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Phytoplankton and protozooplankton on the southern Patagonian shelf (Argentina, 47°–55°S) in late summer: Potentially toxic species and community assemblage structure linked to environmental features

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ABSTRACT

On the southern Patagonian shelf (Argentina, 47°–55°S) phyto- and protozooplankton are key structural and functional components of a complex trophic web that sustains commercially important species. During late summer 2004, spatial structure, assemblage species and their association with environmental characteristics of water masses were studied for the 2–200 µm phyto- and protozooplankton communities. Ultraplankton 2–5 µm was the most abundant size-fraction (90%), followed by the lower nanoplankton 5–10 µm (7.5%), the larger nanoplankton 10–20 µm (1.5%), and microplankton 20–200 µm (1%). Several of the 319 morpho-species found are potentially toxic taxa (the dinoflagellates *Alexandrium tamarense*, *Protoceratium reticulatum*, *Dinophysis acuminata*, *Prorocentrum cordatum*, *Karenia* and amphidomataceans and the diatom genus *Pseudo-nitzschia*), and this is important since the area sustains significant fisheries. A ultraphytoeukaryotic coccal cell (probably chlorophyte/prasinophyte) (3 µm), *P. cordatum*, and a microplankton naked ciliate were the morpho-species with the highest abundance and occurrence. Abundance and biodiversity patterns indicated that the plankton community structure was heterogeneous vertically, cross-shelf, and along-shelf, suggesting shifts in community structure over the region. Five areas with dissimilar plankton assemblages were defined, each corresponding to different environments. Depth, bathymetry, latitude and temperature were the most explanatory variables for the assemblage distribution patterns observed. This south Patagonian region possesses important fisheries and, considering expected environmental changes, our results help to understand the spatial structure of plankton communities over a broad size spectrum.

1. Introduction

Phytoplankton and protozooplankton have key functional and structural roles in marine environments, constituting the base of trophic webs and modulating marine biogeochemical cycles of bioactive elements (*e.g.*, Sherr and Sherr, 2002; Hirata et al., 2011). Phytoplankton represents a large proportion of primary production (Falkowski and Raven, 2007) that underpins marine food webs and regional fisheries (Rippeth, 2005). Protozooplankton, in turn, are a major consumer of primary production, and a central trophic link through the microbial loop (Azam et al., 1983; Sherr and Sherr, 2002; Calbet and Landry, 2004). The structure of phyto- and protozooplankton communities is a major biological factor modulating the functioning of pelagic food-webs and affecting carbon pathways (Legendre and Le Fèvre, 1991), including *in situ* recycling of organic matter, transfer to higher trophic levels, and/or sedimentation (Tremblay and Legendre, 1994). Phyto- and protozooplankton communities are often patchily distributed and structured in assemblages as a consequence of environmental changes (*e.g.*, Montes-Hugo et al., 2009). Correlating hydrographic regimes with each particular plankton size fraction is very valuable for evaluating

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and predicting trophic systems and phyto- and protozooplankton community structure.

Situated in the southwestern Atlantic Ocean from approximately 47°S to 55°S, the southern Patagonian shelf (SPS) is a recognized reference region for fisheries management, which sustains a vastly productive ecosystem (Bisbal, 1995; Lutz et al., 2010; Segura et al., 2013; Dogliotti et al., 2014). A triangular trophic web has been described for the SPS ecosystem (Ciancio et al., 2008, 2010), with commercially important fish and squid species near the top (Hansen et al., 2004; Sánchez and Bezzi, 2004). Phyto- and protozooplankton are at the base and, as they constitute the main food resource for larger plankton, they are essential trophic components (Antacli et al., 2014a, 2014b). Hydrographically, the SPS shows a unique combination of characteristics: high tidal amplitudes, prevalent westerly winds, large freshwater inflows, and advection from the bordering Malvinas Current (Palma et al., 2008; Matano et al., 2010; Palma and Matano, 2012). Another important hydrographic feature of the SPS is the presence of three water masses defined by salinity: 1- Malvinas Water, characterized by salinities of 33.8–34.2 PSU, 2- Coastal Water, with < 33.2 PSU, and 3- Shelf Water, produced by the mixing of the other two, with salinities of 33.2–33.8 PSU (Bianchi et al., 1982). All these characteristics generate a complex circulation system and cross-shelf exchanges, along with fronts of diverse nature (Acha et al., 2004; Sabatini et al., 2004; Belkin et al., 2009). This complex hydrography determines habitat heterogeneity for plankton communities, mainly in terms of nutrients and food availability (Stemmann and Boss, 2012; Wilkins et al., 2013).

Harmful plankton microalgae blooms can influence marine ecosystems and cause structural and trophic changes in natural food webs, which harm fish and shellfish stocks and could lead to animal mortality, and endanger human health from consuming contaminated shellfish (Hallegraeff, 1995). Several dinoflagellates and diatoms have been identified in southern Patagonia as potential producers of toxins (Krock et al., 2018, and references therein). Among these are the dinoflagellates *Alexandrium tamarense* and *A. catenella*, which synthesize paralytic shellfish poisoning (PSP) toxins (*e.g.*, Benavides et al., 1995; Carreto et al., 1998; Santinelli et al., 2002; Fabro et al., 2017), *Protoceratium reticulatum*, which synthesize yessotoxins (YTX) (Akselman et al., 2015), and *Dinophysis acuminata*, whose toxins cause diarrhetic shellfish poisoning (DSP) (Krock et al., 2015), and diatoms of the genus *Pseudo-nitzschia*, which produce the amnesic shellfish poisoning toxin, domoic acid (DA) (Almandoz, 2011; Krock et al., 2015). *Prorocentrum cordatum* (*Prorocentrum minimum* (Pav.) Schiller) is another potentially toxic dinoflagellate (Grzebyk et al., 1997) that sometimes forms monospecific blooms (Gómez et al., 2011; Sabatini et al., 2012). The most significant harmful effects are caused by PSP toxins produced by *A. tamarense*, which affects shellfish resources and causes temporary fishing bans in coastal areas. The attention focused on harmful microalgae is thus important since, besides shellfish, phycotoxins can also affect fishery resources of the region.

Studies of the phytoplankton communities and of chlorophyll-a variability largely encompassing the southern Patagonian shelf have been based on the analysis of remote sensing data (Rivas et al., 2006; Romero et al., 2006; Gonzalez-Silvera et al., 2006; Signorini et al., 2006; D'Ovidio et al., 2010; Dogliotti et al., 2014), and other studies have focused on the phyto- and protozooplankton communities with *in situ* sampling for composition analysis (Garcia et al., 2008; Painter et al., 2010; Santoferrara and Alder, 2009a, 2009b, 2012; Santoferrara et al., 2011; De Souza et al., 2012; Sabatini et al., 2012; Segura et al., 2013; Balch et al., 2014; Gonçalves-Araujo et al., 2016; Antacli et al., 2014b). These show seasonal variation of phytoplankton in the SPS, which has been related to light intensity, nutrient supply, mixed layer depth, stratification and/or the thermohaline structure of the water column. In general, spring communities in the region show high biomasses dominated by diatoms in an environment of high nutrient availability and low stratification, in contrast to early summer communities, which have low biomasses dominated by coccolithophorids and other haptophytes, associated with low nutrient concentration, high stratification of the water column and shallower mixed depth layers. Nevertheless, despite the recognized importance of these communities in the SPS area, their taxonomy, diversity patterns and community structure with their broad size spectrum have received little detailed attention in comparison to other sea-shelf areas.

In a previous study, the 2–200 µm phytoplankton and protozooplankton communities were broadly assessed in the SPS during late summer 2004, but focusing on their potential trophic availability for copepods (Antacli et al., 2014b). Based on the same pool of data, the present work aims to make the first comprehensive assessment of the 2–200 µm phyto- and protozooplankton communities of the SPS in late summer in terms of taxonomy, biodiversity, presence of potentially toxic species, spatial structure (including vertical distribution through depth strata), and their linkage to hydrographic conditions. We hypothesize that the spatial heterogeneity of the environment across the shelf (*i.e.*, characteristic of water masses and fronts between the prevailing major currents) exerts a predominant influence on plankton distribution, driving distinct phyto- and protozooplankton assemblages, by influencing their composition, diversity, and abundance. The differential degrees of the thermocline along the shelf may produce dissimilar habitats for plankton. Specifically, we aim to (1) describe the abundance, composition, biodiversity, and spatial distribution patterns of 2–200 µm phyto- and protozooplankton communities, (2) provide information on toxigenic species already registered in the area and on new records of other potentially harmful taxa, (3) determine cross-shelf, along-shelf and vertical differences in plankton abundance and diversity, (4) define the 2–200 µm phyto- and protozooplankton assemblages, and (5) identify their association with environmental characteristics of the water masses. These observations are interpreted in terms of the physical characteristics of water masses to assess the strength of environmental control of phyto- and protozooplankton communities.

2. Material and methods

2.1. Sampling

The study area covered the continental shelf off southern Patagonia (Argentina) from *ca.* 47° to 55°S. Data were collected in late summer (from 18 March to 2 April 2004) onboard RV "Dr. E. L. Holmberg". Sampling was conducted along four sections covering different hydrological areas across the shelf: (1) off Puerto Deseado (PD) at *ca.* 47°S, (2) off San Francisco de Paula (SFP) at *ca.* 49°S, (3) in the Grande Bay (GB) at 51°S, and (4) off Magallanes (or Magellan) Strait (Mag) at *ca.* 53°S (Fig. 1).

At all oceanographic stations ($N = 99$), continuous profiles of temperature, salinity and fluorometry were recorded using a Sea-Bird 9–11 CTD, and a Sea-Tech fluorometer mounted onto the CTD. Niskin bottles were utilized to collect samples at 18 stations for the analysis of the 2–200 µm phyto- and protozooplankton communities (Fig. 1). Three discrete depths were sampled by station, based on the fluorometric profile, at surface ('S'), maximum *in situ* fluorescence (first depth level at *ca.* 10–25 m, 'D1'), and below at a selected depth (second depth level at *ca.* 25–65 m, 'D2'). Samples were preserved with 25% glutaraldehyde, 0.3% final concentration, to ensure optimal preservation of naked organisms, such as athecate dinoflagellates and aloricate ciliates.

2.2. Assessment of plankton communities

The composition, abundance and spatial distribution of the plankton 2–200 µm were estimated by microscopy according to Utermöhl (1958) and Hasle (1978). Particles in the size range 2–10 µm and > 10–200 µm were counted with an inverted microscope (Olympus IX 70) equipped with epifluorescence and interference differential contrast at 1000× and 200× magnification, respectively, after

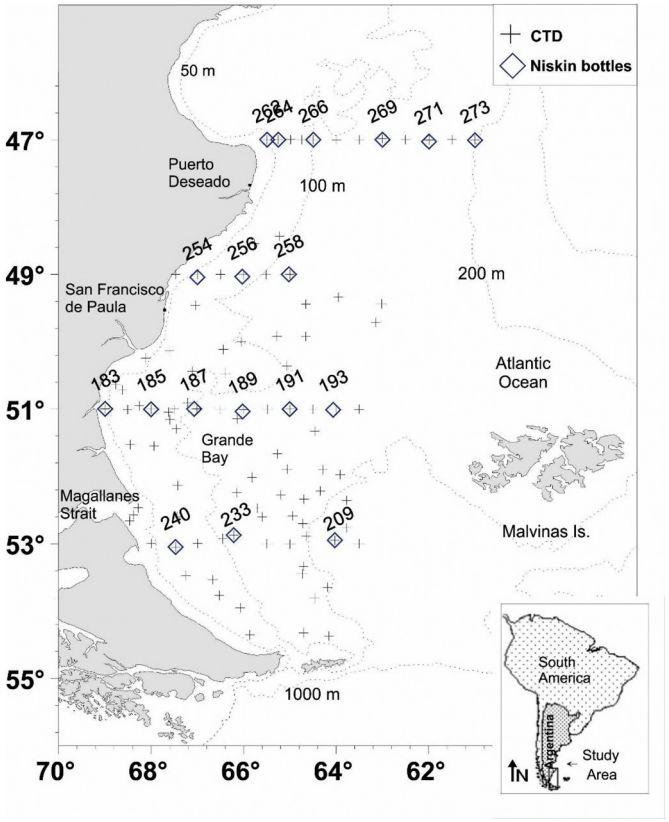

Fig. 1. Oceanographic (crosses: CTD) and plankton (diamonds: Niskin bottles) sampling stations on the southern Patagonian shelf during cruise EH-03/04 in late summer March/April 2004 onboard RV Dr. E.L Holmberg.

sedimentation in 100 mL chambers during at least 48 h to ensure smaller organism precipitation. Cell counts were performed across either the entire, a half or a quarter of the chamber surface depending on sample concentration. Between 250 and 300 cells in the size range 2–200 µm were counted on average for each sample (Venrick, 1978; Edler and Elbrächter, 2010). Organisms were photographed with a digital camera (Olympus DP 71) fitted to the microscope and measured with image analysis software (Image Pro Plus v.6.0). Plankton communities were classified by size (ultraplankton 2–5 µm, small size-fraction of nanoplankton > 5–10 µm, large size-fraction of nanoplankton > 10–20 µm, and microplankton > 20–200 µm) and trophic category (autotrophs and heterotrophs). Organisms not identified taxonomically to species or genus level but recognized as different morphotypes within a group were named with the highest identified taxonomic group accompanied with the abbreviated form of species "sp." and an ordinal number (*e.g.* ciliate sp. 1, ciliate sp. 2). Trophic sorting was based on taxonomic identification and trophic modality reported in the literature for a given taxon. Mixotrophs were not classified separately since experimental procedures with labeled prey are needed for their accurate estimation. Therefore, although some ciliates are known as obligate mixotrophs or functional autotrophs, in this study we have grouped them under the canonical criterion that considers this taxonomic group as heterotrophic.

2.3. Data analysis

2.3.1. Stratification calculation

The extension of either mixed or stratified areas over the shelf was examined through the Simpson stability parameter (Simpson, 1981). It was derived from vertical profiles of density at 1 m depth intervals. The relative contribution of freshwater to the stratification of the water column was additionally estimated by modifying Simpson's equation after Gowen et al. (1995):

$$\Phi s = g\,h - h \int 0\,(\rho' - \rho'0)\,z\,dz$$

where ρ′ is the density at depth z calculated using observed salinity and the mean temperature of the water column.

2.3.2. Phyto- and protozooplankton community structure

The relative abundance (*RA* %), *i.e.* the average contribution of each species/morpho-species to the total abundance, and the frequency of occurrence (*FO* %), *i.e.* the number of samples of a given species/morpho-species occurring in relation to the total number of samples, were calculated.

Spatial distribution of the phyto- and protozooplankton assemblages was examined through multivariate analyses using the PRIMER v.6.1 software package (Clarke and Gorley, 2006) (Primer-E). The initial matrix was composed of all the species/morpho-species identified ($N = 319$), even the rare taxa (*i.e.* those with low relative abundance and low frequency of occurrence) (Clarke and Warwick, 2001), and 54 samples (18 stations, 3 depths each). The abundance data (x_i) for each species/morpho-species (i) were transformed ($x_i' = \log(x_i + 1)$) to reduce the influence of the most-abundant species/morpho-species. The Bray-Curtis similarity measure was calculated and a similarity matrix was then produced from the logarithms of the abundance data. Then, a one-way analysis of similarity (ANOSIM, Clarke and Warwick, 2001) was used to test for differences in the plankton community structures among the following factors considered *a priori*: (1) four latitudinal sections (PD, SFP, GB, and Mag), (2) two bathymetric areas (inner shelf: ≥50–100, and mid-shelf: ≥100–200 m), and (3) three depths (S, D1 and D2). ANOSIM is analogous to one-way ANOVA and based on the statistic *R*, which quantifies the distinctions among the groups (Clarke and Warwick, 2001; Clarke and Gorley, 2006).

2.3.3. Biodiversity

Diversity across samples was compared by calculating the Margalef's species richness index *d* (Margalef, 1977), the Shannon-Wiener diversity index *H′* (Ludwig and Reynolds, 1988), and Pielou's species evenness index *J′* (Pielou, 1975) with the PRIMER v.6.1 software. To analyze the taxonomic relatedness of different taxa in the assemblages, the average taxonomic diversity (Δ) and the average taxonomic distinctness (Δ*) were calculated (Clarke and Warwick, 1995, 1998), following Guiry and Guiry (2018) and the World Register of Marine Species (WoRMS Editorial Board, 2018). Individuals identified to different taxonomic levels (species, genera, family, order, class, subphylum, phylum, kingdom, and empire) were weighted progressively (from 1 to 9 respectively), to put more weight in the shorter branch lengths between species (Clarke and Warwick, 1999).

The existence of differences in the phyto- and protozooplankton diversity patterns through depth strata was explored with Friedman's ANOVA followed by Bonferroni's non-parametric multiple *post-hoc* test; shifts across latitudes and bathymetric areas were both explored through a Kruskal-Wallis ANOVA and Dunn's non-parametric multiple *post-hoc* test (Zar, 1996; Statistica v.8 software package). The factors considered *a priori* were the 4 latitudinal sections, the 2 bathymetric areas and the 3 depths previously stated. The null hypothesis, that no changes in diversity indices were observed between those regions, was tested.

2.3.4. Phyto- and protozooplankton spatial structure in relation to environmental variables

To define the species/morpho-species group profile and to analyze the links between the spatial distribution of those groups and the environmental variables, a multivariate regression tree (MRT) analysis was performed (tree selection by cross-validation using "min", predictive accuracy estimated from cross-validated relative error [CVRE]) (Death, 2002; Borcard et al., 2011). The analysis was carried out using

the biological and environmental data collected in all the samples ($N = 54$). The environmental variables considered were temperature, salinity, density (sigma-t), sampling depth, latitude and longitude. The MRT analysis used the *mvpart* packages of the R statistical software (R Development Core Team, 2011).

Diversity was also compared across the groups derived from the MRT analysis, by calculating the biodiversity indices (*S, d, H′, J′, Δ, Δ**) (see the *Biodiversity* section for details). Then, to test for differences in diversity amongst those groups, a permutation test was performed followed by Bonferroni's non-parametric multiple *post-hoc* test (Zar, 1996), using the R Statistical software (R Development Core Team, 2011).

To identify the species/morpho-species that typified and discriminated the plankton assemblage areas derived from the MRT analysis, a similarity percentage routine (SIMPER, Clarke and Warwick, 2001) was applied to the log-transformed abundance values using the PRIMER v.6.1. Based on the analysis of the Bray-Curtis similarity matrices derived from sample-species compositions, the SIMPER method examines the contribution of species to the total average similarity within each region. In this study, common species were those contributing to the top 70% of average similarity within each region, and discriminatory were those contributing to the top 50% of dissimilarity between regions and having a low ratio of average dissimilarity to its standard deviation (Clarke and Warwick, 2001).

3. Results

3.1. Hydrographic conditions

The temperature fields in the area during the period of this study were reported by Antacli et al. (2014b). In summary, surface temperature decreased gradually with latitude, ranging from 14.5 °C in the northern area to 8.4 °C in the southern area (Fig. 2A, B). A two-layer system separated by a strong thermocline at 40–50 m depth was identified in the water column northern of ca. 52°S, while to the south, the vertical structure was almost isothermal (Fig. 2C–F).

Surface and bottom salinity over the study area increased from coastal waters to the slope, ranging 28.5–33.7 and 32.5–34.2, respectively, in accordance with the three water masses typically identified in the study area (Fig. 2G, H). The marked low salinity values registered inshore extended even to zones relatively distant from the coast. The lowest surface salinity values (< 32) were registered at *ca.* 50°–51°S while the highest values (≥34) were at the deepest stations at *ca.* 52°–53°S. The vertical structure of salinity was relatively homogeneous (Fig. 2I–L).

Density values (sigma-t) ranged 21.6–26.1 at the surface and 24.5–27 at the bottom (Fig. 2M, N). Just as salinity made it possible to characterize water masses, vertical sections showing isotherms and isopycnals with similar patterns indicated that density fields were dominated by temperature. The sigma-t vertical profiles revealed the transition of well-mixed waters near the coast toward stratified waters on the mid-shelf. Stratification gradually decreased southwards, disappearing completely at ca. 53°S (Fig. 2O–R).

Two dynamically different regions were identified based on the distribution of water column stability (Simpson parameter Φ) (Fig. 3). They were separated in general by the isoline of $\Phi = 150\ J\ m^{-3}$. One region was located to the north of *ca.* 52°S, where relatively higher values of the Simpson parameter were recorded, corresponding to stratify and more stable waters. In particular, two strongly stratified sectors were identified in this northern region: in the coastal zone at 50°–51°S ($\Phi > 180\ J\ m^{-3}$), probably related to the fresh water from the Santa Cruz River (mostly saline stratification), and on the mid-shelf in the PD section, due to the high solar radiation warming surface layers (mostly thermal stratification). In general terms, water column stability north of *ca.* 52°S increased from the coast to the mid-shelf as a result of thermal stratification. This gradient is due to the effect of the tides, which homogenize the water column by friction with the bottom, increasing near the coast due to the shallow depth, and wind stress (see Discussion). In contrast, to the south of *ca.* 52°S, the water column was less stable and vertically less homogeneous, as seen in the relatively lower values of the Simpson parameter ($\Phi \leq 40\ J\ m^{-3}$). Coastal waters to the south of 52°S were strongly mixed, while shelf waters were relatively more stratified due to the influence of subantarctic waters that enter the region from the west of the Burdwood Bank.

3.2. Phyto- and protozooplankton community structure

Phyto- and protozooplankton assemblages showed a high numerical dominance of ultraplankton cells over the entire study area, contrasting with the markedly lower numbers recorded for the nano- and microplankton size fractions. A total of 319 species/morpho-species were found belonging to ten taxonomic groups, the most common being dinoflagellates (148 species/morpho-species present in 36% of the 54 samples), followed by diatoms (74 species/morpho-species; 22%) and ciliates (55 species/morpho-species; 21%) (Table 1). Chlorophytes, haptophytes, cryptophytes, chrysophytes, euglenophytes, heliozoans and silicoflagellates were rare groups present in 1–5% of the sampling stations, although some of them reached high abundance.

The spatial distribution and abundance of phyto- and protozooplankton by size-fractions and the average relative abundance of major groups for each section has been shown in Antacli et al. (2014b), see Fig. 4). The composition and abundance of 2–200 μm plankton communities were analyzed by their dimensions, *i.e.* 2–5 μm, > 5–10 μm, > 10–20 μm, and > 20–200, and their trophic condition, *i.e.* autotrophs and heterotrophs (Table 1). The 2–5 μm size fraction comprised diatoms, haptophytes, cryptophytes, chrysophytes, euglenophytes and silicoflagellates, in decreasing order of numerical predominance, headed by a coccal ultraphytoeukaryotic cell (3 μm) (probably chlorophyte/prasinophyte), which was the most important morpho-species in the region (frequency of occurrence $FO = 35\%$, relative abundance $RA = 45\%$). Ultraplankton were distributed all over the study area with higher abundance in surface waters and in the first sampled depth at the maximum fluorescence level, with minor cell concentrations in the southern Mag section (Fig. 4A,B,C). Their highest abundance (4×10^6 cells L^{-1}) was recorded in the inner- and mid-shelf areas of GB, where there were high concentrations of coccal ultraphytoeukaryotic cells at St. 185, 187 and 189 at the surface but especially at the maximum fluorescence level, with up to 2.1×10^6 cells L^{-1}, and diatoms were markedly abundant (Fig. 4A, B). Diatoms were distributed in patches, mostly concentrated at St. 189 in GB, St. 256 in SFP and at St. 269 in PD sections with up to 1.5×10^6 cells L^{-1} (Fig. 4A, B, C). Ultraphytoplankton were markedly more abundant than the heterotrophic part of the 2–5 μm fraction (respective average abundances = 4×10^5 cells L^{-1} and 4×10^3 cells L^{-1}).

Dinoflagellates, diatoms, ciliates, cryptophytes and euglenophytes built up the smaller nanoplankton (> 5–10 μm) size fraction, together with other unidentified heterotrophic and autotrophic taxa. Their maximum abundance was recorded mainly in surface waters and secondarily at the first sampled depth, at the outer-shelf stations of the PD section, with concentrations up to 5×10^5 cells L^{-1} (St. 271) (Fig. 4D, E, F). Autotrophic and heterotrophic groups of the > 5–10 μm size fraction presented similar concentrations (average abundance = 2×10^4 cells L^{-1} in both categories).

The larger nanoplankton (> 10–20 μm) size fraction had relatively low abundance in comparison to the other size groups (up to ~2×10^4 cells L^{-1}) (Fig. 4G, H, I). Its distribution pattern showed lower cell concentrations in the southern Mag section and at the sampling depth below the maximum fluorescence level. There were relatively higher numbers of heterotrophic dinoflagellates in the GB (St. 191, 193) and PD (St. 266, 271) sections, as well as euglenophytes and other phytoflagellates in these same sections (St. 191, 193 and 266, 273, respectively). Photosynthetic and heterotrophic nanoplankton of the >

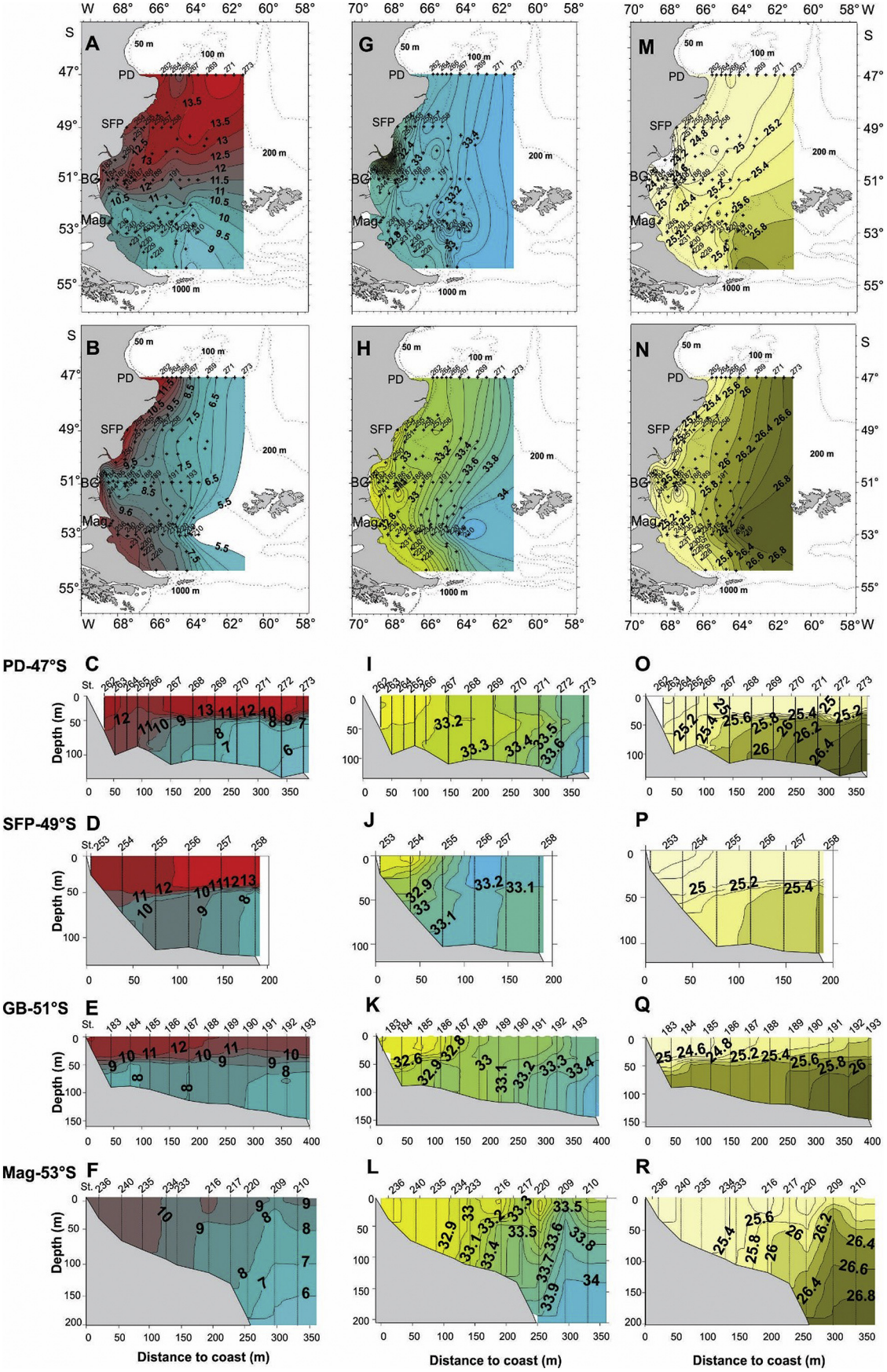

Fig. 2. Temperature (°C) (A–F), salinity (G–L), and density (sigma-t) (M-R) fields on the Southern Patagonian shelf during the March/April 2004 cruise. Surface (A, G, M), bottom (B, H, N), and average vertical distribution values along Puerto Deseado-47°S (C, I, O), San Francisco de Paula-49°S (D, J, P), Grande Bay-51°S (E, K,Q) and Magellan Strait-53°S (F, L, R) transects.

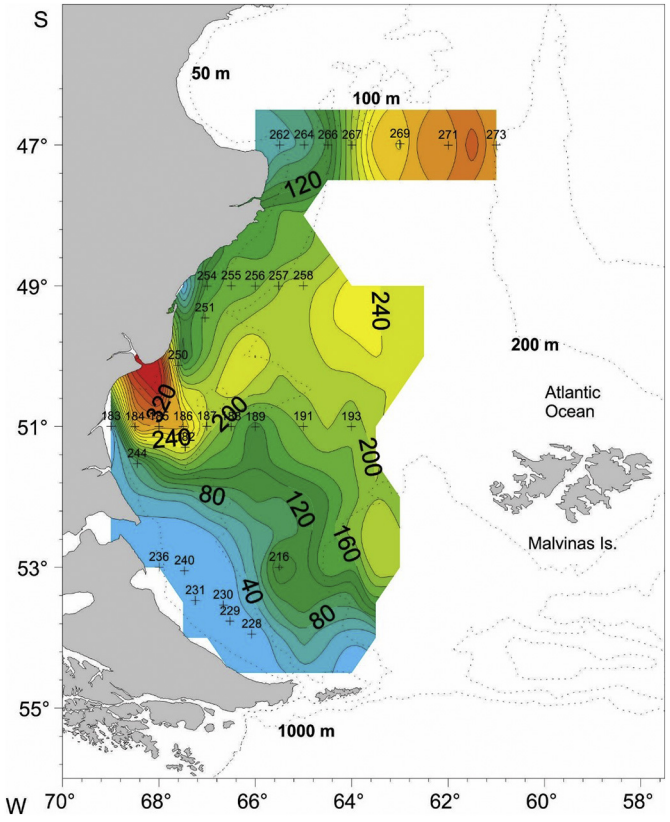

Fig. 3. Simpson stability parameter on the Southern Patagonian shelf during the March/April 2004 cruise.

10–20 µm size fraction presented similar concentrations (average abundance for both trophic categories: $=2 \times 10^3$ cells L^{-1}).

The microplankton (> 20–200 µm) size fraction also showed a generally low abundance, with the exception of some middle shelf and coastal sectors of the PD section where a maximum of $\sim 2 \times 10^5$ cells L^{-1} was recorded (Fig. 4K, St. 266). Similar to other size fractions, their highest values were recorded at the surface and at the maximum fluorescence level as well as in the PD, SFP and GB sections (Fig. 4J, K, L). Autotrophic microplankton showed triple the abundance of the heterotrophic fraction (respective average abundances, 9×10^3 cells L^{-1} and 3×10^3 cells L^{-1}).

Within the larger nanoplankton and microplankton, dinoflagellates and diatoms were respectively the most important autotrophic groups, followed by a miscellanea of euglenophytes, silicoflagellates, haptophytes and cryptophytes among other unidentified phytoflagellates, while dinoflagellates, and aloricate and loricate ciliates, including mixotrophic and functional autotrophic ciliates, showed the highest concentrations among the heterotrophic groups (Table 1). Diatoms had a patchy distribution. *Rhizosolenia setigera* was the only microplankton species with relatively high abundance (up to 1.3×10^5 cells L^{-1} in the water column), causing an exceptional bloom in a restricted area of mid-shelf waters (Fig. 4J, St. 266) (*RA* = 1.4%; *FO* = 18.5%). Other diatoms, *Pseudo-nitzschia* spp., *Dactyliosolen fragilissimus*, *Guinardia delicatula* and *Thalassiosira decipiens*, were relatively important in coastal and inner shelf stations in the PD and GB sections (St. 262, 183). The photosynthetic dinoflagellate, *Prorocentrum cordatum,* was frequently recorded throughout the region but usually in low numbers, being the second most important species in the entire region (*FO* = 56%; *RA* = 0.2%) after the coccal ultraphytoeukaryotic cell. Unidentified heterotrophic and thin-walled dinoflagellates, as well as euglenophytes and other phytoflagellates, contributed in number to the somewhat higher abundance recorded in GB (St. 191, 193) and PD (St. 266, 271, 273). The non-photosynthetic genus *Protoperidinium* showed low abundance ($< 0.3 \times 10^3$ cells L^{-1}, max. 1×10^3 cells L^{-1}), but was present with more than a dozen species (Table 1), *P. bispinum* occurring most frequently (*FO* = 22.2%; *RA* = 0.03%). Taxa of interest were found belonging to other autotrophic groups: *Phaeocystis* colonies (at surface, St. 264), *Emiliania huxleyi* and other unidentified coccolithophorides (frequent in the entire area), and phycoma stages of *Pterosperma* spp. among chlorophytes (registered at several stations).

A total of 51 ciliate taxa, including tintinnids, aloricate and naked ciliates, were recorded, among which *Strombidium* and *Tintinnopsis* were the most important genera by number of morpho-species (Table 1). Different trophic categories were present in the nano- and microplankton size fractions: heterotrophic naked ciliates and tintinnids, the mixotrophs *Laboea strobila* and *Strombidium* spp., and the functional autotrophs *Mesodinium rubrum* and *Mesodinium* spp. Ciliates were widely distributed, with presence in the four latitudinal sections but generally in low abundance ($< 1 \times 10^3$ cells L^{-1}) with higher concentrations at levels of maximum fluorescence. However, high densities of an unidentified naked heterotrophic species (3.2×10^4 cells L^{-1}) and a species of the aloricate *Strombidium* (1.25×10^4 cells L^{-1}) were recorded at 15 m depth in the northern PD section (St 271). This peak number of ciliates was restricted to a single location, which also showed minor abundances of naked heterotrophic ciliates as well as of L. *strobila* and other species of *Strombidium*. In particular, a naked unidentified nanoplankton ciliate (ciliate sp. 17, Table 5) was the third most important species in the region (*FO* = 52%; *RA* = 0.1%) after the coccal ultraphytoeukaryotic and *P. cordatum*. An unidentified aloricate ciliate (ciliate sp. 2, Table 5) was fourth in importance in the region for its relatively high occurrence (*FO* = 38%).

Several morpho-species stood out in the microplankton size fraction for different reasons. The dinoflagellate *Prorocentrum vaginula* (Fig. 5A–C; Appendix A) was recorded for the first time in the southwestern Atlantic Ocean. A mass encystment of a dinoflagellate possibly belonging to the genus *Protoperidinium* (Fig. 5D-F) was recorded in a restricted area of the PD section (St. 266) at high abundances (up to 4.5×10^3 cysts L^{-1} at the maximum fluorescence depth) throughout the sampled water column. Living resting cysts of the dinoflagellates *Polykrikos schwartzii* and *Scrippsiella patagonica* were recorded only at this same station (St. 266), although with markedly low densities (*ca.* 100 cysts L^{-1}). Despite the wide spatial distribution of *P. schwartzii* vegetative cells, a simultaneous presence with its resting cysts was observed only at St. 266. Resting cysts of the mass-encysted unidentified *Protoperidinium* species and those of *P. schwartzii* were also observed in fecal zooplankton pellets (Fig. 5F). Living resting cysts of the dinoflagellate *Protoceratium reticulatum* were recorded at St. 256 (*ca.* 100 cysts L^{-1}).

Potentially toxic species were present in the > 10–200 µm size fraction communities, with the dinoflagellates *Alexandrium tamarense*, *Protoceratium reticulatum, Dinophysis acuminata*, *Prorocentrum cordatum* and species of *Karenia* and amphidomataceans, and diatoms of the genus *Pseudo-nitzschia*. *A. tamarense*, a well known PSP toxins producer in the Argentine sea, showed wide spatial distribution, encompassing nearshore and mid-shelf areas, and reached > 200 m depth in the southern Mag section (Fig. 6). With low abundance (≤ 200 cells L^{-1}) in most stations, the maximum density (1.8×10^3 cells L^{-1}) of *A. tamarense* was in coastal waters (St. 254). All analyzed cells corresponded morphologically to the "tamarense" phenotype; the compressed "catenella" phenotype, including chained cells, was not observed. The motile stage of *P. reticulatum*, a YTX producer, was present in low densities (< 100 cells L^{-1}) in coastal and mid-shelf sectors of the northern area (Fig. 6). Its resting cysts at different stages of development as well as cysts of apparently recent formation were recorded at a station (St. 256) where the abundance of the motile stage was somewhat greater (600 cells L^{-1}). *D. acuminata*, which produces diarrhetic shellfish poisoning (DSP) toxins, had a wide spatial distribution from near coastal to mid-shelf waters and at depths > 200 m (Fig. 6). We recorded the two morphological varieties described for this region, *D. acuminata* var.

Table 1
List of phytoplankton and protozooplankton 2–200 μm taxa registered over the southern Patagonian shelf during late summer 2004 onboard cruise EH-03/04.

Diatoms	Dinoflagellates
Actinoptychus senarius (Ehrenberg) Ehrenberg	*Alexandrium tamarense* (Lebour) Balech
Asterionellopsis glacialis (Castracane) Round	*Amphidinium* sp.
Asteromphalus sarcophagus Wallich	*Amphidomataceae* spp.
Cerataulina sp.	*Cochlodinium* sp.
Ceratoneis closterium Ehrenberg	*Dinophysis acuminata* Claparède & Lachmann
Chaetoceros didymus Ehrenberg	*Dinophysis schroederi* Pavillard
Chaetoceros spp.	*Dinophysis truncata* Cleve
Corethron pennatum (Grunow) Ostenfeld	*Dinophysis* spp.
Coscinodiscus spp.	*Diplopelta pusilla* Balech & Akselman
Dactyliosolen fragilissimus (Bergon) Hasle	Gymnodiniales spp.
Ditylum brightwelli (T. West) Grunow	*Gyrodinium fusus* (Meunier) Akselman
Eucampia zodiacus Ehrenberg	*Gyrodinium spirale* (Bergh) Kofoid & Swezy
Fragilariopsis spp.	*Heterocapsa triquetra* (Ehrenberg) Stein
Guinardia delicatula (Cleve) Hasle	*Heterocapsa* sp.
Gyrosigma sp.	*Karenia* spp.
Helicotheca tamesis (Shrubsole) M.Ricard	*Oblea baculifera* Balech ex Loeblich Jr. & Loeblich III
Hyalodiscus scoticus (Kützing) Grunow	*Oxytoxum gracile* Schiller
Leptocylindrus minimus Gran	*Oxytoxum* spp.
Melosira moniliformis (Müller) Agardh	Peridiniales spp.
Meuniera membranacea (Cleve) P.C. Silva	*Phalacroma scrobiculatum* (Balech) Díaz-Ramos & G.J. Estrella
Nitzschia longissima (Brébisson) Ralfs	*Polykrikos schwartzii* Bütschli
Paralia sulcata (Ehrenberg) Cleve	*Polykrikos* spp.
Phaeodactylum sp.	*Preperidinium meunieri* (Pavillard) Elbrächter
Pleurosigma normanii Ralfs	*Prorocentrum micans* Ehrenberg
Pseudo-nitzschia spp.	*Prorocentrum cordatum* (Ostenfeld) J.D.Dodge
Rhizosolenia setigera Brightwell	*Prorocentrum vaginula* (F.Stein) J.D.Dodge
Rhizosolenia styliformis Brightwell	*Prorocentrum* spp.
Thalassionema nitzschioides (Grunow) Mereschkowsky	*Protoceratium reticulatum* (Claparède & Lachmann) Bütschli
Thalassiosira decipiens (Grunow ex Van Heurck) E.G.Jørgensen	*Protoperidinium aspidiotum* (Balech) Balech
Thalassiosira spp.	*Protoperidinium bispinum* (Schiller) Balech
Triceratium sp.	*Protoperidinium capurroi* (Balech) Balech
Tryblionella coarctata (Grunow) D.G.Mann	*Protoperidinium cassum* var. *decens* (Balech) Balech
Non-identified centric diatoms	*Protoperidinium conicoides* (Paulsen) Balech
Non-identified pennate diatoms	*Protoperidinium depressum* (Bailey) Balech
	Protoperidinium divaricatum (Meunier) Parke & Dodge
Ciliates and heterotrophs	*Protoperidinium excentricum* (Paulsen) Balech
Amphorides quadrilineata (Claparède & Lachmann)	*Protoperidinium mastophorum* (Balech) Balech
Amphorellopsis sp.	*Protoperidinium obtusum* (Karsten) Parke & Dodge
Cymatocylis sp.	*Protoperidinium pentagonum* (Gran) Balech
Eutintinnus sp.	*Protoperidinium pyriforme* (Paulsen) Balech
Favella ehrenbergii (Claparède & Lachmann) Jörgensen	*Protoperidinium* spp.
Laboea strobila Lohmann	*Scrippsiella acuminata* (Ehrenberg) Kretschmann, Elbrächter, Zinssmeister, S.Soehner, Kirsch, Kusber & Gottschling
Leucocryptos sp.	*Scrippsiella patagonica* Akselman & Keupp
Mesodinium rubrum Lohmann	*Scrippsiella* spp.
Mesodinium sp.	*Torodinium robustum* Kofoid & Swezy
Paulinella ovalis (A.Wulff) P.W.Johnson, P.E.Hargraves & J.M.Sieburth	*Tripos lineatus* (Ehrenberg) F.Gómez
	Tripos fusus (Ehrenberg) F. Gómez
Strombidium spp.	Non-identified non-photosynthetic dinoflagellates
Telonema sp.	Non-identified photosynthetic dinoflagellates
Tintinnopsis spp.	Other autotrophs
Xystonella sp.	*Dinobryon* sp.
Heliozoa sp.	*Distephanus speculum* (Ehrenberg) Haeckel
Non-photosynthetic flagellates	*Emiliania huxleyi* (Lohmann) W.W.Hay & H.P.Mohler
Non-identified choanoflagellates	*Nephroselmis* sp.
Non-identified ciliates	*Ollicola vangoorii* (W.Conrad) Vørs
Non-identified heterotrophs	*Pelagocystis oceanica* Lohmann
	Phaeocystis sp.
	Pseudoscourfieldia marina (J.Throndsen) Manton
	Pterosperma cristatum Schiller
	Pterosperma sp.
	Pyramimonas sp.
	Non-identified coccolithoporides
	Non-identified cryptophytes
	Non-identified euglenophytes
	Non-identified haptophytes
	Non-identified phytoflagellates
	Non-identified photosynthetic coccoid cells
	Non-identified photosynthetic flagellates

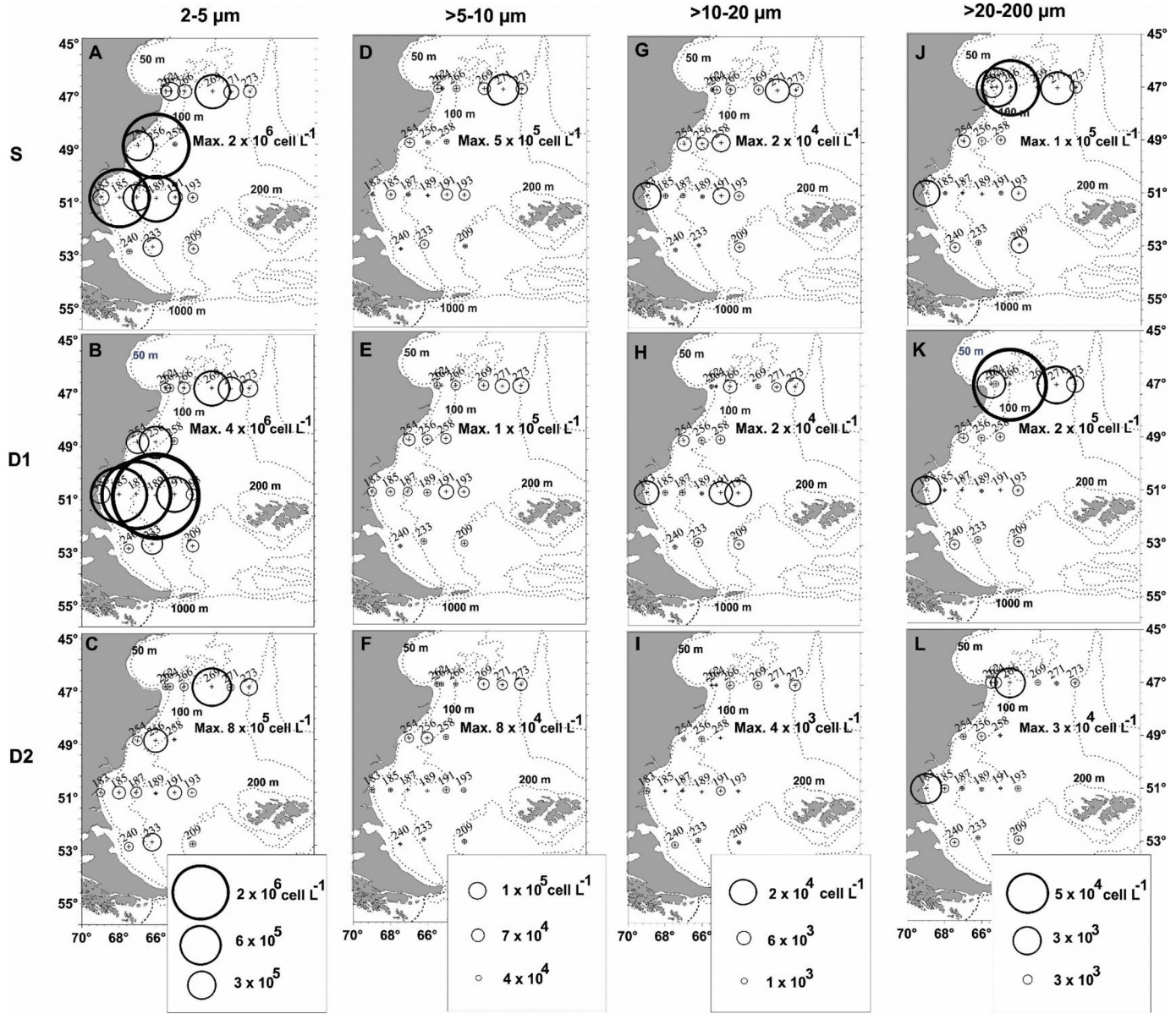

Fig. 4. Spatial distribution and abundance of plankton communities 2–200 µm by size fraction and depth stratum. Surface (A, D, G, J); first depth stratum/ca. 10–25 m (B, E, H, K); second depth stratum/ca. 25–65 m (C, F, I, L). Maximal abundance values are indicated for each case.

acuminata and *D. acuminata* var. *lachmanni* (Balech, 1988), which both had low densities (≤100 cells L^{-1}). *P. cordatum*, a potentially toxic dinoflagellate, also had an extense spatial distribution (Fig. 6). Its density was usually low (≤400 cells L^{-1}) with some higher values (up to 2500 cells L^{-1}) in the northern PD section. Three species of the genus *Karenia* were registered of different morphology and dimensions, but no conclusive identifications could be made. Nevertheless, a species which matched descriptions of the toxigenic *K. mikimotoi* was present in the southeastern area of the cruise (St. 193, 209). *Karenia* spp. were present in a wide area of coastal (St. 262) and mid-shelf waters (St. 187, 189, 191, 193), and at depths > 200 m in the southeastern area (St. 209). *Karenia* cf. *mikimotoi* showed densities of up to 3400 cells L^{-1} at surface and upper levels of the water column, but the other species had lower values (< 100 cells L^{-1}).

Azaspiracid toxins (AZA) are responsible for the most recent shellfish poisoning syndromes and are produced by some species of the family Amphidomataceae. Several members of Amphidomataceae have been recorded in this study but, as features distinguishing genera and species are difficult to examine under light microscopy, we grouped them together. Different morphologies at a range of longitudes of 10–20 µm (with and without an antapical spine) were observed at low total abundances not above 1×10^3 cells L^{-1}. As a whole, amphidomataceans showed a wide spatial distribution and were present in PD (St. 269, 271, 273), SFP (St. 254, 256, 258), GB (St. 187, 193) and Mag (St. 209, 233) sections, in samples collected at the three sampling depths. *Pseudo-nitzschia* is a genus that includes some species known to produce the DA toxin. Several species of *Pseudo-nitzschia* were present but no identifications were made. *Pseudo-nitzschia* spp. showed a large latitudinal distribution (47° to 53°S) and was present in coastal, mid-shelf and outer shelf areas, usually at densities $\leq 2 \times 10^3$ cells L^{-1} but more abundant in coastal areas of the PD and GB transects (maximum: 16×10^3 cells L^{-1}, St. 183).

Interesting trophic relations were detected between organisms of the > 10–200 µm size fraction. *P. cordatum* was the species most frequently found inside the cytoplasm of non-photosynthetic dinoflagellates, such as *P. schwartzii* and other naked heterotrophic dinoflagellates, and in tintinnids such as *Eutintinnus* sp. Intact cells and valves of *P. cordatum* were also found in zooplankton fecal pellets. The

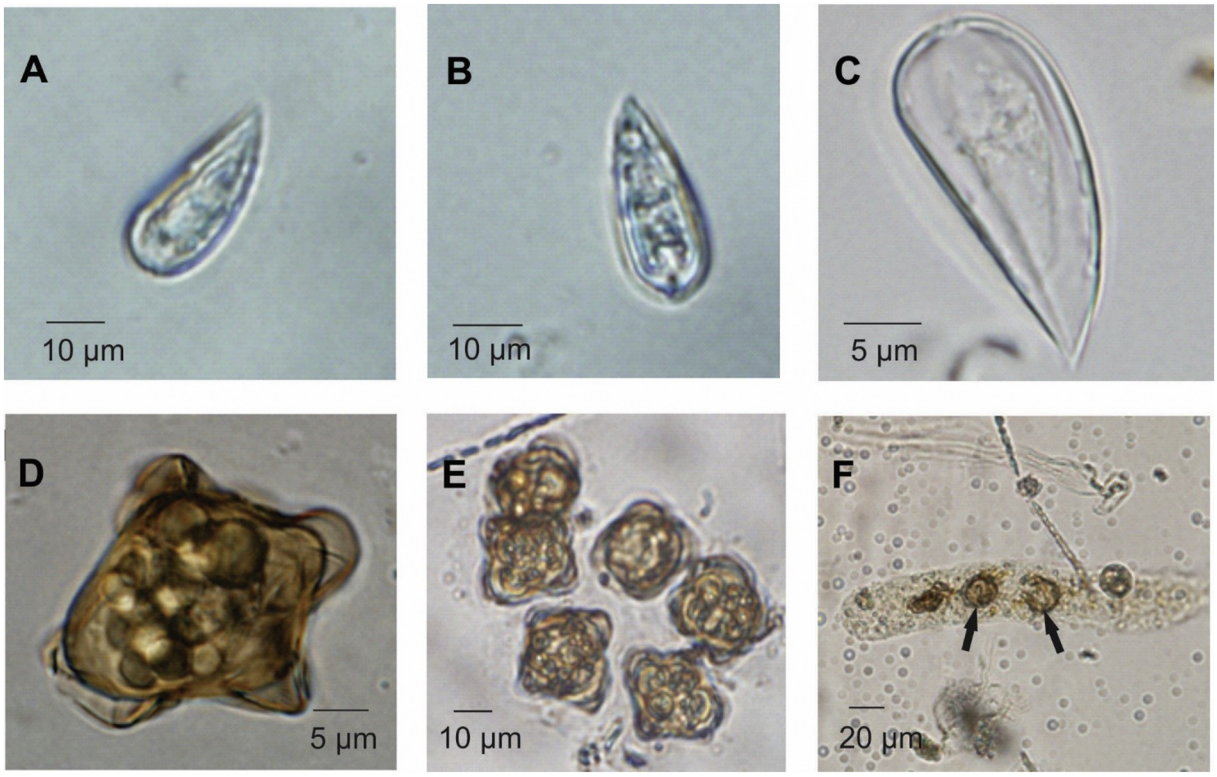

Fig. 5. *Prorocentrum vaginula* and resting cysts of an unidentified species of *Protoperidinium*. Different specimens of *P. vaginula* in valvar (A), sutural (B) and oblique views (C). Free living *Protoperidinium* sp. cysts showing lipid globules inside its cytoplasm (D) and grouped in mass (E), and cysts inside a fecal zooplankton pellet (F, arrowheads). See Appendix A for details on *P. vaginula*.

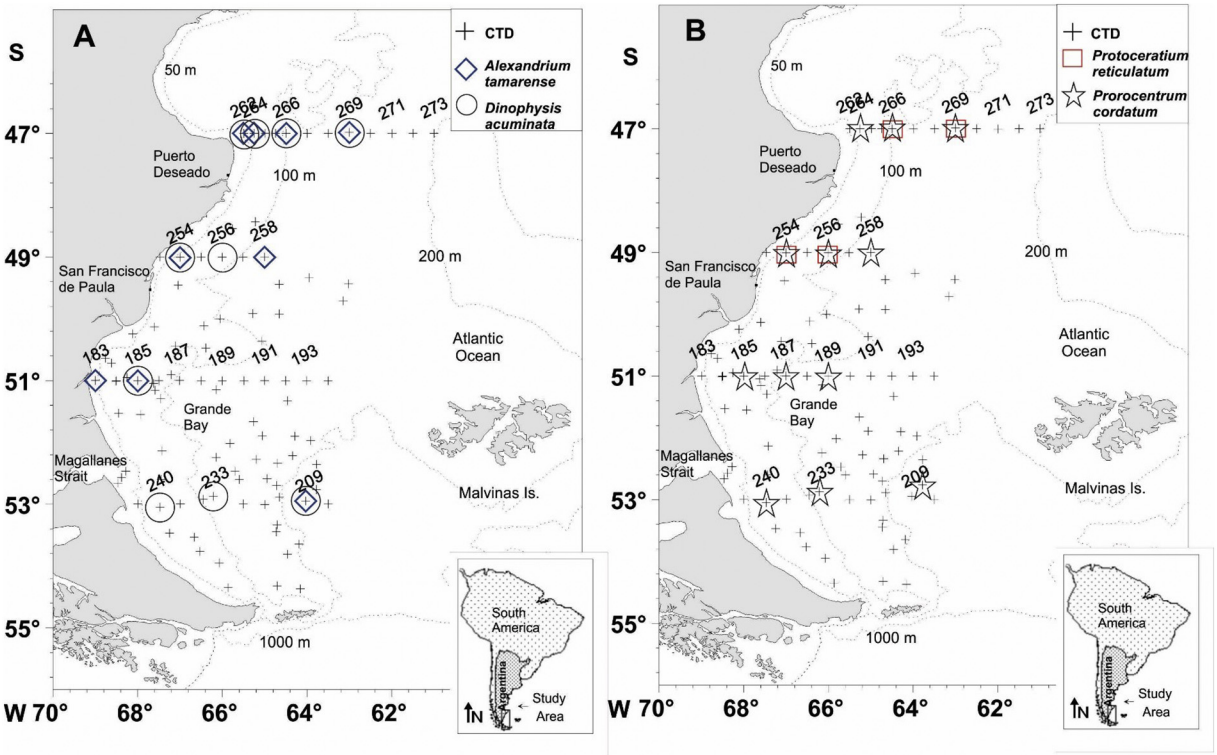

Fig. 6. Spatial distribution and abundance of potentially toxigenic species over the southern Patagonian shelf during March/April 2004. *Alexandrium tamarense* and *Dinophysis acuminata* (A); *Protoceratium reticulatum* and *Prorocentrum cordatum* (B).

Table 2
Analysis of similarity (ANOSIM test) performed to test for significant differences in the plankton community structure across depth strata, latitudinal sections, and bathymetric areas. All values of R in the pairwise tests are significant at $p = .05\%$.

Factors	Global *R*	*R* statistic pairwise test	Significance level *p*	*P* value correction Bonferroni
Depth[a]	0.353		0.001	
Pairwise test:				
S-D1		0.548	0.001	0
S-D2		0.443	0.001	0
D1-D2		0.036	0.155	0.47
Latitude[b]	0.303		0.001	
Pairwise test:				
PD-SFP		−0.008	0.520	3.12
PD-GB		0.446	0.001	0.006
PD-MAG		0.001	0.462	2.772
SFP-GB		0.52	0.001	0.006
SFP-Mag		0.132	0.074	0.444
GB-Mag		0.477	0.001	0.006
Bathymetry	0.185		0.001	

[a] S = surface; D1 = first depth level; D2 = second depth level.
[b] PD = Puerto Deseado; SFP = San Francisco de Paula; GB = Grande Bay; Mag = Magellan Strait.

presence of *P. cordatum* in fecal pellets as well as evidence of its predation by protozooplankton were observed in a wide area covering stations in the four sampled sections, and match its wide plankton distribution in this region (Fig. 6B). Other recorded trophic relations included consumption of *Protoperidinium bispinum* by an unidentified species of the same genus *Protoperidinium*, *Heterocapsa triquetra* by a naked dinoflagellate and resting cysts of the mass-encysted *Protoperidinium* species (see above in 3.2) by *P. schwartzii* and *Eutintinnus* sp.

3.3. Plankton assemblages and biodiversity indices

The analysis of similarity (ANOSIM, Table 2) indicated that latitudinal, bathymetric and vertical differences in the phyto- and protozooplankton communities were weakly significant (Global *R* values, $p < .001$). Only the stations in surface waters (S) were clearly different from those at the first depth level (D1), and the stations at *ca.* 49°S (SFP transect) were clearly separated from those at *ca.* 51°S (GB section) (pairwise test, $R > 0.5$). The other groups were mostly either not separated or barely separated ($R < 0.5$). Negative values of *R* in the PD vs. SFP comparison were indicative of larger differences within groups than between groups. Overall, communities had higher abundances at D1 than at S, and higher numbers at GB than at SFP.

Statistically significant differences ($p < .05$) in species richness (*S*), Margalef's index (*d*), Shannon's index (*H*), and Pielou's evenness (*J*) were detected between the three sampled depth strata (Friedman test, *p*-values, Table 3). Shifts were present mainly between the surface samples and the deeper samples at D1 and D2 (Bonferroni test, Table 3). Generally, surface waters harbored less diverse and less evenly distributed assemblages than the deeper layers, that is, there was a consistent increase in structural diversity in most index values with water depth, which was the most important contributor to the observed variability (Table A, Appendix B). In contrast, no effect of depth was found on the phyto- and protozooplankton communities' taxonomic diversity and taxonomic distinctness (Δ, Δ*) between the three sampled strata (Friedman test, *p*-values, Table 3), indicating consistency in community composition in terms of taxonomic features. The effect of latitude on diversity indices was registered only for Pielou's index, while no differences were detected between latitudinal sections for the remaining biodiversity indices (Kruskal-Wallis test *p*-values, Table 3). Only samples grouping at GB showed evenness values statistically different from those at the Mag section (Dunn test, Table 3). Eveness index values at Mag were double those at the GB transect (Table A, Appendix B), indicating more evenly distributed assemblages at Mag than at GB. The species richness and Margalef's index differed significantly between the two bathymetric areas (Kruskal-Wallis test *p*-values, Table 3). Both indices showed higher values in inner shelf waters than in mid-shelf (Table A, Appendix B). In contrast, no differences for the remaining biodiversity indices were detected between inner and mid-shelf waters (Table 3).

3.4. Environment and species composition. Ordination analysis of phyto- and protozooplankton communities

The multivariate regression tree analysis (MRT) revealed a weak environmental link with the spatial distribution of species/morpho-species groups ($R^2 = 27.1\%$; CVRE = 0.997). Five groups of samples were identified (Fig. 7). The spatial distribution of these groups formed five separate plankton areas: (1) surface waters 'S', including all the surface samples over the area; (2) coastal waters 'C', encompassing two samples located at the only coastal station in the region at < 50 m depth in the GB section (St. 183 at D1 and D2), (3) north of 51°S/depth waters 'ND', comprising samples in the PD and SFP sections at D1 and D2; (4) depth-warmer water 'SW', including five samples located in the GB section at D1; and (5) depth-colder waters 'SC', with samples from the GB section at D2, along with the southernmost samples in the Mag section at D1 and D2. Each area was differentiated by predictor variables, first by depth (5 m), then by longitude (68.5°W), latitude (51°S), and finally by temperature (10.77 °C).

Statistically significant ($p < .05$) differences were found in all the diversity indices between the assemblages defined by the MRT (Table 3). Most differences with the rest of groups were between the S, ND, and SC assemblages (Bonferroni test, Table 3). In general terms, the S group was the least and C the most diverse and evenly distributed assemblage. The ND, SW and SC groups showed intermediate values, as seen in the values of *S*, *d*, *H′* and *J* (Table 4). The taxonomic diversity (Δ) values varied considerably among the five assemblages (Tables 3 and 4), which indicates a shift in community structure in those areas. However, no clear patterns in the distribution of the differences appear through comparisons across groups (Bonferroni test, Table 3). The highest Δ values were found in the SC assemblage, the lowest in SW, while the remaining groups were intermediate (Table 4). In contrast, taxonomic distinctness (Δ*) was similar among sites, ranging 66.1–95.8, (Table 3), indicating that they were equally distinct taxonomically.

There were three common species (the top 70% of cumulative similarity, SIMPER analysis, Table 5) of the surface area: an ultra-heterotrophic cell, the ultraphytoeukaryotic coccal cell, and coccolithophorid sp. 1. The discriminant species (the top 50% of cumulative dissimilarity) at the surface were 20 morpho-species, half of which were diatoms, and half ciliates and other autotrophs. Likewise, the coastal sector was characterized by a large number of species, which therefore exhibited one of the highest average intra-group similarities (41.83%) along with the SW assemblage (44%). The high contribution of diatoms was a notable feature of the coastal sector, in contrast to the low representation and abundance of other taxa. The ciliate sp. 17, *P. cordatum,* and a nanophytoflagellate sp. 1 accounted together for 47% of the cumulative average similarity of the ND group. In this northern area, 8 species were common, of which most were ciliates. Haptophyte sp. 2, *Phaeodactylum* sp. and the ultraphytoeukaryotic coccal cell were the most significant morpho-species in the 'SW' group, accounting for 40% of the cumulative similarity, and were also common and discriminant species. Finally, two unidentified ciliates (ciliate sp. 2 and sp. 17) and the ultraphytoeukaryotic coccal cell contributed most of the similarity in the southern/colder group 'SC'.

Table 3
Biodiversity index statistics. Results (*p* values) of the Friedman test, Kruskal-Wallis test, Permutation test, and Post Hoc comparisons of the biodiversity indices, estimated by depth strata, bathymetric areas, latitudinal sections, and groups derived from the MRT analysis. Correction of the Bonferroni test on the *p* value for pairwise comparison (for Friedman and Permutation tests) is *p* adjust = 3 * *p* value. Statistically significant differences are in bold (*p* adjust < 0.05). nd = no statistically significant differences.

Diversity index Factor/area	S	d	H′	J′	Δ	Δ*
Depth[a] (Friedman test)	**0.01339**	**0.00002**	**0.00002**	**0.00150**	0.31140	0.64220
Bonferrroni's post-hoc test:						
S/D1	**0.02289**	**0.00291**	**0.00048**	**0.01404**	nd	nd
S/D2	**0.02265**	**0.00006**	**0.00048**	**0.01404**	nd	nd
D1/D2	nd	nd	nd	nd	nd	nd
Latitude *(Kruskal-Wallis test)*	0.2298	0.778	0.0846	**0.0221**	0.4732	0.5214
Dunn's post-hoc test:						
PD/SFP	nd	nd	nd	nd	nd	nd
PD/GB	nd	nd	nd	nd	nd	nd
PD/Mag	nd	nd	nd	nd	nd	nd
SFP/GB	nd	nd	nd	nd	nd	nd
SFP/Mag	nd	nd	nd	nd	nd	nd
GB/Mag	nd	nd	nd	**0.0318**	nd	nd
Bathymetry *(Kruskal-Wallis test)*	**0.0019**	**0.0044**	0.5401	0.3871	0.8854	0.5154
Dunn's post-hoc test:						
Inner shelf/Mid-shelf	**0.0019**	**0.0044**	nd	nd	nd	nd
MRT-areas[b] *(Permutation test)*	**0.004**	**0.0137**	**0.0002**	**0.0002**	**0.0033**	0.0534
Bonferroni's post-hoc test:						
S/C	**0.0430**	**0.0325**	**0.0253**	nd	nd	nd
S/ND	nd	**0.0325**	**0.0020**	**0.0000**	nd	nd
S/SW	nd	nd	nd	nd	**0.040**	nd
S/SC	nd	nd	**0.0253**	**0.0163**	**0.0468**	nd
C/SC	nd	**0.0387**	nd	nd	nd	nd
ND/SW	nd	nd	nd	**0.0163**	**0.0255**	nd
ND/SC	nd	nd	nd	nd	**0.0063**	nd
SW/SC	nd	nd	nd	nd	**0.0250**	nd

[a] S = surface; D1 = first depth level; D2 = second depth level.
[b] S = surface waters; C = coastal waters; ND = northern/depth waters; SW = southern/warmer waters; SC = southern/colder waters.

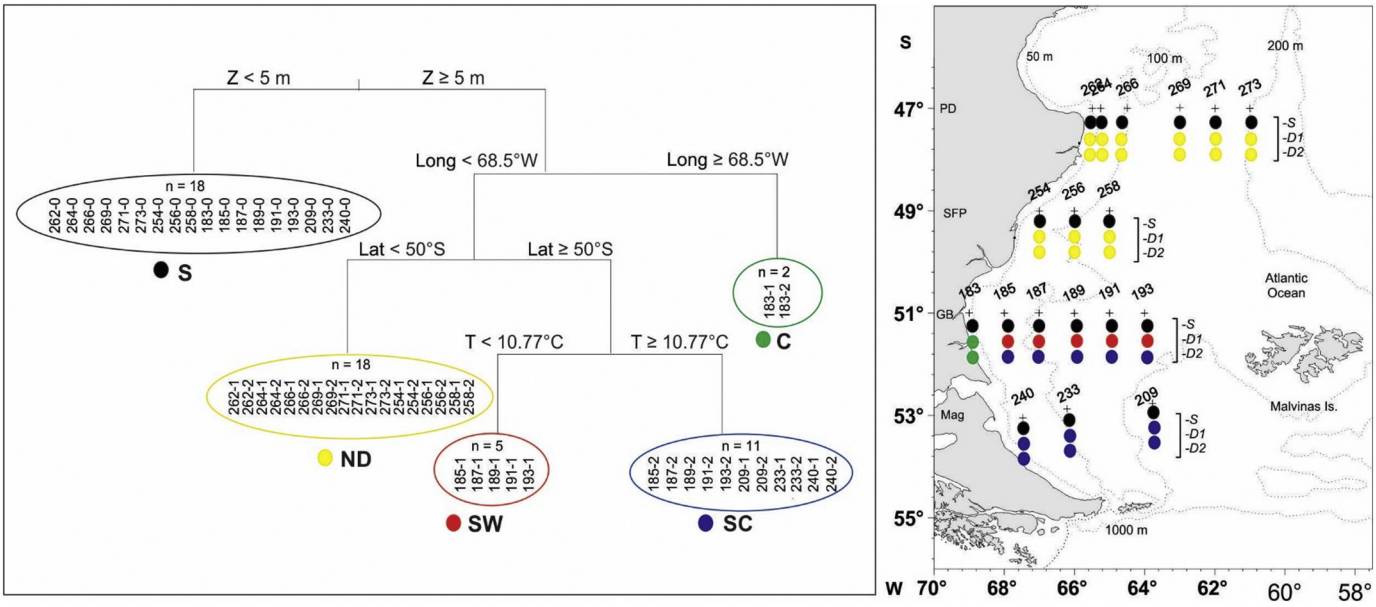

Fig. 7. Multivariate regression tree for links between environmental factors and species/morphospecies groups' data. The number of samples (n) within a leaf are shown. Explanatory variables: sampling depth (Z), longitude (Long), latitude (Lat), and temperature (T). Areas formed: S = surface waters; C = coastal waters; ND = northern/depth waters; SW = southern/warmer waters; SC = southern/colder waters (left panel). The five identified groups correspond to colored symbols (circles) used in the tree, which are geographically located on the map through the vertical depth at each station at surface level (S), first depth stratum/ca. 10–25 m (D1) and second depth stratum/ca. 25–65 m (D2) (right panel).

4. Discussion

Five plankton assemblage areas with major community structure differences were identified in the Patagonian shelf: surface waters, coastal waters, northern/depth waters, southern/warmer waters, and southern/colder waters. According to the vertical structure of the water column properties and the controlling physical processes, two distinct environments for plankton development were recognized: a thermally

Table 4
Range (min.max.), standard deviation (SD) and coefficient of variation (CV %) values of biodiversity indices in the southern Patagonian shelf during late summer 2004 by groups derived from the MRT analysis.

Diversity indices		MRT-groups[a]				
		S	C	ND	SW	SC
S	Range	1–26	34–43	4–43	13–21	4–21
	Median	12	38.5	15	18	16
	SD	7.81	6.36	9.04	3.27	4.68
	CV	61.13	16.53	53.34	17.97	31
d	Range	0–2.26	2.92–3.29	0.52–3.48	0.81–1.67	0.37–2.51
	Median	0.91	3.1	1.62	1.19	1.54
	SD	0.69	0.27	0.77	0.33	0.62
	CV	67.85	8.54	43.27	26.35	39.73
H′(log_{10})	Range	0–0.79	1–1.17	0.45–1.16	0.29–1.00	0.24–1.22
	Median	0.42	1.08	0.88	0.53	0.92
	SD	0.27	0.12	0.2	0.31	0.36
	CV	66.25	11.35	23.17	52.95	45.76
J´	Range	0–0.72	0.61–0.76	0.36–0.92	0.23–0.76	0.24–0.93
	Median	0.41	0.69	0.79	0.43	0.79
	SD	0.21	0.11	0.15	0.22	0.25
	CV	53.86	15.86	20.48	48.3	37.65
Δ	Range	7.01–59.78	8.49–58.39	7.88–62.60	7.89–16.44	23.81–65.88
	Median	38.25	33.44	31	12.78	59.54
	SD	15.16	35.28	15.85	3.89	13.65
	CV	38.85	105.52	48.06	31.5	25.95
Δ*	Range	66.67–90.58	76.76–78.22	66.07–95.78	66.89–85.55	66.67–92.59
	Median	72.58	77.49	74.53	72.78	88.23
	SD	10.98	1.03	9.57	7.11	8.61
	CV	14.05	1.33	12.43	9.58	10.11

[a] S = surface waters. C = coastal waters. ND = northern/depth waters. SW = southern/warmer waters. SC = southern/colder waters.

stratified area with a well-formed thermocline at *ca.* 50 m depth to the north of 52°S, and a colder and thermally homogeneous area to the south of 52°S. Phyto- and protozooplankton community patterns were found to be distinctly defined across-shelf, along-shelf and vertically, as a combination of environmental and geographical variables which included depth, bathymetry, latitude and temperature (MRT analysis, Fig. 7). All these variables are features expected to define the specific area inhabited by plankton communities, and the relationships of species with each biotic and abiotic variable, conditioning selected depths, temperatures, and foods, among other factors.

Oceanic circulation over the southern Patagonian shelf is driven by the predominance of westerly winds, high tidal amplitudes, large freshwater inflows, and the strong influence of the Malvinas Current flowing northwards along the shelf-break (Piola et al., 2018 and references therein). The annual mean wind stress distribution over this region is characterized by a band of strong westerlies, which intensify during the austral winter (Palma and Matano, 2012). Nevertheless, little is known about the wind driven circulation in this region (Palma et al., 2008). The annual mean circulation has an average northeast transport which is controlled by the low-salinity discharges from the Magellan Straits, tidal mixing, and wind forcing (Palma et al., 2008). Glorioso and Flather (1995) and Palma et al. (2004a, 2004b) postulated the existence of a broad northeastward flow with counterclockwise gyres within the GB and the S. Jorge gulf. Considering the seasonal variations of the southern shelf region circulation, experiments indicate a strengthening of the northward flow during the fall and a weakening during the spring, driven mainly by wind forcing in the northern portion (> 48°S) of the inner and middle shelf, and by modulations of the Malvinas current transport in the southern region and offshore of the 100 isobath (Palma et al., 2008). Variations in wind strength could also make substantial modifications in the buoyancy fluxes generated by the Magellan discharge with a weakening (strengthening) in downstream fluxes and intensification (reduction) of upstream fluxes for stronger (weaker) winds. The hydrographic diversity described above translate into habitat heterogeneity for plankton communities, which is reflected in some sense in the MRT results.

Temperature is a major structural factor for plankton communities. In this study, according to the MRT results, temperature was a major factor for discriminating the plankton groups (separating the surface group samples at < 5 m from the other plankton assemblages). In particular, an historical record for this region, based on a long-term monitoring of sea surface temperature and their anomalies data, indicate for the period of our study an accentuated warming of the sea surface layer with the highest positive thermal anomalies (> +2 °C) and the highest thermal differences between surface and bottom (Sanahuja, 2007; unpublished data Regional Oceanographic Data Base–BaRDO, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina), including a maximum vertical gradient recorded for the thermocline at *ca.* 50 m (R. Reta, pers. comm.). The hydrographic pattern described for the time of our study was far from the average of the summer situation for the SPS, which typically shows relatively lower temperature values and low salinity, depicting, in consequence, good mixing of the water column and low stratification (Romero et al., 2006; Palma et al., 2008). Distinct phyto- and protozooplankton biodiversity index values would also explain the differences between the surface and the rest of the subgroups. Most sites in the surface group were characterized by relatively low values of *S, d, H* and *J*, indicating that it was the least diverse and evenly distributed assemblage. The importance of depth as one of the main factors in the observed variability in phyto- and protozooplankton community assemblages was also observed when the effect of this variable on both abundance and diversity data was analyzed separately. Therefore, it is likely that the distribution of phyto- and protozooplankton communities was influenced by differential local environmental characteristics in the vertical stratum (thermal anomalies > +2 °C and thermal differences between surface and bottom; Sanahuja, 2007) in relation to particular adaptations to local characteristics (niche adaptation) of the assemblages (e.g. Thomas et al., 2012; Boyd et al., 2013). It is probable that the anomalous hydrographic conditions, which prevented the water column mixing resulting in higher temperature values, diminished species diversity.

The thermal stratification observed in the region would explain the differences between the northern (ND) and the two southernmost plankton subgroups (SW and SC). This pattern of stability was, overall,

Table 5
Common (to the top 70% of cumulative similarity) and discriminant (to the top 50% of cumulative dissimilarity) plankton species/morpho-species of sample groups derived from the MRT analysis over the southern Patagonian shelf determined using SIMPER analysis. S (%) = Contribution to similarity. AS = Average similarity (%). MRT groups: S = surface waters; C = coastal waters; ND = northern/depth waters; SW = southern/warmer waters; SC = southern/colder waters.

	S (AS = 20%)		C (AS = 40%)		ND (AS = 17%)		SW (AS = 44%)		SC (AS = 16%)	
	Species	S (%)	Species	S (%)	Species	S (%)	Species	S (%)	Species	S (%)
Common	Ultraheterotrophic cell	27	*Pyramimonas* sp.	9	Ciliate sp. 17	18	Haptophyte sp. 2	15	Ciliate sp. 2	17
	Ultraphytoeukaryotic coccal cell	22	*Ollicola vangoorii*	8	*Prorocentrum cordatum*	16	*Phaeodactylum* sp.	13	Ultraphytoeukaryotic coccal cell	15
	Coccolithophorid sp. 1	17	Euglenophyte sp. 1	7	Nanophytoflagellate sp. 1	13	Ultraphytoeukaryotic coccal cell	13	Ciliate sp. 17	14
			Pseudo-nitzschia spp.	7	*Amphidomataceae*	8	Ciliate sp. 17	9	Euglenophyte sp.1	7
			Thalassiosira decipiens	7	Ciliate sp. 1	6	Heterotrophic flagellate sp. 1	8	*Amphidomataceae*	6
			Chaetoceros secc. *Phaeoceros*	7	Ciliate sp. 6	4	Cryptophyte sp. 4	8	*Mesodinium rubrum*	4
			Dactyliosolen fragilissimus	7	Ciliate sp. 2	3			*Karenia* sp. 3	4
			Thalassionema nitzschioides	6	*Strombidium* sp. 1	3				
			Thalassiosira sp. *6*	6						
			Tintinnopsis sp. 2	5						
Discriminant	*Pyraminomas* sp.		Ultraheterotrophic cell				Ultraphytoeukaryotic coccal cell			
	Euglenophyte sp. 1		Coccolithophorid sp. 1				*Phaeodactylum* sp.			
	Pseudo-nitzschia spp.						Haptophyte sp. 2			
	Dactyliosolen fragilissimus						*Fragilariopsis* sp.			
	Calycomonas sp. 2						Heterotrophic flagellate sp. 1			
	Chaetoceros secc. *Phaeoceros*						Phytoflagellate sp. 2			
	Thalassiosira decipiens						Cryptophyte sp. 4			
	Centric diatom sp. 6									
	Thalassionema nitzschioides									
	Thalassiosira sp. *6*									
	Laboea sp.									
	Tintinnopsis sp. 2									
	Mesodinium sp.									
	Euglenophyte sp. 1									
	Dytilum brightwelli									
	Cyst form									
	Leucocryptos sp.									
	Leptocylindricus minimus									
	Paralia sulcata									
	Cryptophyte sp. 5									

in keeping with that described by Sabatini et al. (2000, 2004), although the values of the Simpson stability parameter Φ in this study indicated a markedly stronger stratification than previous records, and that the stratified area extended further south than in other years. In fact, the critical value of Φ considered in this study to separate mixed from stratified waters was much higher than that commonly used ($\Phi = 150\ J\ m^{-3}$ vs. 40–50 $J\ m^{-3}$) (Martos and Sánchez, 1997; Sabatini et al., 2000; Bianchi et al., 2005).

The discrimination of the coastal group from the rest of subgroups may be associated with the prevalent influence of water masses, typically defined by Bianchi et al. (1982) by their saline content, which resulted in the separation of the SPS into three areas by the bathymetry: *i.e.* Coastal Waters, Mid-shelf Waters and Malvinas Waters. In turn, the salinity field and gradients recorded during this study enabled those areas to be recognized. The lowest salinity values registered were found in coastal waters (< 32) due to discharge from the Patagonian rivers and the input of low salinity waters from the Magellan Strait. However, the MRT analysis did not recognize salinity as a factor separating the coastal group from the remaining phyto- and protozooplankton assemblages. At the same time, coastal samples registered a distinctive taxonomic composition. The SIMPER analysis attributed most of the similarity in the coastal group to a relatively large number of species, mostly diatoms (Table 5), which tend to be prevalent in high-nutrient and high-turbulence conditions (*e.g.*,Granéli and Turner, 2007).

Our results suggest that taxonomic composition is another important factor distinguishing the five assemblages, and the explanation is two-fold: firstly, for the significant shifts in diversity indices (Permutation test, Table 4) and, secondly, for the composition of common species (SIMPER, Table 5). In particular, the variation of the taxonomic diversity index (Δ) among most of the assemblages (*e.g.* surface versus both southern subgroups SC and SW; northern versus both southern groups, and differences between the two southern subgroups SC and SW) indicated that the groups were highly diverse taxonomically. In the SW waters, the phylogenetic structure of the assemblages was lower than in the other areas (Table A, Appendix B), the SC group was the highest, while the remaining groups had intermediate values. Lower taxonomic diversity indicates that communities are composed of more closely-related species than those with higher index

values. It is important to note that, like most diversity indices, taxonomic diversity is a relative measure for use in comparisons within a study, rather than an absolute value for comparisons among studies (Warwick and Clarke, 1995). This index was a major factor explaining the heterogeneity of phyto- and protozooplankton communities, emphasizing the importance of using this approach. Taxonomic indices are considered to be less susceptible to variability in sample size (such as disparities in sampling efforts), providing, additionally, a more intuitive measure of biodiversity than conventional measures such as species richness and evenness and, to some extent, species diversity (H'), with Δ being considered a truer measure of "biodiversity" than H' (Warwick and Clarke, 1995, 1998). In general, species richness (S), Margalef's index (d), and Shannon's index (H') showed relatively low values at all stations during the study period, especially in surface samples in the Grande Bay area, which indicates a low specific structure of phyto- and protozooplankton (Badsi et al., 2012). Locations that had high species richness were the most diverse, that is, in general terms, species richness d and species diversity H both followed the same pattern in the samples analyzed. The wide range of values of the species evenness index (0.001 to 0.93) coupled with their spatial variation reflects the heterogeneity of the unevenly distributed plankton populations.

We examined four categories of biodiversity measures: species richness (S, the simplest measure of diversity expressing the number of species encountered per sample, and d which includes the number of species and the total number of individuals in the sample); species diversity, weighting species by abundance (Shannon's index); evenness, that is, the degree to which abundances are divided equally among the species present in samples (Pielou's index); and taxonomic diversity (Δ and Δ*). These approaches provide slightly different slants to the same question: to what extent is the community dominated by just a few or a large number of taxa? The aim of using all these metrics was to examine their behavior and see if any of these differs from the others or displays particularly robust behavior. The biodiversity of phyto- and protozooplankton is, however, often very difficult to estimate, since these assemblages consist of a vast number of species, and the number of species (or taxa) recorded in a sample depends not only on what is present, or on the skill of the analysts, or on the effort allocated to investigate the particular area (*e.g.*, Carstensen et al., 2005), but also on the restrictions of the routine analysis methodology, as many taxa cannot simply be identified to species level by light microscopy of preserved samples (*e.g.*, Ojaveer et al., 2010). Moreover, the turnover rate of phyto- and protozooplankton is fast, and assemblages react quickly to changes in the environment, making the community structure spatially and temporally variable, thus requiring a large number of samples to overcome this high natural variability (*e.g.*, Dybern and Hansen, 1989). This means that we cannot assume to have a complete list of species in the ecosystem at any given point in time. There are three ways in which to approach the problem of having to work with data with variable taxonomic detail: to exclude all except species-level observations; to summarize all data into genus- (or higher) level information; or to use the data as they are and accept the fact that the taxonomic units vary. We consider the third approach is the best available option, since discarding parts of the data or aggregating them means losing information related to biodiversity, precisely the property we aim to estimate.

The size structure of phyto- and protozooplankton communities here recorded, that is, abundance markedly dominated by ultraphytoplankton over nano- and microplankton, matches the overall patterns previously described for the region in late summer (Almandoz et al., 2007; Cefarelli et al., 2010; Vega Moreno et al., 2012; Zingone et al., 2011). A few species dominated the late summer communities. In particular, a coccal ultraphytoeukaryotic cell (3 μm), possibly belonging to the group of chlorophytes/prasinophytes, prevailed over all the morpho-species recorded. Similarly, Zingone et al. (2011) reported the predominance of a small-sized (average 2.5 μm) coccoid form for the Magellan Strait, tentatively identified as the prasinophyte *Pycnococcus provasolii*. The high predominance of haptophytes in this study was in keeping with many other reports in the area identifying coccolithophorids as dominant components in summer (Signorini et al., 2006; Painter et al., 2010; De Souza et al., 2012; Segura et al., 2013; Balch et al., 2014). We found low abundance of nano- and microplankton, also in keeping with other studies, either dinoflagellates, diatoms and silicoflagellates (Olguín and Alder, 2004; Olguín et al., 2005; Zingone et al., 2011; Akselman, unpubl. data) and ciliates (Santoferrara and Alder, 2009a). Analysis of an annual cycle in the nearby S. Jorge gulf showed a decrease in microplankton population levels in summer (Akselman, 1996). Ultraphytoplankton communities were numerous, especially in the GB area, and the reason could be 2-fold. One, the spatially coincident low abundance of their main potential grazers, *i.e.* nano- and microplankton species (Antacli et al., 2014b), in turn consumed by mesozooplankton (especially copepods) which were a notably abundant group in the GB area at that time (Antacli et al., 2014b). Another reason could be the relatively higher stratification in the area (Peterson and Bellantoni, 1987; Huete-Ortega et al., 2010). A two-layer bi-directional flow affects both the distribution of organisms and the manner in which populations are retained within the system (Peterson et al., 1979). Changes in the thermal structure of the water column lead to time-varying changes in stability, which in turn lead to changes in the vertical distribution and abundance of phytoplankton and to changes in phytoplankton species composition and mean cell size. For example, phytoplankton is usually distributed homogeneously with depth in a mixed water column but is concentrated either in the upper wind mixed layer or at the pycnocline in a stratified water column (Holligan et al., 1984). Chain-forming diatoms dominate the phytoplankton assemblage of mixed water columns, but small dinoflagellates and cryptomonads (those < 20 μm in diameter) dominate in stratified water columns (Conover, 1956).

Another reason for the dominance of ultraplankton over larger cells could be the presence of low nutrient concentrations. The Antarctic Circumpolar Current enriches the outer shelf and slope waters through nutrient inputs from the Malvinas Current. Some observations and numerical simulations suggest the onshore spreading of cold and dense waters carrying nutrients (Sabatini et al., 2012 and references therein). In winter and in early spring nitrogen and phosphorus concentrations seem to be non-limiting, although silicate show low values (Sabatini et al., 2012; Gómez et al., 2011). We have no inorganic nutrient data for the cruise under study and to our knowledge there are no synoptic information on nutrients in the SPS for late summer and for hydrographic conditions of water column stability such as those present in the prospected northern area. Despite this and in the nearby S. Jorge gulf, low nutrient concentrations were recorded in the upper layer of highly stratified waters during summer in comparison with other seasons (Akselman, 1996). Small cells have a high surface-to-volume ratio that is favorable for acquiring nutrients at low nutrient concentrations (Raven, 1998), allowing them to thrive under poor nutrient conditions and to dominate plankton communities in oligotrophic seawaters. Consequently, we conjecture that nutrient limitation may be responsible for the dominance of a limited number of small phytoplankton morpho-species at relatively low phytoplankton abundances.

A remarkable feature we documented in certain communities was patchiness in plankton distribution. Examples are the high abundance of the diatom *R. setigera* and of a loricate and a naked ciliate at particular sites in middle shelf and outer shelf areas of the PD section. These spots of enhanced plankton biomass were recorded at maximum fluorescence depths. In general terms, most of the phyto- and protozooplankton populations were also more abundant at maximum fluorescence levels. A maximum of phytoplankton biomass often occurs at depth, which has been attributed to diverse mechanisms or their combination, that may include a local maximum in phytoplankton growth rate near the nutricline, photoacclimation of pigment contents that leads to elevated chlorophyll concentration relative to phytoplankton biomass, and a range of physiologically influenced swimming behaviors

in motile phytoplankton and buoyancy control in diatoms and cyanobacteria that can lead to aggregations in layers (Cullen, 2015). Low surface Chl *a* values (max. 1 μg L^{-1}) recorded during our study cruise (V. Lutz, unpubl. data) indicated a close relationship with the low abundance of autotrophic organisms registered in most of the area. However, several stations located offshore in the southern region (where plankton samples were not obtained) showed higher Chl *a* values (*ca.* 4 μg L^{-1}), which may indicate patchiness in the spatial distribution of autotrophic communities. This patchy distribution could be related to onshore intrusions and subsequent upwelling of nutrient-rich waters of outer-shelf subantarctic waters (Palma et al., 2008).

Production of PSP by *A. tamarense* is a well-known phenomenon in the Argentine sea, including Patagonia and the Beagle Channel in Tierra del Fuego, which affects shellfish resources causing temporary fishing bans in coastal areas (*e.g.*, Carreto et al., 1998; Santinelli et al., 2002; Almandoz, 2011; Turner and Goya, 2015). Maximum abundances for *A. tamarense* in the S. Jorge gulf (2.6×10^6 cells L^{-1}; Akselman, 1996) and for *A. catenella* in the Beagle Channel (821×10^3 cells L^{-1}; Benavides et al., 1995) have been recorded. In this study, adopting a precautionary approach, we use the name *A. tamarense* instead of *A. catenella* (see Moestrup et al., 2009). Its vegetative cells co-occur with their phycotoxins in the water column (Montoya et al., 2010; Krock et al., 2015; Fabro et al., 2017). We found *A. tamarense* widely distributed in south Patagonia, including coastal and middle shelf waters, as well as in areas of > 200 m depth offshore Tierra del Fuego. It is remarkable to record this species in offshore waters, considering the proximity of the Malvinas Islands where high PSP levels were detected in an episode of penguin mortality (Uhart et al., 2004). In Patagonian gulfs north of 47°S, *A. tamarense* is more abundant in spring and autumn (Akselman, 1996; Santinelli et al., 2002). The low late summer densities that we observed may be related to the low mean monthly toxicity values reported for this period by Carreto et al. (1998).

We also found *P. reticulatum* and *D. acuminata* in low abundance. Recently, YTX was reported as occurring in shellfish (Turner and Goya, 2015) and in plankton samples in which *P. reticulatum* was present (Krock et al., 2015). Additionally, it was shown that strains isolated from the S. Jorge gulf have the ability to produce YTX in culture (Akselman et al., 2015). Also recently, the presence of *D. acuminata* was related to pectenotoxins detected in size-fractionated plankton samples (Fabro et al., 2016), and several DSP toxins in shellfish were reported in the S. Jorge gulf and Beagle Channel (Turner and Goya, 2015). This highlights the importance of *P. reticulatum* and *D. acuminata* as potentially harmful species in this region.

Prorocentrum cordatum is another potentially toxic dinoflagellate (Grzebyk et al., 1997; Rodriguez et al., 2017) that was present in most of our analyzed samples. It was the most frequent species over the entire region (*FO* = 55.6%), among the 20 most abundant species (*RA* = 0.2%), and a common species (SIMPER, 70% of similarity). *P. cordatum* has been recorded in coastal and middle shelf waters in Patagonia during different seasons (e.g. Gómez et al., 2011; Sastre et al., 2016), forming sometimes monospecific blooms (e.g. Carreto et al., 2018). The presence of non-identified species of the naked genus *Karenia* and taxa of the family Amphidomataceae is also of interest and we are recording these dinoflagellates for the first time in shelf waters of southern Patagonia. Some species of *Karenia* produce cytotoxic polyethers that can cause fish and invertebrate mortality, among them *K. mikimotoi* (Moestrup et al., 2009). Members of this genus were present in our samples and, although not conclusively identified, one of them matched descriptions of the toxigenic *K. mikimotoi*. As some members of Amphidomataceae are known to produce AZA toxins, its identification, knowledge of its spatial distribution and possible toxigenicity are topics of interest. Several species were recently reported in huge blooms in northern Argentine waters, as well as the presence of a toxic species (*Azadinium poporum*) and traces of AZA-2 in shellfish (Akselman et al., 2014; Turner and Goya, 2015; Tillmann and Akselman, 2016; Tillmann et al., 2016). Although in this study we did not make any identification, observation of different morphologies suggests that more than one species and even genera could have been present.

Potentially toxic species of the diatom genus *Pseudo-nitzschia* are known in the Argentine sea, including the Patagonia region and Tierra del Fuego, with reports of the DA toxin in plankton samples, shellfish, anchovies and in whale feces (*e.g.*, Almandoz, 2011; Krock et al., 2015; Sastre et al., 2007; Wilson et al., 2015). The wide distribution of harmful dinoflagellates and diatoms here recorded highlights the need to pay attention to the potentially noxious species pertaining not only to these taxonomic groups but also to other algal groups which could eventually be present. Although the most significant harmful effects for some decades in southern Patagonia have been caused by PSP produced by *A. tamarense*, recent records of the presence of other species and their toxins as well as our observations recording for the first time potentially toxic dinoflagellates stresses the need to continue taxonomic and chemical studies on biotoxin production. It is clearly important to focus attention on harmful microalgae, as phycotoxins can affect fishery resources and pose a risk of poisoning for humans and marine wildlife.

5. Conclusions

This is the first study assessing in detail the phyto- and protozooplankton community structures in a broad size spectrum of particles (2–200 μm) in the SPS ecosystem during late summer, simultaneously focusing on the abundance distribution, taxonomic composition and biodiversity patterns, and also analyzing hydrographic properties through depth strata. It reveals complex relations between hydrography and phyto- and protozooplankton by the end of summer.

Our results support the initial hypothesis of a major effect of thermal stratification of water columns on spatial differences of plankton distribution. Major conclusions can be drawn related to our specific objectives: 1) the phyto- and protozooplankton communities were dominated by ultraphytoplankton; 2) plankton abundance and biodiversity patterns showed differences cross-shelf, along-shelf and with depth throughout the water column, indicating shifts in community structure over the region; 3) a combination of geographic (latitude, bathymetry) and environmental (temperature) variables influence the spatial distribution of phyto- and protozooplankton assemblages in the SPS, indicating five dissimilar regions; and 4) the wide spatial distribution of known toxigenic taxa and of potentially toxic dinoflagellate groups recorded for the first time in this region poses the need to continue focusing on the study of harmful microalgae.

Despite limitations regarding the relatively low number of stations involved in the analyses in such an extended shelf area, our results fill a gap in the knowledge of phyto- and protozooplankton groups, mainly in the smallest size fractions which have received little attention, and offer valuable information on their structural patterns on the southern Patagonian shelf to contribute to a baseline for future studies.

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Appendix A

Prorocentrum vaginula (F. Stein) J.D. Dodge
Class Dinophyceae
Order Prorocentrales
Family Prorocentraceae
Genus *Prorocentrum*
Basionym
Dinopyxis vaginula F.Stein
Homotypic Synonym
Exuviaella vaginula (F. Stein) Lemmermann
(Fig. 5A-C)

Cell morphology and dimensions correspond to the description given in Schiller (1931–1937). Length range of 27.4–29 μm (10 specimens measured).

Remarks. *Prorocentrum vaginula* is cited for the first time for southern Patagonia and as far as we know for the southwestern Atlantic Ocean. *P. vaginula* has been recorded in the southern Magellan section at St. 209 (52.9477°S–64.0285°W) in bottle samples of the three analyzed depths (0, 15 and 40 m) and with low densities (200 cells L^{-1}). This is a marine species known from the Canary Islands, Black Sea and Adriatic Sea (http://www.algaebase.org; searched on 20 March 2018).

Appendix B

Table A
Ranges (min.–max.), median, standard deviations (SD) and coefficient of variation (CV %) values of diversity indices in the SPS during late summer 2004 by depth stratum, latitudinal section, and bathymetric area. *S = surface (0 m). D1 = first depth level (~10–25 m). D2 = second depth level (~25–65 m).

Indices		Depth strata*			Latitudinal sections (°S)				Bathymetric areas	
		S	D1	D2	47	49	51	53	Inner shelf	Mid-shelf
S	Range	1–26	7–43	4–34	7–43	4–20	1–43	10–23	6–43	1–23
	Median	11	17.5	14.5	16.5	13.0	14.5	17.0	18.0	12.0
	SD	7.8	9.8	7.3	9.02	5.7	10.6	4.5	7.8	6.1
	CV	61.1	50.9	45.3	48.6	46.9	69.4	26.83	42.4	48.2
d	Range	0–2.3	0.7–3.5	0.4–2.9	0.5–3.5	0.3–2.4	0.2–3.3	0.8–2.5	0.4–3.5	0.3–2.5
	Median	0.8	1.6	1.5	1.6	1.2	1.1	1.9	1.7	1.2
	SD	0.7	0.8	0.8	0.8	0.67	0.9	0.6	0.8	0.6
	CV	67.9	44.4	44.4	44.8	54.1	67.7	32.2	45.4	47.8
H′(log_{10})	Range	0–0.8	0.3–1.2	0.2–1.2	0.4–1.2	0.03–1.1	0–1.2	0.3–1.2	0.2–1.2	0.03–1.2
	Median	0.4	0.85	0.87	0.77	0.78	0.47	0.98	0.75	0.8
	SD	0.27	0.26	0.3	0.21	0.36	0.35	0.33	0.32	0.31
	CV	66.3	33.1	37.5	27.9	53.1	65.7	38.8	47.1	45.4
J´	Range	0–0.7	0.3–0.9	0.24–0.93	0.3–0.9	0.04–0.9	0–0.8	0.3–0.9	0.2–0.9	0.04–0.9
	Median	0.4	0.7	0.78	0.58	0.8	0.43	0.8	0.6	0.7
	SD	0.2	0.2	0.2	0.18	0.3	0.24	0.3	0.24	0.2
	CV	53.9	33.3	29.1	29.0	45.55	54.1	35.1	44.8	38.4
Δ	Range	7.0–59.8	7.89–62.6	7.9–65.9	10.1–62.6	7.9–58.4	7.9–65.9	7.0–59.9	7.9–62.6	7.0–65.9
	Median	38.3	26.8	46.1	36.4	29.9	45.2	44.6	34.1	40.9
	SD	15.2	17.7	19.1	14.5	15.5	22.7	17.5	18.3	17.6
	CV	38.9	61.4	43.9	39.8	51.9	58.1	42.1	52.5	47.2
Δ*	Range	66.7–93.5	66.7–92.6	66.1–95.8	66.7–92.9	66.1–95.8	66.7–91.0	66.7–93.5	66.1–93.3	66.7–95.8
	Median	72.6	73.3	85.2	79.7	68.8	76.3	84.8	79.7	74.2
	SD	10.9	8.47	9.5	8.5	12.5	9.3	11.5	9.5	10.5
	CV	14.1	11.2	11.5	10.6	16.5	11.9	14.3	12.0	13.4

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