How physical and biotic factors affect brachiopods from the Patagonian Continental Shelf

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A B S T R A C T

The Patagonian Continental Shelf (PCS) is a dynamic region characterized by the confluence of two western boundary currents (the Brazil and Malvinas currents) and the presence of several oceanographic fronts, giving rise to a large and rich biological area. In this study we analyze the distribution pattern of brachiopod assemblages along a latitudinal range between 39°S and 55°S, including the relationship with different physical factors of the benthic zone, either measured *in situ* (depth, sediment, water temperature, and salinity) or provided by the Bio-ORACLE database (water temperature, salinity, phosphate concentration, nitrate concentration, dissolved oxygen concentration, primary productivity, phytoplankton, and current velocity). Data show that articulate brachiopods were not homogeneous in terms of species composition, body size, relative abundance and taphonomic signatures along the latitudinal gradient, thus indicating environmental sensitivity. The brachiopod assemblages throughout the gradient are characterized by the dominance of *Magellania venosa*, especially in the internal sector of the platform, accompanied by *Terebratella dorsata* towards the slope, and *Liothyrella uva* in the southern sector. Based on all available information, it appears that the main physical factors that affect the distribution of articulate brachiopods from the PCS were sediment grain size and water flow velocities. Also, in *M. venosa* shells, sediment grain size is also associated with fragmentation, abrasion and encrusting by invertebrates. Finally, the larger sizes of *M. venosa* appear to be associated with higher productivity areas rich in phytoplankton and suitable environmental water energy.

1. Introduction

Brachiopods constitute a marine filter feeding group with a long geologic history, with fossil records at least from the early Cambrian (Carlson, 2016; Emig, 2017), and extending to the Precambrian, as suggested by phylogenetic signals (Sperling et al., 2011). According to paleontological records they were among the most successful benthic invertebrates of the Paleozoic. In contrast, in today's marine environments they are a smaller group, having been replaced by molluscan fauna, on which taxonomists and ecologists have focused more. Additionally, brachiopods are not as common as molluscs in the intertidal and shallow marine environments and are thus unnoticed by ecologists studying coastal marine communities. This has meant that many of the compilation works on extant brachiopods (e.g., Emig, 2017) have been carried out by paleontologists.

However, recent studies have paid more attention to brachiopod assemblages since their shells can be used as biological proxies for environmental or paleoenvironmental purposes in the Quaternary (Kowalewski et al., 2002; Rodrigues and Simões, 2010; Simões et al., 2004). One line of research has also focused on evaluating whether modern brachiopods incorporate oxygen isotopes into shell calcite in isotopic equilibrium with their ambient water (Brand et al., 2003; von Allmen et al., 2010), and this indicated that further studies are required due to inter- and intraspecific variations. In addition, there is concern about the rapid acidification of oceans (Orselli et al., 2018), and the need for more frequent monitoring of the calcareous fauna (such as brachiopods) living along the Argentine Continental Shelf.

For the Argentine Continental Shelf there is little information on brachiopods, except for a report by Roux and Bremec (1996), who mentioned the articulate brachiopods collected during four joint expeditions between Japan and Argentina in 1978 and 1979 with the R/V Shinkai Maru. Almost 40 years after these first expeditions, this study

aims to determine the current distribution of articulate brachiopods in the Patagonian sector of the Continental Shelf, and to relate it with the potential factors that regulate and limit their distribution over the studied region.

1.1. The Patagonian Continental Shelf (PCS)

The PCS is located off southeastern South America and is bounded offshore by the Malvinas Current, which extends northward from northern Drake Passage (~55°S) to nearly 38°S (Piola et al., 2010). It is one of the most extensive submarine platforms in the world (1,700,000 km^2), most of which has been repeatedly uncovered during glacial times and flooded again during glacial terminations (Ponce et al., 2011). It has a maximum length of 2300 km and a mean width of 440 km in an east–west direction, with a maximum depth of approximately 250 m, although most of the shelf is < 200 m deep (Ponce et al., 2011). The shelf eastern margin is considered by the 200 m isobath, where a pronounced shelfbreak clearly sets the boundary between the continental shelf and open ocean waters (Ruiz Etcheverry et al., 2016). At present, it is a highly dynamic region characterized by the confluence of two western boundary currents (the Brazil and Malvinas currents), and the presence of several oceanographic fronts: the shelf-break front between shelf subantarctic waters, and Malvinas Current waters (Dogliotti et al., 2014; Martos and Piccolo, 1988; Matano et al., 2010).

The study area covers the Patagonian and the southern sectors of the Argentine Continental Shelf. Within the shelf there are two different zones: a 100 km coastal band which drops sharply down to 100 m, and then a 250–450 km band with a more gradual slope (Parker et al., 1997; Piola and Rivas, 1997; Sabatini and Alvarez Colombo, 2001). Fronts influence the distribution of organisms in a broad range of ways, for example by allowing high biological production, offering feeding and/or reproductive habitats to different marine species, and acting as retention areas for the larvae of benthic species (Acha et al., 2004).

During the last few years, studies of satellite image analysis of the PCS have provided valuable information on the distribution and intensity of biological production over the entire area (Rivas et al., 2006).

1.2. Water masses

The PCS is a highly dynamic region affected by winds, tides, eddies, freshwater discharges, and geomorphological features, which combine to produce an exceptionally large neritic province (Acha et al., 2004; Matano et al., 2010). As mentioned previously, its circulation is dominated by two water masses which flow in opposite directions and converge in this region: the subtropical Brazil Current and the subantarctic Malvinas Current (Acha et al., 2004; Piola et al., 2010). Intense vertical mixing has been registered in this area, especially during spring and summer (Glorioso, 1987; Lasta and Bremec, 1997; Piola and Rivas, 1997; Rivas et al., 2006; Song et al., 2016), and this, together with the local circulation, enhances nutrient availability and induces high primary productivity (Acha et al., 2004; Glorioso, 1987; Rivas et al., 2006). An example of a seasonal thermocline that produces well mixed inshore waters occurs around Península Valdés (Glorioso, 1987).

One of the most distinct characteristics of the PCS is the chlorophyll maximum (spring blooms), which closely follows the 200 m isobaths, with variations still difficult to explain, but at least partly associated with changes in the location of tidal and shelf-break fronts (Bianchi et al., 2005; Matano et al., 2010).

1.3. Previous studies on brachiopods

In a recent revision work of living brachiopods (see Álvarez et al., 2017), the genera mentioned for Patagonia (which includes the Atlantic and the Pacific since it is a region shared by Chile and Argentina) are *Liothyrella, Aerobrochus, Pelagociscus, Terebratulina, Aneboconcha,*

Fosteria, Magellania, Terebratella, Platidia, Abyssothyris and *Neorhynchia,* and probably genera today not recorded like *Novocrania*. In relation to the species living in the study region and southern South America, previous studies (i.e., Cooper, 1973; Foster, 1989, 1974; McCammon, 1973, 1970) also allowed the identification and characterization of the three most common species, which were studied in this contribution. Two of them, *Terebratella dorsata* (Gmelin) and *Magellania venosa* (Solander), belong to the family Terebratellidae, while *Liothyrella uva* (Broderip) belongs to the family Terebratullidae. Subsequently, the three species have been collected during different oceanographic expeditions on the continental shelf (Roux and Bremec, 1996), and even from a submarine canyon (43°35 ′S, 325 m, Bremec and Schejter, 2010). These species live fixed on hard substrates like shells of other brachiopods, boulders, or rock, but they are also able to live on soft bottoms (Bremec and Schejter, 2010; Richardson et al., 2007). Both *T. dorsata* and *M. venosa* occur on the continental shelf around South America and out to the Malvinas Islands, and they have developed well in areas of high productivity such as the Chilean fjords, where in some sites *M. venosa* was found growing on soft sediments, attached to grains of coarse sand (Försterra et al., 2008). In fact, these authors refer to this species living within the area of the fjords as a rarity among living brachiopods, since it is capable of building up monospecific 'living shell beds' reminiscent of the Paleozoic, when brachiopods dominated the benthic communities. The third species, *L. uva,* is a polytypic species living on the continental shelf off southernmost South America, Antarctica, and the islands between South America and Antarctica. It is well represented in the range between 100 and 800 m, and according to Foster (1989, 1974) would have used the islands between South America and Antarctica as stepping stones, since clinal changes have been recognized in a number of characters in populations from north to south.

Two other studies focusing on the biotic interactions of these brachiopod species deserve a mention: Harper et al. (2009) used specimens from the Antarctic Peninsula (*L. uva*), Malvinas Islands (*M. venosa* and *T. dorsata*) and Chile (*M. venosa*) to analyze patterns of shell repair after attacks by predators, while later on, Morán et al. (2017) focused on brachiopod epibionts along the Argentine coast between the latitudes of 40°S and 55°S, and found that higher latitudes had the highest overall rate of occurrence of encrusting organisms, mainly bryozoans.

2. Material and methods

2.1. Stations and sampling

Brachiopod assemblages for taphonomic, size and distribution analyses were collected from the PCS during a campaign aboard the R/V ARA Puerto Deseado in March/April 2012 (Fig. 1, black dots; Supplementary data). Brachiopods were collected from 15 stations using a demersal bottom trawl pilot net (total length 6 m, 25 mm mesh on the wings and 10 mm mesh at the cod end, vertical opening 0.6 m, horizontal aperture 1.8 m).

During the fieldwork, environmental information, such as bottom water temperature and salinity data, was measured using a Seabird SBE 21 thermosalinograph (Sea-Bird Scientific, Bellevue, WA, USA), whereas depth was measured using a SIMRAD EA 600 (Kogsberg Maritime, Horten, Norway) echo-sounder.

Each sample represents a single point in space at each site. Samples were preserved in 4% buffered formaldehyde.

In order to expand the database of brachiopods from the PCS, information provided by Roux and Bremec (1996) was also taken into account. Data used included the number of individuals, and the depth and sediment type per station. For this analysis, the grain size of the sediment, standardized and obtained in the different campaigns, was taken into account. The sampling was performed during four campaigns by R/V Shinkai Maru (1978–1979) and was published by Roux and Bremec (1996). Sediment information of the 2012 campaign was
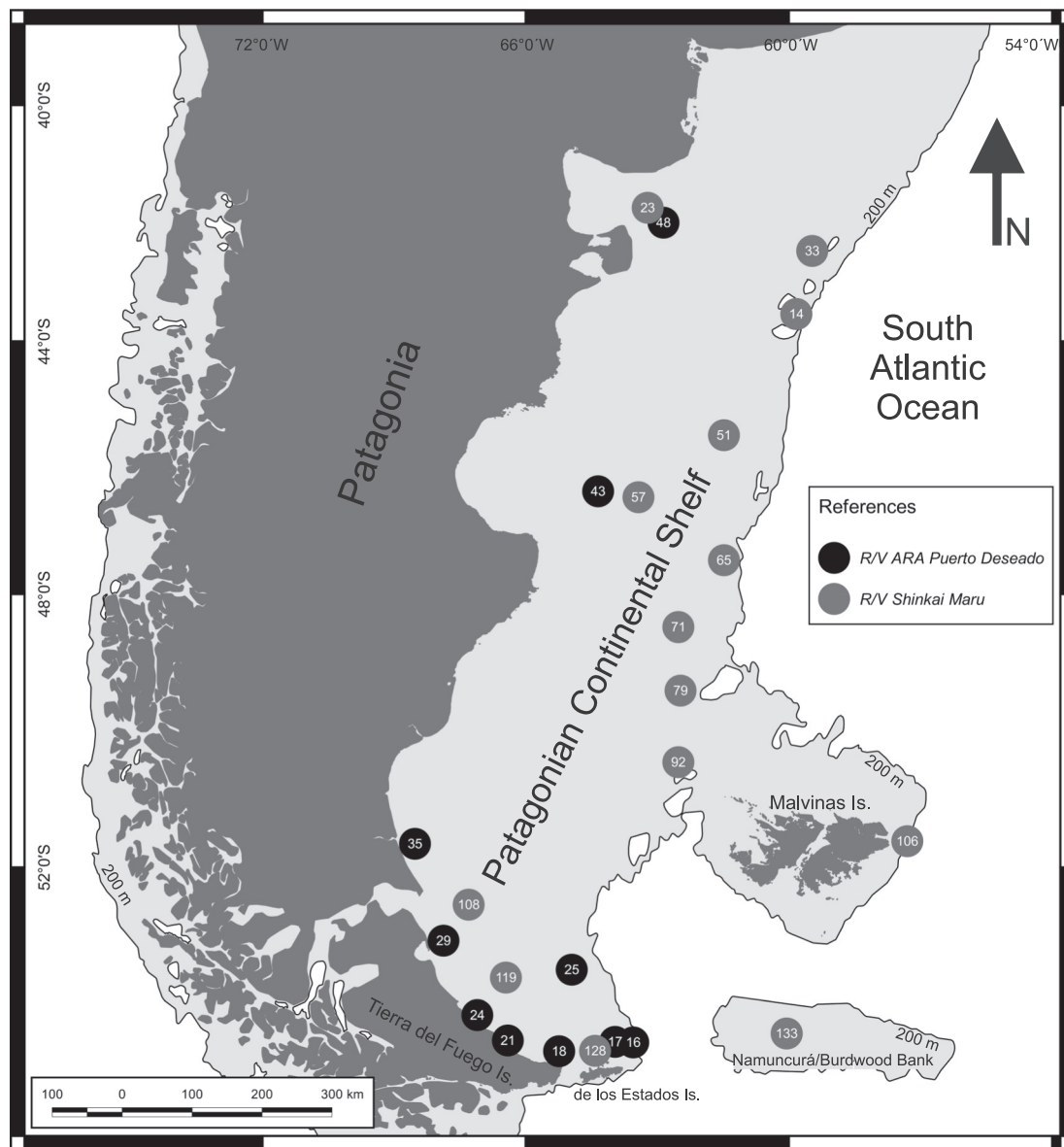
Fig. 1. Sampling sites of brachiopod assemblages collected during the R/V ARA Puerto Deseado expedition in 2012 and the R/V Shinkai Maru expeditions in 1978–1979 (Roux and Bremec, 1996). Only stations with > 20 specimens were plotted.

provided by the Puerto Deseado scientific report (http://www.conicet. gov.ar/wp-content/uploads/Informe-Campa%C3%B1a-BOPD-Patagonia-Austral-2012.pdf). We standardized sea floor information of both ships, coding according to the material available. This allowed analyzing a greater amount of information.

To increase and analyze the information from both ships together, we used benthic environmental information from the Bio-ORACLE database (Assis et al., 2017; Tyberghein et al., 2012) using QGIS v. 2.18 software to process and extract data for each station. The Bio-ORACLE dataset was retrieved on December 19, 2017 from the website: http://bio-oracle.org/downloads-to-email.php.

2.2. Data analysis

We assume that the assemblages of brachiopods represent living individuals and others recently dead. This assumption is based on the fact that a large part of the specimens preserved soft parts and were articulated. However, the age of some specimens, mainly isolated shells and fragments may be variable, from a few years to several hundred

years, that will depend, not only on the composition of the shell and the organic matrix, but also on the environmental conditions, which degrades the shells at different speeds.

2.2.1. Taxa composition, relative abundance and body size

In the laboratory, each element was classified as an articulated specimen, or as a ventral or dorsal valve if disarticulated, and was identified to the species level following Cooper (1973) and Foster (1974). The systematic position was updated according to Emig (2017). The examined material is deposited in the Centro de Investigaciones Paleobiológicas (CEGH-UNC) collection at CICTERRA, in Argentina.

To estimate latitudinal variations of taxa, the relative abundance of species was calculated for each station. In the quantitative analyses, only those stations with > 20 specimens were included. For comparative purposes, the relative abundance of brachiopods obtained by Roux and Bremec (1996) during previous expeditions in the same region (Fig. 1, gray dots) were also considered.

To explore latitudinal trends in body size, the length of each specimen or entire valve was measured using a vernier caliper to the

nearest 0.1 mm. This metric is highly correlated with body mass, together with linear measurements of the brachiopod shell (Foster, 1974). For each sample, the 25–75% quartiles were drawn with the PAST software (Hammer et al., 2001) using a box, with the median as a horizontal line inside the box, and the minimum and maximum values with short horizontal lines ("whiskers"). Taking into account the fact that brachiopods are suspension feeders, sediment grain size and benthic current velocities were also observed in each station in order to compare body size trends. Sediment grain size was obtained from the R/V ARA Puerto Deseado (2012) dataset, and benthic maximum current velocities were taken from the Bio-ORACLE database.

2.2.2. Taphonomic analysis

The taphonomic analysis was carried out in order to describe, understand and interpret the type of elements present in the study material and their preservation quality. *Magellania venosa* valves were therefore examined because this species was dominant and was recorded in high proportions along the latitudinal gradient during the R/V ARA Puerto Deseado expedition (2012); once again, only those stations with > 20 specimens were included. Taphonomic variation between stations was tested using a protocol with five taphonomic attributes for each element. Taphonomic attributes and grades were chosen according to various literature sources (Davies et al., 1989; Gordillo, 2009; Gordillo et al., 1993; Kidwell et al., 1986; Kidwell and Bosence, 1991; Kowalewski et al., 1995; Rodrigues and Simões, 2010; Zuschin et al., 2003, among others). Specimen taphonomic attributes were described using taphonomic grades, when quantifiable, or binary character states.

2.2.2.1. Articulation.
Articulation refers to the presence of two joined shells (dorsal and ventral) (Brett and Baird, 1986; Gordillo and Isla, 2011). The studied species possess cyrtomatodont hinge-teeth (Jaanuson, 1971), which increase the chance of valves remaining articulated after death, until teeth or sockets are broken (Sheehan, 1978). Articulation was coded as disarticulated (0) and articulated (1).

2.2.2.2. Dorsal/ventral valve ratio.
Those brachiopod species with a flat dorsal valve and a convex ventral valve can experience the preferential transport of the convex ventral valve (Hallman et al., 1996), so the dorsal and ventral valves were counted and coded as dorsal (0) and ventral (1). The ratio of dorsal and ventral valves was compared using a *Chi-squared* test in order to infer shell transport and residence time in the sediment water interface (Boyajian and Thayer, 1995; Flessa, 1998; Hallman et al., 1996; Simões et al., 2005).

2.2.2.3. Fragmentation.
This attribute is associated with shell breakage due to the action of mechanical stress. It can be influenced by water energy (Hollmann, 1966; Parsons and Brett, 1991) and biological interactions such as predation and bioturbation (Zuschin et al., 2003). The degree of fragmentation was encoded as complete shells (0), < 50% of the entire shell fragmented (1) and > 50% of the entire shell fragmented (2).

2.2.2.4. Abrasion.
This attribute is defined as the durability of the elements that make up the shell surface. It is associated with physical, chemical and biological factors or a combination of these, for example, environmental energy, time of exposure, particle size of the abrasive agent, and bioerosion (Brett and Baird, 1986; Parsons and Brett, 1991; Rodrigues and Simões, 2010), among others. Abrasion marks on the outer surface of the shell were encoded as unaltered valve surface (0), eroded shells with polished morphological features but without bioerosion (1), and intensely eroded and/or with bioerosion (2).

2.2.2.5. Encrusting.
This attribute evaluates the role of brachiopods in the settlement of other encrusting invertebrates (e.g., bryozoans, polychaetes, balanidae, molluscs) and/or algae. This feature was divided into three states: shells without encrusting (0), shells with encrusters covering < 50% (1) or equal or > 50% (2) of the shell.

2.2.3. Canonical correspondence analyses

Brachiopod relative abundances were calculated for each station (R/V ARA Puerto Deseado and R/V Shinkai Maru expeditions) where the total number of specimens was over 20. The domains of brachiopod species were defined with QGIS software using 60% relative abundance buffering in order to understand brachiopod preference distribution.

To explore whether the environmental variables at each station can explain the presence and the relative abundances of the three brachiopod species, canonical correspondence analyses (CCA) were carried out. Because brachiopods are benthic organisms, only measured benthic data were used. The first CCA considered the physical variables of latitude, temperature, salinity, depth, and sediment type, which were taken *in situ* during the R/V ARA Puerto Deseado campaign (2012). A second CCA was performed using our own data (R/V ARA Puerto Deseado 2012) and data from Roux and Bremec (1996) (R/V Shinkai Maru 1978–1979), who provided information on the number of individuals, the depth and the sediment type for each station. Given the need to use comparable environmental information, data derived from the global marine environment dataset Bio-ORACLE v2.0 (Assis et al., 2017; Tyberghein et al., 2012) was also obtained. The long-term averages of benthic variables such as temperature, salinity, primary productivity and phosphates were selected as potential influences on the distribution of brachiopod communities.

3. Results

3.1. Taxa composition, relative abundance and body size

A total of 902 elements, including articulated specimens and single valves, were recovered from 10 stations between depths of 27 and 169 m within the study region (Supplementary data). There was a remarkable predominance of *M. venosa* with respect to the other two species (Table 1), which represented approximately 70% of the total abundance.

The 2012 expedition found a remarkable dominance of *M. venosa* throughout the stations; in fact, it was the only species along almost the entire gradient, except in the southern sector of the area considered where *L. uva* made its appearance, and was sometimes dominant (Fig. 2). On the other hand, in the expeditions carried out 40 years before, the dominant species was *T. dorsata*, except for a single locality near Malvinas Islands where *M. venosa* was dominant (Fig. 2). It seems from these results that *M. venosa* was found or developed better in the internal part of the platform, while *T. dorsata* preferred the outer area. Given that the older stations sampled were on the outer part of the

Table 1

Taxa composition and relative abundances of brachiopods, distinguishing between articulated specimens and single valves, collected during the 2012 expedition (R/V ARA Puerto Deseado).

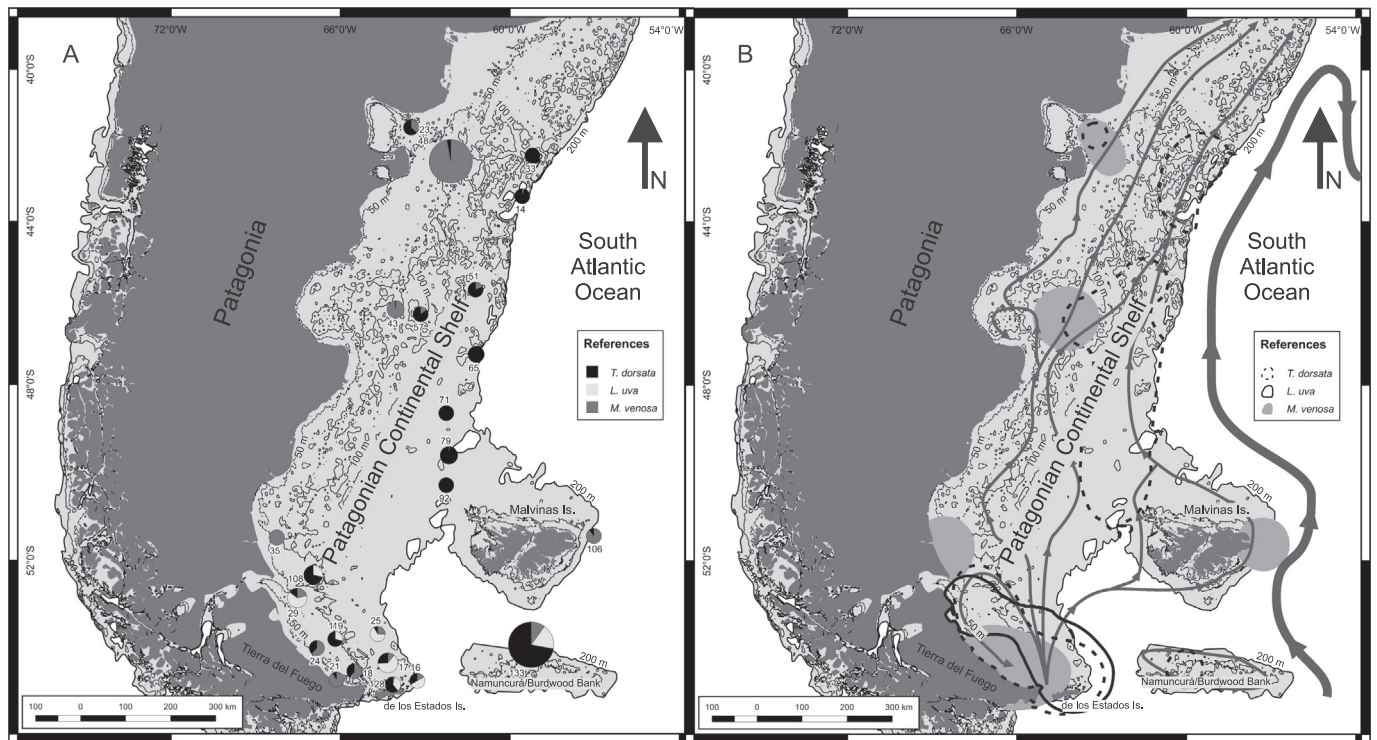| *Magellania venosa*	n	%
Articulated specimens	365	40.47%
Dorsal valves	83	9.20%
Ventral valves	174	19.29%
Single valves indet	9	1%
Terebratella dorsata		
Articulated specimens	30	3.33%
Dorsal valves	33	3.66%
Ventral valves	51	5.65%
Single valves indet	1	0.11%
Liothyrella uva		
Articulated specimens	67	7.43%
Dorsal valves	11	1.22%
Ventral valves	77	8.54%
Single valves Indet	1	0.11%

Fig. 2. A. Distribution and relative abundance of the three brachiopod species over a latitudinal gradient. Graph size is related to the total number of specimens. B. Brachiopod Domains based on > 60% of their relative abundance in each station. Gray arrows represent depth averaged circulation based on Matano et al. (2010).

platform, and separated by several kilometers from the stations sampled in the most recent campaign (2012), these were only analyzed at the regional level (latitudinal gradient, changes over space) and not at the local level (replacement of fauna over time).

Fig. 3 shows the distribution of the three brachiopod species over the latitudinal gradient between 39°S and 54°S, where *M. venosa* was present along the whole latitudinal gradient but with great variability in body size. Recovered *M. venosa* shells showed the highest average values between 46°S and 51°S. The greatest variability in body size was seen at 46°S, while the lowest was registered at 51°S and at 39°S; however, at 39°S the smallest sample size (N = 12) was registered, and therefore should not be taken into account. According to the body size analysis of *M. venosa* shells, there is a slight trend of maximum size increasing towards the south (Fig. 3A; Fig. 4); however, there was a lot of variability in sample size and in brachiopod body size between stations. The other two species, *T. dorsata* and *L. uva* (Fig. 3B and C), showed a lower body size variability than *M. venosa*, but these species were registered in lower proportions and in a limited latitude gradient.

According to datasets from R/V ARA Puerto Deseado (2012) and the Bio-ORACLE database, different grain sizes were recorded at stations 43 and 35. Station 43 exhibited coarse grain sediments (gravel and shell fragments), while station 35 had very fine sediments (cohesive muds). The highest body size averages for *M. venosa* were recorded at these stations, with higher body size variability at station 43 than station 35 (Fig. 3A). Both stations also had equal benthic current velocities (0.046 m/s), coinciding with the highest average values for the whole latitudinal gradient (Fig. 5).

3.2. Taphonomic analysis

3.2.1. Articulation

Throughout the latitudinal gradient, there were differences in articulation as well as in taphonomic attributes and dorsal and ventral valve ratios between these three species of brachiopods. Although articulation was recorded at almost all stations, one station alone (station
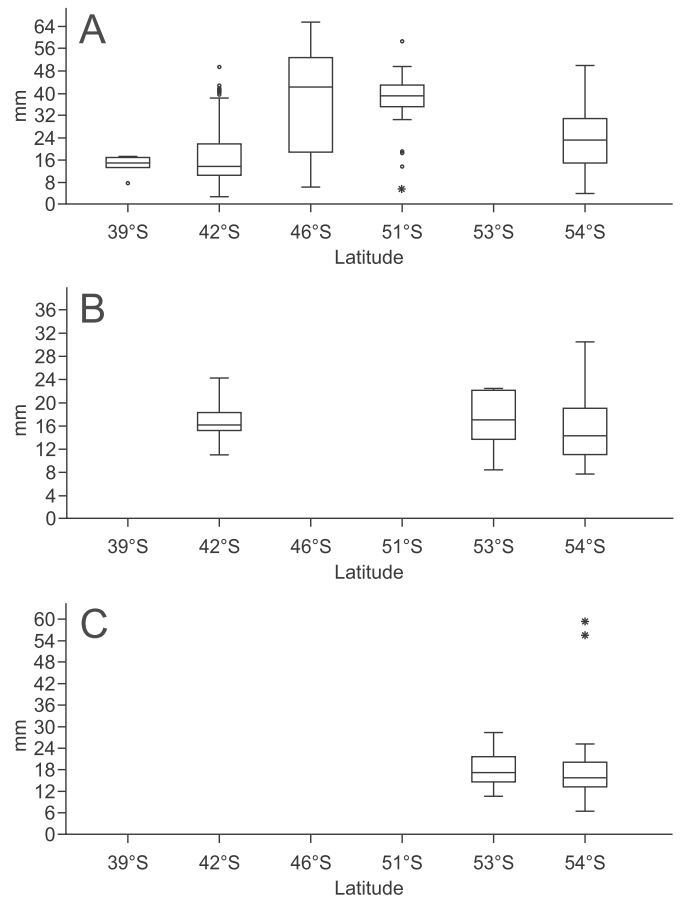

Fig. 3. Distribution of the three brachiopod species by size over a latitudinal gradient. Boxplots showing median, maximum, minimum and outlier values. A. *Magellania venosa*. B. *Terebratella dorsata*. C. *Liothyrella uva*.
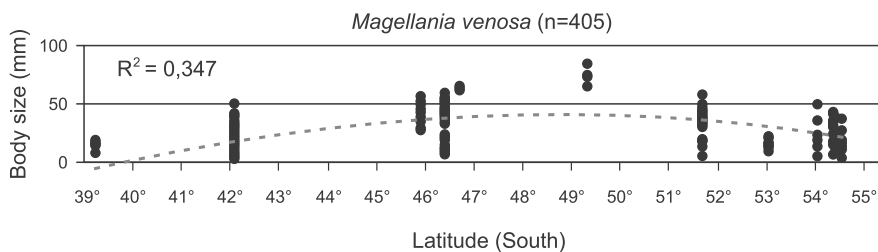
Fig. 4. Relationship between body size and latitude for *Magellania venosa*.

29) contained 100% disarticulated *M. venosa* shells. Some stations showed a slightly higher number of ventral valves over dorsal valves for *M. venosa* (*M. venosa*, station 48 p = 0.035, station 29 p = 0.0001, and station 18 p = 0.039; Table 2). At station 29, 100% of *T. dorsata* and *L. uva* valves were disarticulated; however, the proportion of dorsal/ventral valves tended to be 1:1 for *T. dorsata*. For *L. uva* there were significant differences in the proportion of dorsal/ventral valves at station 18 (station 18 p > 0.0001; Table 2).

Since *M. venosa* was the most abundant taxa and had a continuous

record throughout the latitudinal gradient, the following analyses were only carried out on this species (Fig. 5).

3.2.2. Fragmentation

There were some differences in the fragmentation pattern along the latitudinal gradient. The analyzed assemblages all showed some degree of fragmentation: either whole shells with < 50% fragmentation, or fragmentation of > 50% of the shell. Although brachiopod assemblages were well-preserved, with most of specimens exhibiting complete
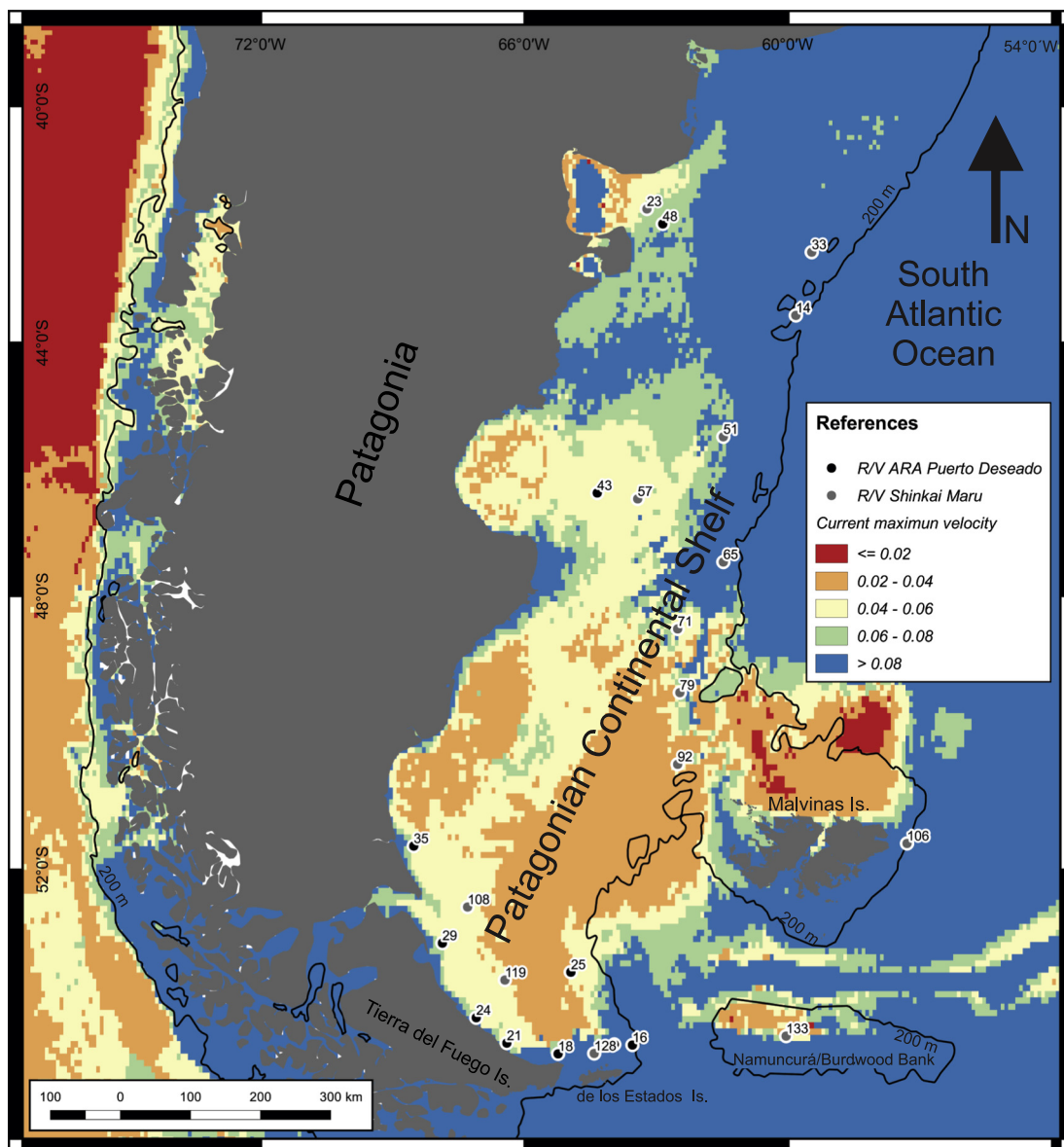

Fig. 5. Map showing benthic maximum current velocities of the studied area. Current velocities taken from the Bio-ORACLE database.

Table 2
p-Values of dorsal/ventral valve ratios obtained by a *Chi-squared* test in the three brachiopod species from stations where there were over 20 *M. venosa* specimens. Asterisks represent statistical differences.

Station	Latitude (°S)	*M. venosa*	*T. dorsata*	*L. uva*
48	42	0.035*	0.12	0
43	45	0.083	0	0
35	51	0.79	0.423	0
29	53	0.0001*	0.052	0
21	54	0.116	0	0
18	54	0.039*	0.4	> 0.0001*

valves, there were some differences in the degree of fragmentation. Stations 48, 43 and 35 contained > 60% complete, or unfragmented, shells. Even though stations 29, 21 and 18 had 40% complete shells, the remaining 60% all had broken valves. In this taphonomic attribute, an interesting pattern emerged: from latitude 42° to latitude 51°S, the fragmentation grade was low, while from latitude 53° this started to rise towards the southern stations, where grades 1 and 2 (fragmentation lower than 50% and fragmentation equal to or higher than 50% of the whole shell) had higher percentages for *M. venosa* valves (Fig. 6A). With respect to *T. dorsata* and *L. uva*, both species also had a good preservation pattern, where a high proportion of shells had complete valves, especially in stations 35 and 21 for *T. dorsata*, and station 29 for *L. uva*.

3.2.3. Abrasion

For this attribute, *M. venosa* had a good preservation pattern. However, as with fragmentation, the degree of abrasion also showed an interesting pattern. While most shells had natural surfaces with no signs of abrasion, there were some eroded shells with polished morphological features, and others which were intensely eroded with completely abraded shell features. Stations 48, 21 and 18 had the highest proportion of abraded shells, while stations 43, 35 and 29 had higher proportions of natural surfaces on their shells, particularly station 29, where 100% of the shells had no abrasion. With respect to latitude, the
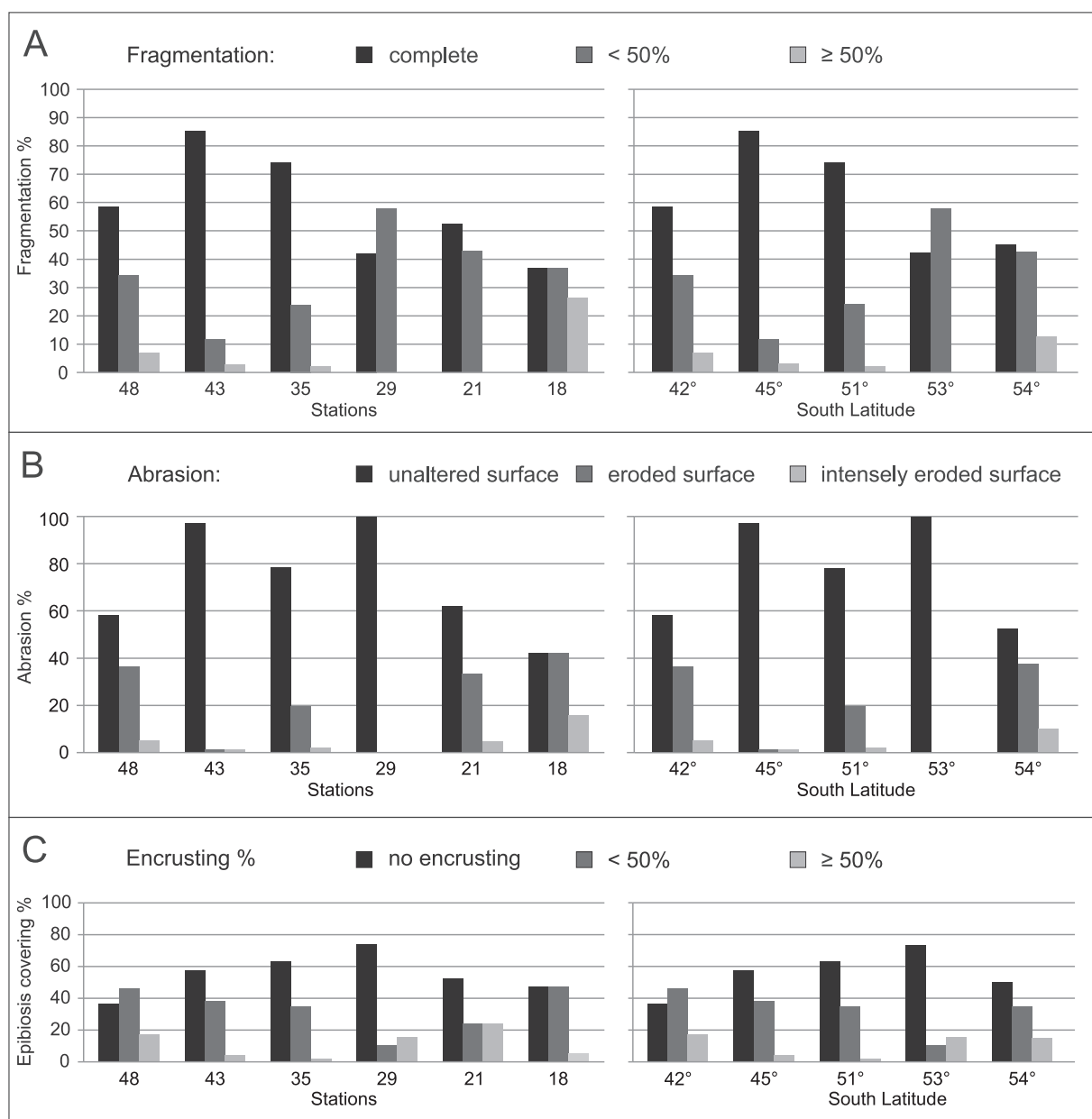

Fig. 6. Taphonomic attributes on *Magellania venosa* shells at each station and along the latitudinal gradient. A. Fragmentation. B. Abrasion. C. Encrusting.

extreme latitudes (latitude 42°S and latitude 54°S) had more abrasion, with higher percentages of grades 1 and 2 (eroded shells with polished morphological features, and intensely eroded with shell features completed abraded) for *M. venosa* valves (Fig. 6B) than the intermediate latitudes (from latitude 45°S to latitude 53°S). *Terebratella dorsata* and *L. uva* shells also had a good preservation pattern, where natural surfaces were seen in a high proportion at station 29. *Liothyrella uva* shells with no abrasion were also found in very high percentages at stations 35 and 21.

3.2.4. Encrusting

The analyzed *M. venosa* assemblages showed three grades of encrusting by organisms: no encrusting, encrusters covering < 50% of the shell, and encrusters covering 50% or more of the brachiopod shell. Stations 43, 35, 29 and 21 had lower percentages of encrusting than stations 48 and 18. Again, at the extreme latitudes (latitude 42°S and latitude 54°S) there was a greater degree of covering by encrusters, with higher percentages of grades 1 and 2 (encrusters covering < 50% of the shell, and encrusters covering > 50% of the shell) for *M. venosa* valves (Fig. 6C) than at intermediate latitudes (from latitude 45° to latitude 53°S). The proportion of encrusting on *T. dorsata* shells was only high at station 48, and medium at station 18. At the rest of stations, encrusting was low for both *T. dorsata* and *L. uva*.

3.3. Canonical correspondence analyses

Conforming to the CCA on the dataset from the 2012 expedition (Fig. 7A, Supplementary data), the relative abundance of *M. venosa* was associated with higher water temperature, lower latitudes and finer grain sediments. Inversely, *L. uva* seemed to be more sensitive to coarser grain sediments, higher latitudes and depths, and lower water temperatures. Finally, *T. dorsata* did not seem to prefer any particular environmental variable, although it could be more sensitive to coarser sediments.

According to the CCA between both datasets from the 2012 expedition and Roux and Bremec (1996), and incorporating data provided by the global marine environment dataset Bio-ORACLE v2.0 (Fig. 7B, Supplementary data), the relative abundance of *M. venosa* was associated with higher water temperatures, higher primary productivity, and a higher concentration of phytoplankton. Its relative abundance also corresponded to shallower depths and lower salinity, as well as lower concentrations of fosfates and nitrates. Inversely, *T. dorsata* seemed to be more sensitive to deeper environments with lower water temperature, higher salinity and higher concentrations of fosfates and nitrates. Finally, *L. uva* seemed to prefer higher latitudes with coarser grain sediments and a high concentration of dissolved oxygen.

4. Discussion and conclusions

4.1. Environmental sensitivity to different factors

The uneven distribution of the articulate brachiopods to depths of over 200 m and covering a great latitudinal range (between 39°S and 55°S) along the PCS, clearly shows their environmental sensitivity.

With respect to the distribution of the three brachiopod species recovered (*L. uva*, *T. dorsata* and *M. venosa*), there are natural physiological elements such as water temperature and available dissolved oxygen that probably explain why *L. uva* only appears in the southern sector. Furthermore, other physical factors, such as sediment type, appear to play an important role in their distribution and development. According to this study, data from the expeditions aboard R/V ARA Puerto Deseado and R/V Shinkai Maru, together with the Bio-ORACLE dataset, offered valuable information on which environmental variables may play a role in the preferences of brachiopods. *Liothyrella uva* showed a preference for coarser sediments, lower water temperature and a high concentration of dissolved oxygen. These three

environmental variables change according to the latitudinal gradient, where water temperature tends to decrease towards the south, while sediment grain size and the concentration of dissolved oxygen tend to increase, coinciding with previous studies (Parker et al., 1997; Podestá, 1997; Sabatini et al., 2016; Violante et al., 2014). This is probably why *L. uva* prefers southern latitudes (lower water temperature with a high concentration of dissolved oxygen and coarser sediments, among other environmental factors). This is also clearly seen in the other two species, which are differentially distributed over the PCS. The distribution of *T. dorsata* (data collected by Roux and Bremec, 1996) seems to be more linked to the Argentine shelf-break front and associated with sandy sediments, whereas *M. venosa* (new data) prefers the Patagonian cold estuarine zone and finer sediments (i.e., mud to muddy sands).

In addition, the distribution and relative abundance pattern of *M. venosa* resulting from the stations studied (provided by the canonical correspondence analyses), also seems to be associated with the concentration of phytoplankton and primary productivity. This species probably prefers high values of these variables. Although the very slight correlation between body size and latitude does not appear to have a significant effect on the mean or on size variance, other authors have found a trend when correlating these variables (Peck and Harper, 2010). This suggests that other physical and/or biological factors also come into play. In the particular case of *M. venosa*, the larger sizes appear to be associated with higher productivity areas, such as the coastal tidal front of Patagonian embayments.

In this respect, phytoplankton would be a crucial ecological factor in the development of brachiopods, since it is the main source of food. High, heterogeneous productivity along the Continental Platform has been supported by previous studies carried out in the region, including both campaign and satellite data. For example, previous studies on scallops and bryozoans also found that the richest stations on the Argentine Continental Platform occurred along the 100 m isobaths (López Gappa, 2000; Lasta and Bremec, 1997), which is an area where a high-productivity shelf-break front has been documented (Podestá, 1997). Acha et al. (2004) also argue that high levels of chlorophyll biomass found near the shelf break area are associated with nutrient supply by the Malvinas Current; nutrient-rich subantarctic water flows northward and provides nutrients to the shelf area through various physical processes, including eddies and mixing. Rivas et al. (2006) mention that the external region, bordering the 200 m isobath, presents elevated concentrations of phytoplankton from spring through fall, supported by the nutrient-rich waters provided by the Malvinas Current; however, the coastal region has less marked seasonal variability, and small, isolated areas with elevated concentrations associated with tidal coastal fronts. Interestingly, those stations where the largest body size for *M. venosa* was recorded in this study (at latitudes 46°S and 51°S) did not coincide with the high values of primary productivity and phytoplankton provided by the Bio-ORACLE database (see Supplementary data). On this point, it is important to note that both phytoplankton and primary productivity have very variable compositions, resulting in great spatial heterogeneity which is difficult to recognize in satellite studies (Segura et al., 2013). Field studies would therefore be necessary to obtain more detailed data, but these would be a huge undertaking, given the large surface area of the platform.

Nevertheless, brachiopod species recorded the lowest metabolic rates among invertebrates, and slow growth (James et al., 1992; Peck et al., 1997), which would offer an advantage in low food availability environments and hence an increase in body size (Peck and Harper, 2010). Moreover, taking into account the studied material together with data from the Bio-ORACLE database, it is proposed that the nutrient concentration would not be the main factor that conditions the distribution and body size (i.e. *M. venosa*). The nature of substrates would therefore be one of the primary factors, as found by Foster (1989). It is also important to note that brachiopods in general show great morphological variability or phenotypic plasticity (Alexander, 1977; Topper et al., 2017; Williams et al., 2006) which allows them to
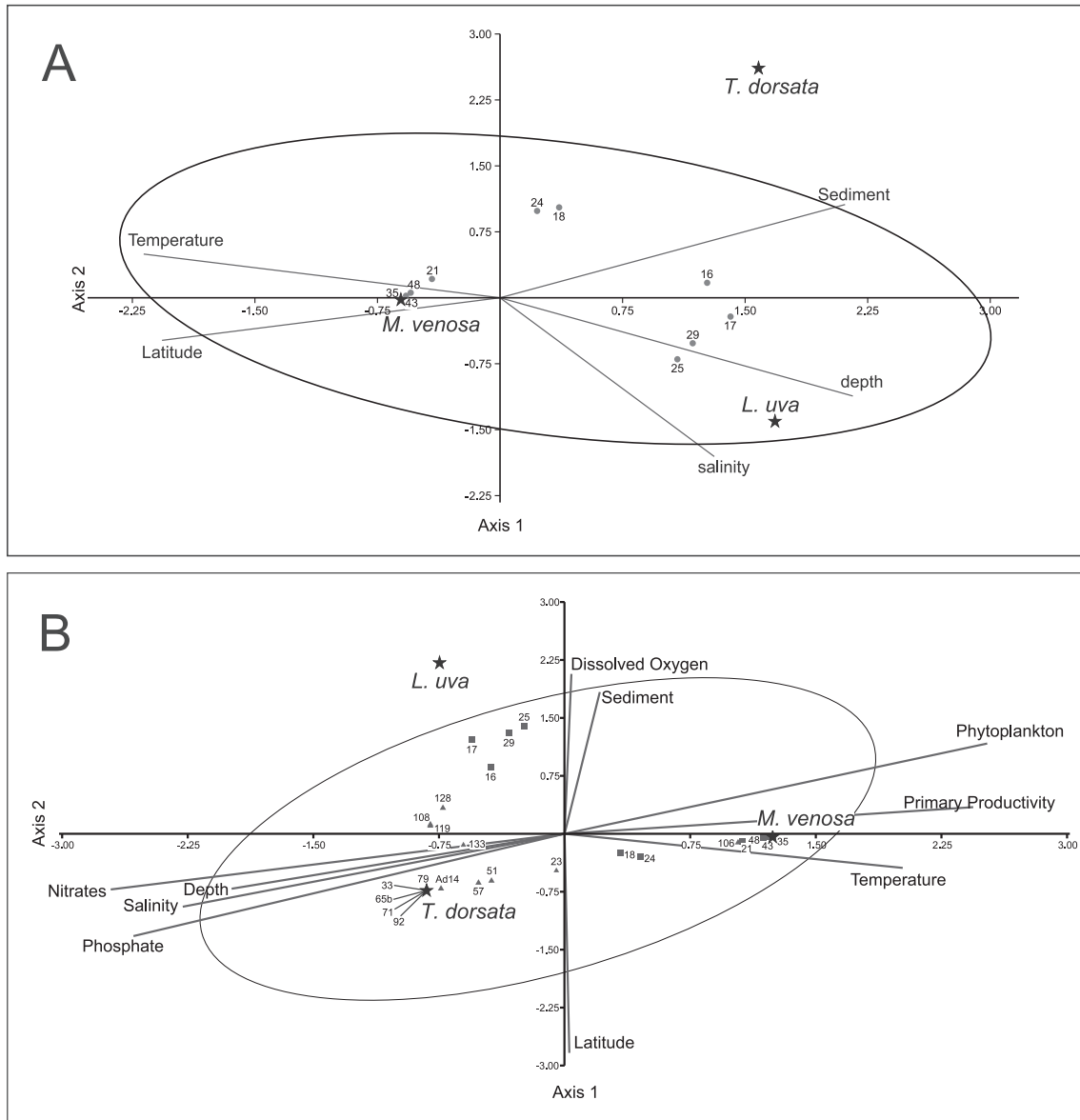
Fig. 7. Canonical correspondence analyses. A. CCA between the three brachiopod species and environmental data from the 2012 expedition (R/V ARA Puerto Deseado). B. CCA which includes our own data (R/V ARA Puerto Deseado, 2012), data provided by Roux and Bremec (1996) (R/V Shinkai Maru 1978–1979), and environmental data provided by the global marine environment dataset Bio-ORACLE v2.0.

adapt to a wide range of habitats (Williams et al., 2006), where substrate type influences by inhibiting or promoting shell growth in a particular direction (Topper et al., 2017). In the case of *M. venosa*, which was registered along the whole latitudinal gradient, the highest values for mean body size were found at two stations (43 and 35), corresponding to 46°S and 51°S latitudes, respectively (Fig. 3A). These stations had different sediment grain sizes, with a coarser sediment grain size at latitude 46°S and very fine sediment at latitude 51°S. Another difference recorded between these stations was body size variability, where higher variability in the body size of this species was recorded in the coarser substrate (see percentiles in Fig. 3A). This may indicate that grain size is not an important environmental factor controlling the mean body size *M. venosa*, although it does contribute to the body size range.

However, environmental energy would affect the brachiopods' feeding and excretion processes; brachiopods need slow and laminar water movement during these processes, and depending on the mainstream speed they would expend more or less energy controlling the energy dissipation from turbulent flow regimens (LaBarbera, 1981,

1978, 1977). This lost energy would represent a cost in terms of animal growth (LaBarbera, 1981). On the other hand, in very low energy environments, some recirculation of excurrent water has been registered as a consequence of the small sizes and low pumping speeds of brachiopods, which try to avoid refiltering the same water repeatedly (LaBarbera, 1981). Based on the benthic maximum current velocity from the Bio-ORACLE database, those stations with the highest current velocity values had the smallest *M. venosa* body sizes. Besides, as mentioned before, stations 35 and 43, which recorded similar current velocities (0.046 m/s, Fig. 5) had the highest mean body sizes (see Fig. 3A, and Supplementary data). This would therefore suggest that environmental energy or water flow control brachiopod body sizes.

One last comment regarding the fishing gear used here, is that the trawl is not the best gear to collect brachiopods when one seeks to prevent the loss of juveniles (we collect the material using the fishing gear available in the vessel at that time). In this regard its absence probably does not affect the results when we compare adult specimens with environmental variables.

4.2. Taphonomy

Following on from the idea that brachiopods could have very variable body shapes and sizes, it was important to understand the type of material recovered from the sampling method for a better interpretation of these organisms. Taphonomic analyses were thus developed which showed that brachiopod assemblages from the PCS contained good quality material, with live organisms and well-preserved dead specimens with a high proportion of articulated valves. In general, this material was probably not affected by sampling or storage methods (Flessa et al., 1992), although there was some degree of deterioration to the valves that could have been due to short-term environmental effects (Carroll et al., 2003; Torello et al., 2002). Articulation was registered at almost all stations and in high proportions, except at station 29 which contained 100% disarticulated *M. venosa* and *T. dorsata* valves. In the case of dead shells, for those that were single valves, the proportion of dorsal and ventral valves of the three species varied depending on each station, although ventral valves were always more abundant than dorsal ones. This coincided with the fact that flat dorsal valves are more likely to be transported or are more fragile (Simões et al., 2005). Moreover, live specimens were found together with empty and disarticulated shells. Carroll et al. (2003), who studied the time-averaging of brachiopod shell assemblages from a modern tropical shelf, elucidated that brachiopods occurred in patches and were found in the same areas as live specimens; those accumulations were thus produced *in situ* by local populations. Here, the assemblages collected during 2012 by ARA Puerto Deseado, could therefore be interpreted as local assemblages or *in situ* brachiopod assemblages, where flat dorsal valves remained in low proportions since they are prone to transport or disintegration.

Considering the taphonomic attributes studied here, these brachiopod assemblages showed a good quality of preservation in general, with some variations that could be a response to environmental pressure. Because these three brachiopod species live in the sediment/water interface, they are located in the taphonomically active zone (Davies et al., 1989) and are prone to be a target for taphonomic processes (Davies et al., 1989; Flessa et al., 1993; Simões et al., 2005; Walker and Goldstein, 1999), depending on the physical and chemical environmental variables. In these brachiopod assemblages, the highest proportion of brachiopods was whole shells with no degree of fragmentation; however, that proportion varied at some stations. Stations 48, 43 and 35 had a high proportion (> 60% of the sample) of complete valves, while at stations 29, 21 and 18 that percentage decreased to 40% of the sample, indicating a greater proportion of broken valves. This fragmentation pattern coincided with the grain size of sediments. Those stations located between latitudes 42°S and 51°S contained sand and mud, which are fine grain sizes, and coincided with the lowest fragmentation grade, while the southern stations located at latitudes 53°S and 54°S, had higher fragmentation of valves coinciding with coarser, sabulitic sediment, with gravel and coarse to fine sand with shells. According to previous studies carried out by the Servicio Hidrografico, Servicio de Hidrografia Naval and other researchers (Parker et al., 1997; Violante et al., 2014), muds are distributed throughout northern Patagonian gulfs, while coarser sediments such as gravels are distributed mainly south of 47°S. It is known that shell breakage is the result of large sediment grain size, among other factors (Parsons and Brett, 1991; Zuschin and Stanton, 2001). Although fragmentation in general was not particularly intense, sediments with a coarse grain size such as shell fragments and sabulitic sand could affect the preservation of those brachiopods on the benthos.

At the same time, stations located at extreme latitudes (stations 48, 21 and 18), latitudes 42°S and 54°S, had the highest degree of abrasion on their shells, while the rest of the stations located in the intermediate latitudes had more natural surfaces on their shells. Again, it seems that sediment plays a role in conditioning the preservation quality of brachiopod valves, and grain size is an important factor in the abrasion grade (Driscoll, 1967; Staff and Powell, 1990). Sediments from stations located at latitude 42°S contained sand with shells, and those from latitude 54°S also had coarse sands, which were probably abrasive sediments. On the other hand, muddy sediments located at intermediate latitudes, which are very fine sediments, would not have been such an abrasive element for brachiopod surfaces.

Keeping in mind the abrasion pattern, the same could be seen for the percentage of encrusting on brachiopod shells. Stations from extreme latitudes (stations 48 and 18) showed higher percentages of encrusting, especially by bryozoans. Those stations with sediments containing larger grain sizes such as shell fragments, gravels and sabulitic sands, have greater surface area available for epibiont colonization that would increase the chance of settlement (Rodland et al., 2014, 2006, 2004), and then could be a suitable substrate for these kinds of encrusters/epibionts. According to some publications, bryozoans prefer hard or firm sea floors, or hard objects such as shells and skeletons (Eggleston, 1972; Hageman et al., 1998; McKinnney and Jackson, 1989; Taylor, 1999). Moreover, Parker et al. (1997) related the distribution of sediment type along the Argentine Continental Shelf with the presence and diversity of bryozoans. They proposed that because the sediments in the southern sector of the shelf are mainly composed of gravel, bryozoans have the richest diversity in that area, while the muddy sediment in the northern Patagonian gulfs (San José, Nuevo and San Jorge Gulfs) has little bryozoan species richness (López Gappa, 2000; Parker et al., 1997). Richiano et al. (2017) associated the bryozoan diversity pattern primarily to sea surface temperature and to enhanced productivity, which is higher southwards. Nevertheless, although our analysis did not evaluate the diversity of epibionts, we found one of the highest encrusting percentages in northern Patagonia, and also in southern Patagonia, where primary productivity at the benthos did not show high values. It is proposed here that one of the main variables conditioning encrusting on brachiopod shells is the type of substrate, where coarse sediments such as gravels, sabulitic sands or shell fragments provide greater surfaces for the settlement of encrusters/epibionts, especially bryozoans. However, other variables should also be taken into account in order to explain which ones determine encrusting on brachiopod shells, for example turbidity and water energy.

4.3. Final remarks

Thus, from this intricate network of physical, biological and ecological factors, brachiopods add no uniformity to the diversity and richness of the PCS. With respect to the role of brachiopods in modern ecosystems, the answers should be sought in the biotic interactions that they maintain with other groups, for example, as substrates for epibionts, or food for other members of benthic communities. In this sense, there are some isolated or recent incipient data for southern South America (e.g., Gordillo et al., 2017; Harper et al., 2009; Morán et al., 2017), but more studies focusing on these topics are necessary. For example, benthic individuals of the decapod *Munida gregaria* were captured in almost all of the benthic sets made during the 2012 campaign, and perhaps this species causes breakage by feeding on some epibionts as polychaetes.

The brachiopod assemblages within the PCS are characterized by the dominance of a single species throughout the gradient, with more variety in the southern sector, where *L. uva* makes its appearance. The dominant species in the internal sector of the platform is *M. venosa*, while in the external sector towards the shelf-break it is *T. dorsata*.

The three studied brachiopod species show great variability in size over the latitudinal gradient between 39°S and 54°S. *Magellania venosa* had the largest individuals at intermediate latitudes (46°S and 51°S), coinciding with equal benthic water flow velocities. Stations with higher benthic current velocities contained lower *M. venosa* mean body sizes. Sediment grain size may affect body size variability.

The degrees of taphonomic attributes considered are not homogeneous along the latitudinal gradient, thus indicating environmental

sensitivity. Finally, sediment grain size is the common factor modulating fragmentation, abrasion and encrusting by invertebrates on brachiopod shells from the PCS.

Our analysis shows that fragmentation is associated with grain size sediments, as shown in previous studies (i.e. Parsons and Brett, 1991; Zuschin and Stanton, 2001). However, we recognize that other types of studies, more sophisticated, particularly experimental (with aquaria) are needed to obtain accurate information on the effect of grain size (?) through the speed of the currents, added to submerged chambers.

Taking into account the material from this study, together with other datasets (i.e., Roux and Bremec, 1996; Bio-ORACLE database) it is proposed here that one of the most important physical factors affecting brachiopods is probably the grain size of sediments, which could determine the distribution of the three brachiopods species. But in addition, other factors associated with productivity (e.g., water energy) would be responsible for the distribution, affecting even its size in the case of *M. venosa*.

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