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BIODIVERSITY RESEARCH

# Species richness of marine Bryozoa in the continental shelf and slope off Argentina (south-west Atlantic)

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**Abstract.** A total of 246 marine bryozoan species was recorded within an area of the south-west Atlantic between 35° and 56°S, and between the coast of Argentina and 50°W. The distribution pattern of benthic stations surveyed during the most important cruises in the area shows that the sampling effort has been biased towards southern shelf areas off Santa Cruz and Tierra del Fuego, as well as around the Malvinas (Falkland) islands. The littoral zone, Patagonian gulfs and the continental shelf off Chubut, Río Negro and Buenos Aires state received less attention, and should be surveyed more intensively in the future. Only 2% of the species can be regarded as non-indigenous, all of them inhabiting biofouling communities in harbour environments. With the exception of some thoroughly surveyed localities, the number of species recorded for different areas of the coast, shelf and slope is estimated to be just a small fraction of the actual number of species present. A distinct diversity gradient was found, with species-rich stations located only in the southern shelf. Highest diversity occurred in shelf areas dominated by coarse sediments, and along a high-productivity shelf-break front. A remarkable decrease in species richness was found in inner and middle shelf areas off Chubut, Río Negro and Buenos Aires state. This pattern may be related to the Pacific origin of the Magellanic fauna, since the diversity of bryozoans is higher in the Pacific than in the Atlantic Ocean. The trend of species richness is, however, overemphasized by the fact that the least diverse faunistic assemblage occurs in areas where surveys have been relatively less frequent. An up-to-date checklist of species recorded for the study area is included.

**Key words.** Argentina, Bryozoa, continental shelf and slope, south-west Atlantic, species richness.

## INTRODUCTION

Based on the analysis of geographical distribution patterns of several groups of marine organisms (Seminario sobre biogeografía de los organismos marinos, 1964; see also references in López Gappa & Lichtschein, 1988), the nearshore area of the south-west Atlantic situated between 35° and 56°S has been divided in two biogeographic provinces: Magellanic and Argentine. The former occupies most of the southern Patagonian shelf off Tierra del Fuego and Santa Cruz, as well as the Malvinas (Falkland) islands and the Burdwood Bank. Following the cold waters of the Malvinas Current, this assemblage of species extends its distribution towards outer and deeper areas of the shelf and slope off Chubut, Río Negro and Buenos Aires state. On the other hand, the Argentine biogeographic province occupies the inner and shallower shelf off Chubut, Río Negro and Buenos Aires state (Fig. 1), and is inhabited by species of warm–temperate affinities, reaching also Uruguay and Rio Grande do Sul (Brazil).

Bryozoans are benthic, clonal invertebrates widely distributed throughout the world oceans. The biogeographic affinities of the Magellanic bryozoan fauna and its relationships with Antarctica and the subAntarctic archipelagos has been discussed in detail by Hastings (1943) and

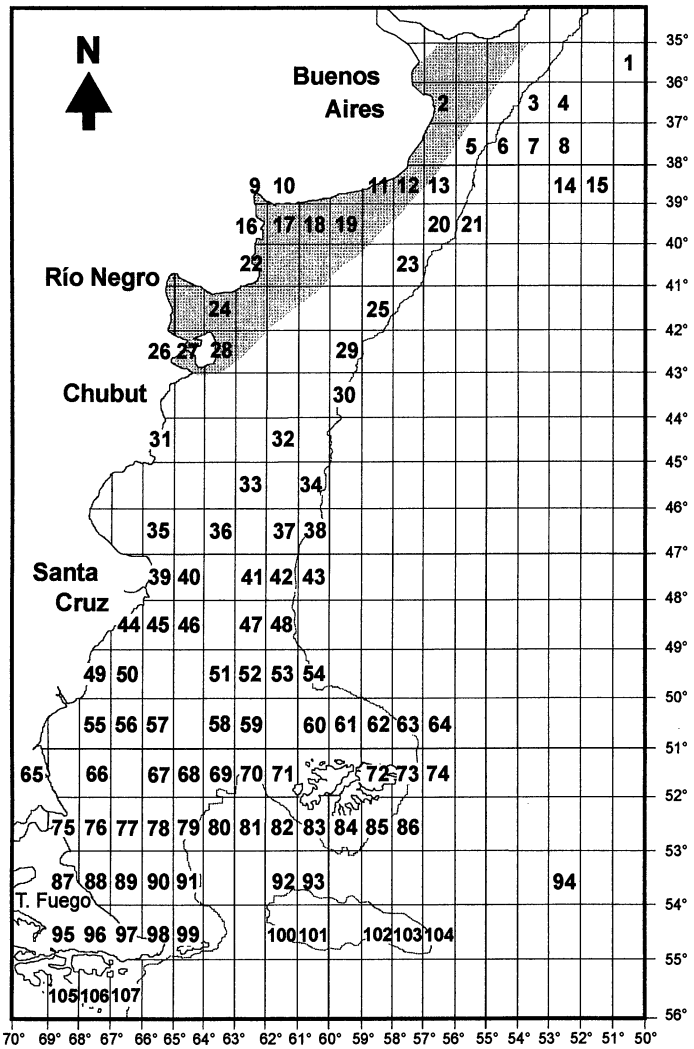


**Fig. 1** One-degree squares containing bryozoan records for precise localities in the taxonomic and ecological literature, numbered from north (35°S) to south (56°S), and from the coast of Argentina to 50°W. The shaded area shows the approximate location of the Argentine biogeographic province. The Magellanic biogeographic province occupies all the remaining shelf area. The 200-m isobath is shown.

Moyano (1982a, 1982b, 1991, 1997). López Gappa & Lichtschein (1988) concluded that within the continental shelf off Argentina, bryozoan diversity was higher in the Magellanic than in the warm–temperate assemblage, and that the boundary between both areas followed a south-west–north-east direction, at a depth of approximately 60–72 m. Bastida *et al.* (1992) reached similar conclusions after studying the distribution of several invertebrate phyla in the Argentine shelf. In addition, they characterized an intermediate area, inhabited by an impoverished Magellanic assemblage, composed by the most tolerant and widely distributed cold–temperate species.

The introduction of non-indigenous marine organisms has increased dramatically in the last

decades, as well as the concern about the ecological consequences brought about by this process on the marine ecosystem (Carlton & Geller, 1993). Since the global transport of benthic marine invertebrates across biogeographic boundaries is increasing steadily, local faunistic inventories are of great value, in order to know the taxonomic composition and the geographical ranges of their species. They constitute the baseline to detect future changes caused by pollution and global climate change.

Since the zoogeographic affinities of the southwest Atlantic bryozoan fauna are well known and have been analysed thoroughly in other publications (Hastings, 1943; Moyano, 1982a, 1982b, 1991, 1997; López Gappa & Lichtschein, 1988), they will not be discussed further in the present study. The purpose of this paper is to (1) compare the distribution of the sampling effort along the continental shelf and slope off Argentina, in order to identify which zones should be more intensively surveyed for bryozoans in future studies; (2) analyse the diversity pattern of marine bryozoans within the study area; and (3) present an up-to-date checklist of the bryozoan species recorded for the area in the taxonomic and ecological literature.

## MATERIALS AND METHODS

A database was prepared after a survey of the taxonomic bibliography published up to 1997, including species names, benthic stations or coastal localities where they were recorded, and bibliographic references. Records involving unprecise localities (i.e. 'Coast of Patagonia', 'Cape Horn Expedition, station unknown', etc.), doubtful or unsettled synonymies, and taxa determined above specific level were not included. Therefore, the number of species per station/locality in Appendix 1 (published on-line at http://www.blackwell-science.com/products/journals/suppmat/ddi/ddi067/ddi067sm.htm) indicates only those included in the present study, and may not be coincident with the actual number of taxa present at each site. Species are listed according to current taxonomic classifications or under the names appearing in the last revision or systematic paper in which they were studied. In addition to the systematic bibliography, distribution records of bryozoan species scattered over the ecological literature (López Gappa *et al.*, 1982; Bremec, 1986, 1989, 1990; Roux *et al.*, 1988; López Gappa, 1989) were also included in the database.

This study was circumscribed to an area comprising the continental shelf and slope off Argentina between 35° and 56°S, and between the coast and 50°W. Several Chilean islands located south of the Beagle Channel were also included, due to their proximity to the Argentine border, as well as some deep stations beyond the slope off Buenos Aires state. The whole area was divided into a 1° square grid. Only squares containing benthic stations or precise localities with published records of bryozoans were numbered from north (35°S) to south (56°S), and from the coast to the slope (Fig. 1). The number of species recorded for each square was counted.

The sampling effort off the Argentine coast was compared by dividing the study area into four sections: (1) off Buenos Aires state, between 35° and 41°S; (2) off Río Negro and Chubut, between 41° and 46°S; (3) off Santa Cruz, between 46° and 51°S; and (4) off Tierra del Fuego and around the Malvinas islands and the Burdwood Bank, between 51° and 56°S. The total number of benthic stations (with and without bryozoans) surveyed by the *Shinkai Maru* (Cousseau *et al.*, 1979) and the *William Scoresby* 1931–32 trawling cruises (Discovery Committee, 1949), were counted in each of these sections. Other cruises were not taken into account for the comparative analysis of sampling effort, due to lower numbers of stations gathered in the study area, or because in many cases the lists of stations were not available to the author.

Non-parametric correlations (Kendall's tau, Sokal & Rohlf, 1981) between the number of species and latitude or depth were calculated for the two most important cruises (*Discovery*/*William Scoresby* and *Shinkai Maru*; published records only).

## RESULTS

### Diversity of the bryozoan fauna

Bryozoans were obtained in 190 benthic stations and 31 coastal localities throughout the study area (Appendix 1). Figures 2 and 3 show that the stations/localities yielding bryozoans were more frequent in southern areas of the

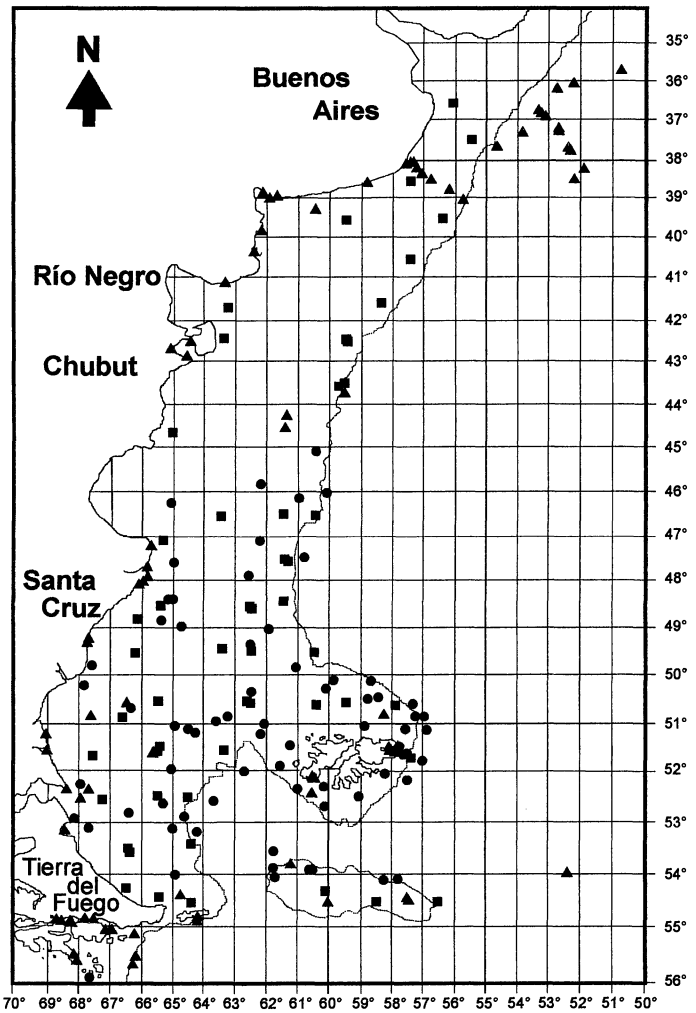


**Fig. 2** Location of benthic stations with bryozoans in the coast, continental shelf and slope off Argentina. Squares: *Shinkai Maru* cruises. Circles: *Discovery*/*William Scoresby* cruises. Triangles: other cruises or localities (see Appendix 1 for the exact position of each station). The 200-m isobath is shown.

continental shelf and slope, mainly off Santa Cruz and Tierra del Fuego, and around the Malvinas islands. The number of sites where bryozoans were recorded decreased northwards, reaching minimum values off Río Negro-Chubut (Fig. 3). Buenos Aires state had an intermediate number of stations/localities, many of which were located in the continental slope or even deeper areas. Table 1 shows that the percentage of benthic stations without published records of bryozoans was lower in the southern shelf areas than in shelf sections off Buenos Aires state and Río Negro-Chubut.

The *Discovery*/*William Scoresby* cruises (Appendix 1; Hastings, 1943, 1946; Hayward & Thorpe, 1988a, 1988b, 1988c, 1989, 1990; Hayward & Ryland, 1990, 1991, 1993; Hayward, 1991, 1992, 1993, 1995), and the *Shinkai Maru* cruises (Appendix 1; Bastida *et al.*, 1981, 1992; López Gappa & Lichtschein, 1988, 1990), made the most comprehensive surveys within the study area (75 and 53 benthic stations with published records of bryozoans,

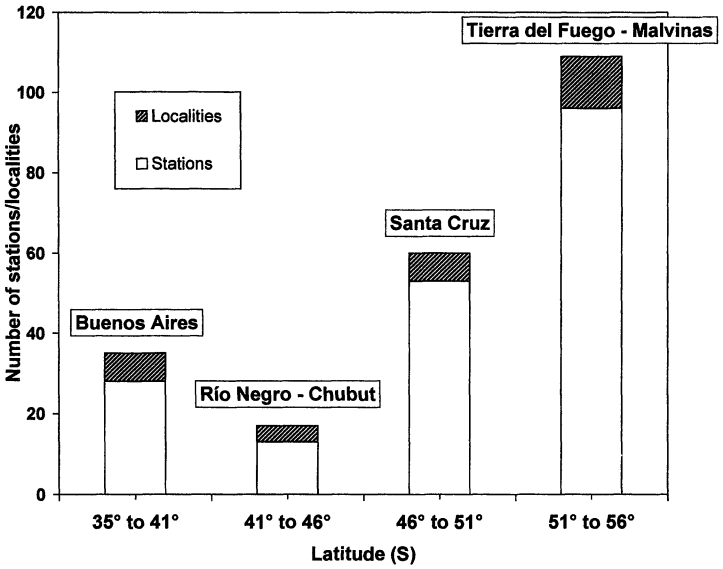


**Fig. 3** Number of benthic stations or localities where bryozoans were recorded in different sections of the coast, shelf and slope off Argentina.

**Table 1** Total number of benthic stations and number of stations without published records of bryozoans during the *Shinkai Maru* and *William Scoresby 1931–1932* cruises, in different sections of the study area. Sources: Discovery Committee, 1949; Cousseau *et al.*, 1979; Bastida *et al.*, 1981

| Cruise/section | Total number (%) of stations | Number (%) of stations without bryozoans |
|---|---|---|
| *Shinkai Maru* | | |
| Buenos Aires | 11 (14.9) | 5 (45.5) |
| Río Negro-Chubut | 17 (22.9) | 9 (52.9) |
| Santa Cruz | 27 (36.5) | 5 (18.5) |
| T. Fuego-Malvinas | 19 (25.7) | 2 (10.5) |
| Total | 74 (100.0) | |
| *William Scoresby 1931–1932* | | |
| Buenos Aires | — — | — — |
| Río Negro-Chubut | 27 (20.3) | 25 (92.6) |
| Santa Cruz | 59 (44.4) | 47 (79.7) |
| T. Fuego-Malvinas | 47 (35.3) | 37 (78.7) |
| Total | 133 (100.0) | |

respectively). The latter sampled throughout the continental shelf from 36°30′S to 54°30′S, while the former made more intensive surveys off Santa Cruz, Tierra del Fuego, and around the Malvinas islands and the Burdwood Bank (Fig. 2). Most other cruises surveyed less than 10 benthic stations in the study area (Appendix 1).

A total of 246 bryozoan species have been recorded for precise localities or benthic stations off the Argentine coast and neighbouring Chilean islands (Appendix 2, published on-line at http://www.blackwell-science.com/products/journals/suppmat/ddi/ddi067/ddi067sm.htm). Twelve species (5%) belong to the order Ctenostomatida, 43 (17%) to the order Cyclostomatida and 191 (78%) to the order Cheilostomatida.

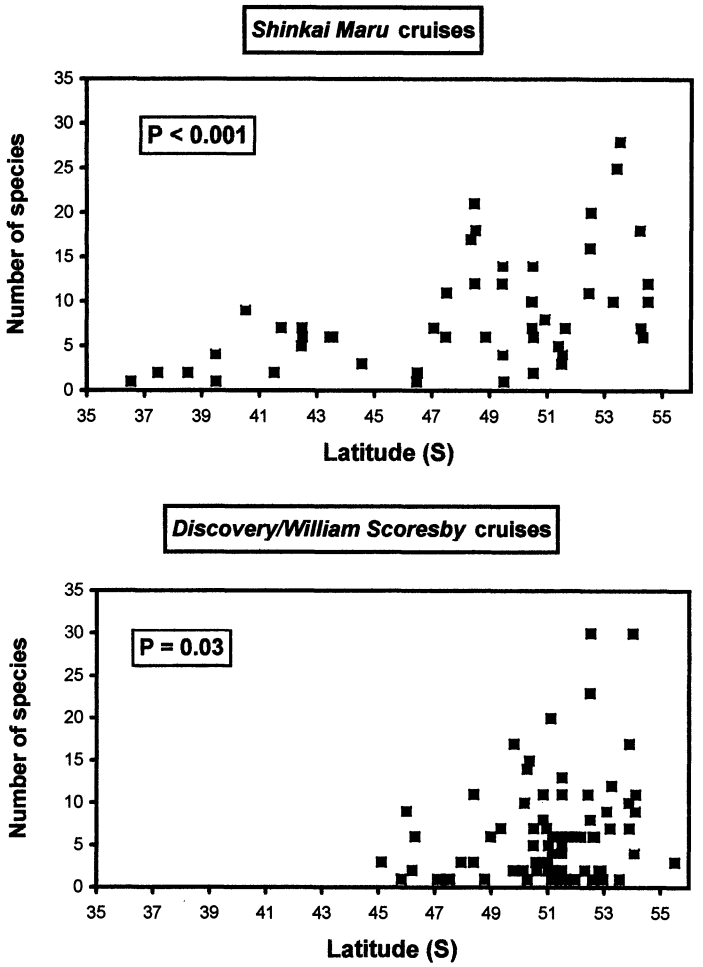


**Fig. 4** Relationship between latitude and number of bryozoan species in the *Shinkai Maru* and *Discovery/William Scoresby* cruises.

The cheilostomes *Microporella hyadesi* (Jullien 1888), *Arachnopusia monoceros* (Busk 1854), *Cellaria ornata* (d'Orbigny 1847), *Menipea flagellifera* Busk 1884, *Caberea darwinii* Busk 1884, *Amastigia benemunita* (Busk 1884) and *Ogivalia elegans* (d'Orbigny 1847) appear as the most frequent species, being present in more than 30 squares (Appendix 2).

Correlation between number of bryozoan species and latitude was positive and significantly different from 0 for the *Shinkai Maru* cruises (Kendall's tau = 0.355, $P < 0.001$; Fig. 4). Samples collected along a narrower latitudinal range (45°–56°S) during the *Discovery/William Scoresby* cruises produced a much lower but still significant correlation (Kendall's tau = 0.167, $P = 0.03$; Fig. 4).

The relationship between species number and depth was nonsignificant (*Shinkai Maru*: Kendall's tau = 0.152, $P = 0.11$; *Discovery/William Scoresby*: Kendall's tau = 0.040, $P = 0.61$, Fig. 5). The richest stations in both surveys, however, were recorded between 80 and 120 m depth.

Species richness of bryozoans along the continental shelf and slope is shown in Fig. 6. The highest number of species was recorded around Port Stanley (Malvinas islands), a locality frequently visited by European cruises (Fig. 2), and Ría Deseado, which has been thoroughly surveyed

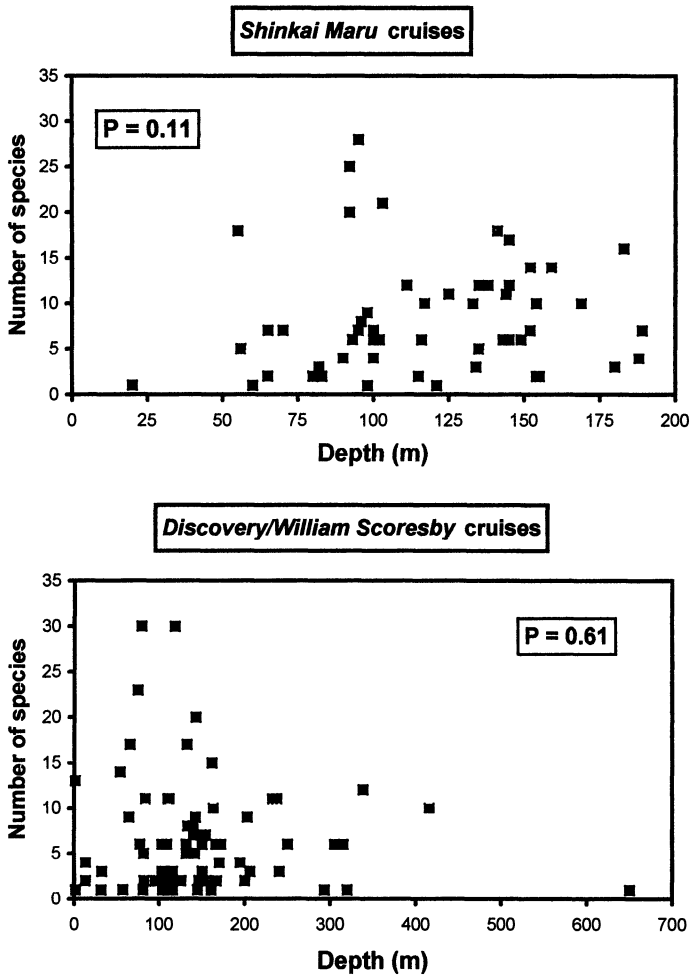


**Fig. 5** Relationship between depth and number of bryozoan species in the *Shinkai Maru* and *Discovery/William Scoresby* cruises.

by Argentine researchers (Amor & Pallares, 1965; López Gappa, 1981a, 1985, 1989; López Gappa *et al.*, 1982).

Specific richness was high in the Chilean islands south of the Beagle Channel, around the Malvinas islands, Burdwood Bank, and on the shelf off Tierra del Fuego and Santa Cruz. On the contrary, species number decreased sharply in relatively shallow shelf areas off Chubut, Rio Negro and Buenos Aires state (Fig. 6).

The most important type localities in the study area were *Challenger* station 320, located on the slope off Buenos Aires state (Busk, 1884, 1886), and Orange Bay in Hoste Island (south of Tierra del Fuego; Jullien, 1888), from which 18 and 15 currently valid bryozoan species have been originally described, respectively.

## Distribution of the sampling effort

The total number of benthic stations surveyed during the *Shinkai Maru* cruises was lower off Buenos Aires state and Rio Negro-Chubut than in the southern sections of the study area (Table 1).

The RRS *William Scoresby* made the most intensive samplings in the Patagonian shelf from November 1931 to April 1932. The shelf off

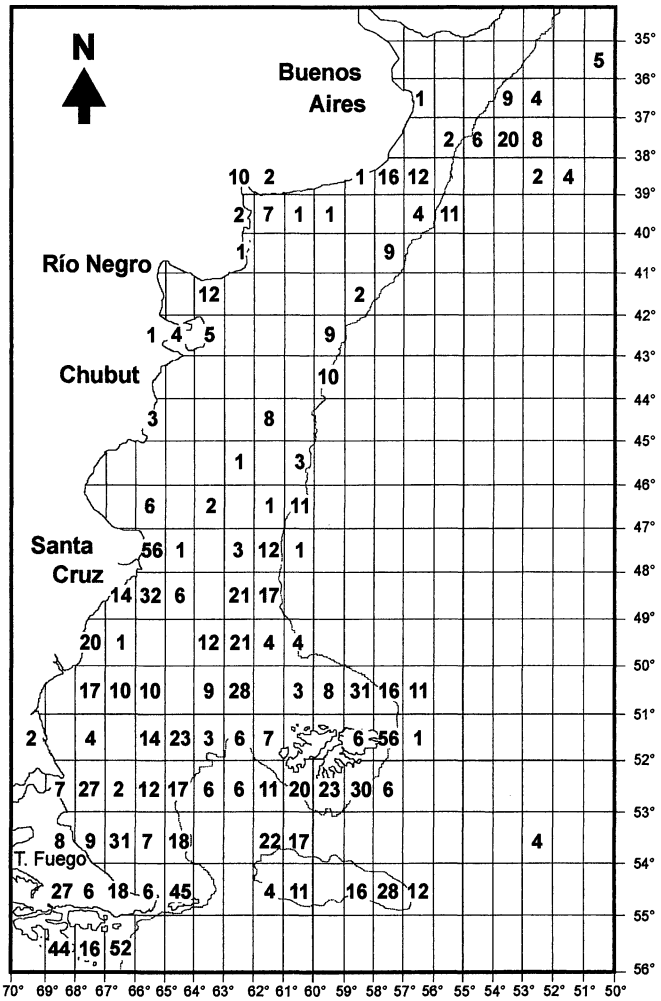


**Fig. 6** Number of bryozoan species in each 1° square of the continental shelf and slope off Argentina. The identity of the species recorded for each square may be ascertained from information included in Appendices 1 and 2. The 200-m isobath is shown.

Buenos Aires state was not explored during these cruises. The southern sections of the study area were more intensively surveyed than the shelf off Río Negro-Chubut (Table 1).

## DISCUSSION

Most species inhabiting this part of the south-west Atlantic show a Magellanic or a warm-temperate distribution (Moyano, 1982a, 1982b, 1983, 1991, 1996, 1997; López Gappa & Lichtschein, 1988, 1990), and may be regarded as native to the study area, according to what is known about their geographical ranges. Only five species from a total of 246 (2%) may be considered as non-indigenous: *Cryptosula pallasiana* (Moll 1803), *Bugula flabellata* (Thompson in Gray 1848), *Bugula simplex* Hincks 1886, *Bugula stolonifera* Ryland 1960 and *Bugula neritina* (Linnaeus 1758) (Appendix 2). The former four species have been recorded only as members of the fouling community in harbours of Buenos Aires state, and the

latter has also been found in a similar environment at Port Stanley (see Lichtschein & Bastida, 1980). It is also possible that other bryozoan species may have been introduced in the study area by human activities, but such instances may be doubtful or almost impossible to prove.

The relationship between species number and depth did not show a simple monotonic trend. On the contrary, the richest stations occurred mainly between 80 and 120 m depth (Fig. 5). Similarly, Lasta & Bremec (1997) found that the largest and richest scallop beds in the Argentine Sea were located along the 100-m isobath, an area where a high-productivity shelf-break front has been documented (Podestá, 1997). Previous studies on other bryozoan faunas have reported contradictory results, since species number was highest between 20 and 80 m in the Western Mediterranean (Ryland, 1970), between 50 and 100 m in the Arctic Ocean (Gontar & Denisenko, 1989), between 50 and 125 m in New England (Schopf, 1969), between 376 and 550 m off South Africa (Hayward & Cook, 1979), and showed either a trend to increase with increasing depth between 22 and 106 m in the English Channel (Grant & Hayward, 1985), or to decrease with increasing depth in a number of circum-Atlantic assemblages (McKinney & Jackson, 1989; Lidgard, 1990). Clearly, several environmental factors requiring further study (i.e. availability of hard substrata) may be important in regulating the bathymetric distribution of bryozoans.

The Cheilostomatida were the most diverse order and had the most frequent species in the study area. The Chilean Magellanic fauna (196 species, Ctenostomatida: 7%, Cyclostomatida: 22%, Cheilostomatida: 71%; Moyano, 1991), has a higher percentage of ctenostomes and cyclostomes and a lower percentage of cheilostomes than those found in the present study. The British bryozoan fauna (267 species, Ctenostomatida: 17%, Cyclostomatida: 13%, Cheilostomatida: 70%; Ryland & Hayward, 1977; Hayward & Ryland, 1979, 1985; Hayward, 1985), has an even higher proportion of ctenostomes than the Argentine bryozoan fauna. It is still not clear whether the low number of ctenostomes represents a real feature of the study area, or its abundance has been underestimated by the scarcity of studies on this group and the inconspicuous nature of its species.

The diversity pattern shown by the bryozoan fauna is partly influenced by the distribution of the sampling effort in the study area. In order to avoid confounding both issues, both stations with and without published records of bryozoans were taken into account, and the relationship between bryozoan diversity and latitude was compared within each of the two most important cruises. Clearly, bryozoans may actually be present in a particular benthic station but may remain unrecorded or unpublished by a number of reasons. Although the percentage of stations without bryozoans may have been overestimated in Table 1, there are no reasons to believe that this bias may be higher or lower in different parts of the shelf. A comparative analysis of the complete list of benthic stations surveyed during the *Shinkai Maru* cruises (Cousseau *et al.*, 1979; pp. 545–555) and the Patagonian trawling stations surveyed during the *William Scoresby* 1931–32 cruises (Discovery Committee, 1949) (Table 1), shows that less effort has been devoted to sampling in northern shelf areas, and that their study should be a priority in the future.

Coastal localities comprise only 14% of the records. Wide coastal extensions have no published records of bryozoans, such as Chubut from Cracker Bay to San Jorge Gulf, and most of the littoral zone of Buenos Aires state, Río Negro and eastern Tierra del Fuego.

Similarly, there are no bryozoan records for the Patagonian gulfs in the results of British or other European oceanographic cruises (San Matías, San José and Nuevo Gulfs not surveyed; WS 770 and WS 777 in San Jorge Gulf without bryozoans, see locations in Discovery Committee, 1949; plate 36). Bryozoans were also absent in the *Shinkai Maru* stations obtained in the San Matías gulf (SM X 22) and the outer part of the San Jorge Gulf (SM XI 48 and SM XI 55) (see Fig. 1 in López Gappa & Lichtschein, 1990).

The biodiversity patterns of bryozoans inhabiting inner and middle areas of the continental shelf off Chubut, Río Negro and Buenos Aires state, at depths lower than 100 m, should be more intensively explored in the future. There are still no published records of any bryozoan species within a wide area extending from 41° to 44°S and from 60° to 63°W (Fig. 6), and only *Cellaria ornata* has been found in the *Shinkai*

*Maru* station V 26 (López Gappa, unpublished; see Fig. 1 of López Gappa & Lichtschein, 1990).

With the exception of some localities that have been sampled intensively (Ría Deseado, Port Stanley, Hoste Island), all evidences suggest that the number of recorded species for squares in Fig. 6 is just a small fraction of the number of species actually present. In fact, less than half of the distribution records of bryozoans collected during the *Shinkai Maru* cruises have been published (López Gappa & Lichtschein, 1990). Therefore, the number of bryozoan species per square is expected to increase in the future, as soon as the results of unworked collections deposited in several museums around the world become published.

Data obtained during the two most important cruises in the study area (Fig. 4) showed that the southern shelf not only has been more thoroughly surveyed, but also shows the highest bryozoan diversity. Although stations yielding few or no species were found throughout the shelf, the richest collections were gathered only in the southernmost areas, between 48° and 56°S. As discussed above, this pattern may have been overemphasized by the fact that shelf sections showing lowest diversity were also the least explored of the study area.

A clear relationship exists between the distribution of sediment types in the Argentine continental shelf (Parker *et al.*, 1997) and the presence and diversity of bryozoans. Mud is the dominant sediment in San Matías, San José, Nuevo and San Jorge Gulfs, where bryozoan species richness is low. On the other hand, gravel is distributed mainly south of 47°, on the shelf off Santa Cruz and Tierra del Fuego, and around the Malvinas islands (Parker *et al.*, 1997), i.e. the area where bryozoans reach highest diversity.

Biodiversity of bryozoans in the Argentine shelf seems to be more influenced by water temperature than by salinity. The shelf near the eastern end of Magellan Strait receives an inflow of low salinity water (32.3 p.s.u.) due to excess precipitation in the South-east Pacific and continental runoff from southern Chile. Salinity increases from the coast to the shelf-break, where it reaches values higher than 33.8 p.s.u. (Piola *et al.*, 2000; see also Fig. 1 in Guerrero & Piola, 1997). This range of salinity values does not seem to influence negatively the distribution of marine bryozoans, since high species numbers have been recorded near the coast of Tierra del Fuego and Santa Cruz (Fig. 6). On the other hand, there is a remarkable agreement between the pattern of species richness shown in Fig. 6 and the hydrological scheme first proposed for the Argentine Sea five decades ago. A pioneer study by Balech (1949) showed that cold–temperate waters occupy the whole shelf south of 47°S, but move away from the coast at lower latitudes, narrowing gradually along the outer margin of the shelf, until reaching at least 35°–36°S. This area is inhabited by the highly diversified Magellanic bryozoan assemblage, and the influence of a narrow band of subAntarctic water flowing northwards (the Malvinas Current) can be followed close to the 200-m isobath between 47° and 39°S in Fig. 6. Vast inner and middle areas of the Patagonian shelf between the coast and the Malvinas Current are influenced alternatively by warm–temperate and cold–temperate waters during summer and winter, respectively (Balech, 1949). This area of fluctuating hydrological characteristics can be seen as an oblique extension of squares with few or no published bryozoan records in Fig. 6.

Maximum surface temperatures have been recorded in the shallow shelf south of Buenos Aires state, and also in San Matías Gulf (Río Negro) (Guerrero & Piola, 1997), which are consequently inhabited by an assemblage of warm–temperate species (Argentine biogeographic province). The relatively low diversity of this warm–temperate area may be related to the fact that many subtropical Brazilian species do not extend their ranges beyond the barrier imposed by the Río de la Plata plume. During the austral winter, the combined discharge of the Río de la Plata and Patos Lagoon (southern Brazil) determines a wide coastal extension of low-salinity water from 37°S to 28°S (Piola *et al.*, 2000).

The importance of bryozoans in the southern part of the continental shelf is also reflected in the composition of biogenic carbonates in the coarse fraction of modern sediments. Bastida *et al.* (1981) studied the characteristics of the sediment in 71 benthic stations surveyed during the *Shinkai Maru* cruises throughout the study area. Bryozoans were the dominant group in the coarse fraction of 13 stations, located exclusively

off Santa Cruz (10) and Tierra del Fuego (3). On the contrary, the biogenic carbonates off Buenos Aires state and Rio Negro-Chubut were mainly dominated by molluscs or other invertebrate groups (Bastida *et al.*, 1981).

The causes of this latitudinal trend in specific richness may be related to the Pacific origin of the Magellanic fauna. Geological and palaeontological evidences show that the disruption and fragmentation of the isthmus connecting the southern Andes with the Antarctic peninsula occurred during the Tertiary (Dalziel & Elliot, 1971). This suggests that the Malvinas Current may have appeared relatively late in the geological history of the region, and that the Magellanic fauna inhabiting most of the shelf off Argentina originated in the South-east Pacific (see Vinuesa, 1977). Based on an analysis of biodiversity gradients, Schopf (1970) has shown that bivalves and bryozoans are twice as diverse in the Pacific as in the Atlantic Ocean.

Although the conclusions of the present study were based exclusively on the analysis of bryozoan distribution patterns, they could also be applicable to other groups of benthic invertebrates, since present biogeographic patterns are a consequence of oceanographic processes and historic events that affected the whole biota of the south-west Atlantic.

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