Diversity and distribution of the Gastropoda Opisthobranchia from the Atlantic Ocean: A global biogeographic approach

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SUMMARY: A zoogeographic study of the Opisthobranchia (Mollusca, Gastropoda) from the Atlantic Ocean was carried out. Data on Opisthobranch occurrence were collated from literature records and databases. An estimated 1066 species were considered for this study, which belonged to the orders Cephalaspidea, Anaspidea, Sacoglossa, Notaspidea and Nudibranchia. Biogeographical patterns were analysed using cluster analysis (TWINSPAN) and ordination MDS (non-metric multidimensional scaling program). The richness of opisthobranchs increases from polar to tropical regions along Atlantic shores. The cluster analysis showed that there is a latitudinal and longitudinal separation of the biogeographical areas. The amphiatlantic species can be separated into four groups according to their distribution: G1.1.- the geographic range of species is limited to cold water on both sides of the Atlantic; G1.2.- species with geographic ranges limited to the western Arctic and Boreal regions, with a wide distribution in the eastern Atlantic, from the eastern Arctic or the eastern Boreal region to the Lusitanian and Mediterranean provinces; G2.1.- species with geographic ranges limited to the Caribbean and Mauritanian-Senegalese areas; G2.2.- species with a wide geographical distribution along both Atlantic shores.

Keywords: amphiatlantism, Atlantic Ocean, Gastropoda, marine biogeography, Mollusca, Opisthobranchia.

INTRODUCTION

Opisthobranch gastropods are well represented in most marine habitats from equatorial to polar regions. Although there are varying levels of knowledge on opisthobranch fauna along the Atlantic shores, it is possible to make generalised comparisons throughout the entire ocean.
There has never been a general zoogeographic study of Atlantic opisthobranch fauna. Prior works have been concerned with the distribution patterns of opisthobranchs from a limited geographical area (i.e. the Mediterranean Sea, Franz, 1970; South Africa, Gosliner, 1987) or with the species’ dispersion capacity (Edmunds, 1977; Clark and Goetzfried, 1978; Templado et al., 1990). Although the data on species distribution and other characteristics vary between the geographical regions, it is nevertheless possible to establish some zoogeographic patterns for Opisthobranchia throughout the Atlantic Ocean. In this paper we present the first global biogeographic analysis of the Gastropoda Opisthobranchia from the Atlantic Ocean and attempt to bring the available information on the Atlantic opisthobranch fauna together into a single database in order to identify whether there are any broad-scale biogeographical patterns.

MATERIAL AND METHODS

Biogeographical areas

This research was conducted by comparing littoral and sub-littoral opisthobranch fauna from Atlantic shores to a depth of 100 m. Species checklists and geographical distribution were compiled by combining information obtained from bibliographical sources (see Supplementary Appendix 1). The bibliography consulted for the faunal lists is referenced in Supplementary Appendix 2. We considered 1066 species that included the orders Cephalaspidea, Anaspidea, Sacoglossa, Notaspidea and Nudibranchia.

Areas were compared according to the classification of zoogeographic areas by Ekman (1953) and Briggs (1974), which has been used by different authors with little variation (i.e. López de la Cuadra and García Gómez, 1994; Naranjo et al., 1998; Boschi, 2000). The geographical limits of these areas are the following:

Eastern Atlantic:

- eastern Arctic: extends to the western Barents Sea (about 72°N).
- eastern Boreal: extends from the Faeroe Islands to the south-western end of the English Channel.
- Lusitanian: extends from the south-western end of the English Channel to the Straits of Gibraltar.
- Mediterranean: the entire Mediterranean Sea.
- Mauritanian: extends from the Straits of Gibraltar to Cape Blanco, including the Canary Islands and Madeira Islands.
- Senegalese: extends from Cape Blanco to about 15°S (Angola), including Cape Verde Islands, São Tomé, Principe, Annobon and Fernando Po Islands.
- south-eastern Atlantic: extends to Cape Town (South Africa).

Western Atlantic:

- western Arctic: extends to the Labrador Peninsula, north of Belle Isle (Lat. 51°37’N).
- western Boreal: extends from the Strait of Belle Isle to Cape Hatteras.
- Carolinian: extends from Cape Hatteras to Cape Canaveral.
- Caribbean: extends from Cape Canaveral to the mouth of the Orinoco River.
- Brazilian: extends from the Orinoco River to Cabo Frio.
- Argentinean: extends from Cabo Frio to latitude 43-44°S (Chubut).
- Magellanic: extends from Chubut to Cabo de Hornos (only the species present in the Atlantic Ocean have been included in this paper).

Faunal affinities

The geographic distribution of the opisthobranchs was compiled into a species-by-biogeographic region matrix for analysis using Two Way Indicator Species Analysis (TWINSPLAN) (Hill, 1979). Ordination analyses were carried out by means of an MDS (non-metric multidimensional scaling program) based on the similarity matrix between stations. The software used was PRIMER (Plymouth Routines in Multivariate Ecological Research) version 5.2.8. for Windows.

RESULTS

The number of opisthobranch species for each Atlantic biogeographic area varies notably, with an apparent tendency to increase in diversity from high to low latitudes (Table 1).

Faunal affinities

TWINSPLAN clustered the sites into seven groups. The cluster shows a first division in which the Magellanic region separates from the remaining
regions (Fig. 1). The second division separates the seven eastern Atlantic regions and western Arctic from the western Atlantic regions. In the first group the northern regions, western Arctic and eastern Arctic, are separate from a group that consists of the eastern Atlantic regions. The remaining divisions separate the south-eastern Atlantic, which is influenced by the fauna from the Indian Ocean and Senegalese regions, from a group consisting of the eastern Boreal, Lusitanian, Mediterranean and Mauritanian regions. The second group, which consists of the western Atlantic regions, can be split into two subgroups. One subgroup includes the northern regions, western Boreal and Carolinian, while the other includes the Caribbean, Brazilian and Argentinean regions. The MDS ordination showed reasonable separation between the TWINSPAN groups (Fig. 2).

Table 2 shows the number and percentage of endemic and amphiatlantic species for each zoogeographic area. Those species considered as endemic have been cited at only one Atlantic zoogeographic area. The geographic distribution in other oceans was not considered for this study. The level of endemism varies notably in the different zoogeographic areas. Although the highest values were found in the Magellanic and south-eastern Atlantic regions, the real endemic percentage for these regions may be lower, as these areas are influenced by fauna from the Pacific and Indian Oceans respectively, which were not considered in this study. High
percentages of endemism were found in the tropical Caribbean, Senegalese and Carolinian areas. The lowest value of endemism was found in the Brazilian area.

According to the bibliography consulted there are 134 known species of amphiatlantic opisthobranchs. The highest numbers of species with an amphiatlantic distribution are found in the western and eastern Arctic regions. Any species present in the Magellanic region was also found in the eastern Atlantic. In the rest of the areas considered, the percentages vary between 19.1% (Mediterranean) and 47.9% (western Boreal).

Species were clustered using TWINSPAN to determine the distribution pattern of the amphiatlantic opisthobranchs (Fig. 3). In this cluster, two main groups can be detected that are made up of species with similar geographic distributions. The G1 group consists of the species present in the northern regions of the western and eastern Atlantic (Arctic, eastern and western Boreal regions), and the G2 group consists of the species distributed along the temperate-warm waters of both Atlantic coasts. Each group divides into two subgroups.

G1.1: In this subgroup the species distribution is limited to the cold waters of the eastern and western Arctic and Boreal regions.

G1.2: Species of this subgroup have a wide geographical distribution on both Atlantic shores. On the eastern Atlantic side, from the Lusitanian province to the Senegalese or south-eastern Atlantic area, and along the western Atlantic in the Caribbean, Brazilian and Argentinean provinces.

G2.1: The species of this group have geographic ranges limited to the Caribbean and Mauritanian or Senegalese areas. Some species are also present along the western Atlantic, Brazilian and Argentinean shores. In the eastern Atlantic a few species extend to the Lusitanian province.

G2.2: Species of this subgroup have a wide geographical distribution on both Atlantic shores. On the eastern Atlantic side, from the Lusitanian province to the Senegalese or south-eastern Atlantic area, and along the western Atlantic in the Caribbean, Brazilian and Argentinean provinces.
DISCUSSION

The number of opisthobranch species for each Atlantic biogeographic area varies notably with an apparent tendency to increase diversity from high to low latitudes. This increase in biological diversity from polar to tropical regions is typical of a wide range of terrestrial and marine organisms (Thorson, 1957; Pianka, 1966; Boschi, 2000; Attrill et al., 2001; Willig et al., 2003; Chown et al., 2004; Giangrande and Licciano, 2004).

The difference in the richness of opisthobranch species in the different Atlantic areas could be due to various factors, such as the intensity and lack of distributional information of some taxonomic and faunistic studies (Gosliner, 1987), as well as the fact that different abiotic factors determine the geographic distribution and richness of opisthobranchs. Thus, the higher diversity of the cold-temperate areas of the eastern Atlantic with regard to the western shores is, according to Miller (1961), Clark (1975) and Templado et al. (1990), due to the lower climatic stability of the north-western Atlantic, where the annual variation in temperature in shallow waters can reach 27°C.

A general vision of the classification analysis based on presence-absence of species in the biogeographical areas considered, shows a latitudinal (north-south) and longitudinal separation (east-west Atlantic shores) of the areas, except in the northern group (western and eastern Arctic).

The relationship between the fauna from the cold water of the western and eastern Atlantic has been known for a long time (Thorson, 1941). In the north Atlantic, many opisthobranch species have populations with continuous geographic ranges along the coasts of Canada, Greenland and Northern Europe. This is probably because the shelf extensions are short, and the larval of many species traverse these distances (Edmunds, 1977).

Although the Arctic region is a homogeneous zoogeographic unit, the geographic range of the species southwards differs on the two sides of the Atlantic. Thus, while 42% of the Arctic species extend to the western Boreal and 10% to Carolinian, along the eastern Atlantic shores, 77.8% of the Arctic species are present in the eastern Boreal and 20% extend to the Mauritanian region. In the Arctic opisthobranch fauna, the Aeolidina, which is the taxa with the highest number of endemic species, show a lower dispersal capacity, while the Cephalaspidea show larger geographical ranges on both sides of the Atlantic.

The dispersal potential of a species is due to several factors, such as food availability and superficial current systems. A possible explanation for the distribution pattern observed in the opisthobranch species is related to temperature. According to Scheltema (1995), temperature plays a significant role in limiting the latitudinal distribution of benthic species. This can be observed in the fauna from the western Arctic and Boreal regions, which mainly consists of cold-temperate fauna. The distribution is limited towards the south by the difference of temperature between these regions and south of the Carolinian region, which is a consequence of the confluence of the cold Labrador current (toward the south) and the temperate Gulf current (toward the north) (Day et al., 1971). Cape Hatteras constitutes the southern boundary for many cold-temperate species of invertebrates and the northern boundary for many subtropical species (Berggreen and Hollister, 1974).

The community of opisthobranchs from the Atlantic-Mediterranean subregion (Lusitanian, Mediterranean and Mauritanian provinces) is constituted mainly by species adapted to cold-temperate waters that extend towards the north to the eastern Boreal. However, the capacity to extend to warm water is more limited. The variation in temperature between the Atlanto-Mediterranean (influenced by the Ca-
nary current) and the warm Senegalese water could be a barrier for the dispersion of opisthobranchs. The cephalaspidans are the species that are generally capable of extending to the Senegalese area, as they frequently live under the sand or mud, which are habitats less influenced by the temperature of the superficial waters.

The Senegalese community consists of warm water species with a limited geographic range toward the north and south. The confluence of the cold-temperate Canary current toward the south, and the cold current of Benguela flowing northward, could be temperature barriers to the tropical Senegalese fauna. However, the Senegalese opisthobranchs show a large percentage of amphiatlantic species; the Doridina and Aeolidina are the most abundant taxa, and extend mainly in Caribbean and Brazilian regions.

Based on the results of the present paper and those of Naranjo et al. (1998), it is possible to consider that ecological changes in cold and temperate waters determine important barriers to the dispersion of opisthobranchs. However, the ecological barriers are not significant in temperate and warm waters, and so the opisthobranch species have wide geographic ranges.

Schrödl (1999) indicates that only 31% of the species are endemic to the Magellanic area (11 species of 36 cited by the author). However, in the present paper we calculated a percentage of 71.87% (23 species of 32 species considered). This difference is because Schrödl considered the Pacific coast for his study, which is not included here.

Boschi (2000) carried out a zoogeographic study of the Crustacea Decapoda from the Pacific and Atlantic littoral zones of America. The endemic percentage of decapods in the different areas considered is lower than the opisthobranch fauna in all the areas except the Brazilian area, where the endemic decapods represent 11.19% of the species cited (Boschi, 2000), while only 6.45% of Brazilian opisthobranchs are endemic. Nevertheless, the tendency of percentages is similar in both taxonomic groups. Thus, as occurs with the opisthobranch fauna, the decapods have the highest percentage of endemism in the Caribbean and Magellanic areas. The lower values of endemic decapods compared to opisthobranchs are explained by the greater dispersion capacity of decapods. In this sense, Tunicata Asciidiacea, which has a low dispersion capacity, shows a higher percentage of endemism. Naranjo et al. (1998), state that 60% and 31% of the species from the Caribbean and Senegalese areas respectively are endemic.

The high percentage of amphiatlantic opisthobranch species in the cold water of eastern and western North Atlantic shores coincides with Franz (1970) and Templado et al. (1990). As was previously pointed out, in these latitudes the shelf extensions are short, and opisthobranch populations are distributed continuously.

The concept of a mid-Atlantic barrier was proposed by Ekman (1953), and later by Briggs (1974), who stated that only 10% of fishes have an amphiatlantic distribution. Naranjo et al. (1998) indicated that few species of ascidians show an amphiatlantic range, which corresponds to cosmopolitan species that are generally associated with shipping traffic or other forms of man-made transport. Knudsen (1956) calculated that 6% of prosobranch gastropods are amphiatlantic. Marcus and Marcus (1966) stated that 29% of the opisthobranch species are transatlantic. However, García-Talavera (1983) cites 102 species of amphiatlantic gastropods, of which only 4 species are Pyramidelloidea (not considered in the present paper) and 7 species are Cephalaspidans. We found 134 species of amphiatlantic species in the bibliography, which represents 12.5%. The difference between our data and those of Marcus and Marcus (1966) is due to the new data on the distribution of the species since the publication of their work.

A TWINSPAN cluster analysis applied to the amphiatlantic species determined two main groups of species: those with geographic ranges along cold-temperate waters (G1), and those that are not so tolerant to cold waters, which extend throughout temperate-warm waters (G2). In group G1 two subgroups were detected. One consists of species with limited geographic ranges in the Arctic and Boreal areas (G1.1) and the other with wide geographic ranges along eastern Atlantic shores and limited to the Arctic-Boreal in the western Atlantic (G1.2). The geographic distribution of the species belonging to subgroup G1.2 in the western Atlantic could be limited southward by factors such as the substrate, as a large part of the Carolinian area is sandy (Day et al., 1971), which is an unfavourable substrate for many opisthobranch species (Franz, 1970). This coincides with the low number of species found in this province.

The discontinuous geographic range of the widely distributed species of subgroup G2.2, could be related to a moderately small increase in sea
temperature, such as that which took place during the most recent post-glacial period 5000 to 7000 years ago (Franz, 1970; Petryashev, 2002). This allowed populations of amphiatlantic species, which are now discontinuous, to have a continuous geographic range via Greenland, Iceland and the Faeroes. Posterior climatic cooling that extends to the present time, might have then caused the extinction of the connecting populations. This change of temperature and organisms along the interglacial periods has also been observed in Pleistocene geologic deposits. Many regions can be seen to be divided into layers with fossil remains belonging to different climates. Thus, in the Arctic region there are layers that contain tree pollen (Bridge et al., 1990) from trees characteristic of north temperate climates and that cannot survive in colder conditions (Peteet et al., 1998). This suggests that Arctic conditions were warmer for some time before becoming colder again.

The classification analysis based on the presence-absence of species in the biogeographical areas considered shows a latitudinal (north-south) and longitudinal separation (east-west Atlantic shores) of the regions, except in the northern regions, which remain joined on both sides of the ocean (western Boreal, western and eastern Arctic). However, at the genus level, the classification analysis only indicates the existence of a latitudinal gradient in the distribution of the genera. Three main endemism areas can be distinguished for Atlantic opisthobranch fauna: south-eastern Atlantic, Magellanic and Caribbean. The Arctic and Boreal areas show the highest percentage of amphiatlantic species. The similarity analysis applied to the amphiatlantic species determined two main groups of species: a group made up of species distributed throughout cold-temperate waters (G1), and a second group with those species that are not so tolerant of cold waters, which extend throughout temperate-warm waters (G2). G1 divides into two subgroups: One consisting of species with a geographic range limited to the Arctic and Boreal areas (G1.1) and the other with wide geographic ranges along the eastern Atlantic shores and limited to the Arctic-Boreal area in the western Atlantic (G1.2). G2 also divides into two subgroups: G2.1, made up of species with geographic ranges limited to the Caribbean and Mauritanian areas, and G2.2 with species which have wide geographical distributions in the temperate-warm waters of both Atlantic shores.

**Eastern Pacific comparisons**

Biogeographic overviews of the opisthobranch fauna from other entire ocean basins are not available. On a smaller scale, comparisons with north-eastern Pacific faunal zones may be relevant. Endemism, vicariance and dispersal events, and trophic structures have been analysed (although with different statistical tools).

A total of 396 opisthobranch species occur in 4 faunal provinces between Point Conception, California, and the Galapagos Islands. Of these, 211 species have been reported from the Californian area (C), 183 from the Sea of Cortez (SofC), 158 from the Mexican area (M), and 220 from the Panamic area (P). These data do not show a N–S latitudinally increasing gradient.

Species in the Sea of Cortez show high N–S faunal affinities: 97 species (53%) occur northward in C, 142 (77.6%) southward in M and P, and 66 (36%) occur in both northerly and southerly regions. SofC species share lower E–W relationships: 13 (7%) are circumtropical, 10 (5.5%) Atlantic-Caribbean, 23 (12.6%) Indo-East-Pacific, and 9 (4.9%) occur in Japan (Bertsch, 2008). Dispersion barriers are more significant than temperature barriers. Endemism in SofC is quite low (11 species, 6%).

The developmental biology of most tropical eastern Pacific opisthobranchs is unknown; data are available on 130 primarily colder-water species (Goddard, 2004).

The trophic structures of opisthobranch communities vary greatly between and within regions (Bertsch and Hermosillo, 2007), but currently there are no comparable Atlantic studies. Local long-term community structure monitoring, such as those conducted at Bahía de los Ángeles, Baja California (Bertsch, 2008), and Bahía de Banderas, Jalisco/Nayarit (Hermosillo, 2006), is needed in Atlantic regions.

**ACKNOWLEDGEMENTS**

This paper has been partially supported by the projects PHB2002-0045-PC and CGL2004-20366-E/BOS, of the Ministerio de Educación y Ciencia (MEC, Spain) and by a project supported by Agencia Española de Cooperación Internacional (AECI) during the years 1998 to 2000.
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Scient. ed.: J.D. Ros.

Received June 11, 2007. Accepted July 17, 2008. Published online January 7, 2009.

SUPPLEMENTARY MATERIAL

The following appendices are available through the web page http://www.icm.csic.es/scimar/supplm/sm73n1153sm.pdf

APPENDIX 1.– Species checklists and geographical distribution. The species are grouped together according to the taxonomic category of Order and Suborder.

APPENDIX 2.– Bibliography consulted for the faunal list of Appen dix 1.