that Senegalian elements, relicts from the Tyrrhenian transgression, are still present in the warmest zones of the Mediterranean, such as the Tunisian coast (Pérès, 1989). However, a great deal of faunistic information, which would be extremely useful for a better understanding of biotic western Mediterranean history, still remains 'buried' in the present-day shallow-water assemblages of the central sector of the Alboran sea (i.e. Alboran Island) due to the scarcity of studies in this area.

As far as the most recent biotic changes are concerned, contemporary authors assume that a certain number of species have entered the Mediterranean with the North Atlantic current in recent times. The presence of most present-day immigrants appears to be restricted to the Alboran Sea (Pérès, 1989). However, little is known about the relative roles of the Moroccan and Lusitanian areas as centres of origin of this recent immigration. Moreover, it would be interesting to try to make a distinction between past and recent biotic influences on the present-day fauna of Alboran Island.

MATERIAL AND METHODS

Areas, communities and data resources

The present study is based on a comparison of the sublittoral demosponge fauna of three marine biogeographical regions (the Lusitanian, Mauritanian and western Mediterranean regions) represented here by six archipelagos. The

set of archipelagos is distributed along an assumed Atlantic-western Mediterranean geographical (latitudinal) axis and consists of the Azores, the Canary Islands, Alboran Island, Cabrera Island, the Medas Islands and Ischia Island (Fig. 1).

Faunistic censuses were elaborated by combining information obtained from authors and from bibliographic sources, as follows:

- Azores: Topsent (1904), Boury-Esnault & Lopes (1985), Weerdt & Van Soest (1986).
- Canary: Cruz & Bacallado (1984a, b, c), Weerdt & Van Soest (1986), Aristegui *et al.* (1987), present study.
- Alboran: Templado *et al.* (1986), Pansini (1987), Griessinger (1971), Maldonado (1992, 1993), Maldonado & Uriz (1992), Uriz & Maldonado (1993), present study.
- Cabrera: Uriz, Rosell & Martín (1992).
- Medas: Olivella (1979), Bibiloni, Olivella & Ros (1984).
- Ischia: Sarà (1960), Pulitzer-Finali (1971, 1977), Pulitzer-Finali & Pronzato (1976).

The elaborated census accounted for a total of 266 species (130 genera) inhabiting the main sublittoral communities of each archipelago between 0 and 120 m depth (Appendix 1). Cavernicola fauna was excluded. The establishment of limits and equivalences between Mediterranean and Atlantic communities involves particularly controversial decisions. Thus, biogeographical conclusions were supported mainly using the whole of fauna in each archipelago. Analyses at the community level were exclusively employed with exploratory and/or confirmatory aims in order to conduct the study at the archipelago level.

Benthic habitats were grouped by combining classifications proposed by Pérès & Picard (1964), Ros, Olivelli & Gigli (1984), Hiscock (1991) and Uriz *et al.* (1992) in order to balance the botanical and zoological

criteria in the recognition of ecological entities. Communities considered here are described using terminology recommended by Lincoln, Boxshall & Clark (1982), as follows.

- Communities of photophilic algae: infralittoral communities between 0 and 10 m in depth dominated by photophilic algae. In most archipelagos, demosponge fauna inhabiting these communities is ubiquitous, extremely poor and often unnoticed in the literature.
- Communities of semi-sciaphilic algae: rocky infralittoral communities settled between 10 and 30 m in depth, depending on exposure to light and water turbidity. Space is shared by fleshy algae with low photophilic affinities and by benthic filter feeders, mainly sponges, bryozoans and tunicates.
- Meadows of macrophytes: bedrocks and boulders with *Laminaria ochroleuca* Pylaie in Alboran Island; sandy or sand-covered rock bottoms with *Posidonia oceanica* (L.) Delile on Ischia Island and the Medas Islands. Both types of meadows have been considered here to be equivalent because they offer similar environmental conditions for demosponges to dwell on. The bathymetrical limits of the *Posidonia* meadows at Medas and Ischia Islands are 15 and 40 m, respectively (Romero, 1985; Colantoni *et al.*, 1982). The lower limit of the *Laminaria* meadows at Alboran Island is 70 m depth (Giaccone, 1972).
- Communities of spatial infra-circalittoral transition: communities settled on hard bottoms usually between 30 and 45 m, in which the spatial dominance of fleshy macrophytes is progressively reversed in favour of crustose calcified algae. They are frequently named 'precoralligenous' in the Mediterranean.
- Upper circalittoral assemblages: coralligenous bio-coenoses in the Mediterranean archipelagos; communities of *Dendrophyllia* or *Axinella* in the Atlantic archipelagos.

In those cases where no community was stated explicitly in the literature for the species, assignation to a given community was made by considering jointly bathymetry and substratum exposure to light of the sampling site. For instance, sponges recorded on overhangs between 0 and 5 m depth (Boury-Esnault & Lopes, 1985) were assigned here to semi-sciaphilic habitat as well as those growing on horizontal surfaces between 20 and 40 m (*l.c.*).

Analyses were carried out both on quantitative (semi-quantitative) and qualitative data. Qualitative data refer to the presence-absence of species either in communities or in archipelagos. Semi-quantitative data were obtained by transforming the original information on the number of collected specimens (e.g. Sará, 1960; Pulitzer-Finali, 1971, 1977; Pulitzer-Finali & Pronzato, 1976; Cruz & Bacallado, 1984b; Boury-Esnault & Lopes, 1985; Pansini, 1987; Maldonado, 1992, 1993; authors' data) into semi-quantitative values ranging from 0 to 3 for each community. Semi-quantitative values were assigned according to the following criteria: 0 = absent species; 1 = species only recorded once in the community (1%); 2 = species moderately fre-

quent in the community (2–35%); 3 = abundant species in the community (> 35%).

When original data were semi-quantitative they were re-scaled to fit the above-mentioned range (e.g. Bibiloni *et al.*, 1984; Cruz & Bacallado, 1984c; Uriz *et al.*, 1992). Purely descriptive taxonomic papers or simple species lists were used to complete the censuses of the communities (e.g. Topsent, 1904; Griessinger, 1971; Olivella, 1979; Cruz & Bacallado, 1981; Weerdt & Van Soest, 1986; Templado *et al.*, 1986; Aristegui *et al.*, 1987; Maldonado & Uriz, 1992). Most of the species included in this way were regarded as rare, unless explicit mention of their abundance had been made by the authors.

It must be realized that an important part of the data was compiled from different studies, in which sampling efforts and methods could vary in accordance with authors and communities. Consequently, transformation of the frequency values of species into semi-quantitative values was achieved separately by communities. This procedure is assumed to have a similar effect to standardization by columns, which minimizes data variability arising from heterogeneity in the samplings.

The semi-quantitative value of a species in an archipelago was finally calculated as the total sum of the abundance values of each community.

The taxonomic acceptability of the species listed in the bibliographical sources was mainly assumed, except for only two cases. (1) The species quoted in the Canary Islands as *Batzella inops* (Cruz & Bacallado, 1984c) was personally confirmed to be *Crambe crambe*, and (2) the species recently described on Alboran Island as *Stylostichon equiosculatum* Pansini, 1987 was reinterpreted as a junior synonym of *Stylostichon plumosum* (i.e. Maldonado, 1993). The species referred to the Appendix as *Sphinctrella* sp. is actually a new species, still unpublished.

Cluster analyses

Cluster analysis was applied to both qualitative and semi-quantitative data in order to examine the main trends in biotic affinity as well as to establish hypotheses on the archipelago inter-relationships. Studied archipelagos are assumed to be arranged along a geographical, and consequently environmental, axis. Therefore, they were expected to display continuous and overlapping patterns of variation. The hierarchical structure inherent to the classification techniques seems a priori to be less appropriate when examining an assumed continuous variation than the ordination methods. However, cluster analysis has the additional advantage of allowing comparisons between results from qualitative and quantitative approaches.

Qualitative approaches to the archipelagos' inter-relationships were based on the Jaccard (similarity) and Simpson (dissimilarity) indices. The Jaccard index is a semi-metric coefficient excluding double-zeros, extremely appropriate for examination of general biotic similarity based on the number of shared taxa. Moreover, this has an additional advantage since its complement (also known as percentage of remoteness) is metric (Pielou, 1984) and, consequently, a good space conserving under ordination

analyses, i.e. non-metric multi-dimensional scaling (NMDS). The Simpson index is postulated to be an objective quantifier of the influence of historical events and ecological factors on the provincialism of distributions (Brown & Gibson, 1983).

Semi-quantitative approaches to the relationships between archipelagos (and also between communities) were based on the application of the Bray–Curtis distance, which is metric, and excludes double-zeros (Legendre & Legendre, 1983). It is recognized as an efficient distance for evaluation of affinities on semi-quantitative data arising from large faunistic assemblages and it is appropriate to support an NMDS ordination (e.g. Warwick & Clarke, 1991; Gamito & Raffaelli, 1992).

The complete list of species was used in qualitative analyses, whereas only those species exclusively present in only one community and, moreover, showing abundance equal to 1 (see Appendix), were discarded in semi-quantitative analyses.

The unweighted arithmetic average clustering method (UPGMA) (Sneath & Sokal, 1973) was applied to the similarity/distance matrices. Goodness of fit between similarity/distance matrices and resulting classifications was assessed by examining their respective coefficients of co-phenetic correlation (Rohlf, 1988).

Ordination analyses

Reciprocal averaging (RA) in R and Q models as well as NMDS were performed in order to examine area relationships in a continuous space. Comparison of the results yielded by both methods was made in order to minimize the risk of possible misinterpretations derived from the inherent assumptions of each analytical method, i.e. monotonicity and linearity in data, respectively.

The mathematical procedure of RA (based on chi-square distances and R–Q balanced) implies that rare species, either by their abundance or their limited distribution, are treated as being extremely distinctive. Such a methodological feature, which is assumed to be undesirable in many ecological studies (i.e. Gauch, 1982), is considered here to be especially useful in dealing with faunistic endemism.

NMDS was applied to matrices containing both percentage remoteness and Bray–Curtis distances between archipelagos. Goodness of fit for the resulting spatial configurations was assessed through stress values (Kruskal, 1964).

Gradient analysis: species richness and beta turnover

The amount of change in species composition from one archipelago to another (i.e. ‘beta turnover’) was examined in pairs of consecutive areas (archipelagos). Two different alignments of areas were considered: (1) a geographical alignment based on the Atlantic–Mediterranean areas location (i.e. latitude scores); and (2) a biotic alignment based on the biotic distances between areas, according to the results of cluster and ordination analyses.

Beta turnover between pairs of areas was computed as proposed by Wilson & Shmida (1984):

$$\beta_t = g + l/2\bar{S}$$

where g and l are gain and loss of species for each step in the gradient, and \bar{S} is the average sample richness between the pairs of involved areas. This index provides an idea of beta diversity along the gradients, combining information on species turnover with standardization by average area richness (Wilson & Shmida, 1984).

Parsimony analysis of endemism

Parsimony analysis of endemism (PAE) was applied to the distribution of taxa in sample archipelagos (operative geographic units = OGU) in order to examine the OGU inter-relationships (Rosen & Smith, 1987; Rosen 1988).

PAE was applied in two different ways. First, a total of 266 species were used as characters to solve relationships between archipelagos. In this case, the presence and absence of each species in an archipelago are the only two possible states of each character (binary characters). Biogeographical conclusions are often drawn from this method (e.g. Rosen, 1988) even when no phylogenetic information about the relationships of the species used as characters is included. Consequently, we have made a tentative methodological modification to this general usage of PAE in order to introduce some phylogenetic information into the data to be analysed. Consequently, the 266 species were grouped into 132 assumed monophyletic species groups (i.e. genera) and were then used as multi-state characters for a new PAE of archipelagos. Absence of the genus in a locality was also considered to be a character state. If more than one species of a genus simultaneously occurs in an area, then such an area is coded as a multiple state OGU. Multiple state OGU were treated as polymorphisms (Swofford, 1989).

Three different assumptions on the biotic status of a hypothetical ancestral area were made in the usage of PAE on binary characters (characters = taxa at the specific level). Assumption 1: no recent species was present in the ancestral area. In this case, relationships between areas would be due mainly to shared speciation events (‘synapomorphies’). Parallelisms and convergences are interpreted as dispersals whereas reversals are considered as extinctions. Assumption 2: all recent species were present in the ancestral area; then, current relationships between areas would be mainly due to shared extinctions. Assumption 3: those recent species occurring simultaneously both in the Azores and the Canary Islands were probably present in the ancestral area. Additionally, those being absent simultaneously in the Azores and the Canary Islands were absent in the ancestral area. The ancestral condition of the remaining species was treated as unknown (?). This assumption is based on the commonly accepted hypothesis which postulates that the most Tethyan fauna of the Mediterranean (Paleomediterranean elements) was extinguished during the Messinian salinity crisis and the Mediterranean was subsequently repopulated with fauna from the Ibero–Moroccan Bay during the Pliocene (Pérès, 1989).

When PAE was carried out on multi-state characters

TABLE 1. Matrix containing real marine geographical distances between OGU's below diagonal (MD) and readjusted marine distances above diagonal (RMD).

	A	B	C	D	E	F	G
A	0	1465	1073	2146	2800	3080	3770
B	1465	0	1660	830	1160	1300	1645
C	2146	1660	0	1073	1320	1880	3260
D	2146	1660	0	0	660	940	1630
E	2800	2320	660	660	0	360	1030
F	3080	2600	940	940	360	0	920
G	3770	3290	1630	1630	1030	920	0

A = Azores, B = Canary Islands, C = ALB-NAS, D = ALB-INT, E = Cabrera Island, F = Medas Islands, G = Island of Ischia.

(characters = taxa at the generic level), a new assumption (Assumption 4) was obtained from Assumption 3 by readjusting the basic premises at the generic level. The resulting Assumption 4 was as follows: the character state present simultaneously in the Canary Islands and the Azores would be the most probable ancestral condition of a character. When more than one character state are present simultaneously in both archipelagos only one of them can be selected as ancestral, because the PAUP program (and other similar packages dealing with parsimony) lacks the option to include multiple states per character in the ancestor. This computational constraint compels us to choose only one of the possible states at random. If no common character state is present simultaneously in the Azores and the Canary Islands, then the ancestral condition of such character was treated to be unknown (?).

The fine phylogenetic relationships among the species of most genera included in the analyses remains practically unexamined and, therefore, no given ordination between states of a multi-state character could be supported logically. Thus, all characters were regarded as unordered both at the specific and the generic level of PAE. However, they were diversely polarized/unpolarized, according to the ancestral assumption used. As a hypothetical ancestral area was always included in the parsimonious searches, yielded cladograms are rooted by ancestral area. This method of rooting was thought to be more appropriate than the 'Lundberg rooting' (Rosen & Smith, 1987) in ensuring the global parsimony in the cladogram (Kitching, 1992). Unlike Rosen (1988), uninformative characters were maintained in our analyses. Such characters, obviously, do not supply information about tree topology, but they become important when patristic distances are examined.

The algorithm used by the PAUP program (version 3.0) to treat the unordered characters is based on that of Fitch (Swofford, 1990). The branch-and-bound method was used to find all optimal trees (Hendy & Penny, 1982).

Correlation analyses between biotic and geographical distances

Geographical distances between archipelagos and those distances yielded on the phenetic and parsimonious tax-spaces (using Jaccard, Simpson and Bray-Curtis indices

and maximal parsimony algorithms, respectively) were jointly examined by non-parametric correlation analysis (Spearman's rank correlation) in order to ascertain the role of the geographical distance in the recent biotic affinity between areas. Correlations were examined repeatedly after tentatively readjusting the geographical pattern of distances between archipelagos by considering the effects that major marine currents may play in the general pattern of biotic affinities. It may be assumed that the occurrence of marine currents facilitates, but also orientates, the dispersal of organisms, resulting, in terms of dispersal efforts, in a 'fictitious' nearness among archipelagos. Sponges are known to have either poor or practically null dispersal ability for covering long distances (e.g. Zea, 1993). We have assumed arbitrarily that the effect of nearness due to the occurrence of major marine currents might result in a 50% reduction for the real geographical distance between the involved areas. Therefore, the North Atlantic water influx entering the Mediterranean translates into a 'fictitious nearness' between the Azores and the infralittoral level of Alboran Island. In addition, it has been postulated that during the maximum of the Quaternary 'glacial periods', as a result of the global climatic modification, a coastal current tended to bring species from the Senegalian and Mauritanian provinces into the Mediterranean fauna (e.g. Pérès, 1989). This fact may be translated into an effect of reduction for the real distances between the Canary Islands and the remaining western Mediterranean sites. The fictitious nearness between the Azores and the infralittoral level of Alboran Island (ALB-NAS) as well as that between the Canary Islands and the remaining sites result in a similar fictitious separation between ALB-NAS and the other Mediterranean sites. The real marine distances between archipelagos (MD) and those readjusted after considering the effects of currents (RMD) are shown in Table 1.

RESULTS

Clustering and ordination results

Congruence between the results from qualitative and semi-quantitative cluster analyses was very high and the conclusions emerging from each one are not significantly

different. Consequently, in avoiding redundancy, we have presented graphically the results of the semi-quantitative approaches only. In the same way, a very close resemblance between the results of RA and NMDS was obtained and, for the same reason, only one of them is graphically displayed. Note that the convergence in the results of RA and NMDS points out that non-linear relationships among variables (taxa) is not a problem in this data set (RA is one of the ordination techniques most susceptible to non-linearity). Results obtained from ordination and cluster analyses were also largely congruent.

The cluster analysis of archipelagos (Fig. 2a) yielded two groups: one consisted of the Azores and Alboran Island, whereas the other contained the remaining archipelagos. Archipelago distribution on the biotic space generated by the two principal ordination axes, accounting for the 53% of the total variance, concurs with the result of the classification (Fig. 2b). The first axis (32.6% of variance) seems to relate to East–West differences in the Mediterranean archipelagos and also to North–South differences in the Atlantic archipelagos. Axis II (21% of variance) discriminates clearly between Mediterranean and Atlantic archipelagos. Note that East–West biotic differences in the Mediterranean (western Mediterranean scenery) are reflected in Axis I, whereas Atlantic–Mediterranean differences, which were found to be less important, occur in Axis II. Both the semi-quantitative and qualitative cluster analyses as well as the ordination analyses (RA and NMDS) concur in finding that the biotic affinity between Alboran Island and the Azores is more important than that between Alboran Island and the remaining Mediterranean archipelagos.

When a classification analysis was performed on communities (Fig. 3), two main sets ('A' and 'B') were found. Group A consisted of the entire sets of communities from Cabrera Island, the Medas Islands and Ischia Island (subgroup A2), along with that of the Canary Islands (subgroup A3) and also the circalittoral community of Alboran Island (subgroup A1). Group B contained all communities from the Azores along with all three infralittoral communities from Alboran Island (3B, 3L, 3C). The A group clearly corresponds to a 'Mediterranean' component in the fauna of the global set of OGU whereas the B group reflects the occurrence of a North Atlantic component. The set of communities of the Canary Islands, in spite of belonging to an Atlantic enclave, was revealed to be closer to those of the typical Mediterranean archipelagos (i.e. Cabrera Island, the Medas Islands, Ischia Island) than to that of the Azores. This result concurs with those from the analyses at the archipelago level.

An unexpected feature revealed by cluster analysis at the community level is that similarity is greater between different communities within the same archipelago than between ecologically equivalent communities of different archipelagos (Fig. 3). Therefore, for instance, the precoral-ligenous community of Ischia Island (6C) is closer to the meadows of *Posidonia* of Ischia Island (6P) than to the precoral-ligenous communities of Cabrera Island (4C) or the Medas Islands (5C). However, this general trend is not matched by the Alboran communities. In contrast, Alboran

Island shows a double biotic affinity: its infralittoral communities are closely related to those from the Azores whereas its circalittoral community lacks such Atlantic affinity and, also, it has low affinity with the typical Mediterranean subgroup (A3).

As a consequence of this double biotic affinity detected for Alboran Island, new cluster and ordination analyses were made at the archipelago level by splitting the Alboranian assemblage into two components (Fig. 4a, b): an infralittoral component subjected to the influence of the NAS water (ALB-NAS = fauna inhabiting the 3B, 3L and 3C communities) and a circalittoral component being free of such influence (ALB-INT = fauna inhabiting the 3D community). The tree resulting from the cluster analysis (Fig. 4a) proved that the Atlantic influence previously detected for Alboran Island (Fig. 2a) affects the infralittoral communities (ALB-NAS) exclusively. The circalittoral community of Alboran Island again displays a distinctive character, lacking noticeable affinities both in the Atlantic and the Mediterranean. A bidimensional ordination accounting for the 48.3% of the total variance corroborated

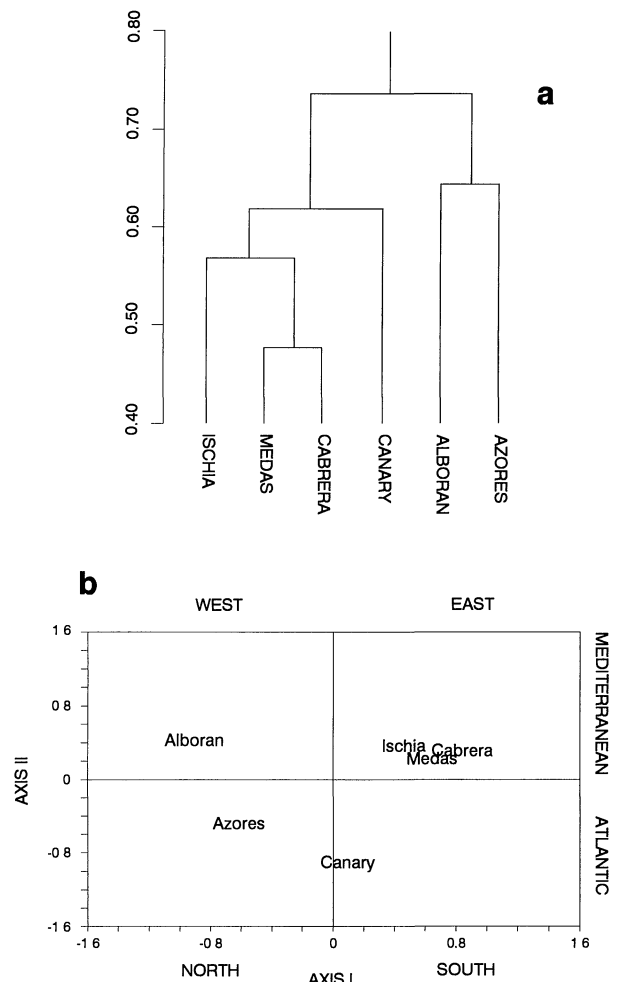


FIG. 2. (a) Dendrogram of biotic inter-relationships among archipelagos based on Bray-Curtis distances. (b) Plot of archipelagos on a bidimensional taxa-space yielded by reciprocal average.

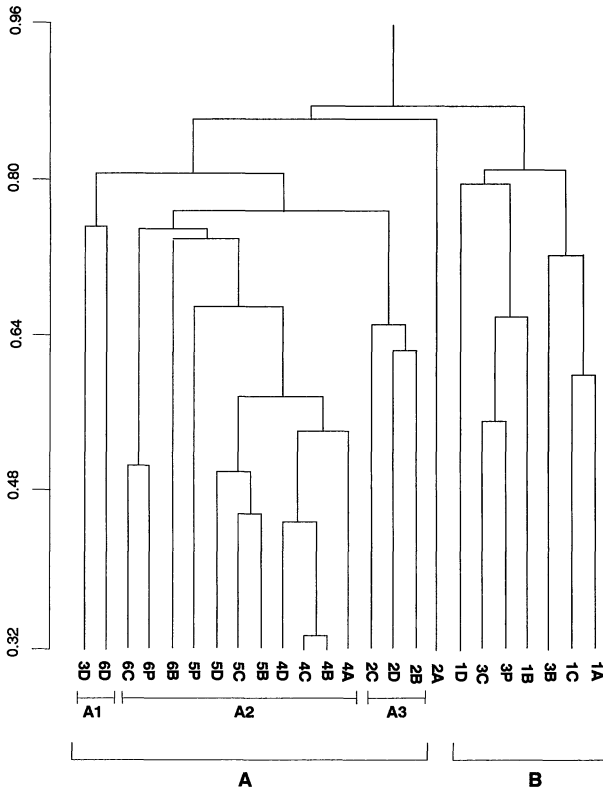


FIG. 3. Dendrogram showing biotic inter-relationships (based on Bray-Curtis distances) in the whole set of communities considered in this study. Numbers in labels represent the archipelago in which communities are located (1 = Azores, 2 = Canary Islands, 3 = Alboran Island, 4 = Cabrera Island, 5 = Medas Islands, 6 = Ischia Island) whereas letters refer to the type of community (A = communities of photophilic algae, B = communities of semi-sciaphilic algae, P = meadows of macrophytes, C = communities of infra-circalittoral transition, D = upper circalittoral assemblages).

this distinctive character (Fig. 4b). Note that these ordination axes may be interpreted in a similar way to those described in Fig. 2b.

A Q-mode ordination (Fig. 5) showed that there is actually a group of species responsible for the distinctive nature found in the circalittoral community of Alboran Island (3D = ALB-INT). The group consisted mainly of species well-represented in the circalittoral community of Alboran Island, but rare or absent in the remaining localities of the Atlantic-Mediterranean region. These species are *Sphinctrella* sp., *Characella tripodaria*, *Isops anceps*, *Stryphnus mucronatus*, *Pseudosuberites hyalinus*, *Prosuberites rugosus*, *Tyloidesma inornata*, *Iophon nigricans*, *Reniera implexa* and *Ircinia pipetta*. The distinctive character was detected by a conservative analysis in which those species present exclusively in the circalittoral community with abundance equal to 1 (i.e. *Plakinastrella intermedia*, *Axinella salicina*, *Crambe tuberosa* and *Leptolabis megachela*) had been discarded.

Gradient analyses results

The number of sponge species per communities in the

different archipelagos is represented in Fig. 6. Species richness increases progressively from the upper infralittoral level towards the circalittoral level in the Mediterranean islands. Conversely, Atlantic archipelagos exhibit maximal species richness in the 'medium' infralittoral level, whereas faunistic impoverishment occurs in the lower infralittoral and circalittoral levels. The number of species associated to the *Laminaria* meadows of Alboran Island is considerably higher than that of the Mediterranean seagrasses of *Posidonia*. The community displaying the highest number of species is the coralligenous of Alboran Island, notably outnumbering any other circalittoral community.

The results of examining species richness and beta turnover at the archipelago level are shown in Fig. 7a, b. Marked changes in species composition along a gradient, reflected by high beta turnover values, have usually been related to ecotones (in ecological approaches), geographical barriers or tension zones (in biogeographical approaches).

When archipelagos were arranged along an Atlantic-

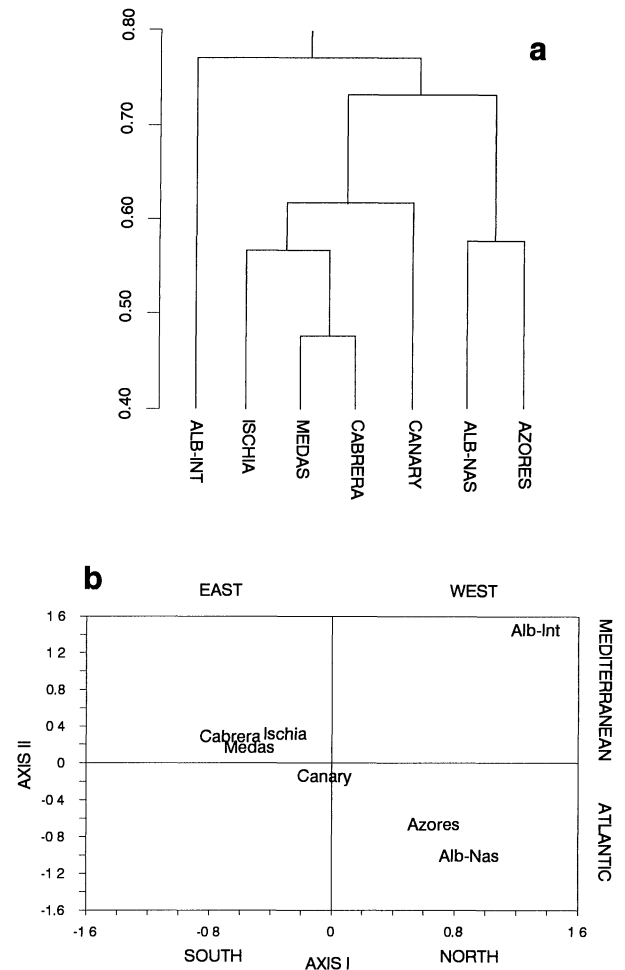


FIG. 4. (a) Dendrogram of biotic inter-relationships among archipelagos (based on Bray-Curtis distances) after splitting the faunistic assemblage of Alboran Island into an infralittoral component (ALB-NAS) and a circalittoral component (ALB-INT). (b) Plot of archipelagos in a bidimensional taxa-space yielded by reciprocal average.

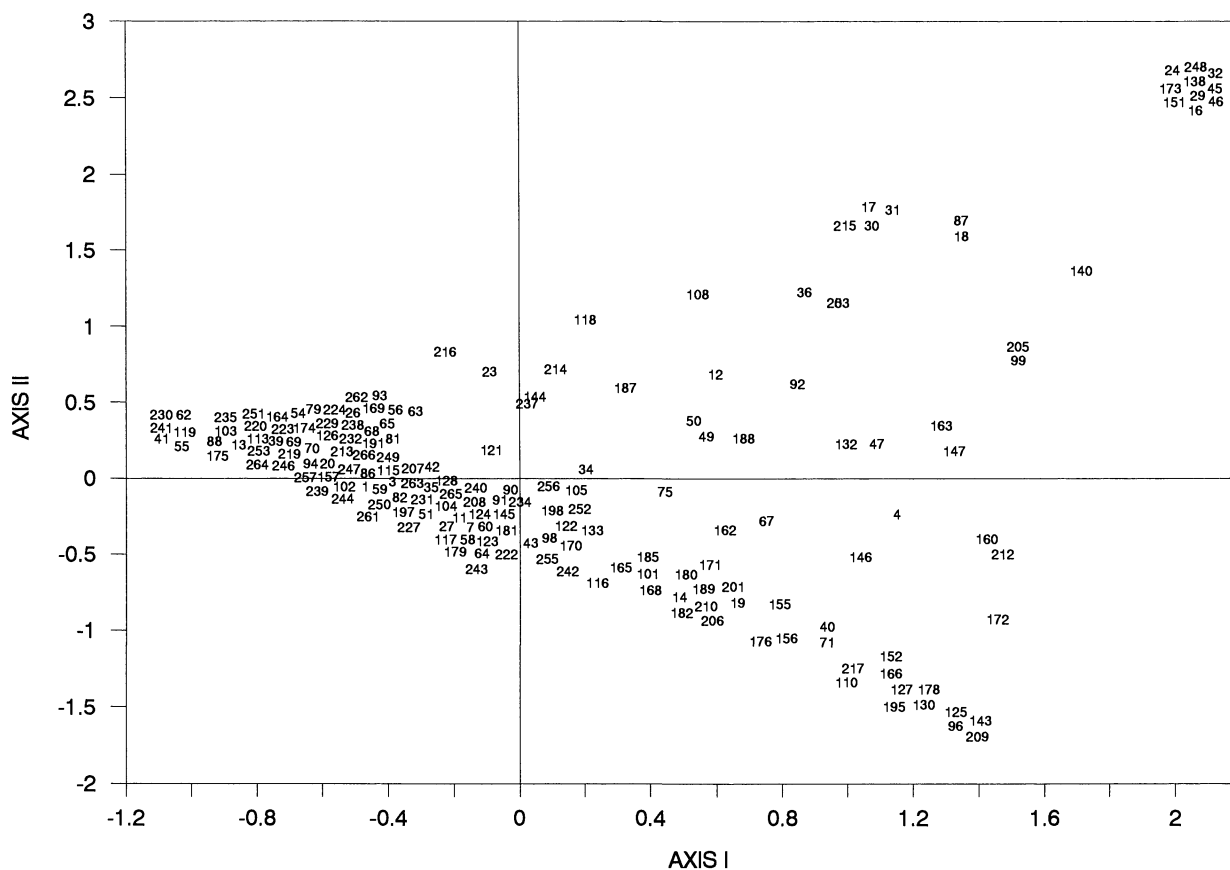


FIG. 5. Bidimensional plot of a Q -mode ordination (RA) displaying the species responsible for the archipelagos ordination yielded in Fig. 4. Numbers refer to species according to codes assigned in Appendix. The original scores yielded by the analyses were slightly modified, when necessary, in order to avoid a complete overlapping of the species codes.

Mediterranean axis according to their latitudinal geographical location, the beta turnover was found to be notably higher in the steps related to Alboran Island (Canary–Alboran; Alboran–Cabrera) than in the remaining steps (Fig. 7a). Since the ordination analyses revealed an Atlantic component in the faunistic affinity of Alboran Island (even greater than that of the Canaries), the purely latitudinal arrangement of the archipelagos was altered subsequently by interchanging the positions of Alboran Island and the Canaries in order to fit more accurately the biotic trends previously detected. Nevertheless, turnover values associated with the steps concerning Alboran Island remained high even after this rearrangement of the archipelagos' alignment. On the other hand, the former turnover value between the Canaries and the Azores (Fig. 7a) was notably higher than that obtained between the Canaries and Cabrera Island in this second alignment (Fig. 7b). This fact clearly shows that the biotic and the geographical relationships at the archipelago level conflict for the position of the Canary Islands.

When Alboran Island was split into its Atlantic and Mediterranean components (ALB-NAS, ALB-INT), as in the cluster and ordination analyses, the turnover value between the Azores and the ALB-NAS notably decreased (Fig. 7c, d). In contrast, turnover values of the steps associ-

ated with the circalittoral community of Alboran (ALB-INT) remained high. Note that turnover values associated with ALB-INT were similarly high whether this component was placed between Atlantic or Mediterranean archipelagos. Moreover, the beta turnover of species was as high between ALB-INT and ALB-NAS as between ALB-INT and the other archipelagos considered (Fig. 7c,d).

Parsimony analysis of endemism

By applying PAE under Assumption 1, only one most parsimonious tree of areas was yielded (length = 408; CI = 0.652). Twenty-six sympleomorphic gains of species were arranged on the root (Fig. 8a). Under Assumption 2, only one most parsimonious tree was also yielded, but this tree was longer and had lower consistency than that yielded under Assumption 1 (length = 524; CI = 0.504). Moreover, a total of 144 sympleomorphic extinctions were arranged on the root, many of which were subsequently unrealistically recovered as reversals on the terminal branches. Under Assumption 3 (Fig. 8c), only one most parsimonious tree was also found. This tree was shorter and more consistent (length: 378; CI = 0.698) than the two previously mentioned. Note that, in spite of being a rooted tree by including into the parsimonious search a

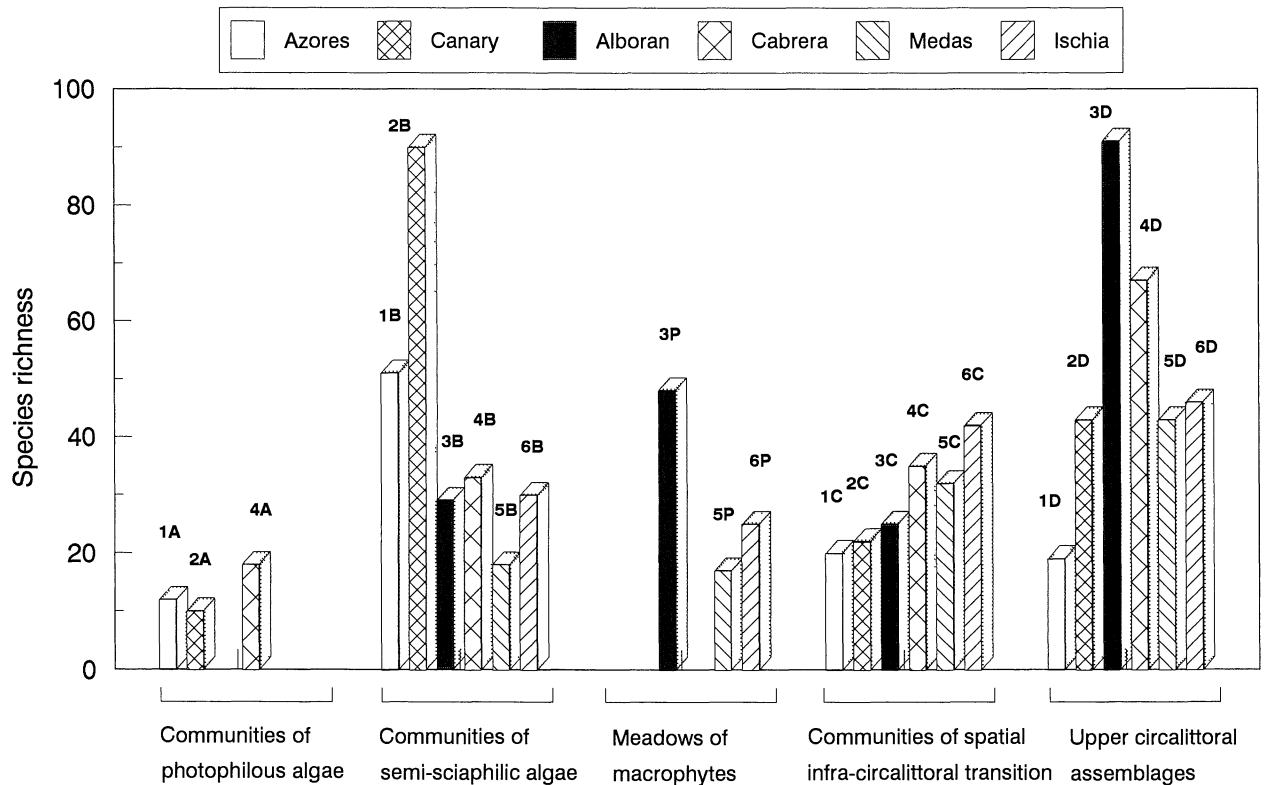


FIG. 6. Bar diagram of species richness per community. Communities are grouped into ecological categories on axis X. Codes at the top of the bars refer to communities as in Fig. 3.

hypothetical ancestral area (Assumption 3), no character change was arranged on the root.

Consequently, it appears obvious that the present-day faunistic status of the Mediterranean and North Atlantic archipelagos is more easily explained, in cost terms of species gains and losses, by assuming that only a certain number of the recent North Atlantic species were present in the ancestral area (as is represented in Assumption 3; Fig. 8c). In this cladogram, the Canaries are found to be arranged far from the root as it would correspond to a relatively 'young area' with a recently acquired biota. Such a resulting position is yielded in spite of the fact that a part of the recent biotic status of the Canaries was assumed to be ancestral (see Assumption 3 in Material and Methods). Moreover, in such a cladogram the Canaries are found to be the sister group of the set of typical Mediterranean archipelagos (Cabrera, Medas, Ischia). The non-Atlantic component of the Alboranian assemblage (ALB-INT) represents the sister group of the set comprised of the Canaries and all three typical Mediterranean archipelagos above-mentioned. In addition, it displays a long and 'distinctive biotic history' as reflected by the accumulation of a total of sixty-two character changes on its terminal branch. From an evolutionary point of view, this OGU may be defined as a 'case of paraphyly'. ALB-INT is even closer to the root than the Canaries, although its present-day sponge fauna were not considered in establishing the biotic status of the ancestral area used (Assumption 3). Finally, the Azores

was found to be the 'virtual' ancestral area (root length = 0). The patristic distance between the Azores and ALB-NAS (eighty-one changes) is low with regard to those of the remaining pairs of areas being adjacent in the tree. Such a low value, which is very near to the minimal value of eighty changes (found between the Cabrera and Ischia Islands), reflects close biotic relationships between the Azores and ALB-NAS.

As a result of applying PAE on generic characters, five most parsimonious trees were yielded. The most probable tree topology was chosen by majority rule consensus (Fig. 9a) and it matched fully one of the five most parsimonious trees (length = 395; CI = 0.838). The Azores and ALB-INT were again closely related to each other, and both were closer to the hypothetical ancestor than the remaining OGU analysed. ALB-INT appeared as a sister group of the remaining typical Mediterranean archipelagos and this overall whole constituted, in their turn, the sister group of the Canaries. Again, the ALB-INT displayed the longest and most distinctive 'biotic history' as reflected by the length of its terminal branch.

The strict consensus between the results from the specific and generic approaches was thought to be an extremely conservative interpretation of the area relationships. A strict-consensus tree was obtained by overlapping the most parsimonious tree yielded at the specific level (under Assumption 3) and the most parsimonious tree yielded at the generic level (selected by the 50% majority

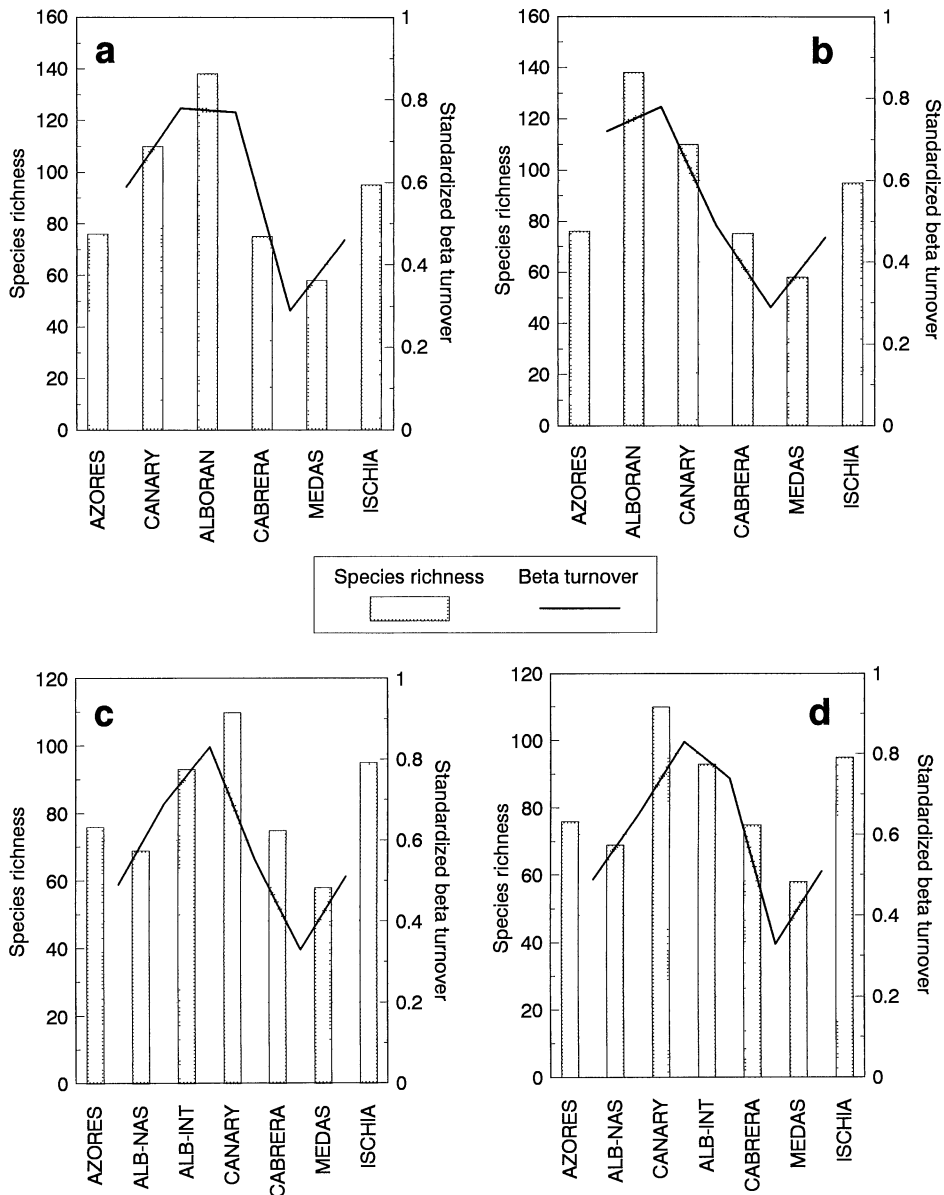


FIG. 7. (a, b) Species richness per archipelagos (left scales) and beta turnover OGU's (right scales) between consecutive arranged according to geographical and biotic alignments, respectively. (c, d) The above-mentioned parameters shown after considering separately the two faunistic components of the Alboranian assemblage. Graphs (c) and (d) represent tentative tests to find the best position (in beta turnover terms) for the controversial ALB-INT on the Atlantic-Mediterranean biotic axis.

rule on the results of applying Assumption 4). In this consensus tree, the relative positions of the pair of OGU, comprising of the Azores/ALB-NAS as well as that of the Canaries/ALB-INT, remained unsolved (Fig. 9b).

In a less conservative procedure, the topology resulting from the specific approach might be accepted as the most probable for the relationships, yielding an entirely solved cladogram. Such an argument is based on the fact that the topology of the most parsimonious tree yielded under Assumption 3 (using species as characters) can be also obtained from Assumption 4 (using genera as characters). In this case, the tree is only one step longer

than the most parsimonious one and it is also largely consistent (length = 396; CI = 0.836). The total number of 396-step trees is four. Conversely, in obtaining from the species approach the topology yielded by the generic approach, it is necessary to accept a tree being six steps longer (length = 384, CI = 0.688) than the most parsimonious one and to accept a greater decrease in the consistency index. Moreover, the number of 384-step trees found, including that used as constraint, is as high as fourteen. Consequently, the topology yielded by the approach at species level seems to be better supported, in parsimony terms, than that arising from approach at the generic level.

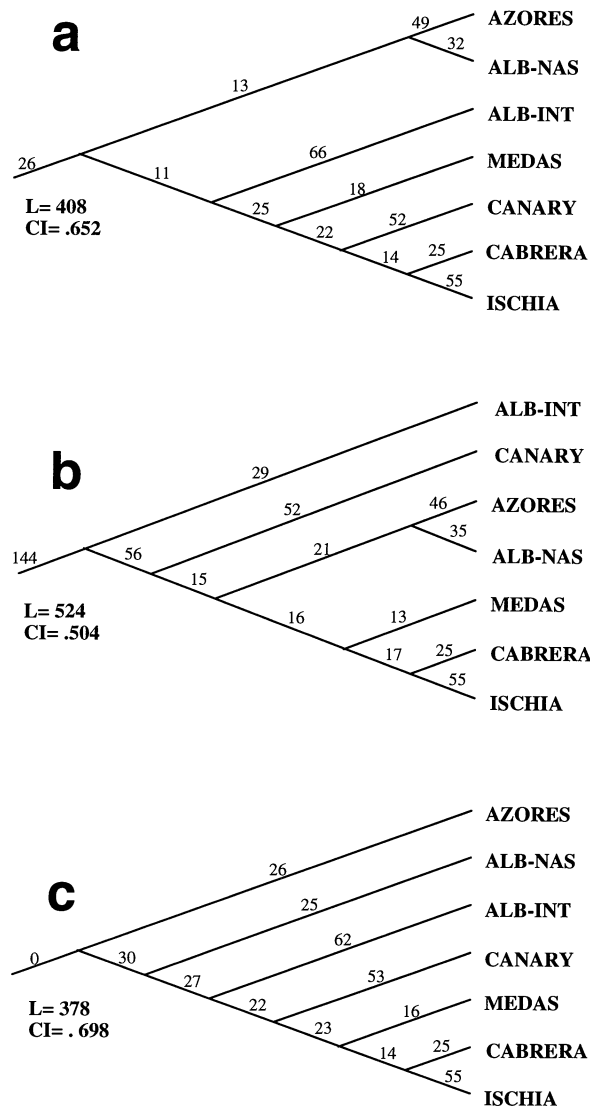


FIG. 8. Most parsimonious area cladograms yielded by PAE under assumptions 'I', 'II' and 'III' are, respectively, shown in (a), (b) and (c). Numbers refer to branch lengths according to the number of character changes. CI = consistency index of the tree; L = total tree length.

Relationships between patristic, phenetic and geographical distances

Relationships between the actual geographical distances existing between archipelagos and various biotic distances calculated from different methods were examined by Spearman's rank correlation, but no significant relationship was found between both distance patterns (Table 2; MD).

On the other hand, after readjusting the marine distances by considering the effect of the currents (see Material and Methods), statistically significant relationships were revealed between such readjusted distances (RMD) and the patristic distances, postulated as reflecting historical events (Table 2; RMD-1). Further examination of the correlation residuals indicated that the biotic distances in which the element ALB-INT was involved notably disturbed the

overall pattern of correlation in all cases. When such distances were removed from the analyses, the remaining biotic distances also became significantly correlated with the RMD (Table 2; RMD-2).

Table 3 shows Spearman's rank correlation values computed pairwise between the various biotic distances employed in the whole of the analyses. It is worth noting that the Simpson index correlates highly with the Jaccard index, in spite of the fact that only the first index has traditionally been postulated as being a good quantifier of the influence of historical events and ecological factors on the regionalism of distributions (e.g. Simpson, 1960; Fallaw, 1978; Flessa *et al.*, 1979).

GENERAL CONCLUSIONS AND DISCUSSION

Ecological interpretations of the biotic inter-relationships

It can be concluded from this study that an important regionalism affects the demosponge distribution in the Atlantic–Mediterranean area, although a better knowledge of the Mauritanian and Senegalian regions might result in a more uniform distribution pattern of the Atlantic–Mediterranean species (e.g. Vacelet, 1980; Weerdt & Van Soest, 1986; Pansini, 1987).

Biotic affinity at the archipelago level reflected latitudinal differences in the Mediterranean and longitudinal differences in the North Atlantic. In addition, analysis at the community level corroborated that the general pattern of biotic affinity was determined mainly by the horizontal distances, while it was hardly affected by the vertical (bathymetric) distances unless special barriers occurred. Surprisingly, all biotic distances between areas were found to be uncorrelated with their marine geographical distances. Such apparent conflict is, to a certain extent, solved when it is granted tentatively that past and recent major marine currents (i.e. African coastal currents associated to Quaternary westerlies and nowadays NAS currents, respectively) have played an important role in determining the present-day pattern of biotic affinity. Moreover, it has also been demonstrated that in the absence of OGU representing ecotones, such as the ALB-INT, the role of marine currents becomes more evident in explaining the affinities.

Marine currents facilitate, but also direct, dispersal of organisms. Consequently, this fact is translated into a 'fictitious' nearness between distant areas, in terms of dispersal efforts. The relevance of this passive transport in determining the biogeographical distribution of a species may be assumed to be inversely related to its ability for an active dispersal. As far as sponges are concerned, it is well known that their dispersal ability is limited (Zea, 1993). Sponge larvae are extremely rare or even absent in coastal oceanic plankton samples (Zea, 1993; Carlton & Geller, 1993) and seldom colonize offshore fouling panels (Sarà & Vacelet, 1973).

As for the biotic relationships of Alboran, both semi-quantitative and qualitative approaches indicate an important affinity between its shallow-water demosponge fauna and that of the Lusitanian region, which is represented in

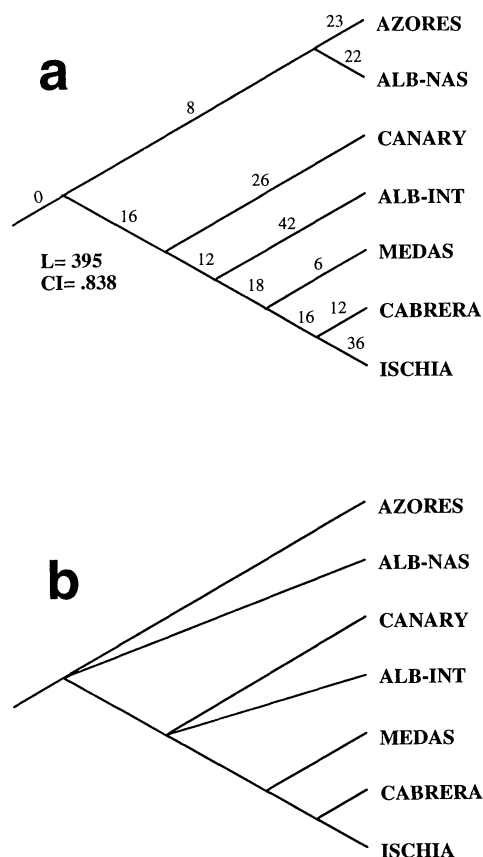


FIG. 9.(a) Area cladogram obtained by majority (50%) rule consensus from the five most parsimonious trees yielded by PAE under assumption IV. Labels and items as in Fig. 8. (b) Strict consensus area cladogram obtained from the specific (assumption III) and generic solutions yielded by PAE for the area inter-relationships.

the study by the Azores. At first sight, such a result is explained by the North Atlantic water inflow coming into the Mediterranean, directly bathing the continental shelf of Alboran Island. However, it was shown that the North Atlantic affinity solely affects the infralittoral level of the continental shelf of Alboran Island. In contrast, the circalittoral level showed a remarkable, distinctive faunistic composition, lacking affinity with the remaining Atlantic and Mediterranean OGU considered in the study. This double affinity detected in Alboranian fauna suggests that the interface water layer residing between the Atlantic and Mediterranean water masses functions as a barrier, thereby hindering the vertical dispersal of the benthos.

From hydrological studies of Alboran Island and nearby seas (e.g. Cano, 1977, 1978a, b; Parrilla, 1984), we now know that the coralligenous community is settled within the interface water layer. Therefore, the distinctive nature of the circalittoral assemblage of Alboran Island is viewed mainly as a result of such peculiar environmental conditions (ecozone). In fact, its high beta turnover values, as well as its high species richness, suggest that this community is an ecotone assemblage within the Atlantic-Mediterranean axis.

Another aspect of the general pattern of affinity is the

relationships found between the Canary Islands and the inner, western Mediterranean settings (Cabrera, Medas, Ischia), in which Alboran Island does not participate. Such discontinuity in the Atlantic-Mediterranean affinity pattern had gone unnoticed in previous biogeographical approaches based on sponges (e.g. Vacelet, 1980; Weerdt & Van Soest, 1986; Pansini, 1987). However, it clearly emerges in this study, probably as a consequence of having performed an ecologically addressed compartmentalization and a magnification of the biogeographical scenery. Similar discontinuous distributions have also been reported, for instance, in fishes (e.g. Postel, 1956) and decapods (e.g. Quignard, 1978). This 'jumping model' of affinity remains unexplainable if present-day environmental conditions are considered exclusively (i.e. climate, marine currents, etc.). Therefore, historical factors should also be taken into account.

Historical interpretation of the biotic interrelationships

The area cladograms yielded by PAE have been interpreted tentatively as historical sequences of biotic divergence between sister localities. The most conservative approach, deriving from a consensus between solutions at the generic and specific levels, supports clearly that the Mediterranean assemblage is posterior to and originated from the North Atlantic assemblage. This interpretation concurs with the hypothesis postulating that 'most' Paleomediterranean fauna was destroyed during the salinity crisis at the Messinian. The persistence of numerous Paleomediterranean species (hypothesis tested under Assumption 2) was viewed from PAE results as an unrealistic possibility.

The current biotic status of the Azores is found by PAE to be ancestral to those of the remaining archipelagos considered in the analyses. The biotic proximity between the ALB-NAS and the Azores is interpreted as being more a consequence of the recent North Atlantic influence than a result of the persistence of ancestral Atlantic fauna in the infralittoral assemblages of Alboran Island. It is, therefore, assumed that the strong present-day influence from the Lusitanian region (i.e. Azores) on the ALB-NAS has removed most living evidence of its Quaternary faunistic history. Unless highly speculative arguments are used, it will not be possible to proceed further in the historical interpretation from this neontological study.

Some authors have postulated that the Senegalian-Mauritanian fauna from the subtropical West African coast, still containing an important Tethyan element, repopulated the Mediterranean at the early Pliocene after the Messinian crisis (e.g. Klausewitz, 1973; Por, 1978). Even if this were found to be true, it is not clearly reflected in the present fauna, probably because later Quaternary events have hidden most traces. In fact, results of PAE indicated that the Lusitanian assemblage is ancestral to the Canarian-western Mediterranean set. The present-day biotic affinity between demosponge fauna of the Canary Islands and the inner western Mediterranean archipelagos (i.e. Cabrera, Medas and Ischia) is commonly explained as a consequence of the important and well-known inflow of Senegalian-Maurita-

TABLE 2. Spearman's rank correlation coefficients (r_s) between marine and biotic distances, both calculated for the set of OGU's considered in Table 1.

	PATRI-SP	PATRI-GE	SIMPSON	BRAY-CUR	JACCARD
MD	0.403	0.251	-0.093	-0.119	-0.036
RMD-1	0.637**	0.590*	-0.431	0.203	-0.379
RMD-2	0.836**	0.726*	-0.747*	0.811**	-0.886**

MD = set of marine distances between archipelagos ($n = 25$), RMD-1 = set of marine readjusted distances between archipelagos ($n = 25$), RMD-2 = set of readjusted marine distances after discarding distances in which ALB-INT was involved ($n = 15$); JACCARD, BRAY-CURT, SIMPSON = faunistic affinity between OGU's yielded by the Jaccard's, Bray-Curtis' and Simpson's indexes, respectively; PATRI-SP, PATRI-GE = patristic distances between OGU's yielded by PAE under assumptions III and IV, respectively. Significant correlations: * $P < 0.005$ and ** $P < 0.001$.

nian elements during the Tyrrhenian, at the end of the Quaternary (Mars, 1963; Por, 1978; Pérès, 1989). Such a hypothesis is supported by the present results. However, the result of PAE at the specific level opens up controversy with regard to a concrete point of this Mauritanian-Mediterranean relationship, because the divergence of the ALB-INT biota was found to be just prior to that of the Canarian and the inner western Mediterranean biota.

From an historical point of view, the ancient divergence of the ALB-INT yielded by PAE agrees with the hypothesis claiming persistence of important amounts of water during the Messinian Paleomediterranean (Rouchy, 1982; Stanley, 1990) and, perhaps, the persistence of a Tethyan biotic stock (Quignard, 1978; Por, 1989). This theory would also be in concordance with recent findings of very ancient species of the genera *Crambe* (*C. tuberosa*, Maldonado & Benito, 1991) and *Discorhabdella* (*D. hindei*, Boury-Esnault, Pansini & Uriz, 1992) in circalittoral and epibathyal assemblages of the Alboran Sea. Such species have, tentatively, been postulated to be Tethyan relicts and interpreted as the most ancient living elements in their respective genera (Boury-Esnault *et al.*, 1992; Maldonado & Uriz, 1993). Thus, this set of items suggests that local areas of the Alboran basin, sporadically connected to the Atlantic by a passageway (Sonnenfeld & Finetti, 1985; Stanley, 1990), would have constituted marine refuges where a Tethyan stock survived the Messinian crisis.

Another possible explanation for the ancient divergence of ALB-INT is that it was due to a methodological artefact. This site was revealed by the ecological approach as an ecozone where western Mediterranean and Atlantic faunistic influences converge. That is, ALB-INT might be assumed to be a relatively recent faunistic assemblage originated by the co-existence of present-day (Holocene) species coming from the nearby biogeographical regions and also some Quaternary relicts from later periods (Silician, Tyrrhenian) of alternating Mediterranean and Atlantic influences (Postel, 1956; Quignard, 1978; Pérès, 1989). It is a well-known fact that cold-water Calabrian fauna disappeared from the upper littoral western Mediterranean bottoms due to the effects of the Later Sicilian transgressive phase, but stock survived in the lower assemblages (Pérès, 1989). Another interesting fact is that, even though the Tyrrhenian transgressive phase allowed intense successive

inflows of littoral Senegalian species, there are signs of a Neotyrrhenian shoreline where the Senegalian element was impoverished (Mars, 1963; Pérès & Picard, 1964; Pérès, 1989). In the light of these two facts, it can be assumed that the environmental changes provoked by the Quaternary events were to some extent attenuated beneath the shallowest bathymetrical level, allowing survival and co-existence for elements of different origin. In contrast, no faunistic co-existence could be possible in shallower assemblages, in which each new event was probably capable of eradicating the previous fauna, as may also be concluded from the present biotic affinities of the ALB-NAS site. In any case, the co-existence of a moderate amount of Mauritanian and western Mediterranean elements in the present-day fauna of ALB-INT, even if it were an exclusive consequence of its present-day condition as ecozone, might be reason enough to find that the most parsimonious solution is to assign to ALB-INT a 'deceptive' ancestral position with regard to the Canary Islands and the remaining Mediterranean archipelagos. Nevertheless, if this interpretation was accepted, the occurrence of species such as *C. tuberosa* and *D. hindei*, which are ancestral to any other species of the same genera inhabiting the Canaries and the Azores, would remain unexplained.

A third interpretation is possible for the ancient divergence of ALB-NAS when the two above-mentioned hypotheses are assumed to be partially true. The current demosponge fauna of ALB-INT could be understood as a result of the co-existence of (1) some very ancient elements (either true Tethyan elements surviving the Messinian crisis or Tethyan elements reintroduced from the Ibero-Moroccan Bay in the Pliocene); (2) Lusitanian, Mauritanian-Senegalian elements arising from the alternating glacial and interglacial Quaternary migrations; (3) Mediterranean elements originated during the Quaternary; and (4) new species evolved from the current peculiar environmental conditions. This interpretation reconciles the conflicting results of PAE at the generic and species levels and also takes into account the postulated Tethyan relicts. The faunistic co-existence claimed for the assemblage of the ALB-INT concurs with the historical conception of Mediterranean fauna as being a 'collage' of Pliocene, Quaternary and Holocene elements (e.g. Furnestin, 1968, 1979;

TABLE 3. Spearman's rank correlation coefficients (r_s) showing pairwise relationships between patterns of biotic distances.

	JACCARD	BRAY-CUR	SIMPSON	PATRI-SP	PATRI-GE
JACCARD	—	-0.676**	0.930**	-0.709**	-0.613*
BRAY-CUR	-0.942**	—	-0.629*	0.509	0.396
SIMPSON	0.937**	-0.877**	—	-0.720**	-0.968**
PATRI-SP	-0.839**	0.815**	-0.756*	—	0.781**
PATRI-GE	-0.720*	0.717*	-0.728*	0.851**	—

All calculated for the entire set of OGU's referred to in Table 1 (below diagonal). Above diagonal: readjustments of the pairwise relationships after discarding those distances in which the element ALB-INT was involved. Significant correlations: * $P < 0.005$ and ** $P < 0.001$. Labels as in Table 2.

Pèrès, 1989). We concede that the chance of persistence of few Paleomediterranean (Tethyan or Pliocene) elements, which is supported from our results, remains a controversial matter, subject to intense debate by the contemporary scientific community. However, the existence of refuge areas in the Mediterranean during the salinity crisis has recently been revived by the discovery and review of some rare benthic species (Por & Dimentman, 1985; Por, 1989; Vacelet, Boury-Esnault & Zibrovius, 1989; Boury-Esnault *et al.*, 1992) as well as by new geological models for explaining the Messinian events (Sonnenfeld & Finetti, 1985; Stanley, 1990).

In fact, every present-day biotic assemblage may be considered to be a result of the overlapping effects of historical events and current ecological processes, whose relative importance cannot often be clearly discriminated. Through time, trails testifying to the past events become either weaker or even lost in the current assemblages, depending on the local intensity of subsequent events. We concede that this is a neontological study, based exclusively on the analyses of living demosponges and, therefore, a refinement of the historical relationships among areas might be obtained by considering fossil fauna along with the recent one, as proposed by Rosen & Smith (1987). Nevertheless, at the present time it is an unrealistic possibility for two major reasons: (1) living and fossil sponges are classified separately into parallel taxonomic systems which, furthermore, remain far from becoming reconcilable; (2) available information on fossil sponge assemblages from the studied archipelagos is either extremely poor or even non-existent. On the other hand, it must also be conceded that sponges are probably one of the best marine groups to support general biogeographical approaches. It may be argued, for instance, that sponges are the sole major marine group not involved in the artificial transoceanic transport of organisms in the water used by ships as ballast (Carlton & Geller, 1993). Regardless of their ecological impact, shipped species may yield an important distortion in the basic information to be analysed by biogeographers.

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APPENDIX 1

Semiquantitative values of species abundance per community. The semiquantitative value of abundance for one species in one archipelago was calculated as the total sum of the abundance value in each community. A, Communities of photophilic algae; B, communities of semi-sciaphilic algae; P, meadows of macrophytes; C, communities of infra-circalittoral transition; D, upper circalittoral assemblages.

SPECIES LIST	AZORES				CANARY				ALBORAN				CABRERA				MEDAS				ISCHIA			
	A	B	C	D	A	B	C	D	B	P	C	D	A	B	C	D	B	P	C	D	B	P	C	D
1 <i>Oscarella lobularis</i> (Schmidt, 1862)	0	2	0	0	0	2	1	0	0	0	0	0	0	2	2	2	0	0	0	2	0	0	0	1
2 <i>Corticium bowerbanki</i> Sarà, 1960	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
3 <i>Corticium candelabrum</i> Schmidt, 1862	0	0	0	0	0	1	2	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
4 <i>Plakina monolopha</i> Schulze, 1880	0	0	0	0	0	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
5 <i>Plakina trilopha</i> Schulze, 1880	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
6 <i>Plakinastrella mixta</i> Maldonado, 1992	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
7 <i>Plakortis simplex</i> Schulze, 1880	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8 <i>Ancorina cerebrum</i> Schmidt, 1862	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
9 <i>Myriastria digitifera</i> Lévi, 1959	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10 <i>Myriastria inermis</i> (Topsent, 1904)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 <i>Myriastria paucistellata</i> Lévi, 1952	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12 <i>Penares candidata</i> (Schmidt, 1868)	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
13 <i>Penares helleri</i> (Schmidt, 1864)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0
14 <i>Stelletta hispida</i> (Buccich, 1886)	0	0	0	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15 <i>Stelletta mediterranea</i> (Topsent, 1894)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16 <i>Stryphnus mucronatus</i> (Schmidt, 1868)	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
17 <i>Stryphnus ponderosus</i> (Bowerbank, 1866)	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0
18 <i>Caminus vulcani</i> Schmidt, 1862	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
19 <i>Erylus discophorus</i> (Schmidt, 1862)	1	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20 <i>Erylus euastrum</i> (Schmidt, 1868)	0	0	0	0	0	1	0	1	0	0	0	0	0	0	2	1	0	0	2	0	0	0	3	0
21 <i>Erylus papulifer</i> Pulitzer-Finali, 1983	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
22 <i>Geodia conchilega</i> Schmidt, 1862	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
23 <i>Geodia cydonium</i> (Jameson, 1811)	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	2	0	0	2	1	1	0	0	0
24 <i>Isops anceps</i> (Vosmaer, 1894)	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
25 <i>Isops intuta</i> (Topsent, 1892)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
26 <i>Calthropella recondita</i> Pulitzer-Finali, 1972	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
27 <i>Calthropella stelligera</i> (Schmidt, 1868)	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28 <i>Pachastrissa pathologica</i> (Schmidt, 1868)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
29 <i>Characella tripodaria</i> (Schmidt, 1868)	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
30 <i>Pachastrella monilifera</i> Schmidt, 1868	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	2	0
31 <i>Poecillastra compressa</i> (Bowerbank, 1866)	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0
32 <i>Sphinctrella</i> sp.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
33 <i>Sphinctrella gracilis</i> Sollas, 1888	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
34 <i>Stoeba plicatus</i> (Schmidt, 1868)	0	1	0	0	0	0	0	1	0	1	0	1	0	0	2	0	0	0	1	0	0	0	0	0
35 <i>Holoxea furtiva</i> Topsent, 1892	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
36 <i>Jaspis johnstoni</i> (Schmidt, 1862)	0	0	0	0	0	2	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0
37 <i>Craniella cranium</i> (Müller, 1776)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
38 <i>Petromica grimaldii</i> Topsent, 1898	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
39 <i>Laxosuberites ectyoninus</i> Topsent, 1900	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
40 <i>Laxosuberites ferrerhernandezii</i> Boury-E. & Lopes, 1985	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41 <i>Laxosuberites rugosus</i> (Schmidt, 1868)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
42 <i>Prosuberites epiphytum</i> (Lamarck, 1815)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
43 <i>Prosuberites longispina</i> Topsent, 1893	0	1	1	0	0	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
44 <i>Prosuberites modestus</i> Pulitzer-Finali, 1977	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
45 <i>Prosuberites rugosus</i> Topsent, 1893	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
46 <i>Pseudosuberites hyalinus</i> (Ridley & Dendy, 1887)	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
47 <i>Pseudosuberites sulphureus</i> (Bowerbank, 1866)	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
48 <i>Rhizaxinella pyrifera</i> (Delle Chiaje, 1828)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
49 <i>Suberites carnosus</i> (Johnston, 1842)	0	2	0	0	1	0	0	0	0	1	1	3	0	0	0	1	0	0	0	1	0	0	1	2
50 <i>Suberites domuncula</i> (Olivi, 1792)	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0
51 <i>Terpios fugax</i> Duchassaing & Michelotti, 1864	0	1	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
52 <i>Polymastia agglutinans</i> Ridley & Dendy, 1886	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

53	<i>Polymastia mamillaris</i> (Müller, 1806)	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
54	<i>Spirastrella cunctatrix</i> Schmidt, 1868	0 0 0 0	0 0 0 0	0 0 0 1	1 2 2 3	0 0 1 2	1 0 0 0
55	<i>Spirastrella minax</i> (Topsent, 1888)	0 0 0 0	0 0 0 0	0 0 0 0	0 1 1 1	0 0 0 0	0 0 0 0
56	<i>Diplastrella bistellata</i> (Schmidt, 1862)	0 0 0 0	0 1 0 0	0 0 0 1	0 0 0 2	0 0 0 3	0 0 0 2
57	<i>Alectona millari</i> Carter, 1879	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
58	<i>Cliona carteri</i> (Ridley, 1881)	0 0 0 0	0 1 0 3	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
59	<i>Cliona celata</i> Grant, 1826	0 1 0 0	1 3 3 3	0 0 0 0	2 2 1 0	2 0 0 1	0 0 0 0
60	<i>Cliona labyrinthica</i> Hancock, 1849	0 0 0 0	0 1 0 3	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
61	<i>Cliona lampa</i> De Laubenfels, 1950	0 0 0 0	0 1 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
62	<i>Cliona schmidti</i> (Ridley, 1881)	0 0 0 0	0 0 0 0	0 0 0 0	0 1 0 1	0 0 0 0	0 0 0 0
63	<i>Cliona vastifica</i> Hancock, 1849	0 0 0 0	0 1 0 1	0 0 0 1	2 1 1 0	0 0 0 0	0 0 0 0
64	<i>Cliona viridis</i> (Schmidt, 1862)	1 2 1 1	1 1 0 0	1 3 3 0	3 2 2 2	0 2 3 3	0 1 2 2
65	<i>Aaptos aaptos</i> (Schmidt, 1864)	0 0 0 0	0 2 0 0	0 0 0 1	0 0 0 2	1 1 2 0	1 0 0 2
66	<i>Pseudotrachya hystrix</i> (Topsent, 1892)	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
67	<i>Tethya aurantium</i> (Pallas, 1766)	0 2 0 1	0 2 0 0	0 3 1 2	0 0 0 0	0 0 0 0	0 2 1 0
68	<i>Tethya citrina</i> Sarà & Melone, 1965	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 2 0 0
69	<i>Chondrilla nucula</i> Schmidt, 1862	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 1 1 0	0 0 1 0
70	<i>Chondrosia reniformis</i> Nardo, 1847	0 0 0 0	0 3 2 1	0 0 0 0	0 2 2 2	2 1 2 2	0 3 3 1
71	<i>Thymosia guernei</i> Topsent, 1895	0 2 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
72	<i>Placospongia decorticans</i> (Hanitsch, 1895)	0 0 0 0	0 1 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
73	<i>Timea cumana</i> Pulitzer-Finali, 1977	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
74	<i>Timea fasciata</i> Topsent, 1934	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 1 0
75	<i>Timea unistellata</i> (Topsent, 1892)	0 1 0 0	0 2 0 1	0 1 0 1	0 0 0 0	0 0 0 1	0 0 0 0
76	<i>Latrunculia citharistae</i> Vacelet, 1969	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
77	<i>Latrunculia insignis</i> Topsent, 1892	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
78	<i>Podospongia lovenii</i> Bocage, 1870	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
79	<i>Acanthella acuta</i> Schmidt, 1862	0 0 0 0	0 0 0 1	0 0 0 1	0 1 2 3	1 1 2 3	1 0 0 0
80	<i>Auletta sessilis</i> Topsent, 1904	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
81	<i>Axinella damicornis</i> (Esper, 1794)	0 0 0 0	0 2 3 3	0 0 0 2	0 1 2 2	1 2 2 3	0 1 1 3
82	<i>Axinella polypoides</i> Schmidt, 1862	0 0 0 0	0 0 0 2	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0
83	<i>Axinella pumila</i> Babic, 1922	0 0 0 0	0 1 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
84	<i>Axinella salicina</i> Schmidt, 1868	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
85	<i>Axinella vasonuda</i> Topsent, 1904	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
86	<i>Axinella verrucosa</i> (Esper, 1794)	0 0 0 0	0 0 2 1	0 0 0 0	0 0 0 0	0 0 1 2	0 0 0 1
87	<i>Phakellia robusta</i> Bowerbank, 1866	0 0 0 0	0 0 0 1	0 0 0 2	0 0 0 0	0 0 0 0	0 0 0 0
88	<i>Phakellia rugosa</i> (Bowerbank, 1866)	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 2	0 0 1 0	0 0 0 0
89	<i>Phakellia ventilabrum</i> (Johston, 1842)	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
90	<i>Bubaris vermiculata</i> (Bowerbank, 1866)	0 0 1 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 1 1
91	<i>Halicnemis patera</i> Bowerbank, 1864	0 0 1 0	0 1 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 2
92	<i>Paratimea constellata</i> (Topsent, 1893)	0 1 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 1
93	<i>Endectyon delaubenfelsi</i> Burton, 1930	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 2 0
94	<i>Raspaciona aculeata</i> (Johnston, 1842)	0 0 0 0	0 2 0 1	0 0 0 0	0 1 1 2	0 0 0 0	0 0 0 2
95	<i>Raspaciona robusta</i> Sarà, 1958	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 1
96	<i>Raspailia(Syringella) agnata</i> (Topsent, 1896)	0 0 0 0	0 0 0 0	0 3 0 0	0 0 0 0	0 0 0 0	0 0 0 0
97	<i>Rhaphidectyon spinosum</i> Topsent, 1927	0 0 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
98	<i>Eurypon cinctum</i> Sarà, 1960	0 0 0 0	0 0 0 0	0 1 0 0	0 0 0 0	0 0 0 0	0 0 1 1
99	<i>Eurypon coronula</i> (Bowerbank, 1874)	0 0 1 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0	0 0 0 0
100	<i>Eurypon lacazei</i> (Topsent, 1891)	0 0 1 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
101	<i>Tricheurypon viride</i> (Topsent, 1889)	0 0 1 0	0 1 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
102	<i>Rhabderemia minutula</i> (Carter, 1876)	0 0 0 0	0 1 0 0	0 0 0 0	0 0 0 1	0 0 0 0	0 0 0 0
103	<i>Agelas oroides</i> (Schmidt, 1864)	0 0 0 0	0 0 0 0	0 0 0 0	0 1 2 2	1 0 2 3	0 0 0 2
104	<i>Merlia normani</i> Kirkpatrick, 1908	0 0 0 0	0 1 0 1	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
105	<i>Batzella inops</i> (Topsent, 1891)	0 0 0 0	0 0 0 0	0 2 1 1	0 0 1 1	0 0 0 2	0 1 1 0
106	<i>Ciocalyptra penicillus</i> Bowerbank, 1864	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	1 0 0 0
107	<i>Halichondria agglomerans</i> Cabioch, 1968	0 0 0 0	0 1 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
108	<i>Halichondria aurantiaca</i> (Schmidt, 1862)	0 0 0 0	0 0 0 0	0 0 0 2	0 0 0 0	0 0 0 0	0 0 1 2
109	<i>Halichondria bowerbanki</i> Burton, 1930	0 0 0 0	0 0 0 0	0 0 1 0	0 0 0 0	0 0 0 0	0 0 0 0

167	<i>Leptolabis megachela</i>	Maldonado, 1992	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0		
168	<i>Stylopus dujardini</i>	(Bowerbank, 1866)	0	0	0	2	0	0	0	2	1	0	0	0	0	0	0	0	0	1		
169	<i>Stylopus nigrescens</i>	Topsent, 1925	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	
170	<i>Phorbas coriaceus</i>	(Fristedt, 1885)	0	2	1	0	0	2	0	0	1	1	0	0	0	0	1	0	0	1	2	0
171	<i>Phorbas fictitius</i>	(Bowerbank, 1866)	1	2	1	0	0	3	1	0	2	3	0	1	0	0	0	1	0	0	0	0
172	<i>Phorbas mercator</i>	(Schmidt, 1868)	0	0	0	0	0	0	0	0	1	3	1	1	0	0	0	0	0	0	0	0
173	<i>Phorbas paupertas</i>	(Bowerbank, 1866)	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
174	<i>Phorbas tenacior</i>	Topsent, 1925	0	0	0	0	0	2	3	0	0	0	0	0	2	3	3	1	0	1	1	0
175	<i>Hamigera hamigera</i>	(Schmidt, 1862)	0	0	0	0	0	0	0	0	2	2	1	0	2	1	0	0	0	0	0	0
176	<i>Pronax dives</i>	(Topsent, 1891)	0	0	0	0	0	2	0	0	0	3	0	0	0	0	0	0	0	0	0	0
177	<i>Pronax fibulatum</i>	Topsent, 1893	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
178	<i>Pronax plumosum</i>	(Montagu, 1818)	2	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0
179	<i>Acanthacarnus sourieji</i>	Lévi, 1952	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
180	<i>Acarnus tortilis</i>	Topsent, 1892	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0
181	<i>Antho involvens</i>	(Schmidt, 1864)	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0
182	<i>Clathria coralloides</i>	(Olivi, 1792)	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
183	<i>Clathria toxistricta</i>	Topsent, 1925	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
184	<i>Microciona armata</i>	Bowerbank, 1866	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
185	<i>Microciona cleistochela</i>	(Topsent, 1925)	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
186	<i>Microciona duplex</i>	(Sarà, 1958)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
187	<i>Microciona gradalis</i>	(Topsent, 1925)	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	1
188	<i>Microciona spinarcus</i>	Carter & Hope, 1889	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
189	<i>Microciona strepsitoxa</i>	Hope, 1889	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
190	<i>Microciona toximajor</i>	(Topsent, 1925)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
191	<i>Microciona toxitenuis</i>	(Topsent, 1925)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0
192	<i>Ophlitaspongia seriata</i>	(Grant, 1826)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
193	<i>Plocamilla elegans</i>	(Ridley & Dendy, 1887)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
194	<i>Plocamilla cf. novizelanica</i>	(Ridley, 1881)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
195	<i>Acervochalina limbata</i>	(Montagu, 1818)	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0
196	<i>Acervochalina nigra</i>	Boury-E. & Lopes, 1985	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
197	<i>Dendroxea lenis</i>	(Topsent, 1892)	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
198	<i>Gellius angulatus</i>	(Bowerbank, 1866)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
199	<i>Gellius apertus</i>	Sarà, 1960	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
200	<i>Gellius cucurbitiformis</i>	Kirkpatrick, 1907	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
201	<i>Gellius fibulatum</i>	(Schmidt, 1862)	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
202	<i>Gellius flagellifer</i>	Ridley & Dendy, 1886	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
203	<i>Gellius lacazei</i>	Topsent, 1893	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
204	<i>Gellius marismedi</i>	Pulitzer-Finali, 1972	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
205	<i>Haliclona citrina</i>	(Topsent, 1892)	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
206	<i>Haliclona elegans</i>	(Bowerbank, 1866)	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
207	<i>Haliclona mediterranea</i>	Griessinger, 1971	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
208	<i>Haliclona parasimulans</i>	Lévi, 1959	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
209	<i>Haliclona subtilis</i>	Griessinger, 1971	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
210	<i>Haliclona aqueductus</i>	(Schmidt, 1862)	1	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
211	<i>Haliclona arenata</i>	(Griessinger, 1971)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
212	<i>Haliclona cinerea</i>	(Grant, 1826)	0	0	0	1	0	0	0	0	3	2	2	0	0	0	0	0	0	0	0	0
213	<i>Haliclona cratera</i>	Schmidt, 1862	0	0	0	0	2	0	1	0	0	0	0	0	0	2	0	0	1	0	2	2
214	<i>Haliclona fulva</i>	(Topsent, 1893)	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1
215	<i>Haliclona implexa</i>	(Schmidt, 1868)	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	2
216	<i>Haliclona mucosa</i>	(Griessinger, 1971)	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	0
217	<i>Haliclona perlucida</i>	(Griessinger, 1971)	0	0	0	1	0	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0
218	<i>Haliclona pocilliformis</i>	(Griessinger, 1971)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
219	<i>Halichona rosea</i>	(Bowerbank, 1866)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
220	<i>Haliclona sarai</i>	(Pulitzer-Finali, 1969)	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1
221	<i>Adocia reptans</i>	Griessinger, 1971	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
222	<i>Adocia simulans</i>	(Johnston, 1842)	0	0	0	0	3	0	0	0	2	0	0	0	2	0	0	0	0	0	0	1
223	<i>Adocia varia</i>	Sarà, 1958	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	2	0

224	<i>Adocia venata</i>	Sarà, 1960	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
225	<i>Amphimedon rustica</i>	(Schmidt, 1868)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
226	<i>Callyspongia septimaniensis</i>	Griessinger, 1971	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
227	<i>Callyspongia balearica</i>	(Ferrer-Hernández, 1916)	0	0	0	0	0	0	0	2	0	0	3	2	0	0	0	0	0	0
228	<i>Callyspongia coriacea</i>	(Schmidt, 1868)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
229	<i>Callyspongia expansa</i>	(Sarà, 1960)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
230	<i>Callyspongia subcornea</i>	(Griessinger, 1971)	0	0	0	0	0	0	0	0	0	0	1	2	0	2	0	0	0	0
231	<i>Petrosia ficiformis</i>	(Poiret, 1789)	0	2	0	2	0	3	2	0	0	0	0	0	1	2	0	1	3	0
232	<i>Oceanapia perforata</i>	(Sarà, 1960)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
233	<i>Pellina fistulosa</i>	(Bowerbank, 1866)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
234	<i>Pellina semitubulosa</i>	(Lieberkühn, 1859)	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1
235	<i>Hippospongia communis</i>	(Lamarck, 1813)	0	0	0	0	0	0	0	0	0	0	2	2	1	0	0	2	2	0
236	<i>Spongia nitens</i>	(Schmidt, 1862)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
237	<i>Spongia officinalis</i>	Linné, 1759	0	0	0	0	2	0	1	0	1	0	3	0	0	2	0	0	1	0
238	<i>Spongia virgultosa</i>	(Schmidt, 1868)	0	0	0	0	0	0	1	1	0	1	1	2	2	2	3	2	3	1
239	<i>Cacospongia mollior</i>	Schmidt, 1862	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
240	<i>Cacospongia scalaris</i>	Schmidt, 1862	0	2	0	0	0	1	0	1	0	0	0	0	0	2	0	0	0	0
241	<i>Faciospongia cavernosa</i>	(Schmidt, 1862)	0	0	0	0	0	0	0	0	0	0	2	2	3	0	0	0	0	0
242	<i>Hyrtios collectrix</i>	(Schulze, 1879)	0	0	0	0	0	2	0	2	2	0	0	0	0	1	0	0	0	0
243	<i>Ircinia dendroides</i>	(Schmidt, 1862)	0	2	1	0	0	0	3	0	1	0	0	1	0	0	2	0	0	0
244	<i>Ircinia fasciculata</i>	(Pallas, 1766)	0	1	0	0	0	3	0	0	2	0	0	3	2	2	1	3	2	3
245	<i>Ircinia foetida</i>	(Schmidt, 1862)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
246	<i>Ircinia muscarum</i>	(Schmidt, 1864)	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	1	0
247	<i>Ircinia oros</i>	(Schmidt, 1864)	0	0	0	0	0	2	2	3	0	0	0	0	2	2	0	0	2	1
248	<i>Ircinia pipetta</i>	(Schmidt, 1868)	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
249	<i>Sarcotragus spinulosum</i>	(Schmidt, 1862)	0	2	0	0	0	2	0	0	0	1	0	1	3	2	2	1	2	0
250	<i>Ircinia variabilis</i>	(Schmidt, 1862)	0	0	0	0	0	2	0	0	2	2	0	0	3	2	2	3	0	2
251	<i>Dysidea avara</i>	(Schmidt, 1862)	0	0	0	0	0	0	0	0	0	0	0	2	3	2	0	0	1	2
252	<i>Dysidea fragilis</i>	(Montagu, 1818)	0	1	0	0	0	2	0	0	2	1	1	0	0	2	2	0	0	0
253	<i>Dysidea tupa</i>	(Martens, 1824)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0
254	<i>Spongionella gracilis</i>	(Vosmaer, 1883)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
255	<i>Spongionella pulchella</i>	(Sowerby, 1806)	0	1	0	1	0	3	3	2	2	1	1	0	0	0	0	0	1	3
256	<i>Aplysilla sulfurea</i>	Schulze, 1878	0	0	0	0	0	2	0	2	2	0	0	1	0	0	0	1	1	1
257	<i>Chelonaplysilla noevus</i>	(Carter, 1876)	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
258	<i>Pleraplysilla</i> sp.		0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
259	<i>Darwinella australiensis</i>	Carter, 1885	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
260	<i>Hexadella detritifera</i>	Topsent, 1913	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
261	<i>Hexadella racovitzai</i>	Topsent, 1896	0	0	1	0	0	1	2	3	0	0	0	0	0	1	2	0	0	0
262	<i>Pleraplysilla minchini</i>	Topsent, 1905	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
263	<i>Pleraplysilla spinifera</i>	(Schulze, 1878)	0	0	0	0	1	3	1	0	1	0	0	0	1	1	2	0	1	0
264	<i>Halisarca dujardini</i>	Johnston, 1842	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	1
265	<i>Aplysina aerophoba</i>	(Schmidt, 1862)	1	1	0	0	2	3	0	0	0	0	0	0	0	0	2	0	1	2
266	<i>Aplysina cavernicola</i>	(Vacelet, 1959)	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0