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# Distribution patterns in Atlantic hydroids

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Key words: Hydrozoa; zoogeography; faunal affinities; Atlantic Ocean.
The present study is a first attempt to comparing the hydroid faunas of the various zoogeographic areas of the Atlantic Ocean. We restricted ourselves to species of the orders Antho- and Leptomedusae, of which 1050 species were taken into account. The classification of zoogeographic areas used follows Ekman and Briggs, with slight modifications; thus, the Strait of Gibraltar is here considered as a separate zoogeographic area due to its character of a transition zone between several areas in the North-eastern Atlantic Region. Species were arranged into zoogeographic groups to compare the faunal composition of the various zoogeographic areas. The Dice similarity index was used for each comparison.
The fauna of North-eastern Region can be split into three groups of similarity: 1) that of the Mediterranean and Lusitanian Provinces plus the Boreal Subregion, 2) that of the Strait of Gibraltar and the Mauritanian Province, and 3) that of the Senegalian Subregion (probably due to the lack of knowledge of its fauna). Just like in Senegalian Subregion, the South-eastern Atlantic Region takes an isolated position (presumably at least in part because the vast majority of data is from South Africa alone). In the North-western Region, the North American and Caribbean Provinces are closely related to each other and to the Brazilian Subregion. The Arctic and Antarctic (together with the Argentinian Subregion) are the most isolated regions.
As a general rule, widely distributed species dominate in each region. In the North-eastern Region, the number of such species increases from higher latitudes to the Equator. In the Mediterranean, their number decreases in favour of endemic species. The fauna of the Strait of Gibraltar is more related to that of the Atlantic part of the North-eastern Region than to that of the Mediterranean Province. The high number of endemics in the South-eastern Region and in the Caribbean Province is remarkable. It is also noticeable that the Brazilian Province shares more species with the North-western Region than with the South-eastern Region. The Antarctic presents a similar percentage of endemics as the Arctic. Some distribution patterns of Antho- and Leptomedusae can be explained by the general current system in the Atlantic Ocean.

## Introduction

The unexplored portions of the world's oceans are so vast that the descriptive stage of their faunas is far from being completed (Van der Spoel: in Boero & Bouillon, 1993). Nevertheless, knowledge of the hydrozoan fauna of both the North-eastern Atlantic and the Mediterranean Sea is at present such to allow an attempt to sketch their affinities. Moreover, several other areas of the Atlantic have been the target of sampling efforts during the present century, offering the possibility of making preliminary comparisons throughout the whole ocean.

In the present work, affinities of the Antho- and Leptomedusae fauna of the main zoogeographic areas of the North-eastern Atlantic are discussed. The Strait of Gibraltar, limited by the meridians of 7°W and 4°E, and by the Iberian and African coasts, is recognised as a distinct zoogeographic area due to its character of a transition zone between the Mediterranean Sea and the Atlantic.

A latitudinal comparison of the hydroid faunas of the main zoogeographic regions (see Methods) in the Atlantic is attempted, even though the faunas of some regions are not very well known.

## Methods

The species of Antho- and Leptomedusae considered for the present study number 1050. As many reliable records as possible, mainly from recent authors, have been taken into account. We have basically followed zoogeographic area classification by Ekman (1953) and Briggs (1974) with slight adaptations (e.g. López de la Cuadra & García-Gomez ,1992; Carballo et al., 1997). This classification, comprising 6 main zoogeographic regions, 4 subregions and 7 provinces, is presented below (tab. 1). Added to this table are the literature references that formed the basis for the faunal census made for each of these areas. Some other papers, providing useful taxonomic reviews and additional information on distribution, were also consulted (Bouillon, 1985; Petersen, 1990; Bouillon et al., 1995; Sengonzac & Vervoort, 1995; Schuchert, 1997). Faunal records from the Strait of Gibraltar are based on Ramil & Vervoort (1992), Medel (1996), Patriti (1970), and Medel & López-González (1996).

Table 1. Classification of zoogeographic regions, subregions and provinces in the Atlantic Ocean used in the present paper, modified after Ekman, 1953, and Briggs, 1974 (cf. fig. 1).

ARCTIC REGION (AR): Fraser, 1921; Kramp, 1961; Calder, 1971; Stepanjants, 1989; Zibrowius & Cairns, 1992.
NORTH-EASTERN REGION:
- BOREAL SUBREGION (BO): Leloup, 1952; Kramp, 1961; Teissier, 1965; Bouillon, 1971; Christiansen, 1972; Cornelius & Ryland, 1990; Svoboda & Cornelius, 1991; Zibrowius & Cairns, 1992; Cornelius, 1995a, 1995b.
- ATLANTO-MEDITERRANEAN SUBREGION:
  - a. *Lusitanian Province* (LU): Kramp, 1961; Rees & White, 1966; Castric-Fey, 1969, 1970; Svoboda & Cornelius, 1991; Cornelius, 1992a; Ramil & Vervoort, 1992; Zibrowius & Cairns, 1992; Medel & López-González, 1996.
  - b. *Mediterranean Province* (ME): Kramp, 1961; Svoboda & Cornelius, 1991; Ramil & Vervoort, 1992; Zibrowius & Cairns, 1992; Boero & Bouillon, 1993; Medel & López-González, 1996.
  - c. *Mauritanian Province* (MA): Kramp, 1961; Patriti, 1970; Ramil & Vervoort, 1992; Zibrowius & Cairns, 1992; Medel & Vervoort, in prep.
- SENEGALIAN SUBREGION (SE): Vervoort, 1959; Kramp, 1961; Gili et al., 1989.

SOUTH-EASTERN REGION (SA): Millard, 1975.
NORTH-WESTERN REGION:
- a. *North-American Province* (NA): Nutting, 1900, 1904, 1915; Fraser, 1944; Kramp, 1961; Calder, 1971, 1972, 1983, 1986, 1988, 1991; Vervoort, 1972.
- b. *Caribbean Province* (CA): Kramp, 1961; Vervoort, 1968, 1972; Cairns, 1986.

SOUTH-WESTERN REGION:
- BRAZILIAN SUBREGION (BR): Kramp, 1961; Migotto, 1996.
- ARGENTINIAN SUBREGION:
  - a. *Bonaerensian Province* (BN): Kramp, 1961; Blanco, 1967a, 1967b, 1968; Vervoort, 1972; Genzano & Zamponi, 1997.
  - b. *Magellanic Province* (MG): Kramp, 1961; Blanco, 1967a, 1967b, 1968; Stepanjants, 1970; Vervoort, 1972; Genzano & Zamponi, 1997.

ANTARCTIC REGION (AT): Kramp, 1961; Stepanjants, 1979; Peña Cantero, Garcia Carracosa & Vervoort, 1995, 1997; Peña Cantero & Vervoort, 1995; 1996a, 1996b; Peña Cantero, Svoboda & Vervoort, 1996, 1997.

The Dice similarity index was applied to determine faunal affinities between regions. The computer programs Microsoft Excel, Harvard Graphics 1.0 and NTSYS-PC 1.8 were used for calculations.

In order to study the faunal composition of the regions considered, species were arranged into zoogeographic groups. These groups were based on and modified after Aristegui & Cruz (1986) and López de la Cuadra & García-Gómez (1992) (cf. table 2).

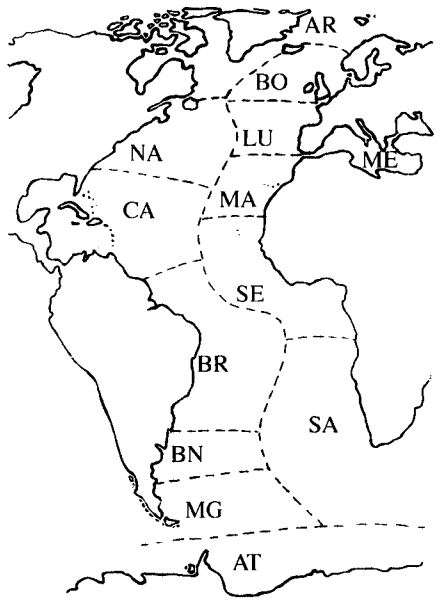


Fig. 1. The zoogeographical areas considered of the Atlantic Ocean. Abbreviations on the map: AR = Arctic Region; AT = Antarctic Region; BN = Bonaerensian Province; BO = Boreal Subregion; BZ = Brazilian Subregion; CA = Caribbean Province; LU = Lusitanian Province; MA = Mauretanian Province; ME = Mediterranean Province; MG = Magellanic Province; NA = North-American Province; SA = South-eastern Region; SE = Senegalian Subregion.

## Results

Table 2 shows comparatively the zoogeographic composition of species of Antho- and Leptomedusae in the different zoogeographic regions in the Atlantic. Although not shown in this table (to keep it conveniently arranged), the numbers and percentages of subtropical and relatively cold water species in the groups *AM* and *NE* were also taken into account for comparison. This was also done for the groups *WA* and *AA*, but separately for the two hemispheres.

The widely distributed groups (*AA, CT, WD, CO*) are dominant in the North-eastern Atlantic. In the Boreal Subregion and in the Lusitanian Province, the percentage of North-eastern Atlantic species absent (*NE*) and present (*AM*) in the Mediterranean Sea is similar. In the Strait of Gibraltar, there are more North-eastern Atlantic species (*NE*) than Mediterranean endemics (*ME*). In the South-eastern Region, endemics together with Indo-Pacific species (exclusively present in this region of the Atlantic) constitute the highest percentage (34.4% and 15.4%, respectively). In accordance with the North-eastern Region, the widely distributed groups are also the dominant ones in the North-western Region. In the Brazilian Subregion, the percentage of endemic species is higher (species of *WA* with a subtropical character). This is also so in the Arctic Region (35.5%). In the Antarctic Region endemics (33%) and species shared with the Magellanic Province (*WA*, 53%) predominate.

Figure 2a shows the faunal affinities of the regions analysed using the total presence/absence species data by applying the Dice similarity index. Three groups of similarity are differentiated. The first includes most areas from the North-eastern Region and can be split into two subgroups: a) comprising the Strait of Gibraltar and the Mauritanian Province, and b) comprising the Boreal Subregion and the Lusitanian and Mediterranean Provinces. The Senegalian Subregion is excluded from this group.

Table 2. Absolute numbers (upper part of table) and percentages (lower part of table) of zoogeographic groups of species in the different zoogeographic areas of the Atlantic Ocean.

Abbreviations for zoogeographic groups : *AA* = Amphi-Atlantic; *AM* = North-eastern Atlantic present in the Mediterranean; *AR* = Arctic endemic; *AT* = Antarctic endemic; *CO* = Cosmopolitan; *CT* = Circumtropical; *EA* = Widely distributed in Eastern Atlantic; *ME* = Mediterranean endemic; *NE* = North-eastern Atlantic absent in the Mediterranean; *SE* = South-eastern Atlantic; *WA* = Western Atlantic; *WD* = Widely distributed in warm temperate waters around the World; ? = Unknown.

Abbreviations for zoogeographic areas: AR = Arctic Region; AT = Antarctic Region; BN = Bonaerensian Province; BO = Boreal Subregion; BZ = Brazilian Subregion; CA = Caribbean Province; LU = Lusitanian Province; MA = Mauretanian Province; ME = Mediterranean Province; MG = Magellanic Province; NA = North-American Province; SA = South-eastern Region; SE = Senegalian Subregion.

| Group / Area | *ME* | *AM* | *NE* | *SE* | *EA* | *WA* | *AT* | *AR* | *AA* | *CT* | *WD* | *CO* | ? | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AR | 0 | 7 | 17 | 0 | 1 | 7 | 0 | 62 | 34 | 0 | 2 | 42 | 3 | 175 |
| BO | 0 | 39 | 42 | 0 | 4 | 0 | 0 | 0 | 52 | 1 | 47 | 37 | 1 | 223 |
| LU | 0 | 34 | 37 | 0 | 7 | 0 | 0 | 0 | 41 | 2 | 58 | 35 | 1 | 215 |
| Str. Gib. | 4 | 23 | 9 | 0 | 3 | 0 | 0 | 0 | 17 | 2 | 42 | 22 | 4 | 126 |
| ME | 57 | 60 | 0 | 0 | 7 | 0 | 0 | 0 | 46 | 5 | 89 | 34 | 10 | 308 |
| MA | 0 | 11 | 16 | 0 | 4 | 0 | 0 | 0 | 19 | 4 | 30 | 21 | 0 | 105 |
| SE | 0 | 2 | 28 | 0 | 3 | 0 | 0 | 0 | 26 | 3 | 33 | 14 | 0 | 109 |
| SA | 0 | 0 | 0 | 126 | 7 | 0 | 0 | 0 | 38 | 6 | 51 | 25 | 0 | 253 |
| NA | 0 | 0 | 0 | 0 | 0 | 65 | 0 | 0 | 70 | 4 | 44 | 37 | 2 | 222 |
| CA | 0 | 0 | 0 | 0 | 0 | 132 | 0 | 0 | 47 | 10 | 40 | 23 | 3 | 255 |
| BR | 0 | 0 | 0 | 0 | 0 | 35 | 0 | 0 | 31 | 5 | 26 | 8 | 0 | 105 |
| BN | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 13 | 0 | 14 | 13 | 0 | 60 |
| MG | 0 | 0 | 0 | 0 | 0 | 94 | 0 | 0 | 17 | 0 | 12 | 17 | 1 | 141 |
| AT | 0 | 0 | 0 | 0 | 0 | 45 | 28 | 0 | 3 | 0 | 0 | 7 | 2 | 85 |

| Group / Area | *ME* | *AM* | *NE* | *SE* | *EA* | *WA* | *AT* | *AR* | *AA* | *CT* | *WD* | *CO* | ? |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AR | 0 | 4 | 9.7 | 0 | 0.6 | 4 | 0 | 35.5 | 19.4 | 0 | 1.1 | 24 | 1.7 |
| BO | 0 | 17.5 | 18.8 | 0 | 18 | 0 | 0 | 0 | 23.3 | 0.5 | 21 | 16.6 | 0.5 |
| LU | 0 | 15.8 | 17.2 | 0 | 3.2 | 0 | 0 | 0 | 19.1 | 0.9 | 27 | 16.3 | 0.5 |
| Str. Gib. | 3.2 | 18.2 | 7.1 | 0 | 2.4 | 0 | 0 | 0 | 13.5 | 1.6 | 33.3 | 17.6 | 3.1 |
| ME | 18.5 | 19.5 | 0 | 0 | 2.3 | 0 | 0 | 0 | 14.9 | 1.6 | 29 | 11 | 3.2 |
| MA | 0 | 10.5 | 15.2 | 0 | 3.8 | 0 | 0 | 0 | 18.1 | 3.8 | 28.6 | 20 | 0 |
| SE | 0 | 1.8 | 25.7 | 0 | 2.8 | 0 | 0 | 0 | 23.8 | 2.8 | 30.3 | 12.8 | 0 |
| SA | 0 | 0 | 0 | 49.8 | 2.8 | 0 | 0 | 0 | 15 | 2.4 | 20.2 | 9.8 | 0 |
| NA | 0 | 0 | 0 | 0 | 0 | 29.3 | 0 | 0 | 31.5 | 1.8 | 19.8 | 16.6 | 1 |
| CA | 0 | 0 | 0 | 0 | 0 | 51.8 | 0 | 0 | 18.4 | 3.9 | 15.7 | 9 | 1.2 |
| BR | 0 | 0 | 0 | 0 | 0 | 33.3 | 0 | 0 | 29.5 | 4.8 | 24.8 | 7.6 | 0 |
| BN | 0 | 0 | 0 | 0 | 0 | 33.3 | 0 | 0 | 21.7 | 0 | 23.3 | 21.7 | 0 |
| MG | 0 | 0 | 0 | 0 | 0 | 66.7 | 0 | 0 | 12 | 0 | 8.6 | 12 | 0.7 |
| AT | 0 | 0 | 0 | 0 | 0 | 53 | 33 | 0 | 3.5 | 0 | 0 | 8.2 | 2.3 |

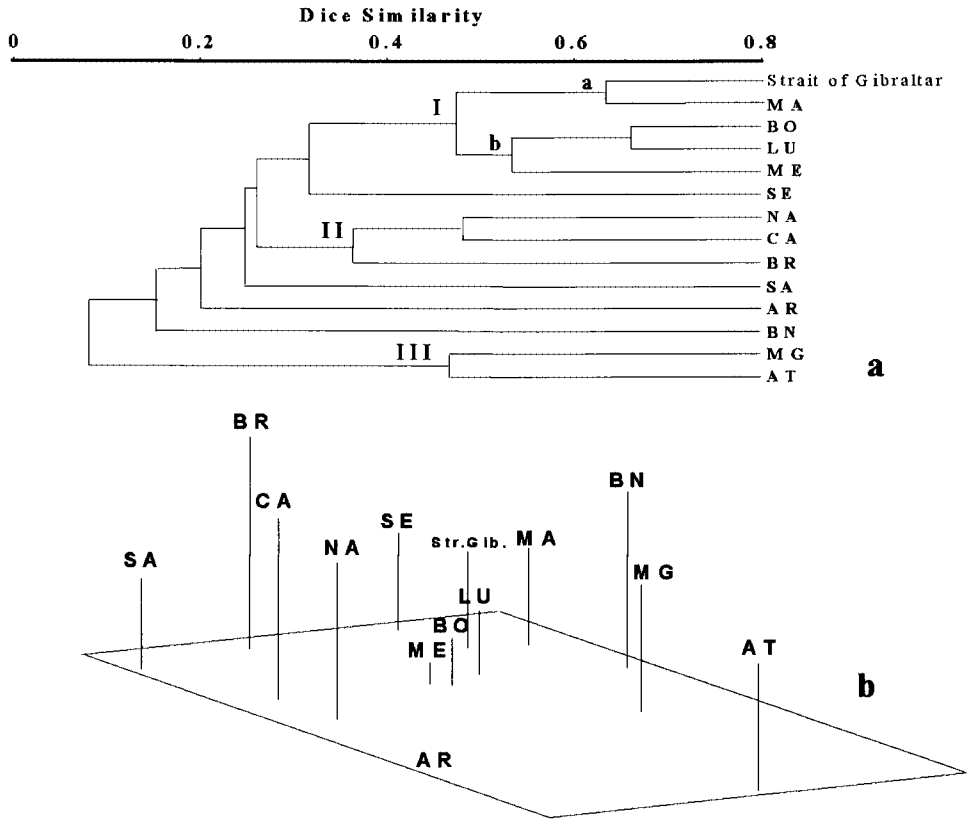


Fig. 2. Dice similarities between the zoogeographical areas: a, dendrogram. b, MDS-3D. Abbreviations: AR = Arctic region; AT = Antarctic Region; BN = Bonaerensian Province; BO = Boreal Subregion; BZ = Brazilian Subregion; CA = Caribbean Province; LU = Lusitanian Province; MA = Mauretanian Province; ME = Mediterranean Province; MG = Magellanic Province; NA = North-American Province; SA = South-eastern Region; SE = Senegalian Subregion; Str. Gib. = Strait of Gibraltar.

The South-eastern Region and the Bonaerensian province also take an isolated position. The second group comprises the North-western Region and the Brazilian subregion, and the third group the Antarctic Region and the Magellanic Province.

The results obtained from the dendrogram are to a considerable extent corroborated by MDS-3D analysis (fig. 2b). Here too, the Arctic and Antarctic Regions are the most isolated ones, followed by the Magellanic and Bonaerensian Provinces (together forming the Argentinian Subregion), which are close to each other. The areas of the North-eastern Region form a group, with the Senegalian Subregion and the Mauritanian Province in a relatively isolated position. The North American and Caribbean Provinces form a group with the Brazilian Subregion, the latter two being more close to each other. In accordance with the dendrogram (fig. 2a), the South-eastern Region takes an isolated position.

## Discussion

The high proportion of Antho- and Leptomedusae with a wide distribution in the world is well known (Cornelius, 1992b, 1995a, 1995b). These wide distributions are often explained by high dispersive capability of the species, by certain aspects of their life cycle or life history such as resting stages or encystment, rafting, or even fouling (Cornelius, 1992a, 1992b; Boero et al., 1992; Boero & Bouillon, 1993; Gili & Hughes, 1995).

The best known parts of the Atlantic as far as hydroids are concerned are the North-eastern Region (cf. Cornelius, 1992b) and the Mediterranean (cf. Boero & Bouillon, 1993). Other areas are less well explored. Thus, comparisons with these are tentative and preliminary.

### North-eastern Region

The zoogeographic areas of the North-eastern Atlantic Region show a high uniformity in general terms, which is especially true with regard to the Mediterranean and Lusitanian Provinces and the Boreal Subregion (fig. 2a). The cumulative percentage of widely distributed groups (*AA+CT+WD+CO*) increases from higher latitudes to the Equator from about 61% to 70%. Considering each of these groups separately, this pattern is shown mainly by the groups *CO* and *CT*, less so in *WD*, and not in *AA*. The lower percentage of widely distributed species in the Mediterranean Province (56.5%) is probably due to the particular conditions of this sea, and will be discussed below. The Mauritanian province has a lower percentage of endemic species [group *NE* with a subtropical character, 3.8% (4 of 105 species)] than have the Boreal Subregion and the Lusitanian Province [group *NE* with a cool-temperate character, 17% (38 of 223 species) and 11.1% (24 of 215 species) respectively]. These results might be due to the greater sampling effort in the last mentioned areas since the second half of the 19th century, whereas data from the African coasts are still scarce (e.g. Vervoort, 1959; Patriti, 1970; Gili et al., 1989).

Taking into consideration the similar number of records from the Senegalian Subregion and the Mauritanian Province (about 100 species for each area), the high percentage of endemics counted for the Senegalian Subregion [16.5% (18 of 109 species)] is surprising. This may be explained by most records from the latter region bearing upon medusae (the study of which has often been neglected in other regions) whereas mainly bearing upon the hydroid phase in the Mauritanian Province.

### Mediterranean Province and the Strait of Gibraltar

The Mediterranean hydrozoan fauna is more similar to the Atlantic fauna of Europe than to that of Africa. Boero & Bouillon (1993) found that the Hydroidomedusae have a faunal composition dominated mainly by endemic, boreal and Atlanto-Mediterranean species (in this order), if the widely distributed groups are excluded. Nevertheless, the fauna of the Mediterranean coasts of Europe is better known than that of the African side, which influences the discussion.

The Mediterranean fauna takes a special position within the North-eastern Region. The percentage of amphi-Atlantic (*AA*) and cosmopolitian (*CO*) species

decreases, not following the same pattern shown for the remaining areas of the North-eastern Region This decrease is due to a higher percentage of species with a more restricted distribution (endemic and Atlanto-Mediterranean), as a consequence of the particular geographic character of this almost closed sea. Another interesting faunal aspect of the Mediterranean may be commented upon, viz. the presence of Indo-Pacific species which are absent from the Atlantic. Indo-Pacific species were considered non-existent in the Mediterranean by Picard (1958) and very few by Por (1978) (perhaps 3 species). However, recently their number was stated to comprise 8% by Boero & Bouillon (1993). In respect of the two orders analysed in the present paper (Antho- and Leptomedusae), 5.5% (17 of 308 species) of the Mediterranean species are absent from the Atlantic but well distributed throughout Indo-Pacific areas. This may be due to Lessepsian migration (Boero & Bouillon, 1993), even though no information on the Eastern Mediterranean hydrozoan fauna is available from before the Suez Canal was established as a route between the Mediterranean and the Red Sea.

The Strait of Gibraltar is not considered an important biogeographic barrier but rather a boundary or transition zone between the Atlanto-Mediterranean provinces (Naranjo et al., 1998). A preliminary study of the faunal affinities of the hydrozoan fauna of the Iberian Peninsula was carried out by Medel & López-González (1996). In that first attempt, the Iberian side of the Strait of Gibraltar was identified as a separate faunal unit, though closely resembling the fauna of the Mediterranean Iberian coasts. In the present study, both sides (European and African) of the Strait of Gibraltar are considered, and a greater similarity to the Mauritanian fauna is shown. Comparable results were obtained by Carballo et al. (1997) from study of littoral sponges. These authors commented on the possible origin of Mediterranean endemics from a subtropical Atlantic stock in the Pliocene that lived near the present Strait, and which could have entered when it opened (see also Pérès, 1989). Subtropical affinities of the Mediterranean fauna have been previously suggested for other taxa (Ballesteros, 1989; Bibiloni et al., 1989). Affinities of the fauna of the Strait of Gibraltar with adjacent areas were discussed for cheilostomate bryozoans (López de la Cuadra & García-Gómez, 1992), anthozoans (López-González, 1993) and ascidians (Naranjo et al., 1998), suggesting a high affinity with the Lusitanian (bryozoans) and Mediterranean Provinces (anthozoans and ascidians). However, as shown by Medel & López-González (1996), the conclusions of these authors were biassed by the limits of the area studied, mainly restricted to the European side of the Strait. Further studies on these and other benthic invertebrate groups, considering both sides of the Strait, should be carried out to establish the affinities of its fauna more accurately.

In the present study, the faunal composition of the Strait of Gibraltar was found to include a percentage of widely distributed species (66%; *AA+CT+WD+CO*) intermediate between that of the Boreal Subregion (61.4%) and the Mauritanian Province (70.5%), and by showing a percentage of endemics similar to that of other Atlantic areas of the North-eastern Region, with a number of Atlantic species twice that of Mediterranean species. Ramil & Vervoort (1992) also found more Atlantic species. In their opinion, the depth preference of some species is more decisive than bottom or hydrographic conditions to enable crossing of the barrier of the Strait of Gibraltar. Finally, the majority of the Atlanto-Mediterranean species have a cool-temperate character (15 of 23 species).

## South-eastern Region

The South-eastern Region (SA) takes an isolated position within the various Eastern Atlantic zoogeographic areas (fig. 2a). The detailed available knowledge of the fauna of South Africa (Millard, 1975) may explain the low similarity between this region and the rest of the Eastern Atlantic.

A unique combination of factors causes the marine invertebrate fauna of South Africa to be one of the richest in species in the world (Williams, 1992). These factors include: 1) the importance, in the present and the past, of its harbours as a transit station for international shipping, 2) the influence of two major current systems (the cold upwelling Benguela Current on its west coast, and the warm Agulhas Current on its east coast), and 3) the expanse and isolation of the Agulhas bank.

The special situation with regard to the currents and the Agulhas Bank might explain the great number of endemics in South African waters [34.4% (87 of 253 species)]. Further, the confluence of Indo-Pacific and Atlantic waters, explains the high percentage of Indo-Pacific species [15.4% of the total (39 of 253 species)] in this area, which are absent from the rest of the Atlantic.

## North-western and South-western Regions

In the present study a close relationship is determined between the North-western Region (*NA* and *CA*) and the Brazilian Subregion (fig. 2a). Whereas the Caribbean Province shows a higher percentage of endemics [*WA* with a subtropical character, 40.8% (104 of 255 species)], widely distributed species are dominant in the North American and Brazilian areas, with endemics as the second important group [14.4% (32 of 222 species) and 20% (24 of 105 species) respectively].

The relatively high percentage [8.6% (9 of 105 species)] of Brazilian species in common with the North-western Region, and the very low percentage [about 1% (1 of 105 species] in common with the Argentinian Subregion is remarkable. Thus, Migotto (1996) found that the hydroid fauna of shallow water around São Sebastião (Brazilian Subregion) was typically tropical and more similar to that of the Caribbean than to that of Patagonia. The remaining areas of the South-western Atlantic, and especially the Magellanic Province, show a similar reduction in the percentage of widely distributed species, and a tendency towards a narrower distribution. A particular similarity is shown between the Magellanic Province and the Antarctic Region, explained by the close proximity of the Antarctic Peninsula, connected with the South American continent by a chain of islands. A striking difference in species diversity occurs between the Magellanic and Bonaerensian Provinces (141 versus 60 species). This was also noted by Genzano & Zamponi (1997), who exclusively studied the continental shelf species (94 versus 48 species). They explained this difference by the Magellanic Province being influenced by colder and more productive waters, and they further suggested that the general absence of extensive regions of hard substrate on the Argentine continental shelf might explain the apparent absence of some groups of species in the Bonaerensian Province, thus adding to the relatively low number of species in that province. This low number of species explains the isolated position of the Bonaerensian Province in fig 2a.

### Arctic and Antarctic Regions

The Arctic and Antarctic regions differ strikingly in the character of their hydroid faunae. The Arctic has 44.5% of widely distributed species, with another 13.7% also present in the North-eastern Atlantic Region (*AM, ME*). These high percentages are explained by the proximity of the American and Eurasian continents. Arctic endemics make out 35.5% of the species.

In contrast, the Antarctic is rather isolated from the American and African continents, and only its strong relation to the Magellanic Province is worth mentioning; no less than 53% of species is shared by these two areas (*WA* in tab. 2). Only 11.7% of Antarctic species may be considered of wide distribution (tab. 2: *AA+CO*). In addition, a historical faunal stock inhabiting the shores and shelf of the Antarctic continent must have made possible the evolution of 33% of strictly Antarctic species.

## Distribution patterns of Antho- and Leptomedusae in relation to the general current system in the Atlantic Ocean.

The general current system throughout the Atlantic Ocean (fig. 3) contributes to an explanation of some of the distribution patterns of hydroid species within it.

The North-American Province is characterised by a high percentage of amphi-Atlantic species and the same is true for the Arctic, Boreal, and Lusitanian areas, all of them influenced by the Gulf Stream. The surface water of this current originates along the North American coast, and flows in north-eastern and eastern direction (giving rise the North Atlantic Current), even reaching the Arctic Region, and providing an excellent means of transport for the different dispersal stages. The relative proximity of these coasts contributes to this. Most of the amphi-Atlantic species in subtropical areas have a cool-temperate character. This distribution pattern presumably resulted from transportation via the Equatorial Current that crosses the Atlantic in East-West direction. There are few amphi-Atlantic species in the Southern Hemisphere. This is perhaps partly due to the great breadth of the South Atlantic, but more likely first of all because of lack of knowledge of the South Atlantic hydroid fauna.

In the Western Atlantic, the higher similarity of the North-American and Caribbean Provinces and the Brazilian Subregion, might be due in part to several connected warmer currents bathing the great part of these areas (fig. 3). In this way, in the Brazilian Subregion, the percentage of species in common with the Northern and Southern Hemispheres is 8.5% (9 of 105 species) and 1% (just 1 of 105 species) respectively.

In the Southern Hemisphere, the similarity between the Magellanic and Antarctic areas is probably due to the influence of colder currents, which affect both areas at higher latitudes. The percentage of species with a wide distribution along the Western Atlantic coast is negligible. Only a single species (*Sertularella conica* Allman, 1877), absent in the Arctic and Antarctic Regions, is known to occur throughout the Northwestern and South-western Regions, so far excepting the Bonaerensian Province. However, the coastline of the Western Atlantic is very long, extending from the Arctic almost to the Antarctic, and its hydroid fauna has been studied well only in a few places. Hence, further knowledge is needed to confirm the present conclusions.

In the North-eastern Region, the higher similarity of the hydroid fauna of the Boreal Subregion to that of the Lusitanian Province may partly result from the influence of the North Atlantic Current, which affects both areas. Figure 2a shows the high similarity between the Antho- and Leptomedusae fauna of the Strait of Gibraltar and the Mauritanian Province. The relatively cool Canary Current flows from the western Iberian coast (Lusitanian Province) to the Mauretanian Province, contributing to the faunal similarity of these areas. Although the west coast of the Iberian Peninsula is slightly affected by the Canary Current, the scant knowledge of the hydrozoan fauna of this coast hinders derivation of a higher similarity between the Lusitanian and Mauretanian Provinces. The Mediterranean has its own pattern of currents. The role of water exchange with the Atlantic through the Strait of Gibraltar was recently discussed by Medel and López-González (1996).

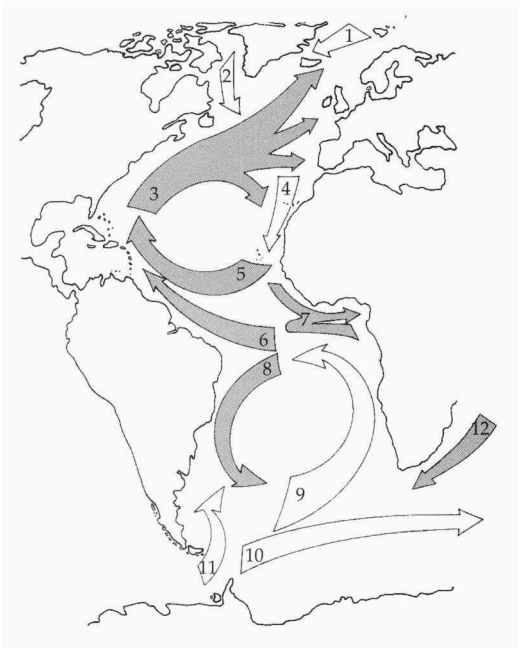


Fig. 3. General current pattern in the Atlantic Ocean: 1, Greenland Current; 2, Labrador Current; 3, Gulf Stream; 4, Canary Current; 5, North Equatorial Current; 6, South Equatorial Current; 7, Guinea Current; 8, Brazil Current; 9, Benguela Current; 10, Occidental Drift; 11, Falkland Current; 12, Agulhas Current. Relatively warm currents shaded, relatively cold currents unshaded.

The low percentage of widely distributed species in different areas along the Eastern Atlantic coast (group *EA*) is remarkable, the highest being 3.8% (Mauritanian Province). This may be caused by interruptions of oceanic currents (fig. 3) in the Eastern Atlantic, with the alternation of warmer and cooler water masses, which might limit a wider distribution of many species throughout the area.

Considering the high capacity of dispersion of Hydroidomedusae in general, and the plasticity of their life cycles (i.e. to disappear in unfavourable seasons), a higher similarity of faunas throughout the Atlantic Ocean may be expected if these become better known. On the other hand, more intense collecting efforts would improve our knowledge of local faunas, and presumably increase the number of endemic species.

It is to be regretted that the study of hydrozoan diversity in general is increasingly being abandoned by the scientific community (Boero et al., 1997), despite taxonomic studies being the base of zoogeographic knowledge.

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