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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.

RESUMEN: Diversidad y distribución de los Gasterópodos Opistobranquios del Océano Atlántico. Un enfoque biogeográfico global. – Se realiza un estudio zoogeográfico de los Opistobranquios (Mollusca, Gastropoda) del Océano Atlántico. Los datos de distribución proceden de referencias bibliográficas y de bases de datos. El número de especies consideradas es de 1066, pertenecientes a los órdenes Cephalaspidea, Anaspidea, Sacoglossa, Notaspidea y Nudibranchia. Los modelos biogeográficos fueron analizados empleando análisis de agrupamiento (TWINSPAN) y de ordenación (MDS). A lo largo de los márgenes del océano, se detecta un incremento de la riqueza de especies desde las regiones polares hacia las tropicales. Los análisis mostraron la existencia de separaciones latitudinales y longitudinales de las áreas biogeográficas a partir de las comunidades de opistobranquios. Según la distribución que presentan las especies anfiatlánticas, éstas se pueden reunir en cuatro grupos: G1.1, especies cuyo rango de distribución están limitados a las aguas frías más septentrionales; G1.2, especies con rango de distribución estrecho en el Atlántico Occidental (regiones Ártica y Boreal) y amplio en el Atlántico Oriental (desde el Ártico o Boreal hasta las provincias Lusitánica y Mediterránea); G2.1, especies con rango de distribución geográfica limitado a las áreas Caribeña, en el Atlántico Occidental y Mauritánica o Senegalense en el Atlántico Oriental; G2.2, especies con amplio rango de distribución en ambos lados del Atlántico.

Palabras claves: anfiatlantismo, biogeografía marina, Gastropoda, Mollusca, océano Atlántico, 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 72ºN).

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 15ºS (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. 51º37'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 43-44ºS (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 (TWINSPAN) (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

TWINSPAN clustered the sites into seven groups. The cluster shows a first division in which the Magellanic region separates from the remaining

TABLE 1. – Total number of species according to Order or Suborder for each zoogeographic area.

	Cephalaspidea	Sacoglossa	Anaspidea	Notaspidea	Doridina	Dendronotina	Arminina	Aeolidina	TOTAL
Western Arctic	14	1	1	0	10	3	0	8	37
Western Boreal	45	7	4	3	18	5	0	14	96
Carolinian	23	0	2	1	7	2	2	5	42
Caribbean	95	51	17	15	80	28	5	38	329
Brazilian	40	5	12	9	20	3	1	3	93
Argentinean	25	12	7	5	40	10	3	25	127
Magellanic	11	1	0	1	15	3	0	1	32
Eastern Arctic	8	0	0	0	3	0	0	5	16
Eastern Boreal	52	11	4	6	53	29	7	53	215
Lusitanian	104	20	9	10	88	30	7	65	333
Mediterranean	72	30	13	9	94	31	5	69	323
Mauritanian	75	33	15	15	70	14	4	35	261
Senegalese	30	15	8	5	33	8	3	19	121
South Eastern Atlantic	23	7	7	5	34	8	5	18	107

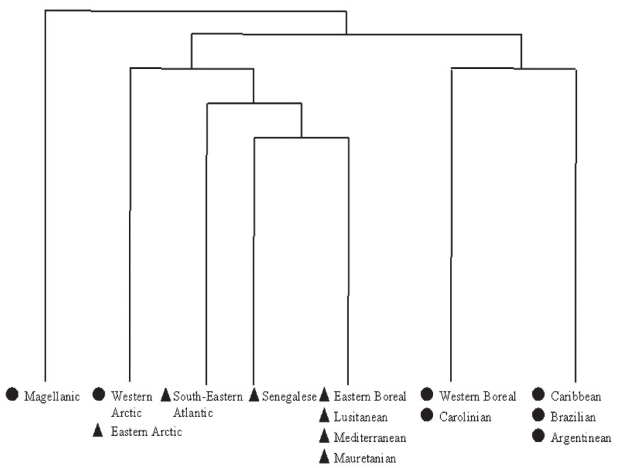

FIG. 1. – Results from TWINSPAN analysis based on the presence-absence of species in the biogeographic areas. Circles, western regions; triangles, eastern regions.

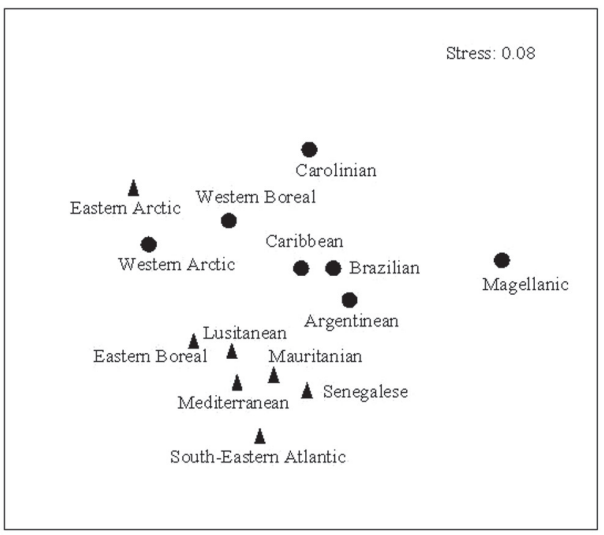

FIG. 2. – Multidimensional scaling (MDS) ordination of the similarity of the biogeographic areas based on the presence-absence of species.

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).

Endemism and amphiatlantism of opisthobranchs in the Atlantic Ocean

Table 2 shows the number and percentage of endemic and amphiatlantic species for each biogeographic area respectively. 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

TABLE 2. – Number and percentage of endemic and amphiatlantic species for each faunistic area. Areas influenced by adjacent oceans are identified by an asterisk.

	Species	Endemism	% Endemism	Amphiatlantic	% Amphiatlantic
Western Arctic	37	4	10.81	31	83.7
Western Boreal	96	20	20.83	46	47.9
Carolinian	42	15	35.71	12	28.5
Caribbean	329	156	47.56	86	26.2
Brazilian	93	6	6.45	33	35.4
Argentinean	127	31	24.4	38	31.6
Magellanic*	32	23	71.87	0	0
Eastern Arctic	16	2	12.5	13	81.2
Eastern Boreal	215	54	25.11	49	22.7
Lusitanian	333	49	14.71	69	20.7
Mediterranean	323	55	17.02	62	19.1
Mauritanian	261	58	22.22	66	25.2
Senegalese	121	43	35.53	36	29.7
South-Eastern Atlantic*	107	57	53.27	27	25.2

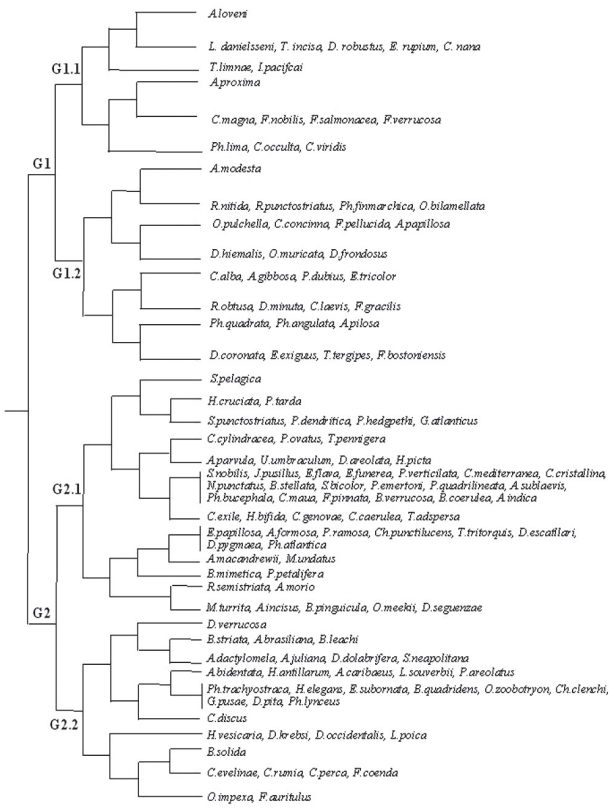

FIG. 3. – Results from TWINSPAN analysis based on the presence-absence of amphiatlantic species in the biogeographic areas.

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: Made up of species with geographic ranges limited to the western Arctic and Boreal regions, while in the eastern Atlantic the distribution area extends from the eastern Arctic or eastern Boreal regions to the Lusitanian and Mediterranean 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.

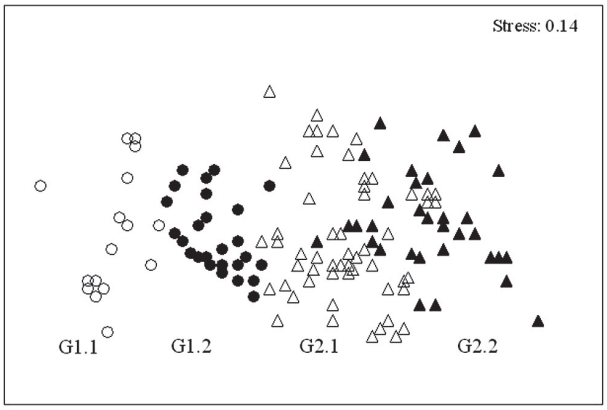

FIG. 4. – MDS ordination of the amphiatlantic species based on their presence-absence in the zoogeographic areas. White circles, species of subgroup G1.1; black circles, species of subgroup G1.2; white triangles, species of subgroup G2.1; black triangles, species of subgroup G2.2.

The two-dimensional representation of the ordination analysis (MDS) (Fig. 4) showed reasonable separation of the TWINSPAN groups.

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 varies 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 27ºC.

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 opisthobranchs 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 larvae 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 dispersion 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 opisthobranchs 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 Atlanto-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 cephalaspideans 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 Shrödl 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 Ascidiacea, 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 Cephalaspideans. 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 northeastern 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.

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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 Appendix 1.