SHORT COMMUNICATION

Latitudinal diversity patterns of diatoms in the Southwestern Atlantic and Antarctic waters

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Latitudinal changes in the species richness of planktonic diatoms in Southwestern Atlantic and Antarctic waters (29°–76° S) were analyzed from local to regional scale in three spring and one summer seasons. A total of 220 diatom species (16–87 per station) were recorded. Despite the noticeable interannual variability, species richness showed a maximum in the northern sector of the Brazil-Malvinas Confluence Zone and a highly significant decrease with latitude.

Global diversity patterns and, more specifically, latitudinal gradients of species richness are ecological phenomena that have been the subject of recent study (e.g. Gaston, 2000; Barton *et al.*, 2010). Some previous studies on the distribution of planktonic organisms (e.g. diatoms, foraminifers, copepods, bacterioplankton) have detected clear latitudinal trends (e.g. Rutherford *et al.*, 1999; Martiny *et al.*, 2006; Rombouts *et al.*, 2009), whereas others have suggested very weak or non-existent latitudinal diversity gradients (e.g. Hillebrand and Azovsky, 2001; Cermeño *et al.*, 2008; Rodríguez-Ramos *et al.*, 2015). The aim of this work was to assess the latitudinal species richness of planktonic diatoms from Subtropical to Antarctic waters of the Southwestern Atlantic Ocean (SWA). Diatom biogeography is poorly known in this region which has unique features (e.g. Cermeño *et al.*, 2008; Chust *et al.*, 2012).

The surface circulation of the SWA is driven by two of the largest and most energetic western boundary currents
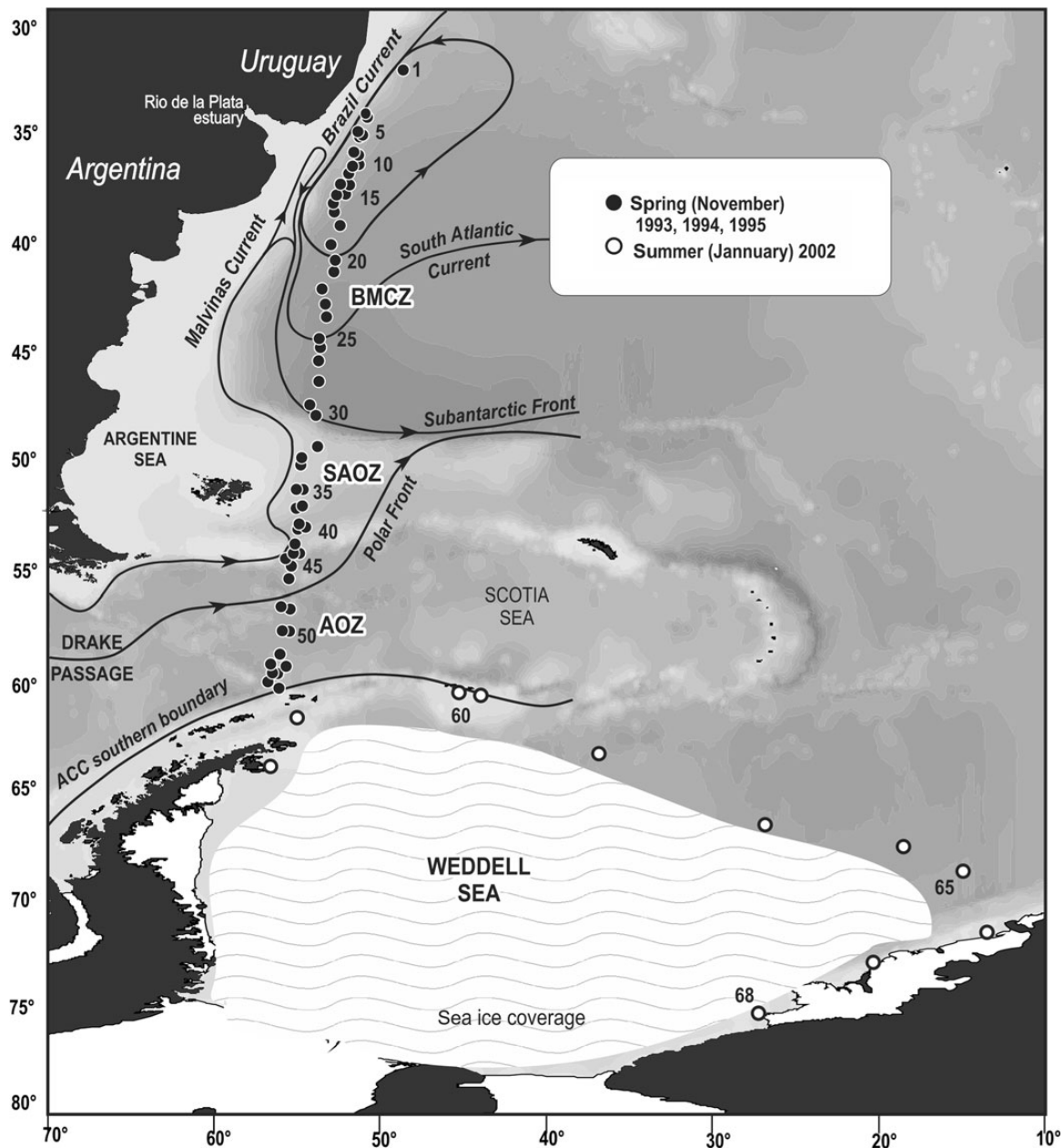
Fig. 1. Location of oceanographic stations in the Southwestern Atlantic during the 1993, 1994 and 1995 spring surveys, and in the Weddell Sea during the summer of 2002 and general surface circulation patterns (Peterson and Stramma, 1991).

of the world: the Malvinas Current and the Brazil Current (Peterson and Stramma, 1991), which flow in opposite directions (Fig. 1). These currents transport organisms of Antarctic/Subantarctic and Subtropical origin, respectively, and meet ∼34–35° S to generate a hydrologically complex area, rich in spatial structure (d'Ovidio *et al.*, 2010), known as the Brazil-Malvinas Confluence Zone (BMCZ). South of this area, the Antarctic Circumpolar Current (ACC) flows permanently from west to east connecting three large ocean basins.

Latitudinal gradients of diatom species richness were assessed through regression analysis (least squares method) of the number of diatom species versus latitude. Since the patterns obtained in this way are known to depend, among other factors, on the spatial scale considered (Macpherson, 2002), the analyses were made at three different spatial scales: individual samples (at each depth and site), stations (at each site) and biogeographic zones.

The analyses of the individual samples and stations were based on each survey carried out in austral spring

1993, 1994 and 1995 in an oceanic area next to the Argentine Shelf and extending from the BMCZ to Antarctic waters ($\sim$29°S$-$47°W to 62°S$-$57°W; Fig. 1). Samples were collected at different depths between 0 and 50 m either by means of Niskin bottles (1993: 3$-$8 L; 1995: 18 L), followed by reverse filtration (10-μm-mesh gauze), or by means of a 30-μm-mesh closing net (1994: 200$-$300 L) and preserved with neutralized 5% formaldehyde. A seawater volume of at least 2 L of each sample was completely examined for the species richness estimation. This volume exceeds that recommended by recent methodological reviews (Cermeño *et al.*, 2014; Rodríguez-Ramos *et al.*, 2014) to avoid bias due to undersampling, especially of rare species. The present study is supported by an appropriate sampling, identification and counting effort (methodological details are provided in Supplementary data, Appendix S1). The station scale was derived after pooling the 0- to 50-m-depth samples for each survey.

The analysis at the biogeographic scale was based on the above spring samplings plus an additional survey carried out in the Weddell Sea during summer 2002 (Fig. 1). For the latter, water samples (180$-$300 L) were collected at 9-m depth and filtered through a 20-μm-mesh gauze. The boundaries between biogeographic zones were defined by the location of those fronts strong enough to affect diatom distribution (indicated by cluster analysis; Jaccard's Similarity Index) (Olguín *et al.*, 2006, 2015; Olguín and Alder, 2011). The zones considered were the BMCZ, divided into Northern (BMCZ-N; 34°$-$37° S); Central (BMCZ-C; 37°$-$42° S) and Southern sectors (BMCZ-S; 42°$-$47° S); the Subantarctic Oceanic Zone (SAOZ; 47°$-$56° S); the Antarctic Oceanic Zone (AOZ; 56°$-$62° S) and the Weddell Sea (WS; south of 62° S) (Fig. 1). The number of species within each zone was based on all identifications, regardless of the sampling year. The diatom species richness in each biogeographic zone (Fig. 2; Supplementary data, Appendix S2 in color) was estimated by sample-size-based rarefaction and extrapolation using the Chao2 nonparametric estimator of asymptotic richness (Colwell *et al.*, 2012; Chao *et al.*, 2014). The endpoint (sample size that is the endpoint for extrapolation) was specified as twice the smallest original sample size. The 95% unconditional confidence intervals were estimated by a bootstrap method based on 200 repetitions, using the iNEXT software (Hsieh *et al.*, 2013). The sample coverages (Chao *et al.*, 2014) for the six zones (BMCZ-N, BMCZ-C, BMCZ-S, SAOZ, AOZ and WS) were estimated as 96, 92.5, 97, 96, 98.5 and 99%, respectively (Supplementary data, Appendix S3), indicating that sampling is nearly complete for all zones.

A total of 220 diatom species (16$-$87 species per station) were recorded in the studied region. On average,
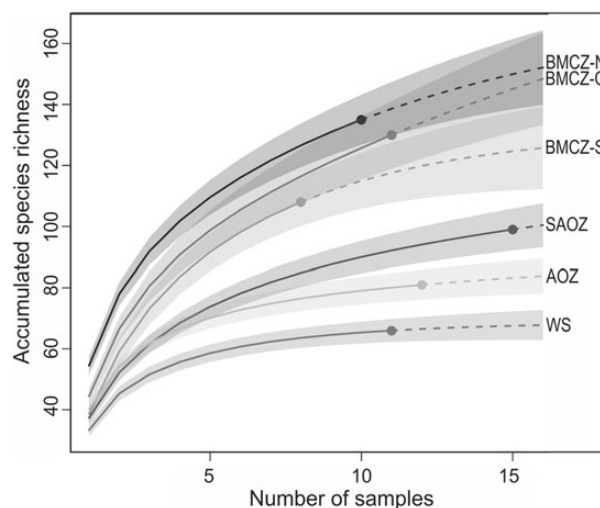

Fig. 2. Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines, up to twice the smallest reference sample size) of diatom species richness based on the Chao2 for each biogeographic zone. Reference samples are denoted by solid dots. The 95% unconditional confidence intervals (gray-shaded regions) were obtained by a bootstrap method based on 200 repetitions (Colwell *et al.*, 2012; Chao *et al.*, 2014).

nearly 70% of all species present at each station showed a relative density below 1% and may thus be classified as rare (Rodríguez-Ramos *et al.*, 2014). The high proportion of species with low density values stresses the relevance of the well-known effect of sample size on species richness estimates (e.g. Rodríguez-Ramos *et al.*, 2014). This effect may partially explain the lower mean number of diatom species per station based on 100-ml samples previously reported (Chust *et al.*, 2012) for the same latitudinal range and similar longitude (at 7-m depth; spring 1995, 1996, autumn 1996) than the mean recorded in our surveys: 15 (estimation from a figure in Supplementary data, Appendix S2, *op. cit.*) vs. 35 species at 10 m depth; 15 vs. 43 species at 0$-$50 m depth.

Diatom densities spanned 5 orders of magnitude (up to 700 000 cells L^{-1}) with peaks mainly at some BMCZ stations and in Antarctic waters (Olguín *et al.*, 2006, 2015; Olguín and Alder, 2011). Diatom density and species richness showed a nonsignificant linear correlation along the transect, thus suggesting that density is a poor predictor of species richness, as also biomass seems to be (Cermeño *et al.*, 2013).

Whereas the 1993 survey showed the highest species richness values for the northern BMCZ stations (69/87 species per sample/station), the 1995 survey showed low overall species richness values in most of the transect stations (Fig. 3A and B). At the level of biogeographic zones, the northern BMCZ showed the highest number of species (150), while the Weddell Sea showed the lowest (67) (Figs 2 and 3C). Estimated species richness values
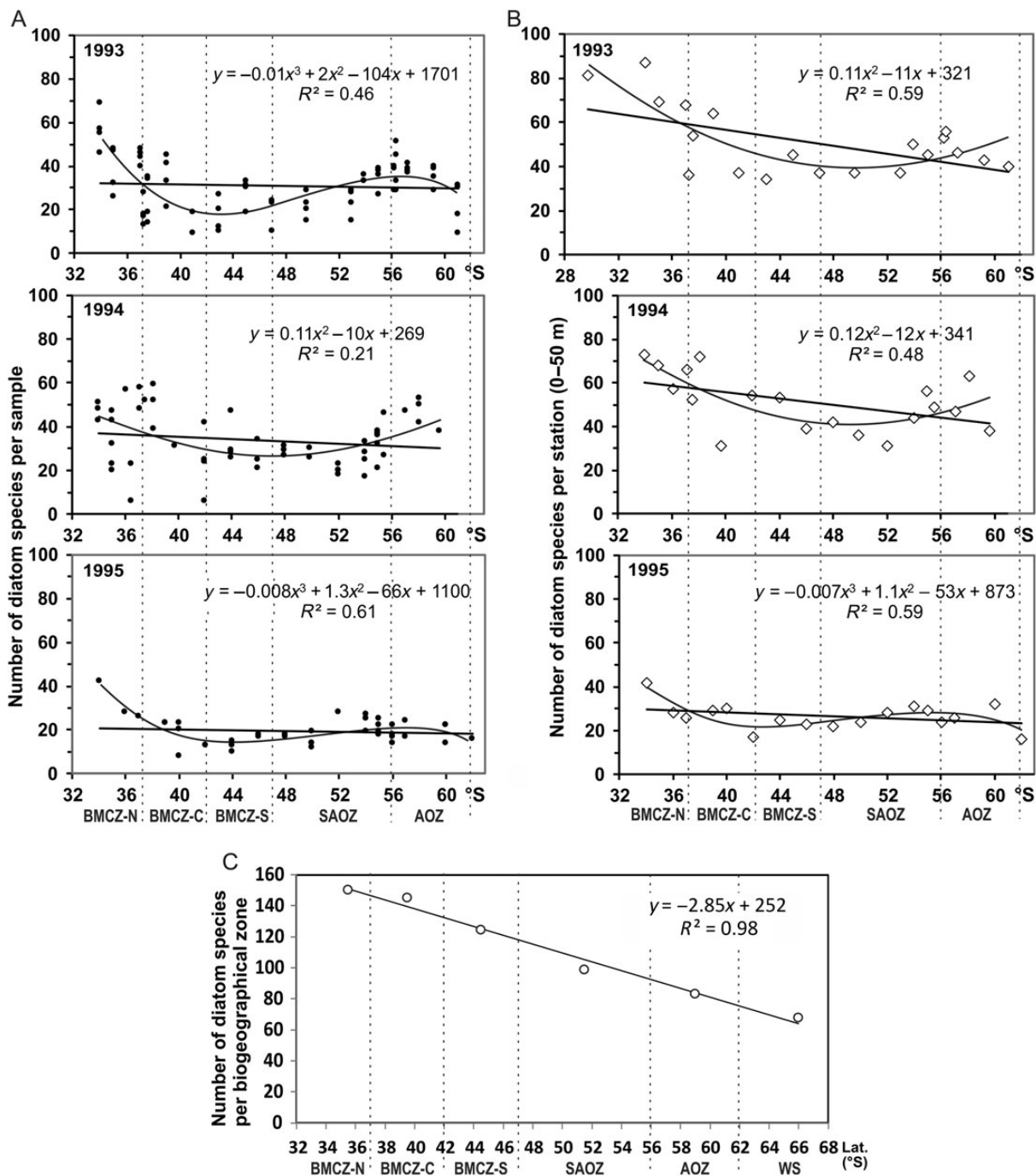
Fig. 3. Regression analysis of species richness as a function of latitude, showing the least squares regression fitted line ($P < 0.05$) to a linear and/or polynomial model. (**A**) At sample level, (**B**) at station level and (**C**) at level of biogeographic zones, including also the Weddell Sea. Estimated species richness according to the endpoints shown in Fig. 2 (based on station 0–50 m pooled data of the spring surveys). BMCZ, Brazil-Malvinas Confluence Zone; N, Northern; C, Central; S, Southern; SOZ, Subantarctic Oceanic Zone; AOZ, Antarctic Oceanic Zone; WS, Weddell Sea.

consistently and significantly decreased with increased latitude (based conservatively on nonoverlapping confidence intervals): BMZC-N > BMCZ-S > SAOZ > AOZ > WS (Fig. 2). Within the BMCZ zone, the species richness estimated at the endpoint also followed the latitudinal trend

(Figs 2 and 3C); however, the unconditional confidence intervals overlapped with the BMCZ-C subzone, reflecting the transitional nature of this area. In general, similar results were also obtained for data at 10-m (springs) and 9-m depth (WS) (Supplementary data, Appendix S2).

Most of the diatoms that characterized the BMCZ, especially its northernmost stations, were warm- and temperate-water species (e.g. *Asterolampra marylandica*, *Asteromphalus heptactis*, *A. sarcophagus*, *Alveus marinus*, *Chaetoceros diversus*, *C. messanensis*, *Hemiaulus membranaceus*, *Planktoniella sol*, *Pseudosolenia calcar-avis*, *Rhizosolenia clevei*, *Roperia tesselata*, *Thalassiosira lineata*, *Pseudo-nitzschia multiseries*), reflecting the strong influence of the Brazil Current waters. Cold-water species were more conspicuous in the southern part of the BMCZ (*Fragilariopsis kerguelensis*) and became clearly dominant in the assemblages south of the Subantarctic Front (e.g. *Asteromphalus hookeri*, *A. parvulus*, *Dactylosolen antarcticus*, *Eucampia antarctica*, *Rhizosolenia simplex*, *Thalassiosira gravida*, *T. lentiginosa*, *T. tumida*) (Olguín *et al.*, 2015).

Latitudinal patterns of species richness in diatom assemblages varied across both the surveys and the spatial scales considered (Fig. 3). At the level of samples and stations, species richness decreased toward higher latitudes up to ~52° S (mainly in 1993 and 1994). Farther south, species richness increased slightly and then decreased again. Due to this pattern, the fit of the model increased when adjusted to a second- or third-order polynomial function and reached a higher total variability explained at the level of station (up to ~60%) (Fig. 3B). At the station level, the latitudinal decrease in species richness was weaker in 1995 (Fig. 3B).

At the level of biogeographic zones, a highly significant linear decrease of species richness with increasing latitude was apparent, jointly with a remarkable increase in the percentage of variability explained by this regression (up to 98%) (Fig. 3C, Supplementary data, Appendix S4).

Specific diversity (Shannon-Weaver H' index, log_2) for each survey varied from <1 to >4 and, unlike species richness, did not decreased with latitude (not shown). In general, diversity tended to associate with evenness values rather than with the number of species. However, a similar analysis performed on the tintinnids from the same samples of our study (Thompson, 2004) showed a strong southward decrease of both diversity (Shannon-Weaver H' index) and species richness.

Several historical, evolutionary and ecological mechanisms have been proposed to explain latitudinal gradients in species richness (e.g. Barton *et al.*, 2010; Chust *et al.*, 2012). For marine organisms, accumulated evidence identifies temperature as a useful environmental predictor of species richness in various groups of organisms (Rutherford *et al.*, 1999; Mittelbach *et al.*, 2007; Rombouts *et al.*, 2009). In our study, temperature ranged from ~−1 to 21°C and covaried significantly with species richness ($r = 0.44$; $P < 0.05$, Pearson's correlation coefficient). The temperature hypothesis postulates that, at higher temperatures, increased metabolic rates may promote higher rates of speciation (e.g. Mittelbach *et al.*, 2007), thus accounting, in part, for the greater species richness of the BMCZ. Nevertheless, a recent investigation attributes a minor role of temperature in affecting species richness distribution (Rodríguez-Ramos *et al.*, 2015).

Hydrological features have been found to play an important role in determining species richness (Clayton *et al.*, 2013). Due to the oceanographic features of the SWA, microplanktonic species richness in the BMCZ is likely enhanced by its complex hydrodynamics, which provides a high heterogeneity both in space and time as a result of processes operating at different spatio-temporal scales. The BMCZ is fed by water masses of different origin (Subtropical and Subantarctic), with contrasting physical, chemical and biological characteristics. This fact results in strong gradients and particular habitats, including restricted areas where algal growth is favored by local enhancements in the vertical stability of the water column, cyclonic and anticyclonic vortices, upwelling cells and cold and warm water tongues (Thompson, 2004). These features of the BMCZ favor a large, though ephemeral, regional pool of species which can account for the high diversity values observed at a local scale. The above-mentioned processes combine to support the high diversity associated in this region, as previously suggested (Barton *et al.*, 2010; Chust *et al.*, 2012; d'Ovidio *et al.*, 2010), maintained by the confluence of upstream populations, the associated supply of nutrients and the environmental variability associated with mesoscale eddies (Clayton *et al.*, 2013). Due to the transitional nature of the BMCZ, endemics are either absent or very scarce and local populations are mainly made up of expatriates from neighboring areas (Boltovskoy, 1998).

The ACC waters (~53°−58°S) that showed a slight increase in species richness hosts both several species restricted to it (e.g. *Rhizosolenia curvata*, *R. antarctica*, *R. chunii*) as well as others from different sources. It represents the southern limit for a number of temperate species (e.g. *Chaetoceros decipiens*, *Nitzschia bicapitata*, *N. sicula*, *Stephanopyxis turris*) and the northern limit of several cold-water species (e.g. *Chaetoceros castracanei*, *C. flexuosus*, *C. criophilus*, *Porosira pseudodenticulata*, *Fragilariopsis curta*).

The latitudinal gradient of diatom species richness at the level of biogeographic zones found in our study disagree with Hillebrand and Azovsky's postulate (e.g. Hillebrand and Azovsky, 2001; Rodríguez-Ramos *et al.*, 2015) that organisms with a small size and high dispersion capability do not exhibit latitudinal gradients in species richness. However, our results indicate that, although the latitudinal gradient of species richness may now be regarded as a paradigm in ecology (Gaston, 2000; Macpherson, 2002), such gradients may represent

a simplification of complex patterns influenced by a great number of factors that are overlooked in pursuit of generalization (Gaston, 2000). One of the factors affecting the intensity of these latitudinal gradients in the region of our study is the temporal change of the SWA circulation patterns. These changes occur from subseasonal to seasonal and interannual scales, impacting on the biological and environmental characteristics of the BMCZ and adjacent areas. For instance, the weaker latitudinal decrease in species richness in 1995, in comparison with the other two springs studied, was associated with differences in the hydrological regime that resulted in a water cooling process in this year (Olguín et al., 2015). These results suggest that the gradient may be stronger or weaker depending, for example, on the macroscale climatic and oceanographic prevailing conditions and, therefore, these conditions should be considered as a potential source of discrepancy among different studies on diatom latitudinal diversity gradients.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt. oxfordjournals.org.

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