

# Bryozoa from the continental shelf off Tierra del Fuego (Argentina): Species richness, colonial growth-forms, and their relationship with water depth

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## ABSTRACT

As bryozoans have a rich fossil record, the analysis of their bathymetric ranges and the occurrence of different colonial growth-forms in living assemblages may be valuable for palaeoecological interpretation. The bryozoan fauna from 58 benthic stations (18–92 m) collected on the Atlantic continental shelf off Tierra del Fuego (Southwest Atlantic) was analyzed to assess its biodiversity and the relationship of species richness and colonial growth-forms with depth. In the 58 stations analyzed here, which covered an area of ~5600 km<sup>2</sup>, 90 species were found. Of these, 43 species were already known for this area, whereas the remaining 47 are new records. Therefore, the present study increases by 87% the known biodiversity for the study area, which now reaches 101 species. There is a clear increase in bryozoan species richness with depth, but the ratio of erect-rigid/encrusting species remained unchanged, as all the growth-forms increased with depth. Stations were classified by cluster analysis in three groups differing mainly in species richness. Taxonomic turnover (beta diversity) increased with increasing differences in depth between stations. This was due to the presence of a new set of deeper species, but not to the demise of the shallower fauna in the deeper stations. Twenty-two potentially habitat-forming species were found along the bathymetric range surveyed in this study. They were absent at the shallowest station, its number was relatively low at intermediate depths (31–64 m) and then experienced a sharp increase at 70 m. Palaeoecological interpretations should take into account that fragile, calcareous growth-forms could be expected to occur at shallower depths in more protected areas.

## 1. Introduction

Diversity is a measure of the compositional complexity of an assemblage and its fundamental parameter is species richness (Chao and Jost, 2012). The compilation of a complete list of species present in a community is one of the major issues in biology, but requires excessive efforts and is an almost unattainable goal in practical applications (Chao, 2005; Chao and Chiu, 2016). As it is rarely possible to collect sufficient samples to encompass all the species present, the total species number can be estimated statistically by computing the asymptotic species richness (Chao et al., 2009). In this sense, species richness estimators try to compute the exact value of species richness from a comprehensive sampling, and are widely used in ecology (e.g. Chao, 2005; Walther and Moore, 2005).

Bryozoans, with almost 6000 extant species (Bock and Gordon, 2013), are colonial filter-feeding invertebrates composed of clonal zooids which, in most cases, secrete calcareous skeletons (Taylor et al., 2015). From an ecological point of view, bryozoans are important

components of marine benthic ecosystems since they are food items for a variety of predators (Lidgard, 2008), are good indicators of environmental conditions both in fossil (Hageman et al., 1997) and in recent (Amini et al., 2004; Wood and Probert, 2013) communities, are relevant habitat providers (Cranfield et al., 2003; Cocito, 2004; Wood et al., 2012), and also may be useful to predict the effect of ocean acidification on calcified biota and carbonate sediments (Smith, 2009; Figuerola et al., 2015; Fortunato, 2015).

To comprehend the complexity of nature, the description and quantification of ecological patterns are important first steps (Fortin and Dale, 2005). Biodiversity patterns are usually related to disturbance levels (Connell, 1978) and, in a marine boulder field, disturbance is related both to the near-bottom hydrodynamic conditions and to substrate size (Sousa, 1979; McGuinness, 1987). Bryozoan species richness has been reported as controlled mainly by depth, but also by other environmental parameters such as temperature, salinity and the availability of substrates and food (e.g. Schopf, 1969a; Grant and Hayward, 1985; Amini et al., 2004; Denisenko et al., 2016). Large bryozoan

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colonies are considered habitat-forming organisms, as they increase the complexity of the environment (Kuklinski, 2009). Bryozoan colony morphology has been regarded as a good indicator of disturbance level in a habitat since wave action and strong currents have been shown to hinder the development of species susceptible to mechanical damage, such as erect-rigid growth-forms (Stach, 1936; Kuklinski, 2009). As bryozoans have a rich fossil record and their colonial growth-forms can be correlated with different environmental conditions, their value in palaeoenvironmental interpretation has been widely acknowledged (Hageman et al., 1997; Taylor, 2005).

A relatively high benthic biodiversity has been reported in the continental shelf off Tierra del Fuego, Argentina (López Gappa, 2000), although an insufficient sampling effort has also been demonstrated (Souto et al., 2014). The biodiversity and geographic distribution of bryozoans between 52° and 54°S and 69°–67°W have been compiled by López Gappa (2000). Additional information can be found in several taxonomic (López Gappa, 2002; López Gappa and Liuzzi, 2013) and ecological studies (López Gappa and Sueiro, 2007; Centurión and López Gappa, 2011).

The present study assessed the relationship of bryozoan biodiversity and colonial growth-forms with depth on the continental shelf off Tierra del Fuego. In particular, the following hypotheses were tested: (1) bryozoan species richness in the area is higher than previously reported, (2) bryozoan species richness and the proportion of growth-forms change with depth, (3) the differences in the composition of bryozoan assemblages and the species turnover (beta diversity) are related to depth differences between stations.

## 2. Materials and methods

### 2.1. Study area

The material under study was collected in an area of around

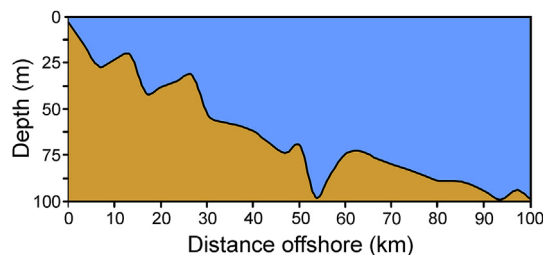


Fig. 2. Bathymetric profile off the Atlantic coast of Tierra del Fuego, at a latitude of 53°06'S.

70 × 80 km on the continental shelf off the Atlantic coast of Tierra del Fuego, Argentina (Fig. 1). The water masses in this area are nutrient-rich, strongly diluted, and characterized by vertical mixing due to the action of tides and wind stress (Acha et al., 2004; Palma et al., 2004; Sabatini et al., 2004; Rivas and Pisoni, 2010). Temperatures between 9.5 and 10.0 °C and salinities from 32.8 to 33.0 have been recorded in bottom waters during late summer (Sabatini et al., 2004). Satellite-measured surface chlorophyll-*a* has shown concentrations higher than 1 mg m<sup>-3</sup> throughout the year (Rivas et al., 2006). Persistent fronts in the study area have been identified from sea surface satellite data (Acha et al., 2004; Palma et al., 2004; Rivas and Pisoni, 2010).

The bathymetric profile of the continental shelf off the Tierra del Fuego Atlantic coast shows a gradually decreasing seafloor, reaching 100 m depth at 102 km offshore (Fig. 2). The wave climate is relatively benign due to the dominance of strong winds from the west. The frequency of wave heights higher than 3.5 m is very low. Gales of 41–47 knots were estimated to generate an extreme wave of 12 m height at a depth of 50 m, with a return period of 50 years (Bujalesky, 2007).

Siliciclastic gravel is the predominant coarse fraction sediment in this region (Parker et al., 1997). Its origin is associated with re-

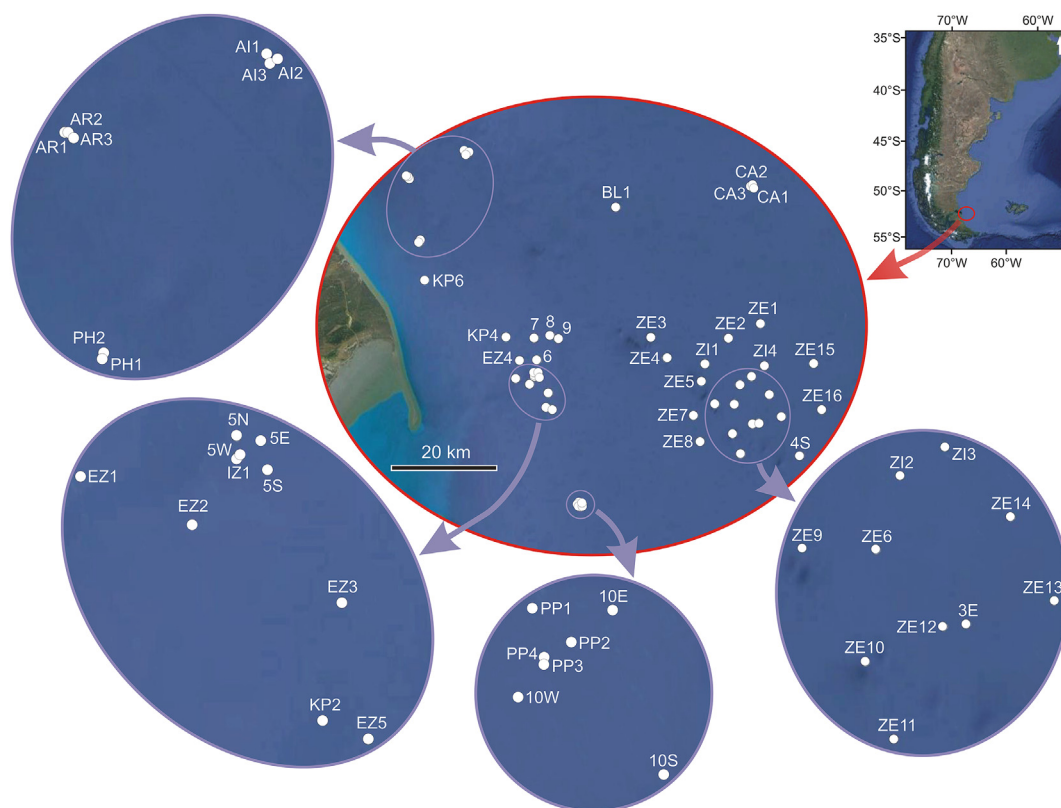


Fig. 1. Continental shelf off the Atlantic coast off Tierra del Fuego, Argentina, showing the distribution of the 58 stations. Depth range is 18–92 m. Detailed bathymetric data can be found in Table 1.

**Table 1**

List of stations collected on the continental shelf off Tierra del Fuego and the number of bryozoan species found in each.

Station	Date	Latitude (S)	Longitude (W)	Depth (m)	Species richness
PP1	Oct 11, 2011	53° 17.889'	67° 44.784'	52	8
PP2	Oct 11, 2011	53° 17.941'	67° 44.680'	52	8
PP3	Oct 11, 2011	53° 17.975'	67° 44.755'	52	14
PP4	Oct 11, 2011	53° 17.965'	67° 44.752'	52	14
PH1	Oct 12, 2011	52° 50.279'	68° 10.821'	33	15
PH2	Oct 12, 2011	52° 50.105'	68° 10.729'	34	11
KP4	Oct 13, 2011	53° 00.523'	67° 56.380'	35	21
KP6	Oct 13, 2011	52° 54.306'	68° 10.090'	18	9
KP2	Oct 14, 2011	53° 07.937'	67° 49.805'	40	22
AR1	Oct 14, 2011	52° 43.300'	68° 12.734'	70	21
AR2	Oct 14, 2011	52° 43.331'	68° 12.537'	70	22
AR3	Oct 14, 2011	52° 43.484'	68° 12.283'	70	30
CA1	Oct 15, 2011	52° 45.539'	67° 12.853'	80	38
CA2	Oct 15, 2011	52° 45.353'	67° 13.087'	80	46
CA3	Oct 15, 2011	52° 45.464'	67° 13.206'	80	41
AI1	Oct 15, 2011	52° 40.883'	68° 2.483'	70	18
AI2	Oct 15, 2011	52° 41.034'	68° 1.933'	70	11
AI3	Oct 15, 2011	52° 41.151'	68° 2.294'	70	14
BL1	Oct 15, 2011	52° 47.287'	67° 36.698'	73	32
ZI1	Dic 03, 2011	53° 03.904'	67° 22.268'	78	55
ZI2	Dic 03, 2011	53° 06.144'	67° 16.366'	72	41
ZI3	Dic 03, 2011	53° 05.366'	67° 14.348'	79	59
ZI4	Dic 03, 2011	53° 04.263'	67° 12.025'	90	48
ZE1	Dic 03, 2011	52° 59.889'	67° 12.459'	84	47
ZE2	Dic 03, 2011	53° 01.289'	67° 18.094'	71	57
ZE3	Dic 03, 2011	53° 01.008'	67° 31.450'	70	57
ZE9	Dic 03, 2011	53° 08.098'	67° 20.778'	84	46
ZE10	Dic 03, 2011	53° 11.191'	67° 17.918'	89	53
ZE11	Dic 03, 2011	53° 13.282'	67° 16.640'	81	55
ZE12	Dic 03, 2011	53° 10.234'	67° 14.400'	84	56
ZE13	Dic 03, 2011	53° 09.539'	67° 09.401'	76	54
ZE14	Dic 03, 2011	53° 07.266'	67° 11.359'	91	53
ZE15	Dic 03, 2011	53° 04.143'	67° 03.532'	90	59
ZE16	Dic 03, 2011	53° 08.954'	67° 02.432'	82	45
ZE4	Dic 04, 2011	53° 03.187'	67° 28.839'	64	31
ZE5	Dic 04, 2011	53° 05.723'	67° 23.026'	74	62
ZE6	Dic 04, 2011	53° 08.154'	67° 17.436'	79	34
ZE7	Dic 04, 2011	53° 09.223'	67° 24.538'	78	63
ZE8	Dic 04, 2011	53° 11.896'	67° 23.573'	80	53
EZ1	Dic 04, 2011	53° 04.855'	67° 54.896'	31	19
EZ2	Dic 04, 2011	53° 05.461'	67° 52.542'	46	20
EZ3	Dic 04, 2011	53° 06.453'	67° 49.397'	37	32
EZ4	Dic 04, 2011	53° 02.994'	67° 54.206'	43	26
EZ5	Dic 04, 2011	53° 08.165'	67° 48.863'	47	14
IZ1	Dic 04, 2011	53° 04.590'	67° 51.563'	42	30
5N	Jul 08, 2014	53° 04.352'	67° 51.613'	41	26
5S	Jul 08, 2014	53° 04.775'	67° 50.967'	46	29
5E	Jul 08, 2014	53° 04.405'	67° 51.098'	43	27
5W	Jul 08, 2014	53° 04.625'	67° 51.593'	44	33
6	Jul 08, 2014	53° 03.016'	67° 51.154'	42	23
7	Jul 08, 2014	53° 0.705'	67° 51.534'	40	19
8	Jul 08, 2014	53° 0.487'	67° 48.744'	39	14
9	Jul 08, 2014	53° 0.859'	67° 47.407'	47	12
4S	Jul 10, 2014	53° 13.614'	67° 06.498'	92	53
10S	Jul 15, 2014	53° 18.148'	67° 44.440'	55	8
10E	Jul 15, 2014	53° 17.890'	67° 44.574'	56	9
10W	Jul 15, 2014	53° 18.028'	67° 44.821'	52	12
3E	Jul 16, 2014	53° 10.165'	67° 13.359'	74	54

transport and re-deposition processes of glacio-fluvial sediments during the late Pleistocene (Violante et al., 2014). A major percentage of the carbonate bioclasts in this area consists of bryozoan remains (Bastida et al., 1981).

## 2.2. Sampling and laboratory analyses

A total of 58 bottom samples (one at each station) ranging from 18 to 92 m were collected by one of the authors (JLG) onboard the AHTS *Lenga* with a 13.49 dm<sup>2</sup> Van Veen grab during three surveys (October 11–15, 2011, December 3–4, 2011 and July 8–16, 2014; Table 1). There is a small gap in the depth gradient, with only one station between 56

and 70 m. The sediment fine fraction was sieved out onboard by washing the samples with seawater through a 1 mm mesh. The coarse fraction was fixed in 7% neutralized formaldehyde in seawater. In the laboratory, clasts  $\geq 1$  mm were rinsed, dried and stored in plastic bags. Bryozoan colonies were identified to the highest taxonomic level possible under stereoscopic microscope (Table 2). Taxa identified to genus or family level represent only one species each.

## 2.3. Data analyses

Statistical analyses were performed based on species presence/absence data. Frequency is expressed as the percentage of samples where

**Table 2**

Growth-forms, frequency and bathymetric ranges observed in this study for 90 bryozoan species found on the continental shelf off Tierra del Fuego. ER: erect-rigid, EF: erect-flexible, EN: encrusting, MA: massive. \*Potentially habitat-forming species.

Species	Order	Growth-form	Frequency (%)	Bathymetric range (m)
<i>Adeonella</i> sp.	Cheilostomata	ER*	32.8	70–92
<i>Aetea anguina</i> (Linnaeus)	Cheilostomata	EN	1.7	37
<i>Alcyonidium</i> sp.	Ctenostomata	EN	6.9	40–70
<i>Alderina simplicissima</i> López Gappa & Liuzzi	Cheilostomata	EN	17.2	70–90
<i>Amastigia benemunita</i> (Busk)	Cheilostomata	EF*	37.9	41–92
<i>Amastigia nuda</i> Busk	Cheilostomata	ER*	6.9	74–90
<i>Andreella patagonica</i> López Gappa	Cheilostomata	EN	91.4	18–91
<i>Andreella uncifera</i> (Busk)	Cheilostomata	EN	31.0	70–92
<i>Antarctothoa</i> sp.	Cheilostomata	EN	3.4	44–46
<i>Arachnopusia monoceros</i> Busk	Cheilostomata	EN	98.3	18–92
<i>Aspidostoma giganteum</i> (Busk)	Cheilostomata	ER*	19.0	70–92
<i>Beania costata</i> (Busk)	Cheilostomata	EF	6.9	70–80
<i>Beania inermis</i> Busk	Cheilostomata	EF	1.7	90
<i>Beania magellanica</i> (Busk)	Cheilostomata	EF	22.4	37–91
<i>Beania maxilla</i> (Jullien)	Cheilostomata	EF	27.6	71–92
<i>Bicrisia biciliata</i> (MacGillivray)	Cyclostomata	EF	3.4	71–90
<i>Bientalophora regularis</i> (MacGillivray)	Cyclostomata	ER*	32.8	70–92
<i>Buffonellodes glabra</i> Hayward	Cheilostomata	EN	74.1	35–92
<i>Buffonellodes simplex</i> (d'Orbigny)	Cheilostomata	EN	31.0	64–91
<i>Caberea darwinii</i> (Busk)	Cheilostomata	EF	34.5	37–90
<i>Callopora deseadensis</i> López Gappa	Cheilostomata	EN	29.3	70–92
<i>Calloporina bicristata</i> Hayward	Cheilostomata	EN	41.4	64–92
<i>Calvetia dissimilis</i> Borg	Cyclostomata	ER*	60.3	37–92
<i>Carbasea ovoidea</i> Busk	Cheilostomata	EF*	22.4	70–92
<i>Cellaria malvinensis</i> (Busk)	Cheilostomata	EF*	74.1	31–92
<i>Cellaria scoresbyi</i> Hastings	Cheilostomata	EF*	3.4	74–80
<i>Cellaria variabilis</i> (Busk)	Cheilostomata	EF*	63.8	31–92
<i>Cellarinella dubia</i> Waters	Cheilostomata	ER*	25.9	70–92
Celleporidae sp. 1	Cheilostomata	MA	32.8	44–92
Celleporidae sp. 2	Cheilostomata	MA	1.7	80
<i>Celleporina bicostata</i> Hayward	Cheilostomata	MA	1.7	92
<i>Chaperiopsis galeata</i> (Busk)	Cheilostomata	EN	17.2	33–90
<i>Chaperiopsis</i> sp.	Cheilostomata	EN	1.7	90
<i>Chondriovelum angustilobatum</i> (Moyano)	Cheilostomata	EN	72.4	31–91
<i>Crisia</i> sp.	Cyclostomata	EF	29.3	70–91
<i>Disporella fimbriata</i> (Busk)	Cyclostomata	EN	74.1	18–92
<i>Disporella</i> sp.	Cyclostomata	EN	25.9	70–92
<i>Electra monostachys</i> (Busk)	Cheilostomata	EN	37.9	18–70
<i>Ellisina antártica</i> Hastings	Cheilostomata	EN	22.4	64–91
<i>Ellisina incrustans</i> (Waters)	Cheilostomata	EN	44.8	42–92
<i>Escharella spinosissima</i> (Hincks)	Cheilostomata	EN	37.9	70–92
<i>Exochella longirostris</i> Jullien	Cheilostomata	EN	82.8	31–92
<i>Fasciculipora ramosa</i> d'Orbigny	Cyclostomata	ER*	34.5	70–92
<i>Fenestrulina dupla</i> Hayward & Ryland	Cheilostomata	EN	63.8	31–92
<i>Fenestrulina horrida</i> Moyano	Cheilostomata	EN	43.1	37–92
<i>Fenestrulina majuscula</i> Hayward	Cheilostomata	EN	13.8	70–84
<i>Fenestrulina</i> sp.	Cheilostomata	EN	19.0	70–91
<i>Foveolaria terrifica</i> (Hincks)	Cheilostomata	EN	6.9	70–81
<i>Galeopsis pentagonus</i> (d'Orbigny)	Cheilostomata	ER*	8.6	74–92
<i>Hippoporina aulacomyae</i> López Gappa	Cheilostomata	EN	1.7	79
<i>Hippothoa flagellum</i> Manzoni	Cheilostomata	EN	37.9	70–92
<i>Hornera</i> sp.	Cyclostomata	ER*	46.6	55–92
<i>Jolietina latimarginata</i> (Busk)	Cheilostomata	EN	36.2	70–92
<i>Kenoaplousina fissurata</i> López Gappa & Liuzzi	Cheilostomata	EN	39.7	64–92
<i>Lacerna hosteensis</i> Jullien	Cheilostomata	EN	67.2	31–92
<i>Metroperiella galeata</i> (Busk)	Cheilostomata	EN	15.5	52–79
<i>Micropora brevissima</i> Waters	Cheilostomata	EN	10.3	64–90
<i>Microporella armata</i> (d'Orbigny)	Cheilostomata	EN	44.8	64–92
<i>Microporella hyadesi</i> (Jullien)	Cheilostomata	ER*	60.3	37–92
<i>Neothoa chiloensis</i> Moyano	Cheilostomata	EN	74.1	31–92
<i>Nevianipora milneana</i> (d'Orbigny)	Cyclostomata	ER*	46.6	42–92
<i>Odontoporella adpressa</i> (Busk)	Cheilostomata	EN	60.3	40–92
<i>Ogivalia elegans</i> (d'Orbigny)	Cheilostomata	ER*	31.0	42–92
<i>Orthopordroides erectus</i> (Waters)	Cheilostomata	ER*	6.9	70–91
<i>Osthimosia bicornis</i> (Busk)	Cheilostomata	MA	91.4	18–92
<i>Osthimosia eatonensis</i> (Busk)	Cheilostomata	MA	94.8	31–92
<i>Osthimosia magna</i> Moyano	Cheilostomata	ER*	1.7	90
<i>Parasmittina dubitata</i> Hayward	Cheilostomata	MA	93.1	31–92
<i>Plagioecia</i> sp.1	Cyclostomata	EN	51.7	37–92
<i>Plagioecia</i> sp.2	Cyclostomata	EN	39.7	64–92
<i>Platonea elegans</i> (Borg)	Cyclostomata	EN	70.7	31–92
<i>Reteporella magellensis</i> (Busk)	Cheilostomata	ER*	39.7	70–92
<i>Romancheina labiosa</i> (Busk)	Cheilostomata	EN	32.8	44–92

(continued on next page)

Table 2 (continued)

Species	Order	Growth-form	Frequency (%)	Bathymetric range (m)
<i>Smittina jullieni</i> Moyano	Cheilostomata	EN	63.8	18–84
<i>Smittina lebruni</i> (Waters)	Cheilostomata	ER*	6.9	74–79
<i>Smittina monacha</i> (Jullien)	Cheilostomata	EN	60.3	18–92
<i>Smittina oblita</i> López Gappa	Cheilostomata	EN	43.1	37–92
<i>Smittina portiuscula</i> Hayward & Thorpe	Cheilostomata	EN	8.6	37–84
<i>Smittina smittiana</i> (Busk)	Cheilostomata	ER*	79.3	31–92
<i>Smittina stigmatophora</i> (Busk)	Cheilostomata	EN	41.4	31–80
<i>Smittoidea rhynchota</i> Hayward & Thorpe	Cheilostomata	EN	56.9	37–92
<i>Smittoidea sigillata</i> (Jullien)	Cheilostomata	MA	58.6	37–92
<i>Stephanollona longispinata</i> (Busk)	Cheilostomata	EN	10.3	40–92
<i>Stomatopora eburnea</i> (d'Orbigny)	Cyclostomata	EN	36.2	64–92
<i>Tricellaria aculeata</i> (d'Orbigny)	Cheilostomata	EF	12.1	40–90
<i>Tubulipora organisans</i> d'Orbigny	Cyclostomata	EN	69.0	18–90
<i>Tubulipora</i> sp.	Cyclostomata	EN	1.7	80
<i>Turbicellepora patagonica</i> Hayward	Cheilostomata	MA	1.7	79
<i>Umbonulla alvareziiana</i> (d'Orbigny)	Cheilostomata	EN	24.1	18–70
<i>Valdemunitella lata</i> (Kluge)	Cheilostomata	EN	3.4	90–92

each species was found. The Diversity menu of the *EstimateS 9.1* software was used to compute the Chao 2, ICE (incidence-based coverage), and the first- and second-order Jackknife estimators of species richness (Colwell, 2013 and references therein) based on the same data matrix. These estimators are widely used in ecology and have good performances in assessing the sampling effort (e.g. Walther and Moore, 2005; Yurkov et al., 2011). Nine hundred randomizations and a curve-fitting method were used to estimate these parameters in an asymptotic species accumulation graph (Chao et al., 2009). Their values are obtained after reaching stabilization, i.e. in the asymptotic part of the curve. The Chao 2 estimator relies on the number of uniques and duplicates (species found once or twice, respectively), while the ICE estimator measures the degree of sample completeness by computing the fraction of the total incidence probabilities of the detected species in the reference sample. Jack-knife techniques were developed to reduce the bias of a biased estimator (Chao and Chiu, 2016).

To assess the relationship between taxonomic turnover (beta diversity) and depth, the number of shared species and the Sørensen Similarity Index were calculated using the Shared Species menu of the *EstimateS 9.1* program (Colwell, 2013). The calculations were performed (1) between all pairs of stations (totalling 1.653 interactions) and (2) between stations located within three depth ranges (< 50 m, 50–75 m and > 75 m) sampled with a similar effort (19, 20 and 19 stations, respectively). The scarcity of stations between 56 and 70 m was compensated in the intermediate group (50–75 m) by including samples from either side of the depth break.

The statistical distributions of (a) species richness, (b) number of shared species between stations, and (c) the Sørensen Similarity Index were tested for normality with the Lilliefors (Kolmogorov-Smirnov) test (Thode, 2002) using the *nortest* package v1.0-4 of R (Gross and Ligges, 2015). As normality was not met ( $p \leq 0.01$ ), the Spearman's rank correlation was used to assess the relationship between these variables and depth (or differences in depth) (Zar, 2010). Tests were performed using the R statistical environment software (R Development Core Team, 2013). Trend lines were calculated using least squares fit (lsfit) in R.

A cluster analysis of stations using group average linking based on presence/absence data was performed using the Sørensen similarity measure (option Bray-Curtis in the PRIMER package, Clarke and Warwick, 2001; see Yoshioka, 2008). The significance ( $p < 0.05$ ) of clusters obtained in the dendrogram was tested with similarity profile analyses (SIMPROF) using the *clustsig* package in R (Whitaker and Christman, 2015).

To analyze the relationship between the different colonial growth-forms and depth, bryozoan species were classified as encrusting (EN), erect-flexible (EF), massive (MA) and erect-rigid (ER) following Amini

et al. (2004) and depths were divided in three ranges, as explained above. The number of species belonging to each growth-form was plotted against depth, and the null hypothesis of independence between growth-forms and depth ranges was tested with a Chi-square test on a  $3 \times 4$  contingency table (Zar, 2010) using R.

Species capable of building colonies greater than 5 cm in 3-dimensions were defined as 'large' (Batson and Probert, 2000), i.e. potentially habitat-forming (Kuklinski, 2009), and their frequency at different depths was analyzed.

### 3. Results

#### 3.1. Species richness

The sediment was always very poorly selected, consisting of a mixture of mud, sand and gravel. Its composition, however, was remarkably similar across samples, suggesting that all came from the same type of habitat. The bryozoan taxocenosis on the study area consisted of 90 species (74 cheilostomes, 15 cyclostomes, 1 ctenostome, Table 2). The cheilostomes *Arachnopusia monoceros*, *Osthimosia eatonensis* and *Parasmittina dubitata* were the most frequent species, being present in 98.3%, 94.8% and 93.1% of the stations, respectively (Table 2).

Species accumulation curves were close to saturation (Fig. 3) showing that bryozoan sampling was comprehensive. Both Chao 2 and ICE species richness estimators predicted 97 species while the first- and second-order Jack-knife forecast 99 and 104 species respectively,

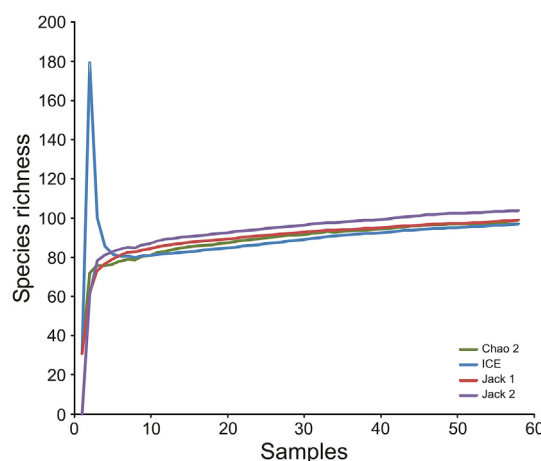
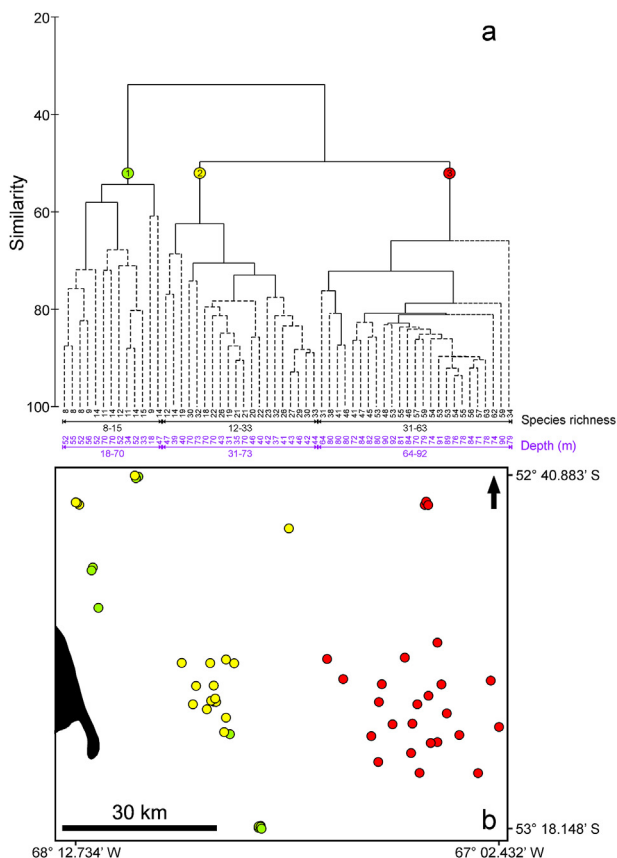


Fig. 3. Species accumulation curves comparing the values of Chao 2, ICE, first and second Jackknife estimators computed using the *EstimateS 9.1* software.



**Fig. 4.** (a) Cluster analysis using group-average linking based on Sørensen similarities between stations. Station labels were replaced by the value of species richness (upper, black) and depth (lower, violet). Significant clusters (SIMPROF test,  $P < 0.05$ ) are connected with solid lines. (b) Map showing the location of the three groups of stations. Green circles: group 1, yellow circles: group 2, red circles: group 3. See also Fig. 1 for details. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

meaning that between 86.5 and 92.8% of the species present in the study area were sampled. Only 10% of species were found just in one sample (Uniques = 9). Eight of them occurred only in the deepest samples (> 75 m, Table 2). *Aetea anguina* appeared only in one shallow station (Table 2).

**3.2. Relationship between species richness and depth**

The SIMPROF analysis resulted in 16 significant clusters which in turn merge in three main groups of stations at a similarity level greater than 50% (Fig. 4a). Groups differed greatly in species richness but overlapped broadly in depth. Group 1 is composed of 13 stations with low species richness (8–15 species) and depths ranging from 18 to 70 m. Group 2 has 20 stations with intermediate values of species richness (12–33 species) and ranging in depth from 31 to 73 m. Group 3 is represented by the deepest (64–92 m) and most speciose (31–63 species) 25 stations. While Group 3 is a geographically well defined set of relatively deep stations located eastwards, there is a considerable spatial overlap between groups 1 and 2, which are mainly distributed towards the west and shallower parts of the study area (Fig. 4b).

When dividing the 58 stations in three depth ranges of similar sampling effort an increase in species richness is observed, with 45 species at depths < 50 m, 79 between 50 and 75 m, and 85 at depths > 75 m. The maximum bryozoan richness value in a single station was 63 species, which was obtained at 78 m (Table 1). The most marked change in bryozoan species richness occurred between the

**Table 3**  
Taxonomic turnover parameters between depth ranges.

Comparison	Shared species	Sørensen Index
< 50 m vs. 50–75 m	42 (52%)	0.683
< 50 m vs. > 75 m	40 (44%)	0.615
50–75 m vs. > 75 m	75 (85%)	0.920

shallowest and the intermediate ranges, with an increase of 34 species (76%, Table 2). However, as most species present in the shallowest range were also found between 50 and 75 m, the taxonomic turnover parameters do not decrease as would be expected (Table 3). The slight increase in species richness observed between the intermediate and the deepest ranges, with the inclusion of only 6 more species (~8%, Table 2), resulted in high values of shared species and the Sørensen Index (Table 3). In these two cases, the taxonomic turnover is produced by adding a new set of species in the deeper ranges but maintaining most species present in the preceding range. Only five shallow species were not found in the deepest range: *Aetea anguina*, *Antarctothoa* sp., *Alcyonidium* sp., *Electra monostachys* and *Umbonula alvareziana*, with the two former only observed at depths lower than 50 m. No species is exclusively present in samples between 50 and 75 m. The information supplied by this intermediate depth range is thus redundant in terms of species richness, as all species are already represented in the stations belonging to the shallowest and deepest ranges.

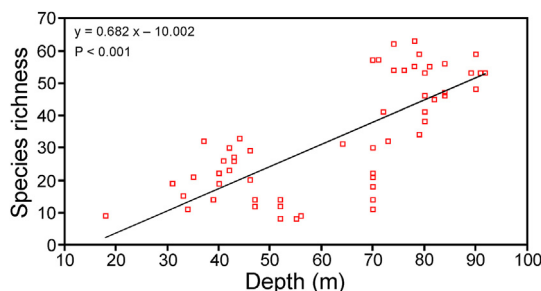
The correlation between species richness and depth was positive and highly significant (Spearman's rank correlation,  $\rho = 0.69$ ,  $p < 0.001$ ), meaning that biodiversity of bryozoans increases with depth between 18 and 92 m (Fig. 5).

The correlations between differences in depth between samples and both the number of shared species and the Sørensen Similarity Index were negative and highly significant (Spearman's rank correlation:  $\rho = -0.26$ ,  $p < 0.001$ ;  $\rho = -0.48$ ,  $p < 0.001$ , respectively), meaning that the smaller the depth differences between stations, the more similar is the species composition and higher the number of species shared (Fig. 6).

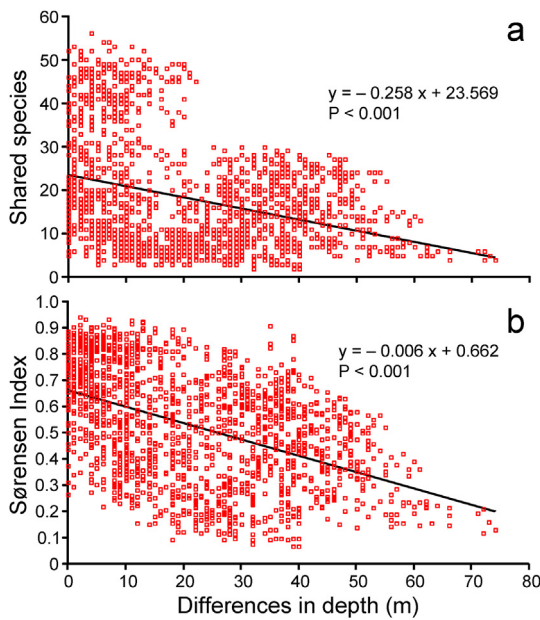
**3.3. Relationship between growth-forms and depth**

The encrusting growth-form was the most common in the study area (57.8%), followed by erect-rigid (17.8%), erect-flexible (15.6%) and massive (8.9%) colonies (Table 2). Changes in the proportion of growth-forms with depth were non-significant (chi-square test,  $\chi^2 = 2.76$ ,  $df = 6$ ,  $p = 0.84$ ; Fig. 7). Although the total species number increased with depth, the ratio of species with different growth-forms remained unchanged because the increase occurred not only for the erect-rigid but also for the remaining growth-forms, particularly the encrusting species (Fig. 8a).

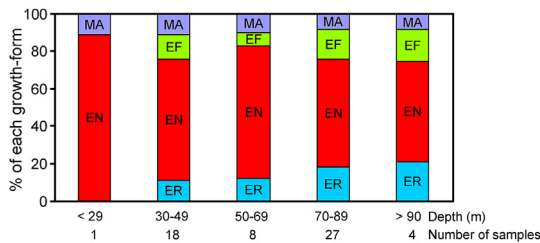
Twenty-two potentially habitat-forming species were found along the bathymetric range surveyed in this study (Table 2). Bioconstructor bryozoans (*sensu* Cocito, 2004) were absent at the most shallow station



**Fig. 5.** Relationship between depth and bryozoan species richness between 18 and 92 m. Trend line was added.



**Fig. 6.** Indicators of species turnover between samples and its relationship with differences in depth. (a) Shared species. (b) Sørensen Similarity Index. Trend lines were added.



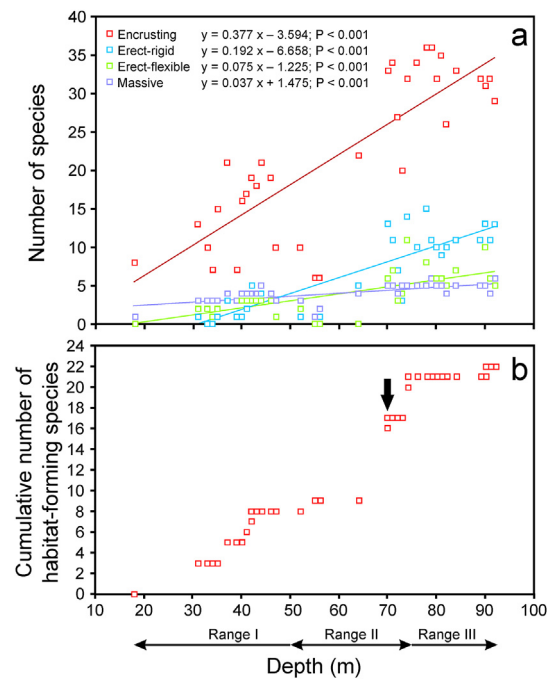
**Fig. 7.** Changes in the proportion of each growth-form at different depths. MA: massive, EF: erect-flexible, EN: encrusting, ER: erect-rigid.

(i.e. 18 m, Fig. 8a). Its cumulative number was relatively low from 31 to 64 m and then experienced a sharp increase at 70 m (Fig. 8b). At the shallowest range, however, bioconstructor species were mainly represented by unilaminar (i.e. young) colonies of *Smittina smittiana*, *Microporella hyadesi* and also by small stubs of *Calvetia dissimilis*.

## 4. Discussion

### 4.1. Bryozoan biodiversity

The continental shelf off Tierra del Fuego has been relatively better sampled than other locations of the southern Southwest Atlantic (López Gappa, 2000). Before this study, a total of 54 bryozoan species had been reported from 22 sampling stations in the study area and surroundings (López Gappa, 2000; Centurión and López Gappa, 2011; López Gappa and Liuzzi, 2013). In the 58 stations analyzed here, which covered an area of  $\sim 5600 \text{ km}^2$ , 90 species were found. Of these, 43 species were already known for this area, whereas the remaining 47 are new records. Therefore, the present study increases in 87% the known biodiversity for the study area, which now reaches 101 species. This number is similar to the mean predicted values obtained with Chao 2, ICE and first- and second-order Jackknife estimators (97, 97, 99 and 104 species, respectively). In a recent study, Figuerola et al. (2017) reported 66 cheilostome bryozoan species around the Malvinas/Falkland isles, an area relatively close to the shelf off Tierra del Fuego. Although the number of cheilostome species is similar (66 vs. 74), biodiversity comparisons between these areas should be made with caution, as they



**Fig. 8.** Relationship between depth and species richness. Samples collected at the same depth were pooled. (a) Number of species of each growth-form. Trend lines were added. (b) Cumulative number of habitat-forming species. The arrow indicates the sharp increase observed at 70 m. Note that the horizontal axis begins at 10 m.

involve different sampling efforts, bathymetric ranges and taxonomic expertise.

Bryozoans are suspension feeders and on the continental shelf their diet is based on diatoms, flagellates and other phytoplankters (Schopf, 1969a). Therefore, the association between bryozoan diversity and areas of high productivity is not unexpected (López Gappa, 2000; Rowden et al., 2004). The availability of food derived from primary productivity could be a key variable explaining the high bryozoan species richness found off the Fuegian coast (López Gappa, 2000), as the study area is near to the Atlantic Patagonia cold estuarine front (see Acha et al., 2004), where very high summer values of surface chlorophyll-*a* have been recorded ( $2\text{--}5 \text{ mg m}^{-3}$ ; see Rivas et al., 2006).

It is well-known that a mid-domain peak or plateau in species richness occurs in virtually any set of distributional ranges when those are randomly placed within a bounded domain, even in the absence of any environmental gradient (Colwell and Lees, 2000). Patterns of diversity produced by these null models, however, are sensitive to the relative position of the hard boundaries chosen for the model (McClain and Etter, 2005). In our case, 1097 m (St. 320 of the *Challenger* Expedition) can be regarded as the most realistic value for the lower domain bound, since it is the greatest depth known for 5 of the species of the assemblage under study: *Foveolaria terrifica*, *Jolietina latimarginata*, *Ogivalia elegans*, *Reteporella magellensis* and *Smittina smittiana*. Stations deeper than 1097 m collected in the Southwest Atlantic during the *Challenger* and *Atlantis II* expeditions did not share any of the bryozoan species present in the Fuegian assemblage (see López Gappa, 2000). Since the bathymetric range of the present study (18–92 m) represents less than 10% of the depth domain, the application of the mid-domain effect model would produce unrealistic results (see Colwell and Hurtt, 1994; Dunn et al., 2007). Although the application of the mid-domain effect model seems to be not advisable, some considerations about the relationship of bryozoans to depth can anyway be made.

#### 4.2. Relationship between species richness and depth

Bryozoans from the continental shelf off Tierra del Fuego show a significant trend for species richness to increase with increasing depth, as has previously been found at similar bathymetric ranges in the English Channel (Grant and Hayward, 1985) and Greenland (Kuklinski, 2009). Our results suggest that this does not occur gradually, since a clear increase in species richness is observed at a depth of around 64–70 m. The fact that the shallowest samples are the least speciose agrees with reports of the bryozoan fauna from Western Norway (Ryland, 1963), the English Channel (Grant and Hayward, 1985), the Arctic Ocean (Kuklinski et al., 2005) and the northwestern Mediterranean (Madurell et al., 2013). A lack of a significant relationship between bryozoan species richness and depth (Hageman et al., 1995; Denisenko and Grebmeier, 2015), as well as maximum species richness in shallow waters (Lidgard, 1990) have also been reported elsewhere.

The species turnover observed in our study was mainly due to the inclusion of new taxa, without the replacement of the set of shallower species. The deepest range proved to be the most speciose (85 species) and included the sample with the maximum bryozoan species richness. This agrees with a biogeographic study of the bryozoan fauna of the southern Southwest Atlantic, which found the highest richness at stations around 100 m depth (López Gappa, 2000). Other studies report different conclusions. In Western Norway, an extremely small number of species is shared between shallow and deeper waters (Ryland, 1963). In the North Atlantic, the highest bryozoan diversity was found between 10 and 75 m (Clarke and Lidgard, 2000). Maximum values of species richness occurred a little deeper both in the English Channel (95 m; Grant and Hayward, 1985) and in the Faroe Islands (101–150 m; Denisenko et al., 2016). These apparently contradictory results may be due to the fact that bryozoan diversity increases with depth on the continental shelf but then decreases as a function of the availability of suitable substrata (Schopf, 1969a) and habitat heterogeneity (Clarke and Lidgard, 2000).

Based on similarity of species composition, three groups of samples arranged mainly according to species richness were found. The most clearly defined group was the deepest assemblage, which is composed of samples with highest species richness and depths of at least 64 m. A strict bathymetric separation of bryozoan assemblages with depth, as shown by Ryland (1963) and Kuklinski et al. (2005), was not found. Some of the samples from 70 to 73 m, which were expected to have a higher number of species, showed relatively low biodiversity values and did not cluster together with the deepest group. Our results suggest that other factors besides depth may be controlling the distribution of species in the area. Taylor et al. (2004) state that the bathymetric distribution of bryozoans could be controlled by depth-correlated factors instead of depth *per se*. The availability of suitable substrates is a key factor for the settlement of these sessile organisms (Schopf, 1969a). Larval behaviour during dispersion, competition, predation, food availability, as well as physical factors such as temperature, salinity, hydrodynamics and sediment deposition may also be critical in structuring bryozoan bathymetric distribution (Ryland, 1963; Hageman et al., 1995; Kuklinski et al., 2005). Kuklinski et al. (2006) reported that substrate hardness and size influence bryozoan distributions since the highest bryozoan richness was found on more stable substrates such as large rocks. Similarly, bryozoan abundance, species richness and diversity were also highest on the largest substrata in Banco Sarmiento, located off the Atlantic mouth of the Magellan Strait (Centurión and López Gappa, 2011).

#### 4.3. Relationship between growth-forms and depth

A major factor that may potentially control growth-form distribution is the depth of storm wave bases. Shallower habitats undergoing stronger water motion may be expected to deter the development of erect colony-forms susceptible to mechanical damage. Hence, the

proportion of fragile morphotypes may increase with increasing water depth, where more stable conditions would be present. The fact that the ratio of erect to encrusting colonies increases with depth has been widely reported (e.g. Schopf, 1969b; McKinney and Jackson, 1989; Kuklinski et al., 2005; Lepoint et al., 2014). In the present study, however, this ratio showed only non-significant changes, as the number of encrusting species also increased with depth. Colony growth-forms were not found to be delimited to a single depth range either.

Although all bryozoans can potentially generate habitats for other benthic organisms, erect three-dimensional colonies may contribute significantly to benthic complexity (Batson and Probert, 2000; Fortunato, 2015). Their calcified structures provide substrate and refuge for a great variety of organisms, enhancing biodiversity (Batson and Probert, 2000), including economically important fish and oyster stocks (Bradstock and Gordon, 1983; Cranfield et al., 2003). For this reason, they are known as bioconstructors (Cocito, 2004) or habitat-formers (e.g. Wood et al., 2012). In the present study, erect bryozoan species capable of attaining sizes over 5 cm in three-dimensions were first found as encrusting colonies or stubs at 31 m depth, but their richness showed a remarkable increase from 70 m onwards, i.e. in the most suitable habitat for their development. A similar situation was reported in Otago Peninsula, New Zealand, where habitat-forming bryozoans occur from 65 m (Batson and Probert, 2000) but the same species, capable of attaining more than 5 cm in 3-dimensions, occurred elsewhere in shallow waters (see Wood and Probert, 2013). These authors suggested that the distributions of the habitat-forming species may be related to the characteristics of substrate type, which could be relatively stable and heterogeneous with depth. In the Greenland Sea the presence of this particular and fragile bryozoan forms are more common at depths greater than 50 m (Kuklinski, 2009). In shallower waters of Banjole Island (Croatia), however, *Cellaria salicornioides* forms dense mats at 35 m depth (McKinney and Jaklin, 2000) and in La Spezia (Italy) giant colonies of *Schizoporella errata* forms large 3-dimensional incrustations from 0.3 to 8 m (Cocito et al., 2000). In addition, in a comprehensive study carried out in New Zealand the presence of 11 species of bryozoan habitat-formers was reported between 1.1 and 30.1 m (Wood et al., 2013).

Bryozoan calcified skeletons have an extensive presence in the fossil record since the early Ordovician (Taylor, 2005). Due to their excellent preservation, the colony growth-form has proved to be a valuable tool for palaeoenvironmental interpretations (Smith, 1995; Hageman et al., 1997; Amini et al., 2004). Patterns reported here, as well as in previous studies (Hageman et al., 1997; Taylor et al., 2004) are commonly used as a tool in palaeoecological analysis. It is of note, however, that the depth of 64–70 m at which a sharp increase in species richness and in the presence of fragile species was found, will not be the same in environments with different hydrodynamic stress. Fragile, calcareous growth-forms could be expected to occur at shallower depths in calmer waters.

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