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BENTHIC FORAMINIFERAL MORPHOGROUPS ON THE ARGENTINE CONTINENTAL SHELF

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ABSTRACT

The aim of this study is to evaluate the relative influence of abiotic factors on the association and spatial distribution of recent benthic foraminiferal morphogroups in the Argentine continental shelf at ∼40°S environments as a first step towards establishing their paleoecological significance. Foraminifera are classified into five morphogroups: tapered, elongate-flattened, milioline, planoconvex, and rounded-planispiral. Compositional data analysis techniques were used to define morphogroup assemblages, and Classification and Regression Tree Analysis was used to identify environmental variables. The distribution of the morphogroup assemblages were recognized was driven by complex interactions between environmental factors. The most important factor is temperature, although salinity, substrate grain size, and hydrodynamic energy also correlate with the distribution of morphogroups. The morphogroups analysis shows potential for determining present and past environments where the autoecology of the species is unknown or where there is doubt regarding their taxonomic classification.

INTRODUCTION

Foraminifera are one of the most widely used groups of organisms for studying marine environments and reconstructing coastal paleoenvironments, including those of Argentina (e.g., Ferrero, 2006; Bernasconi and Cusminsky, 2007; Laprida and others, 2007). The distribution of the different living foraminiferal species is related to, and mainly controlled by, variations in the physicochemical properties of the marine environment such as temperature, salinity, substrate, dissolved oxygen, and nutrients (Boltovskoy, 1966; Murray, 1991, 2006). This has led to many studies of foraminifera involving issues related to community ecology (e.g., Hayward and others, 1996, 2002; Bernasconi and Cusminsky, 2005; Bernasconi, 2006; Alperin and others, 2008; Bernasconi and others, 2009).

A morphogroup is an aggregation of forms with similar test morphology, independent of systematic relationships (Murray, 1973, 2006). Reolid and others (2008) note that using morphological categories in paleoenvironmental analyses may be preferred over the use of formal species identifications because: 1) the morphological approach enables reliable comparisons to be made among assemblages of different ages, reducing the effect of taxonomical divergence caused by biological evolution, 2) identifications of species are not required, and 3) using a small number of morphogroups instead of a large number of species reduces the amount of data to be analyzed. In an earlier study, Severin (1983) noted that morphogroups have great potential for determining paleoenvironments, microhabitat patterns, and feeding strategies because the categories are independent of taxonomy and thereby avoid much of the subjectivity involved in identifying species; thus, specimens can be classified quickly and easily.

The relationship between benthic foraminiferal test morphology and characteristics of the physical environment has been the subject of numerous studies. Years after Bandy (1960) pioneered the morphogroup concept, Severin (1983) used it to infer four biofacies related to bathymetry, which Bernhard (1986) then used in relating morphogroups to oxygen levels. Corliss (1985) and Corliss and Chen (1988) used shape and mode of coiling to determine microhabitat patterns (epifaunal vs. infaunal) and linked them to organic content. Corliss (1985) found test shape and pore distribution, are related to the microhabitat preferences of the different species. Kaiho (1991, 1994, 1999) noted that changes in oxygen concentration at the water-sediment interface play an important role in controlling benthic foraminiferal populations. Kaiho (1991) estimated oxygenation conditions of the water-sediment interface by means of the Benthic Foraminifera Oxygen Index (BFOI), which is based on morphological and taxonomical differences among benthic foraminifera, and extrapolated estimates of oxygenation to the past. Bernasconi (2006), Bernasconi and Cusminsky (2009), and Bernasconi and others (2009) also used BFOI to infer levels of paleo-oxygenation in Quaternary sediments of Nuevo Gulf, Argentina.

The spatial distribution of benthic foraminiferal morphogroups is variable. In addition to small-scale changes that may be caused by oxygenation conditions at the water-sediment interface, there are other local factors that intervene, such as salinity, temperature, nutrient availability, substrate, bioturbation, and currents. Further studies are needed to determine what factors cause joint occurence of benthic foraminiferal morphogroups. Therefore we chose to study the distribution of foraminiferal morphogroups on the Argentine Continental Shelf, as it includes different environments that are closely linked and suitable for the development of benthic foraminifera. San Matías Gulf has oceanographic dynamics characterized by large tide amplitudes that have a major effect on the vertical mixing of waters and circulation, while the shelf has local and seasonal variations in water temperature, salinity, and productivity. The aim of this study is to evaluate the relative influence of abiotic factors on the association and spatial distribution of benthic foraminiferal morphogroups in these shelf environments as a first step towards establishing their paleoecological significance.

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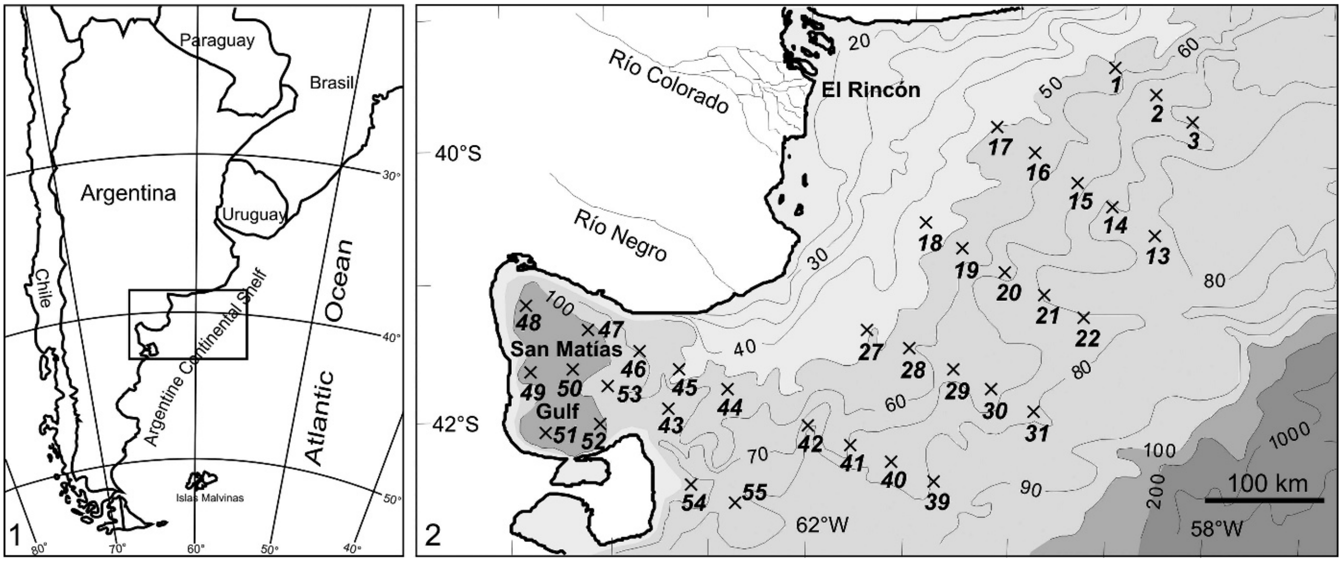

FIGURE 1. **1** Location map. **2** Position of stations. Bathymetric contours are in meters.

STUDY AREA

The study area is located between 39–43° S and 58–65° W and includes San Matías Gulf and part of the Argentine continental shelf (Fig. 1.1). The shelf gently slopes with a fairly uniform gradient. Its sedimentary cover is mainly sand, with mean grain size decreasing towards the continental slope. The sediment also becomes siltier towards Bahía Blanca and San Matías Gulf. Sandy sediment spreads from the mouth of Negro River to the coast (Aliotta, 1983). At the mouth of San Matías Gulf, the sediment contains gravel while the coarse fraction decreases toward the northeast (Gelós and others, 1988).

The hydrology in the region is complex. Water masses over the continental shelf are of subantarctic origin and mean circulation is northward, although the San Matias Gulf and semi-protected coastal area of El Rincón are characterized by local conditions. Martos and Piccolo (1988) differentiated two domains on the shelf: 1) a coastal or inner domain, and 2) an outer domain. The coastal domain includes the littoral zone down to the 40–50 m isobaths with vertically homogenous waters. In this area, Guerrero and Piola (1997) and Lucas and others, (2005) recognized Coastal Water 1) of low salinity (<33.4) in El Rincón estuary due to discharge from the Negro and Colorado rivers; and 2) of high salinity (33.8–34.0) at the mouth of San Matías Gulf and near the coast area east of the estuary. The coastal water is separated from the continental shelf water by the Coastal Front (Guerrero y Piola, 1997; Guerrero, 1998; Lucas and others, 2005). Coastal circulation is SSW to NNE. The outer domain extends from depths of 40–50 m to 100 m (approximate shelf edge). This sector was described by Guerrero and Piola (1997) as Middle Shelf Water (S 33.4–33.7) comprising the northward-flowing Patagonian Current. This water is homogenous in winter and stratified in summer. During spring–summer, surface-water temperatures and salinity are typical of the Río de la Plata (T >15°C; S <33) and flow southwestward. In autumn–winter, surface waters are cooler (mean T 12°C) and the water column is vertically mixed by convection and influenced by the Malvinas Current. The salinity values are typical of a continental shelf (Martos and Píccolo, 1988). Between the Middle Shelf Water and the Malvinas Current, the Outer Shelf or Continental Slope Water (T<15°C and S 33.7–34.0) (Guerrero and Piola, 1997) is present. The thermohaline shelf-break front (which separates the shelf waters from the colder, more saline waters of the Malvinas Current) lies between the 80–100 m isobaths (Martos and Píccolo, 1988). The Malvinas Current flows along the shelf break and carry subantarctic water to the north and it had the same direction over the total water column with velocities of the order of 30 cm/s. The current has a dominating effect on adjacent shelf waters (Martos and Piccolo, 1988).

San Matías Gulf, in the southwest of the study area (40°47′ S–42°13′ S), is a 18,000 km^2, semi-closed basin, deeper than the adjacent continental shelf with which it communicates over a sill at a depth of 70 m (Parker and others, 1996). About 45% of the Gulf is shallower than 100 m, and there are large depressions that are >160 m deep in the middle, with maximum depths >200 m (Piola and Scasso, 1988). Substrates in the gulf are mainly mud, gradually becoming fine sand towards the littoral zone (Gelós and others, 1988). Sandy sediment spreads from the mouth of Negro River to the coast (Aliotta, 1983). At the mouth of the gulf, the substrate is sandy to gravelly (Gelós and others, 1988; Achilli and Aliotta, 1992). There are two different water masses in the gulf: the water to the north and east is characterized by high temperature and salinity (33.9–44.1) with a marked seasonal thermocline, while the water to the south and southwest are unstratified and of lower temperature (9–13°C) and salinity (Carreto and others, 1995). The two water masses are separated by a tidal front located in the northern part of the mouth of the Gulf (Piola and Scasso, 1988; Gagliardini and Rivas, 2004). Shelf waters flow in through the southern end of the mouth

TABLE 1. Geographic location and physicochemical characteristics of water (Pucci and others, 1985) and substrate at each studied station (Gelós and others, 1988).

Sample	Latitude S	Longitude W	Depth (m)	Minimun distance to coast (km)	Silt %	Sand %	Gravel %	Temp °C	Salinity (psu)	D.O. (ml/l)	Cluster
1	39°19.3′	59°13.2′	57	65.2	5	95	0	18.23	34.08	5.72	5
2	39°30.7′	58°49.4′	72	93.8	3	97	0	9.71	33.65	6.05	2
3	39°42.0′	58°28.0′	78	123.3	4	96	0	7.34	33.74	4.82	1
13	40°32.5′	58°46.5′	82	206.1	8	92	0	7.13	33.77	3.70	1
14	40°20.8′	59°11.5′	78	175.8	5	95	0	7.55	33.71	4.48	1
15	40°10.4′	59°32.2′	67	150.5	2	98	0	11.20	33.65	5.60	2
16	39°58.2′	59°57.2′	51	122.1	1	99	0	17.22	33.82	5.33	4
17	39°47.3′	60°19.3′	46	96.7	6	94	0	17.87	33.95	3.87	4
18	40°30.0′	60°59.5′	42	97.3	1	94	5	17.16	33.75	5.59	4
19	40°41.2′	60°37.7′	53	130.6	2	98	0	16.91	33.66	5.12	4
20	40°51.1′	60°12.6′	66	167.5	3	97	0	16.99	33.71	3.96	5
21	41°01.2′	59°49.3′	74	202.9	5	95	0	9.08	33.69	3.53	2
22	41°10.0′	59°25.5′	75	239.0	8	92	0	8.56	33.79	5.40	1
27	41°18.5′	61°32.9′	48	80.6	5	85	10	16.85	33.68	5.40	4
28	41°26.1′	61°07.2′	54	118.2	4	90	6	16.19	33.61	4.80	4
31	41°52.6′	59°53.2′	82	231.9	5	95	0	7.18	33.67	3.25	2
39	42°24.6′	60°50.9′	80	209.7	6	94	0	8.05	33.51	4.19	5
41	42°09.2′	61°41.3′	69	149.6	9	91	0	12.85	33.57	5.52	5
42	42°01.2′	62°06.1′	69	120.8	6	81	13	17.39	34.04	5.21	4
44	41°45.0′	62°54.5′	54	67.7	1	72	27	17.12	33.98	5.40	3
45	41°36.5′	63°22.5′	48	49.3	1	59	40	17.14	34.20	5.80	3
46	41°28.5′	63°46.2′	56	34.6	1	99	0	16.05	34.12	4.92	2
47	41°18.2′	64°16.3′	125	32.8	85	15	0	11.62	34.05	4.53	5
48	41°07.1′	64°52.4′	96	24.4	49	51	0	15.71	34.08	3.89	4
49	41°37.1′	64°50.2′	88	15.0	18	82	0	15.57	34.03	5.07	5
50	41°32.9′	64°30.6′	160	42.6	98	2	0	10.68	34.09	4.68	5
51	42°04.1′	64°42.6′	139	16.1	98	2	0	12.85	34.02	4.52	5
52	41°59.9′	64°10.1′	106	20.8	13	87	0	13.38	34.03	4.65	4
53	41°43.2′	64°04.9′	84	43.6	20	80	0	14.55	34.04	5.79	3
54	42°27.4′	63°16.4′	60	27.4	2	36	62	15.54	33.72	5.16	4
55	42°35.8′	62°49.3′	69	62.9	4	78	18	15.01	33.66	5.14	4

and out through the northern end, producing a semi-permanent gyre (Piola and Scasso, 1988; Scasso and Piola, 1988). This flow is more intense (~3.5 m/s) near the entrance to the Gulf (Tonini and others, 2006).

MATERIALS AND METHODS

In 1984, 31 samples of surface sediment were obtained using a Shipek sampler by the Argentine Institute of Oceanography aboard the oceanographic ship *Puerto Deseado* (Fig. 1.2). Table 1 presents sedimentological data prepared by Gelós and others (1988) from these samples, as well as physicochemical parameters of the bottom water surveyed during the oceanographic campaign by Pucci and others (1985). Samples were screen-washed and the >63 μm residue was air dried. Five grams of dry sediment from each sample were examined under a stereomicroscope. All foraminiferal specimens (i.e., the total assemblage) were extracted (Alperin and others, 2008).

Specimens previously classified according to taxonomic criteria (Alperin and others, 2008) were reclassified using only the outer morphology of their tests, a criterion independent of traditional taxonomy. Agglutinated species are excluded from this classification because none were present. Specimens belonging to the species in Table 2 and Figure 2 were sorted into the following morphogroups:

Tapered (TA): rounded or angular shapes in apertural view (Severin, 1983).

Elongate-flattened (EF): oval to compressed tests in apertural view with parallel to subparallel sides (Severin, 1983).

Milioline (MI): ovate tests with apical aperture (Corliss and Chen, 1988), comprising porcelaneous foraminifera with a flattened discoid coil and an elongate test (Reolid and others, 2008).

Planoconvex (PC): tests with one side flat and the other convex (Severin, 1983).

Rounded-planispiral (RP): planispiral and trochospiral tests in which neither the spiral or the umbilical side is visible in apertural view (Severin, 1983).

The data matrix obtained from counting the specimens in each sample was presented in proportions of PC, PR, MI, AG, and EA (Appendix 1). Data expressed as proportion are known as an Aitchison's composition (Aitchison, 1986). By definition, the proportions of a composition are relative values adding up to one; thus, there is a statistical dependence between the proportions. Aitchison (1986, 1997, 1999) warns that the study of its correlations provides spurious results and analyzing the parts in isolation could lead to erroneous interpretations. Instead, the analysis should focus on the relations between the parts (Aitchison, 1986, 1999; Aitchison and others, 2000, Pawlowsky-Glahn and Egozcue, 2001); Aitchison and Greenacre (2002), Pawlowsky-Glahn and Egozcue, 2002; von Eynatten and others, 2002). Utilization of log-ratios has proven to be a good strategy (Aitchison, 1986, 1999; Kucera and Malgram, 1998, Aitchison and others, 2000, Pawlowsky-Glahn and Egozcue, 2001, Aitchison and Greenacre, 2002, Pawlowsky-Glahn and Egozcue and others, 2002; von Eynatten and others, 2002, Murray, 2006).

TABLE 2. Morphogroup classification of benthic foraminifera: TA = tapered, EF = elongate-flattened, MI = milioline, PC = planoconvex, RP = rounded-planispiral.

Genus and species	Morphogroup
Ammonia beccarii	PC
Angulogerina angulosa	TA
Bolivina compacta	EF
Bolivina lomitensis	EF
Bolivina marginata	EF
Bolivina ordinaria	EF
Bolivina pseudoplicata	EF
Buccella peruviana f. *campsi*	PC
Bulimina gibba	EF
Bulimina patagonica	EF
Buliminella elegantissima	EF
Cassidulina laevigata	RP
Cassidulinoides parkerianus	RP
Cibicides aknerianus	PC
Cibicides dispars	PC
Cibicides fletcheri	PC
Cibicides kullenbergii	PC
Cibicides mckannai	PC
Cibicides sp.	PC
Discorbis peruvianus	PC
Elphidium discoidale	RP
Elphidium sp.	RP
Epistominella exigua	RP
Florilus atlantica	RP
Globobulimina affinis	EF
Globocassidulina subglobosa	RP
Lenticulina clerichii	PC
Lenticulina limbosa	PC
Miliolinella subrotunda	MI
Nonionella auris	RP
Pyrgo nasuta	MI
Quinqueloculina frigida	MI
Quinqueloculina patagonica	MI
Quinqueloculina seminulum	MI
Triloculina sp.	MI
Uvigerina peregrina	TA

Statistical Compositional Analysis was not possible because 36% of the data matrix show zero values. As per Martín-Fernández and others (2003), a replacement multiplicative strategy was taken in which zero values were input as 0.005. To break statistical dependence and achieve independent parts, we followed Aitchison (1986) by performing the centered log ratio transformation (clr) (for a sample log ratio between each part and sample geometric mean):

$$clr\, x_i = \left(\ln\frac{p_1}{g(x_i)}, \ln\frac{p_2}{g(x_i)}, \ldots, \ln\frac{p_d}{g(x_i)}\right) = z_1, z_2, \ldots, z_d;$$

$$g(x_i) = \left(\prod_{i=1}^{d} p_i\right)^{1/d}$$

where: x_i = sample i, p_i = morphogroup proportion, and $g(x_i)$ = geometric mean for sample *i*.

The composition of morphogroups was described according to Aitchison (1986, 1997), using Center (closed geometric mean of the compositional data matrix) and a measure of total variability TotalVar (trace of the symmetric centered logratio covariance matrix). The variability of each morphogroup was described using the variance *clr* (Var-*clr*).

A principal component analysis (PCA) was performed on the *clr*-transformed data and the covariance matrix. Subsequently, two-dimensional biplots were constructed using principal components (PC). Biplots are graphical displays of the four-dimensional morphogroups and samples space. Biplots can be used to identify the existence and nature of relationships between the morphogroups and clusters of samples (Aitchison and Greenacre, 2002).

Classification and regression trees analysis (C&RT; Breiman and others, 1984) was performed in order to capture and model potential non-additive interactions and nonlinear relations among the clusters of samples identified on the biplot and six explanatory variables. The explanatory variables selected were location (depth and minimum distance from shore), substrate ratio of sand:silt (ln(sand/silt)), and three variables describing the physicochemical conditions of the water (temperature, salinity, and dissolved oxygen) (Table 1). The classification tree is constructed using an algorithm that recursively searches values in all explanatory variables to split the samples into two groups, called nodes, such that the variance or impurity within the node is minimized. The Gini diversity index (Gini, 1912) was used to calculate node impurity. This splitting procedure was repeated until node size reached a minimum two samples or until the variance was reduced to 0.001. The classification tree was generated when one of these criteria was either reached or surpassed on all branches. In this way, the final grouping was guaranteed to contain a reasonable sample size and each variable added some explanatory power to the model. Criteria for tree growth and pruning are used to find out how much a tree must grow and how many final nodes are reasonable. For a small number of samples, Breiman and others (1984) propose a V-fold cross-validation method with V = 10. This procedure starts by dividing the 31 stations in 10 equal size groups. It continues by generating a tree with 9 of the 10 groups and utilizing the 10th group to test the tree's precision. This process is repeated 10 times, utilizing a different group each time to test the tree's precision. For each test, the error in the tree's prediction is given by the increment on the number of terminal nodes. The tree with the smallest classification risk calculated with this procedure was displayed.

RESULTS

The 4690 classified specimens are distributed among the morphogroups as 43% rounded-planispiral (RP), 41% planoconvex (PC), 11% elongate-flattened (EF), 4% tapered (TA), and 2% milioline (MI). The PC morphogroup is present in all samples; RP is in 28 samples, and absent only from samples from the mouth of San Matías Gulf (44, 45, 53); EF occurs in 20 samples from the shelf, but is absent from samples from San Matías Gulf (45, 46, 53) and the deepest part of the outer shelf (2, 3, 13, 14, 15, 21, 22, 31); MI is in 12 samples from San Matías Gulf (45, 48 and 52), the coastal zone, and the shallowest part of the outer shelf (16–19, 27, 28, 42, 54, 55); TA is in eight samples from the northernmost area that coincides with the deepest part of the outer shelf (1, 3, 13, 14, 16, 19, 22), and in one sample from San Matías Gulf (52) (Fig. 3).

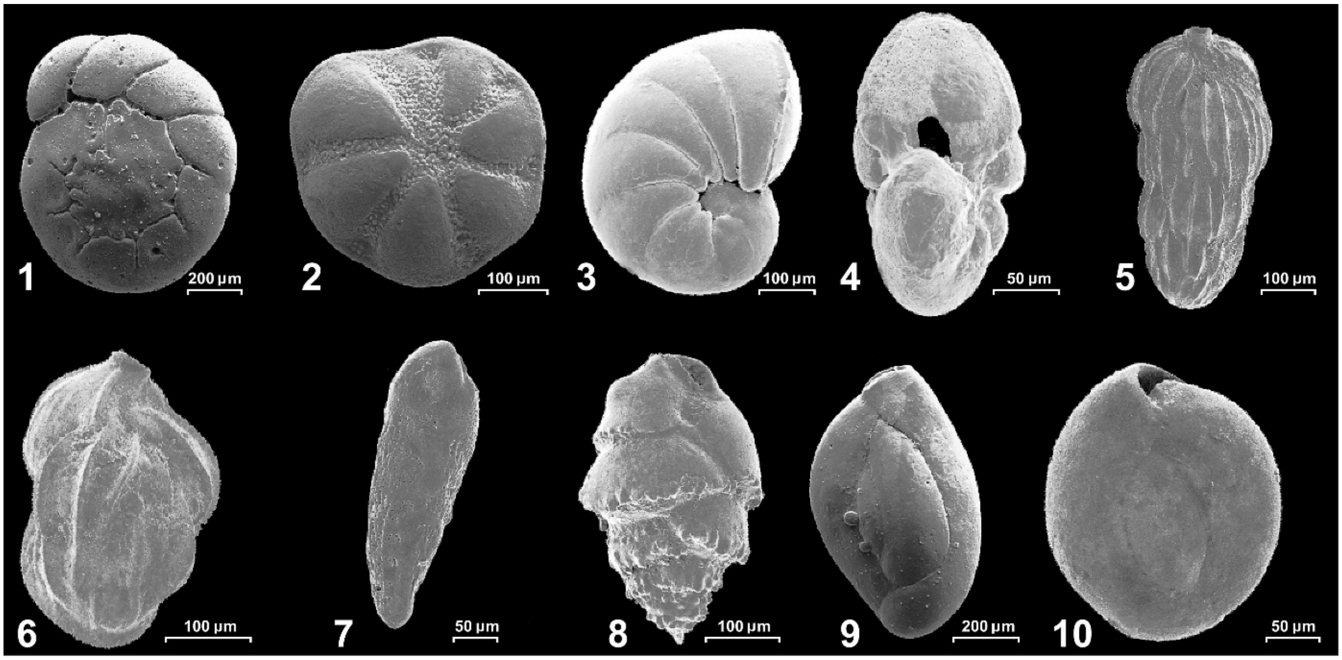

FIGURE 2. Examples of each morphogroup. **1, 2** Planoconvex (PC): 1, *Ammonia beccarii* (Linné); 2; *Buccella peruviana* f. *campsi* (Boltovskoy). **3, 4** Rounded-planispiral (RP): 3, *Nonionella auris* (d'Orbigny); 4, *N. auris* (d'Orbigny). apertural view. **5, 6** Tapered (TA): 5, *Angulogerina angulosa* f. *angulosa* (Williamson); 6, *Uvigerina peregrina* Cushman. **7, 8** Elongate-flattened (EF): 7, *Bolivina striatula* Cushman; 8, *Bulimina marginata* d'Orbigny. **9, 10** Milioline (MI): 9, *Quinqueloculina patagonica* d'Orbigny; 10, *Miliolinella subrotunda* (Montagu).

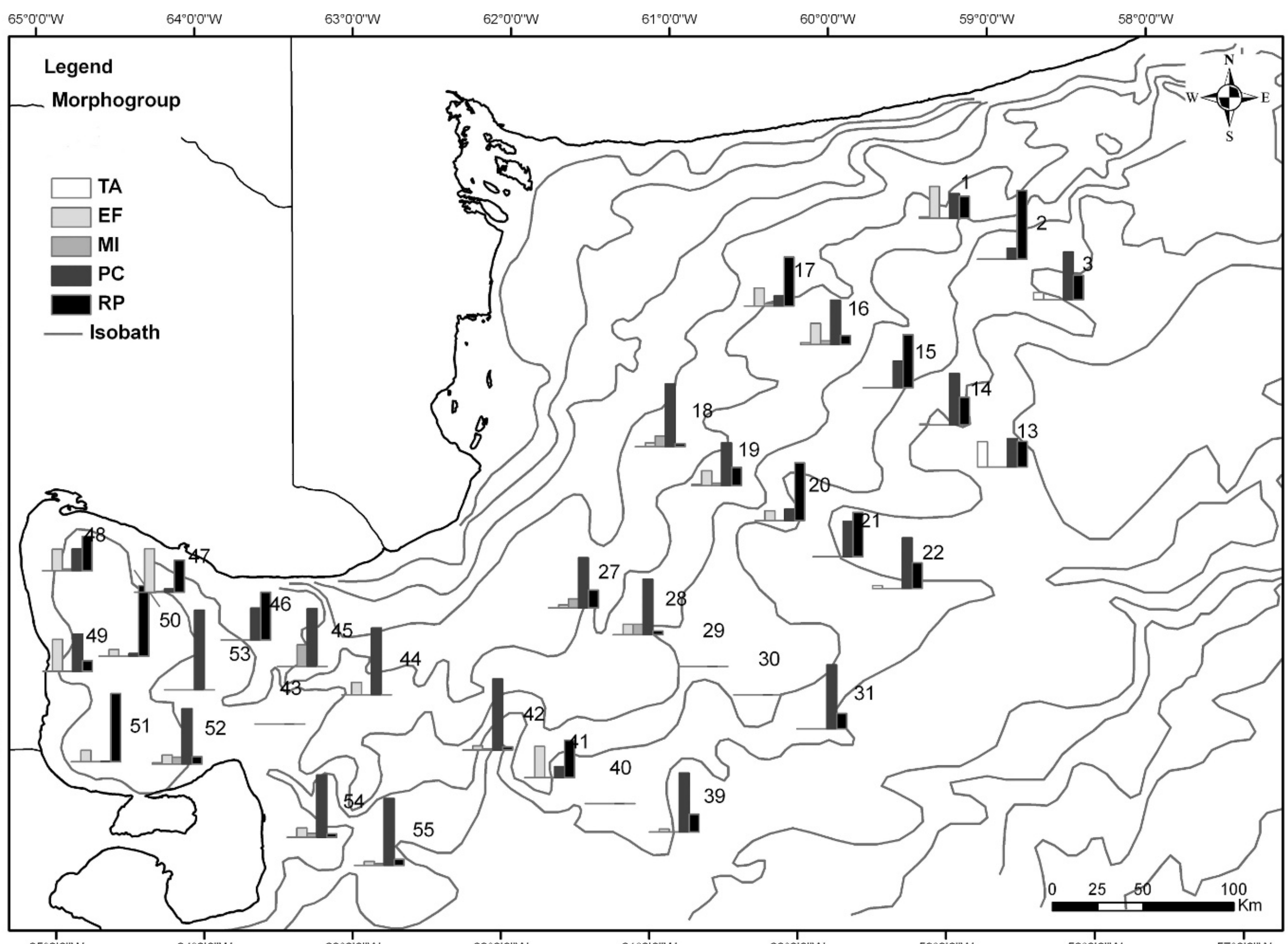

FIGURE 3. Map showing morphogroup composition in stations.

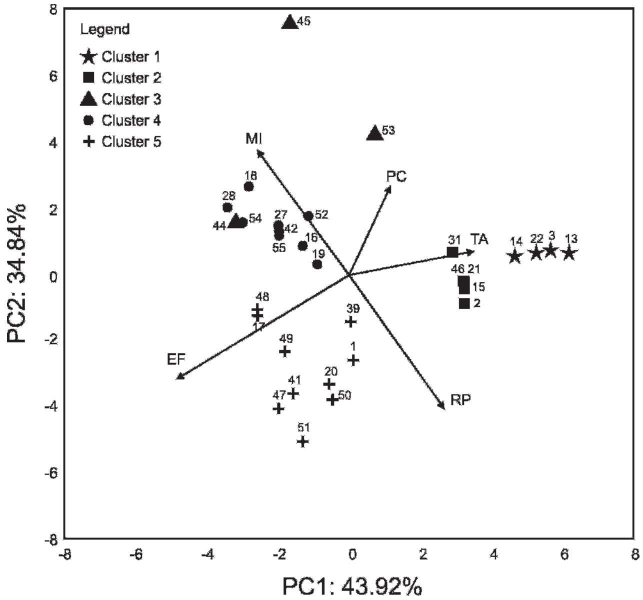

FIGURE 4. Biplot of 31 sample composition of morphogroups. TA = tapered, EF = elongate-flattened, MI = milioline, PC = planoconvex, RP = rounded-planispiral.

Morphogroup mean composition for the samples studied (Center) is dominated by PC (68%) and RP (27%), followed by much lower percentages of EF (3.7%), MI (0.6%), and TA (0.3%) (Appendix 1). The PCA results show that the first principal component (PC1) accounts for 44%, and the second principal component (PC2) for 35%, of the variance. The PC1 log-contrasts was *0.49 TA + 0.37 RP + 0.16 PC = 0.67 EF + 0.36 MI*, and PC2 log-contrasts *0.54 MI + 0.39 PC = 0.58 RP + 0.45 EF* (Table 4). The most variable morphogroups are EF and TA, while the least variable is PC (Fig. 4, Appendix 1). The most variable ratios are EF/TA and MI/RP, followed by EF/PC and EF/RP; the least variable are PC/TA and PC/MI (Fig. 4). It is of particular interest to characterize the PC/RP ratio because both morphogroups are present in most samples and it is highly variable (variance ln(PC/RP) = 8.55), and PC tends to be more abundant than RP (0.99), as verified in a considerable number of samples using the following equation:

$$mean\ \ln(PC/RP) > \sqrt{\mathrm{var} - \ln(PC/RP)}$$

The samples with the highest TA/EF ratio are placed on the positive PC1 together with those that have neither EF nor TA, while the samples with the greatest EF/TA ratio are placed on the negative PC1 with those that have EF and no TA as well as those that have both but contain higher proportions of EF. For PC2, samples with positive PC/RP are placed on the positive PC2 and samples with negative PC/RP are located on the negative PC2. The biplot analysis allows for differentiating five clusters of samples, each of which has a different morphogroup composition. In Figure 4, there are five well-differentiated clusters, four of which are easily discernible in the plane shown, while the fifth (cluster 3) appears scattered from the chosen plane.

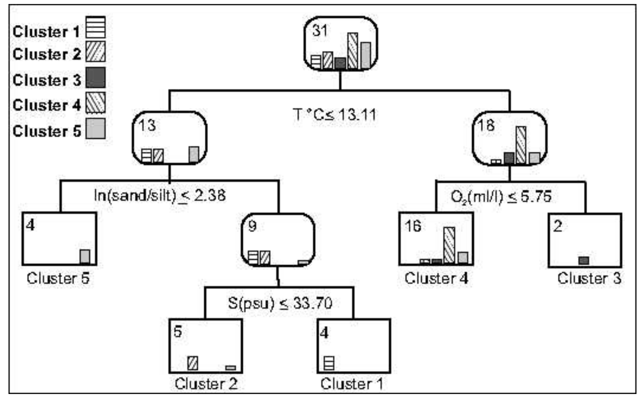

FIGURE 5. Classification Tree model predicting sample location of a cluster of morphogroups. Number of samples per node is shown at left. In the node, the length of the bar indicates the number of samples of the cluster. The variables included in this model are temperature (T), salinity (S), dissolved O_2 in water, ln(sand/silt).

RELATIONSHIPS BETWEEN SAMPLE CLUSTERS AND ENVIRONMENTAL VARIABLES

The classification tree analysis showed that the most significant variables for the morphogroup composition of each cluster of samples were the three physicochemical attributes of water: temperature, salinity, quantity of dissolved oxygen with 100%, 82%, and 76% importance respectively, and substrate, measured as ln(sand/silt) with 74% in importance. Depth, classified as having 77% importance, is masked in this tree because the substrate's characteristic is negatively correlated with its depth ($r(depth;\ ln(sand/silt)$ $= -0.9194$, $p > 0.01$). The lowest explanatory power was attributed to distance from shore (72%). The cross-validation procedure provided a tree with 4 partitions and 5 terminal nodes as the best fit to data (CV cost = 0.52; s.d. CV cost = 0.09). The first split, based on water temperatures, separates samples of clusters 1, 2, and 5 (T $\leq$13.1°C) from samples of clusters 3 and 4 (T >13.1°C). The second partition, in the sample groups from colder water, is based on substrate and separates samples of cluster 5 with finer sediment (ln(sand/silt) $\leq$2.4) from samples of clusters 1 and 2. The third partition separates samples of cluster 1 (salinity $\geq$33.7) from samples of cluster 2, which has lower salinity. The samples from warmer waters (clusters 3 and 4) were split as a function of dissolved oxygen, with those of cluster 3 representing waters with a higher level of oxygen (O $\geq$5.75 ml/l) than cluster 4 (Fig. 5).

It should be noted that only the terminal node labeled cluster 1 is pure, and it comprises all of the samples in cluster 1. In contrast, the pure terminal node labeled cluster 5 only contains those cluster 5 samples from cold and muddy waters (47, 50, 51), leaving out four samples: one from cold, less-saline waters (41), and three from waters with T >13.1°C and a sandy substrate (1, 20, 49). The terminal node labeled cluster 3 is also pure, but includes only well-oxygenated samples (43, 44), leaving out a sample with lower oxygen content (53). On the other hand, the terminal node labeled cluster 2 is impure, but includes four of the five samples in the cluster (2, 15, 21, 31) and one cluster 5 sample (41). Finally, the node labeled cluster 4 is the most impure, and in addition to all the samples in the

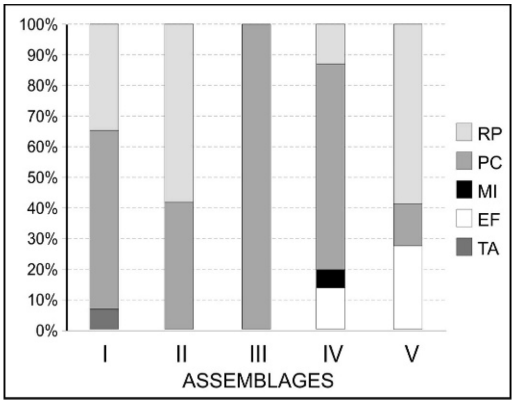

FIGURE 6. Mean morphogroup composition of each assemblage.

cluster, it contains one cluster 2 sample (46), one cluster 3 sample (54) and three cluster 5 samples (1, 20, 49).

ASSEMBLAGES

According to Murray (2006), an assemblage is the group of species found together in the same sample. Our study uses morphogroup assemblages to refer to groups of samples that have a similar composition of calcareous benthic foraminiferal morphotypes. The absence of agglutinated specimens agrees with the observations of Boltovskoy (1976) on the Argentine Shelf, off Tierra del Fuego (Boltovskoy and others, 1983; Murray, 2006), and in estuaries along the Argentine coast (Calvo Marcilese and Protologo, 2009).

Five benthic foraminiferal morphogroup assemblages are distinguished below according to the composition of the clusters of samples, classification tree results, and geographical distribution of the samples. For each assemblage, we have also determined the mean compositional morphogroup composition (Fig. 6).

Assemblage I (PC-RP-TA; cluster 1 samples 3, 13, 14, 22). This assemblage is composed only of PC (59%), RP (35%), and TA (6.3%) (Fig. 6). The proportion of TA is the most variable, followed by the proportion of PC. In nearly all samples there is a greater proportion of PC than RP (mean ln(PC/RP) = 0.51) (Fig. 4). This assemblage corresponds to water temperature <13.1°C, salinity >33.7, and predominantly sandy substrate (Fig. 5, terminal node cluster 1).

Assemblage II (RP-PC; cluster 2 samples 2, 15, 21, 31, 46). It contains only RP (59%) and PC (41%) forms (Fig. 6). Although the PC/RP ratio is variable among the samples in the group, it is always slightly below the mean for the set of samples, indicating that there is a greater proportion of RP than PC (mean ln(PC/RP) = −0.35) (Fig. 4). This assemblage matches to water temperature <13.1°C, salinity <33.7, and predominantly sandy substrate (Fig. 5, terminal node cluster 2).

Assemblage III (PC; cluster 3 samples 44, 45, 53). 99% are PC forms, with very low percentages of MI and EF (0.5% and 0.4% respectively) (Fig. 6). This assemblage corresponds to water temperatures >13.1°C and oxygen content ≥5.7 (Fig. 5, terminal node cluster 3).

Assemblage IV (PC-RP-EF-MI; cluster 4 samples 16–19, 27, 28, 42, 48, 52, 54, 55). This is the most diverse of the assemblages because it includes the five morphogroups, PC (67.3%), RP (13.5%), EF (13.2%), MI (5.7%), and TA (0.2%) (Fig. 6) The PC/RP ratio is variable, although in most samples there is a higher proportion of PC than RP (mean ln(PC/RP) = 1.60). When ln(PC/RP)>1, EF forms appear (Fig. 4). The assemblage is present in the coastal domain (extending the coastal domain to the 55 m isobath) and from the shallowest part of the outer shelf (Fig. 7). This assemblage occurs where water temperature is >13.1°C and oxygen content is ≤5.7 ml/l (Fig. 5, terminal node cluster 4) Substrates are gravelly for sample 54 and sandy-gravelly for 55, 42, 27, 28, and 18.

Assemblage V (RP-EF-PC; cluster 5 samples 1, 20, 39, 41, 47, 49–51). Includes RP (58%), EF (27%), and PC (13%) (Fig. 6). Most samples contain a higher proportion of RP than PC (mean ln(PC/RP) = −1.46). RP predominates in four of the samples, PC and EF in two. The ratios between morphogroups vary a lot (Fig. 4). The assemblage is present in the outer shelf and in samples from San Matías Gulf (Fig. 7). No similarities were found among the environmental characteristics of the samples that would allow the assemblage to be related to a single set of abiotic features. Samples 39, 47, 50, and 51 are found at water temperatures <13.11°C and salinity >33.70 (Fig. 5, terminal node cluster 5). Sample 41 also has water temperature under 13.11°C, but salinity <33.70 (Fig. 5, terminal node cluster 2). Samples 1, 20, and 49 have water temperature >13.11°C and oxygen content ≤5.7 ml/l (Fig. 5, terminal node cluster 4). The substrate also varies; it is silty for samples from San Matías Gulf, and sandy for samples from the outer shelf.

DISCUSSION AND INTERPRETATION

Planoconvex (PC) and rounded-planispiral (RP) calcareous foraminiferal morphogroups predominate throughout the study area. This finding agrees with others investigations such us Nigam and others (2000) and Fernández (2006). However, the abundance distribution of these forms is contrary to the spatial pattern found by Severin (1983), where the relative abundance of PC on the Texas coast decreases with increasing depth. As mentioned previously, the PC/RP ratio is highly variable without any determined relation to any explanatory factor. A plausible explanation for this behavior may be found in the morphological symmetry of both morphogroups (similarities in apertural view, which is biconvex to planoconvex in both groups). Severin (1983) pointed out that the morphologies of PC and RP may be those of generalists, as symmetric forms are more common than asymmetic forms in undisturbed sediment, while the reverse occurs in disturbed sediment. Elongate-flattened (EF) forms have been found over an extensive shelf area corresponding to rather shallow depths. Tapered forms (TA) are found in a low proportion and are limited geographically to deeper parts of the gulf zone and the outermost, deepest sector of the shelf. EF and TA are only found together in four samples, with a higher proportion of EF. It is worth noting that in most samples, when EF is present, TA is lacking, and vice versa.

Morphogroups PC and RP, which have no predominant axis in their morphology, may be considered symmetrical, while those like TA and EF, which do have a predominant axis, are considered asymmetrical. Undisturbed sediments (Reineck-Singh, 1980) favor the development of asymmetrical forms because they can maintain a preferential position, while disturbed sediments are more likely to have symmetrical forms, which can more easily reposition themselves after disturbance (Severin, 1983; Nigam and others, 2000; Fernández, 2006). The increase in asymmetrical forms with depth has been related to bottom-water turbulence and consequential disturbance of the sediment (Severin, 1983). In this context, the presence of TA forms, limited to deeper shelf zones, suggests an environment with little turbulence and low disturbance rate, but the presence

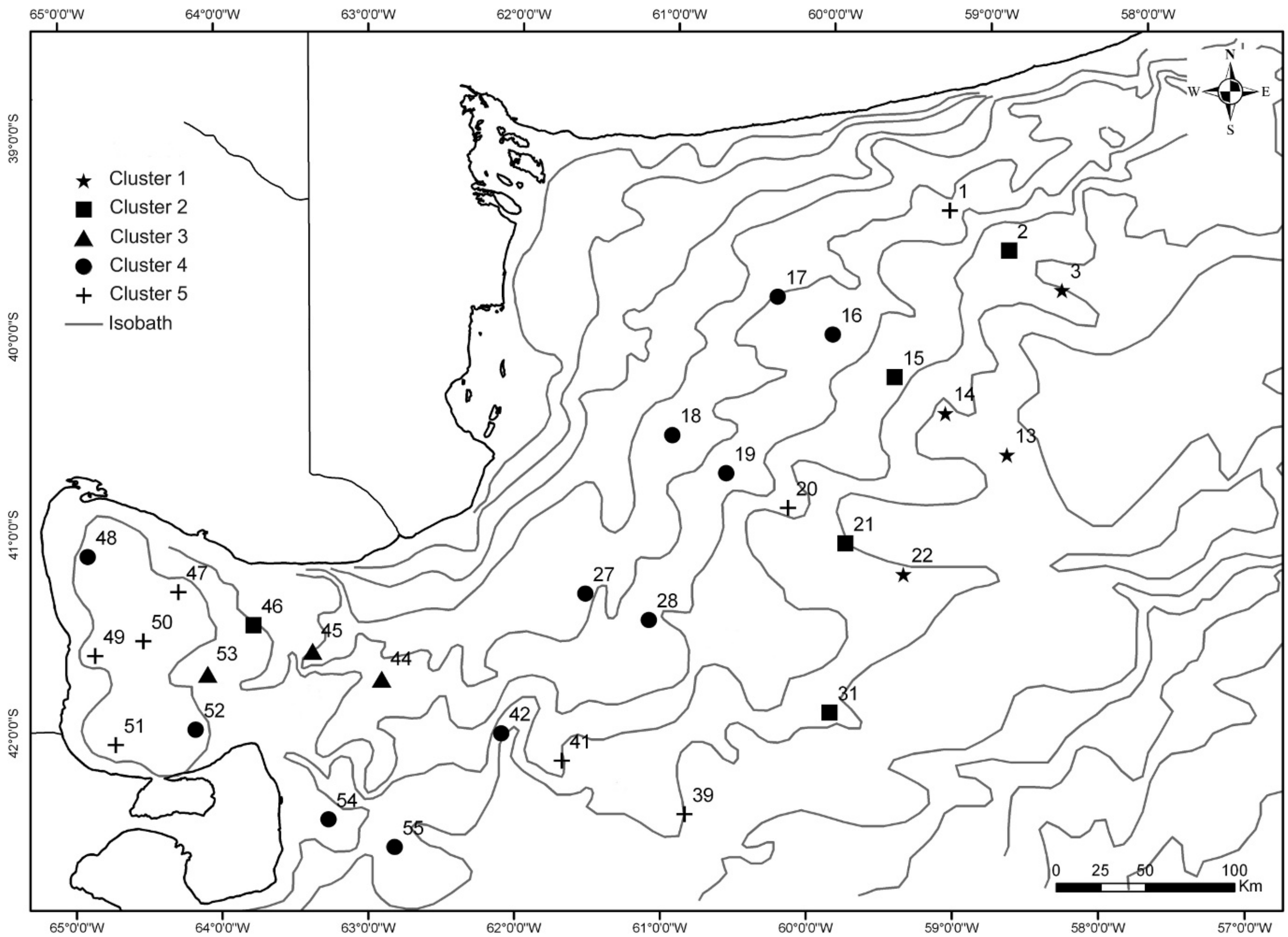

FIGURE 7. Map showing distribution of sample clusters based on morphogroups.

of EF forms in shallower parts of the shelf cannot be interpreted in the same way. The MI forms are limited to samples from the mouth of San Matías Gulf and the shallowest part of the inner shelf nearest the littoral zone. Principal Component Analysis is interpreted by analyzing asymmetry. Asymmetric forms (EF and TA) are the morphogroups with the greatest weight in PC1, while symmetric forms (RP and PC) and miliolines (MI) have the greatest weight in PC2 (Fig. 4, Table 3). Clusters 1, 3, and 4 are found on the positive PC2s with PC and MI forms. On the positive PC1s are clusters 1 and 2, whose samples have a clearly sandy substrate, suggesting environments with similar energy. This differs from those of cluster 5, which are placed on the negative PC2s and whose samples have sandy or sandy-gravelly sandy-silty to silty substrates.

TABLE 3. Eigen values. Eigen vectors and proportion of the accounted variation of each principal component (PC) using the covariance matrix derived from the centered log-ratio data. TA = tapered, EF = elongate-flattened, MI = milioline, PC = planoconvex, RP = rounded-planispiral.

	Eigen vector			
Morphogroup	PC1	PC2	PC3	PC4
TA	0.496	0.099	0.579	0.456
EF	−0.673	−0.450	0.371	−0.079
MI	−0.363	0.544	−0.449	0.410
PC	0.165	0.3892	0.064	−0.785
RP	0.375	−0.582	−0.565	−0.001
Eigen value	8.356	6.628	2.553	1.487
Absolute total variance (%)	43.92	34.84	13.42	7.81
Cumulative total variance (%)	43.92	78.76	92.18	100.00

Many factors have been proposed to explain the presence of benthic foraminifera, such as temperature, salinity, microhabitat, food availability, and substrate type. Water temperature, salinity, and dissolved oxygen, as well as the type of substrate play an important part in the structure of the morphogroup assemblages we have identified. Others authors suggest the food availability is one of the most important factor of the benthic foraminiferal distribution (Jorissen and others, 1995; Van der Zwaan and others, 1999). We do not have information about food supply to include in our analysis to consider as proxy data. It follows that:

Assemblage I (PC-RP-TA) is dominated by the symmetrical morphogroups PC and PR and is the only assemblage that contains asymmetrical TA individuals. It appears on the outer shelf, on a sandy substrate, where Middle Shelf Water is influenced by the Malvinas Current, which is associated with the accumulation production of detritus between the 80-100 m, just before the shelf break. The

TABLE 4. Comparison between morphogroups (this paper) and species assemblages according to Alperin and others (2008) (sample number in brackets).

This paper	Alperin and others. 2008	Oceanographic conditions
Assemblage I (3, 13, 14, 22)	Group 1 (3, 13, 14, 21, 22, 39)	Outer shelf; cooler waters strong influence of Malvinas Current
Assemblage II (2, 15, 21, 31, 46)	Group 2 (2, 15, 17, 20, 31, 41)	Transition between outer and inner shelf; little influence of Malvinas Current
Assemblage III (44, 45, 53)	Group 5 (44, 45, 53)	Coastal water with higher salinity and temperature; high sedimentary dynamics
Assemblage IV (16, 17, 18, 19, 27, 28, 42, 48, 52, 54, 55)	Groups: 4 (18, 19, 28, 42, 52, 54, 55); 2 (17); 3 (16); 6 (48)	Influence of middle-shelf water and coastal water of high salinity
Assemblage V (1, 20, 39, 41, 47, 49, 50, 51)	Groups: 1 (39); 2(20, 41); 3 (1, 49); 6 (47, 50, 51)	Wide range of temperature salinity and environment energy

presence of TA forms coincides with the greatest depths of the outer shelf for the area. The preponderance these symmetrical forms on sandy substrates, indicates that they tolerate an environment disturbed by the Malvinas current, which has velocities in the order of 30 cm/s.

Assemblage II (RP-PC) is composed exclusively of the symmetrical forms PC and RP. This assemblage occurs on the outer shelf where Middle Shelf Water is above a sandy substrate. The exclusive presence of symmetrical morphogroups suggests that these forms are able to inhabit a high-energy environment because they can adapt to disturbance.

Assemblage III (PC) comprises mainly symmetrical morphogroup PC and a few milioline and asymmetrical TA forms. The preponderance of PC forms, the presence of MI forms, which tolerate high energy environments (Boltovskoy, 1966; Gómez and others, 2005; Cusminsky and others, 2009), plus a coarse-grained substrate suggest the fauna tolerates intensive deposit-erosion processes (Scasso and Piola, 1988) resulting from the strong currents (~3.5 m/s) generated by the tidal front (Tonini and others, 2006).

Assemblage IV (*PC*-RP-EF-MI) is composed of has a large proportion of symmetrical morphogroups PC and RP, a smaller proportion of asymmetrical EF, and few TA and miliolines. The assemblage present in the San Matías Gulf is linked to the saline gulf waters. The assemblages located in the shallower part of the outer shelf could be related to the Coastal Water with high salinity, and associated with the production of detritus generated at the Coastal Front zone between the 40–50 m isobaths. The predominance of symmetrical forms and the presence of miliolines on sand to gravelly sand suggest that this association prospers in a high-energy environment.

Assemblage V (RP-TA-PC) comprises mainly of symmetrical RP, subordinate PC forms, and asymmetrical EF forms. This assemblage occurs in the deep parts of San Matías Gulf and on the outer shelf. It is found in a wide range of water temperature and salinity, on silty and sandy substrates, but does not appear to be linked in any definitive way to any of these variables. In the deep parts of the Gulf, the assemblage inhabits silty substrates and its generalist character would allow the specimens to behave like as though they were asymmetric, suggesting either a eutrophic environment most likely caused by a deficit in current circulation or waters with restricted circulation typical of deep, engulfed zones (Bernasconi and Cusminsky, 2005; Bernasconi and others, 2009). On the shelf, the assemblage develops on sandy sediments where there is an EF morphogroup, and its patchy spatial pattern may be associated with local factors.

Alperin and others (2008) studied the same material with statistical analysis of compositional foraminiferal species census data, and defined six assemblages of benthic foraminiferal species whose characteristics are believed to be responses to oceanographic conditions at the site. This would show that the inferences based on the autoecology of the species are similar to the ones in this work that are based on shell morphology (Table 4). On the other hand, several workers, including Corliss and Chen (1988), Jorissen and others (1995), and Van der Zwaan and others (1999), have found food supply to be a major driver of benthic foraminifera assemblage composition and distribution. Food availability is a complex factor with different components (e.g., type, quality, and quantity) that enable different morphogroups to coexist. The coastal and shelf-break fronts, which are areas of high primary productivity favorable to the development of benthic foraminifera, would be the main sources of food supply. Food could still be another driver in this case but there was no proxy information on food supply needed to include it in these analyses.

CONCLUSIONS

The distribution pattern of benthic foraminiferal morphogroups on the Argentine continental shelf between 39–43°S is the result of complex interactions with different environmental parameters. Temperature appears to be the most important factor in structuring the assemblages, although salinity, substrate grain size, and environmental energy also play important roles. These factors, especially temperature and salinity, could be related to different water masses.

The geographical distribution pattern of the benthic foraminiferal assemblages defined by autoecological characteristics is maintained when the analysis uses morphological criteria. Both species assemblages and foraminiferal morphogroups allow inferences to be made about water mass such as temperature and salinity, substrate characteristics, and environmental energy.

Our study is the first attempt to use taxon-free criteria of benthic foraminifera on the Argentine continental shelf.

Foraminiferal morphogroup analysis shows potential for determining recent environments and paleoenvironments when species autoecology is unknown or when there is uncertain taxonomy. Further study of the spatial patterns and factors that structure modern benthic foraminiferal morphogroup assemblages in different environments and zones of the Argentine continental shelf will allow them to be integrated with taxonomically based studies in order to achieve more precise ecologic and paleoecological interpretations.

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APPENDIX 1. Compositional data of morphogroups. TA = tapered, EF = elongate-flattened, MI = milioline, PC = planoconvex, RP = rounded-planispiral. Var-clr = variance of centered log-ratio data.

Sample	Number of specimens	Cluster	Morphogroup				
			TA	EF	MI	PC	RP
1	58	5	0.017	0.397	0.000	0.310	0.276
2	22	2	0.000	0.000	0.000	0.136	0.864
3	78	1	0.090	0.000	0.000	0.603	0.308
13	462	1	0.320	0.000	0.000	0.357	0.323
14	179	1	0.011	0.000	0.000	0.642	0.346
15	12	2	0.000	0.000	0.000	0.333	0.667
16	45	4	0.022	0.267	0.044	0.556	0.111
17	264	4	0.000	0.227	0.030	0.125	0.617
18	224	4	0.000	0.045	0.134	0.786	0.036
19	65	4	0.015	0.185	0.031	0.538	0.231
20	48	5	0.000	0.125	0.000	0.146	0.729
21	86	2	0.000	0.000	0.000	0.442	0.558
22	105	1	0.038	0.000	0.000	0.638	0.324
27	27	4	0.000	0.037	0.111	0.630	0.222
28	46	4	0.000	0.130	0.130	0.696	0.043
31	31	2	0.000	0.000	0.000	0.806	0.193
39	27	5	0.000	0.037	0.000	0.741	0.222
41	66	5	0.000	0.394	0.000	0.136	0.470
42	372	4	0.000	0.054	0.013	0.892	0.040
44	19	3	0.000	0.158	0.000	0.842	0.000
45	11	3	0.000	0.000	0.273	0.727	0.000
46	10	2	0.000	0.000	0.000	0.400	0.600
47	133	5	0.000	0.549	0.000	0.045	0.406
48	244	4	0.000	0.270	0.020	0.275	0.434
49	15	5	0.000	0.400	0.000	0.467	0.133
50	900	5	0.000	0.082	0.000	0.031	0.887
51	419	5	0.000	0.143	0.000	0.002	0.854
52	250	4	0.016	0.112	0.084	0.696	0.092
53	300	3	0.000	0.000	0.000	1.000	0.000
54	134	4	0.000	0.119	0.052	0.784	0.045
55	38	4	0.000	0.053	0.026	0.842	0.079
Samples	31		8	20	12	31	28
Specimens	4690		168	505	93	1916	2008
Geometric mean			0.003	0.038	0.006	0.682	0.271
Var-clr			3.29	5.49	3.84	2.16	4.24