Distribution of dinoflagellate cysts and other aquatic palynomorphs in surface sediments from the Beagle Channel, Southern Argentina

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ABSTRACT

Palynological analyses of 22 surface sediment samples from the Beagle Channel, Tierra del Fuego, Argentina, were performed in order to investigate the distribution of dinocyst assemblages and other aquatic palynomorphs and to explore their relationships with sea-surface conditions, which are regionally characterized by cold and low salinity conditions (4–9 °C and 27–33.5, respectively). Results show relatively low dinocyst concentrations (253 to 5568 cysts/g) and species diversity (19 taxa identified). The assemblages are mostly composed of Protoperidiniaceae and appear typical of a marginal marine environment with surface waters characterized by low to moderate salinity and high nutrient content due to river inputs. The assemblages are thus compatible with the occurrence of freshwater to brackish water taxa *Botryococcus braunii*, *Botryococcus* sp., *Polyasterias* sp., *Halodinium* sp., and *Radiosperma corbiferum*. The dinocyst assemblages are dominated by *Brigantedinium* spp., *Echinidinium* spp. and *Selenopemphix quanta* accompanied by cysts of *Pentapharsodinium dalei*, *Islandinium minutum*, *Votadinium spinosum*, *Polykrikos kofoidii* and *Polykrikos schwartzii*. The assemblages from the Beagle Channel show similarities with those of high latitude regions of the Northern Hemisphere. However, some taxa, which were exclusively reported from relatively warm environments in the Northern Hemisphere, occur in relatively high percentages in the Beagle Channel (e.g. *Echinidinium delicatum* and *Votadinium spinosum*). The absence of *Selenopemphix antarctica* in the Beagle Channel is consistent with its known ecological affinities, since it characterizes environments marked by seasonal sea-ice cover.

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1. Introduction

Dinoflagellates inhabit surface waters in a wide range of marine environments. The abundance and distribution of their cysts (dinocysts) depend upon the primary production and physico-chemical conditions such as sea-surface temperature (SST), sea-surface salinity (SSS) and sea ice cover (e.g. de Vernal et al., 2001, 2005; Radi and de Vernal, 2008). The distribution of dinocysts in surface sediments of the Northern Hemisphere including polar and circumpolar areas is relatively well documented and has contributed to the understanding of their relationships with sea-surface conditions (e.g. Matthiessen, 1995; de Vernal et al., 1997; Matthiessen et al., 2000; de Vernal et al., 2001; Radi et al., 2001; Marret and Zonneveld, 2003; Radi and de Vernal, 2004; de Vernal et al., 2005; Radi et al., 2007; Radi and de Vernal, 2008; Grøsfjeld et al., 2009; Solignac et al., 2009; Bonnet et al., 2010). Studies on dinocyst assemblages in surface sediments and in late Quaternary deposits of the Southern Ocean are still limited to a few studies (McMinn, 1992,

1995; Marret and de Vernal, 1997; McMinn and Wells, 1997; Harland et al., 1998; Harland and Pudsey, 1999; Marret et al., 2001), and do not yet offer a comprehensive documentation of the modern dinocyst distribution. Here, we present the results of palynological analyses in surface sediments from the Beagle Channel, Tierra del Fuego, Argentina with the aims of documenting the distribution of dinocysts and exploring their relationships with SST and SSS. Since standard preparation techniques were used, the results of the present study should complement the modern database that has been developed for palaeoceanographical reconstructions in the Southern Hemisphere (cf. Marret and de Vernal, 1997; Marret et al., 2001). Ultimately, these results will be helpful for reconstructing the past environmental conditions in the Beagle Channel area during the Holocene (Borromei et al., 1997; Borromei and Quattrocchio, 2001; Grill et al., 2002; Borromei and Quattrocchio, 2007; Candel et al., 2009; Rabassa et al., 2009; Candel, 2010).

2. Environmental setting

The Argentine sector of Isla Grande de Tierra del Fuego is located between 52°40'S and 55°7'S and between 65°05′W and 68°40′W.

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The southernmost coasts of Tierra del Fuego (northern Beagle Channel coast and southern Atlantic coast) extend over 220 km from west to east, and constitute a connection between the Atlantic Ocean and the Pacific Ocean (Fig. 1). The Beagle Channel is a former tectonic valley that was completely covered by ice during the last glaciation, with ice limits reaching a maximum extent of about 20–22 ka ago (Rabassa et al., 2000). After ice-melt, around 8200 14C year B.P., the valley was occupied by lakes, peat bogs and rivers. During the Holocene transgression, around 7500 14C yr B.P., the valley was submerged by the sea and the whole area turned into a fjord (Rabassa et al., 1986).

The Beagle Channel shows typical characteristics of a fjord with estuarine dynamics controlled by important fluvial inputs and by tidal currents from both the east (Atlantic) and the west (Pacific) sides (Isla et al., 1999). Two layers of different salinity and temperature develop in the water column during summer, east of Isla Gable. A lower salinity (25) and temperature (4 °C) and vertical mixing down to a depth of 22 m were observed westwards of Isla Gable during summer. The topographic sills of Isla Gable, Canal Murray and the northwestern and southwestern Beagle Channel branches play a role in the fjord dynamics by restricting water exchanges and limiting the relative effects of the eastern and western tidal currents and the gravity waves from the west (D'Onofrio et al., 1989). The Isla Gable sill constitutes the meeting point of the Atlantic and Pacific tidal waves (D'Onofrio et al., 1989).

The Beagle Channel receives input from numerous rivers that drain the intermontane basins of Grande, Navarino and Hoste islands. These basins have a nival regime with increased rainfall between October and December and a dry season in March–April. The water column is stratified mainly during the summer season. The average sea-surface temperature is about 6.5 °C with a maximum of 9 °C in January and a minimum of 4 °C in August. Sea-surface salinity varies from 27 to 33.5 with minimum values during summer due to the meltwater discharge into the channel. The Beagle Channel is ice-free throughout the whole year (Iturraspe et al., 1989; Isla et al., 1999).

3. Materials and methods

3.1. Sampling and laboratory treatments

The 22 surface sediment samples were collected in the Beagle Channel, between Bahía Lapataia and Punta Navarro, Tierra del Fuego (Fig. 1) during two cruises of the Argentine Coast Guard ships, Río Uruguay and Canal Beagle, using a Clamshell Grab-type sampling device. The samples were grouped into three sectors: western, central and eastern, according to the sampling localities (Table 1). The western sector includes Bahía Lapataia (BL), Bahía Golondrina (BG) and Bahía Ushuaia (BU). The central sector comprises Punta Remolino (PR) and Punta Paraná (PP). The eastern sector includes Isla Gable (IG) and Exterior Isla Gable (EIG). In general, the sediment lithologies consist of fetid dark gray clays and dark brown medium-coarse sands with the presence of abundant mollusk shells. The sediments in the western sector (samples FCB4, FCB5, FCB7, FCB8, FCB9, FCB24, FCB27, FCB28 and FCB29) are characterized by greenish gray clays and gray fine sands, with the exception of sample FCB6 which consists of medium to coarse sands. In the central sector, the samples (FCB3, FCB10, FCB11, FCB21 and FCB22) consist of dark
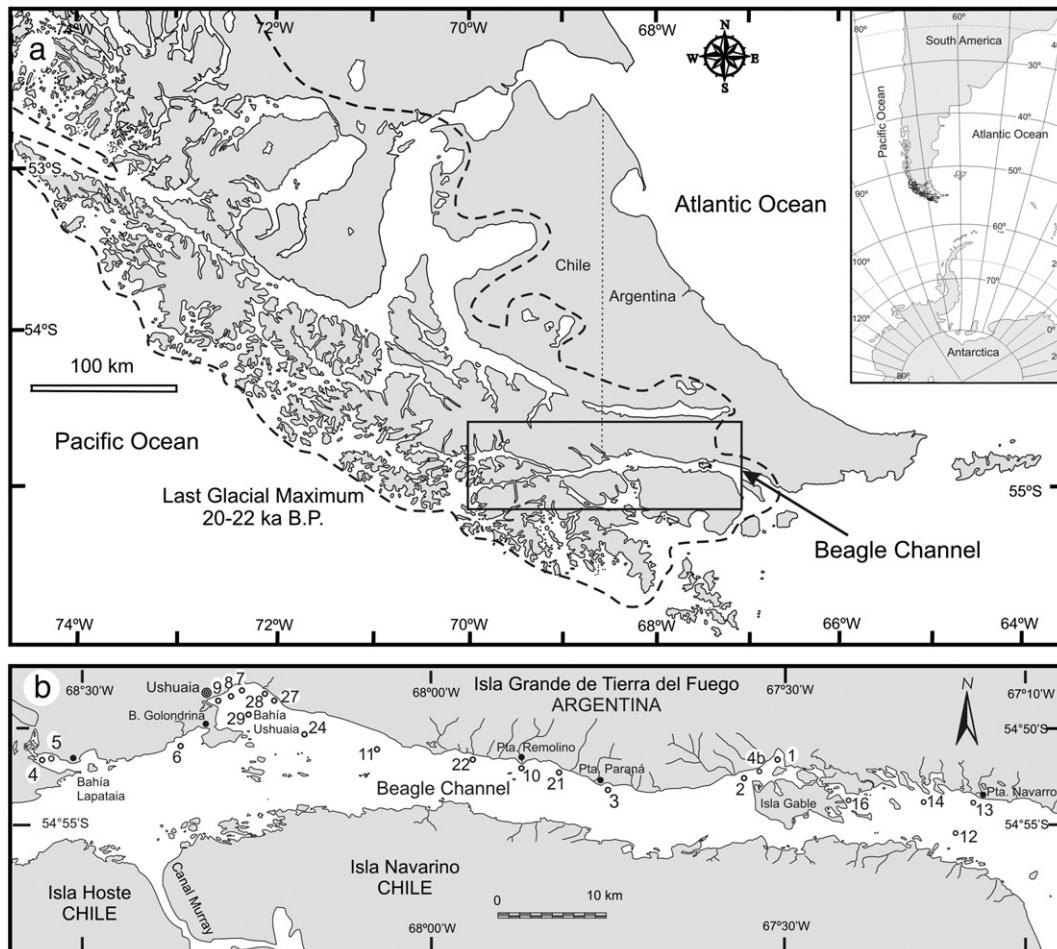

Fig. 1. Map of the study area and location of sampling sites. a) Isla Grande de Tierra del Fuego and position of the Last Glacial Maximum ice limit (Rabassa et al., 2000). b) Beagle Channel and sediment sample locations.

Table 1
Sampling site number, location and sediment type. Dinocyst and other aquatic palynomorph counts and concentrations.

Locality name		Sample number	Laboratory number	Latitude	Longitude	Sediment type	Dinocyst counts	Other aquatic palynomorph counts	Dinocysts/g	Other aquatic palynomorphs/g
Western sector	Bahía Lapataia (BL)	FCB5	2347-5	54°51′08″S	68°33′46″W	Clay	319	1244	4318	16839
		FCB4	2347-4	54°51′37″S	68°33′32″W	Clay	283	1373	1599	7760
	Bahía Golondrina (BG)	FCB6	2349-2	54°50′24″S	68°21′35″W	Medium-coarse sand	4	50	7	88
	Bahía Ushuaia (BU)	FCB9	2347-1	54°48′45″S	68°18′30″W	Silty-clay	219	144	2036	1339
		FCB8	2349-4	54°48′40″S	68°17′40″W	Silty-clay	130	120	612	565
		FCB7	2349-3	54°48′10″S	68°16′30″W	Clay	292	251	2277	1957
		FCB29	3867	54°48′38″S	68°16′28″W	Clay with mollusk shells	231	373	936	1512
		FCB28	3866	54°48′01″S	68°15′07″W	Clay with mollusk shells	221	412	904	1686
		FCB27	3865	54°48′25″S	68°13′57″W	Fine sand with mollusk shells	115	120	292	305
		FCB24	3864	54°50′18″S	68°11′58″W	Fine sand with mollusk shells	129	167	253	328
Central sector	Punta Remolino (PR)	FCB11	3167	54°51′23″S	68°03′21″W	Clay with mollusk shells	321	394	1640	2013
		FCB22	3862	54°51′37″S	67°56′02″W	Silt with mollusk shells	155	505	516	1682
		FCB10	3166	54°52′16″S	67°51′36″W	Clay with mollusk shells	309	228	3196	2379
		FCB21	3172	54°52′11″S	67°49′13″W	Silty-clay with mollusk shells	353	404	3569	4085
	Punta Parana (PP)	FCB3	2347-3	54°52′45″S	67°45′30″W	Sandy-silt with mollusk shells	314	306	3706	3611
Eastern sector	Isla Gable (IG)	FCB2	2347-2	54°52′15″S	67°33′00″W	Clay with mollusk shells	297	247	5568	4630
		FCB4b	3165	54°52′32″S	67°33′18″W	Clay with mollusk shells	391	462	5026	5939
		FCB1	2349-1	54°51′30″S	67°30′30″W	Silty-clay	276	336	3172	3862
	Exterior Isla Gable (EIG)	FCB16	3171	54°53′53″S	67°22′32″W	Clay with mollusk shells	345	388	3135	3526
		FCB14	3170	54°53′52″S	67°17′24″W	Silt with mollusk shells	296	513	1177	2040
		FCB12	3168	54°55′20″S	67°13′53″W	Fine-medium sand	6	16	49	131
		FCB13	3169	54°54′20″S	67°12′32″W	Clay	332	328	3116	3078

gray and dark brown sediments, mainly clays and silts, with abundant mollusk shell fragments in all samples. The eastern sector (FCB1, FCB2, FCB4b, FCB12, FCB13, FCB14 and FCB16) is characterized by dark gray clays and silts, with the presence of abundant mollusk shells (Table 1). All samples were processed for palynological analysis following the standard procedure of the micropalaeontological laboratory at GEOTOP (de Vernal et al., 1999). Samples of 5 to 10 g of dry sediment were wet sieved at 106 and 10 µm in order to remove particles above and below this size range. To dissolve carbonates and silicates, the 106–10 µm fraction was treated several times with HCL (10%) and HF (49%). A tablet containing a known number of *Lycopodium clavatum* spores was added to each sample for the calculation of palynomorph concentrations (Stockmarr, 1971). The final residue was sieved at 10 µm to eliminate particles smaller than this size and was mounted between a slide and cover slide in glycerine gel. In most samples, a minimum of 200 dinocysts and other aquatic palynomorphs were counted using a transmitted light microscope at 400 and 1000× (Table 1). Due to low dinocyst and aquatic palynomorph concentrations of sediments from Bahia Golondrina (sample FCB6) and Exterior Isla Gable (sample FCB12), the counts were less than 50 palynomorphs and were excluded from the analysis. In this study, we present only the relative frequencies (%) and concentrations based upon counts of total aquatic palynomorphs (organic-walled dinoflagellate cysts, acritarchs, Chlorophyta algae, copepod eggs and foraminiferal linings). Further information on pollen and spores, and their ecological implications for the Beagle Channel area are given by Candel (2010). The relative frequencies (%) of dinocysts and other aquatic palynomorphs, as well as the concentrations (specimens/g) were represented using the program TILIA 2.0.b.4 (Grimm, 1991) and TGview 2.0.2 (Grimm, 2004). Principal component analysis (PCA) was performed on selected taxa representing variables using the software Past (Hammer and Harper, 2009). The results showed that the reconstruction percentage of the variables (taxa) was not optimal and there was not optimal and there was no relevant correlation among the different variables.

3.2. Taxonomy of dinocysts

The taxonomic nomenclature of dinoflagellate cysts used in this study conforms to that presented in Rochon et al. (1999), Zonneveld

(1997) and Head et al. (2001). The assemblages include *Islandinium cezare minutum*, *Islandinium? cezare*, *Echinidinium granulatum*, *Trinovantedinium applanatum*, *Pentapharsodinium dalei*, *Selenopemphix nephroides*, *Selenopemphix quanta*, *Votadinium spinosum*, *Votadinium calvum*, *Brigantedinium cariacoense*, *Brigantedinium simplex*, *Spiniferites lazus*, *Spiniferites* sp., *Polykrikos schwartzii*, *Polykrikos kofoidii*, among others (Figs. 2, and 3 and Table 2). Some identified dinocysts in this study show morphological differences from the species type described for the Northern Hemisphere and other sites. The most important morphological features are explained in Appendix A and a summary is provided in Table 3.

Owing to difficulties of identification at the species level, some taxa were grouped together for the analyses. This is the case for *Echinidinium* spp., which comprises *Echinidinium granulatum*, *Echinidinium* cf. *E. granulatum*, and *Echinidinium* cf. *E. delicatum*. The *Spiniferites* spp. group includes *Spiniferites lazus*, *Spiniferites ramosus*, cf. *Spiniferites mirabilis*, and unidentified specimens that show an affinity to the genus *Spiniferites*. Many specimens belonging to Protoperidiniales were grouped as undifferentiated protoperidinioids due to the difficulty in identifying them to a genus or a species level. The spherical shape and brown color of these cysts suggested a protoperidiniacean affinity in spite of scientists not being able to recognize the archeopyle, and the unsuitable orientation or inability to distinguish important taxonomic features. Similarly, proximochorate and chorate dinocysts that could not be properly assigned to a given genus were included within the categories of undifferentiated proximochorate cysts and undifferentiated chorate cysts, respectively. Cysts characterized by high degradation, compression and dark yellow to brownish color were grouped as reworked dinocysts.

3.3. Other aquatic palynomorphs

The recorded acritarchs include Acritarch sp. 1, Acritarch sp. 2 and ?*Cyclopsiella* sp. (Candel, 2010). Acritarch sp. 1 includes organic-walled vesicles, psilate to microgranulate, characterized by the presence of a large pylome with circular to oval outline. The operculum occurs usually in the interior of the vesicle (Fig. 3). Acritarch sp. 2 comprises palynomorphs with a sub-circular outline and dark brown color (Fig. 3). The wall is thick and evenly granulated

giving it a "honeycomb" appearance, covered by a thin and smooth membrane. No opening was observed. This form has similarities with *Cyclopsiella granosa* due to the presence of an inner granulated wall and an outer smooth veil, but a pore was not observed and the body size is greater than *Cyclopsiella*. On the other hand, there is a similarity to the "honeycomb"-type wall of *Tasmanites* although it differs in the presence of an outer veil. ?*Cyclopsiella* sp. includes discoidal cysts, with the body wall being microgranular, thin and pale yellow. The body is surrounded by a thin and diaphanous flange with ragged outer margin. The sub-circular pylome has a smooth edge located in a sub-polar position, near one edge of the cyst (Fig. 3).

Organic-walled zoomorphs include *Halodinium* sp., which possibly belong to the thecamoebians (e.g. de Vernal et al., 1989), benthic foraminiferal linings and copepod egg envelopes. Other aquatic palynomorphs are represented by tasmanids and *Polyasterias* sp., which are both associated with algal protists.
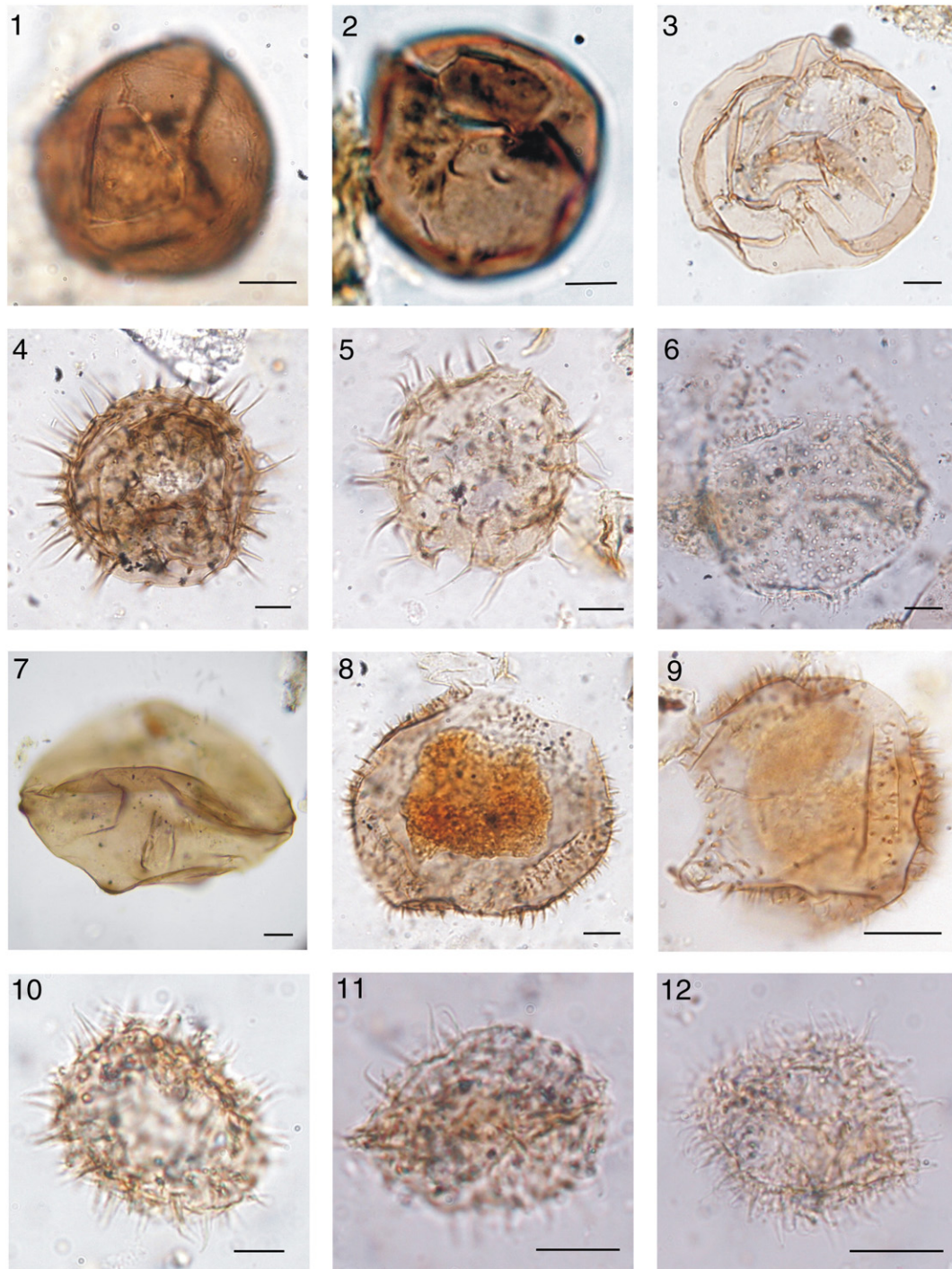

Fig. 2. Scale bar is 10 μm. Sample number followed by England Finder coordinates. 1, *Brigantedinium simplex* FCB2347-2: Y19/2. 2, *Brigantedinium cariacoense* FCB2347-2: M28. 3, *Selenopemphix nephroides* FCB2347-3: J59/3. 4, *Selenopemphix quanta* FCB2347-5: J15. 5, *Selenopemphix* cf. *S. quanta* FCB2347-5: J25. 6, *Trinovantedinium* cf. *T. applanatum* FCB2347-5: Y36/1. 7, *Quinquecuspis concreta* FCB3166: B47. 8, *Votadinium spinosum* FCB2347-5: N20/4. 9, *Islandinium minutum* FCB2347-2: C48. 10, *Echinidinium granulatum* FCB2347-3: L17/3. 11, *Echinidinium* cf. *E. granulatum* FCB2347-5: M12/4. 12, *Echinidinium* cf. *E. delicatum* FCB2347-3: Q9.
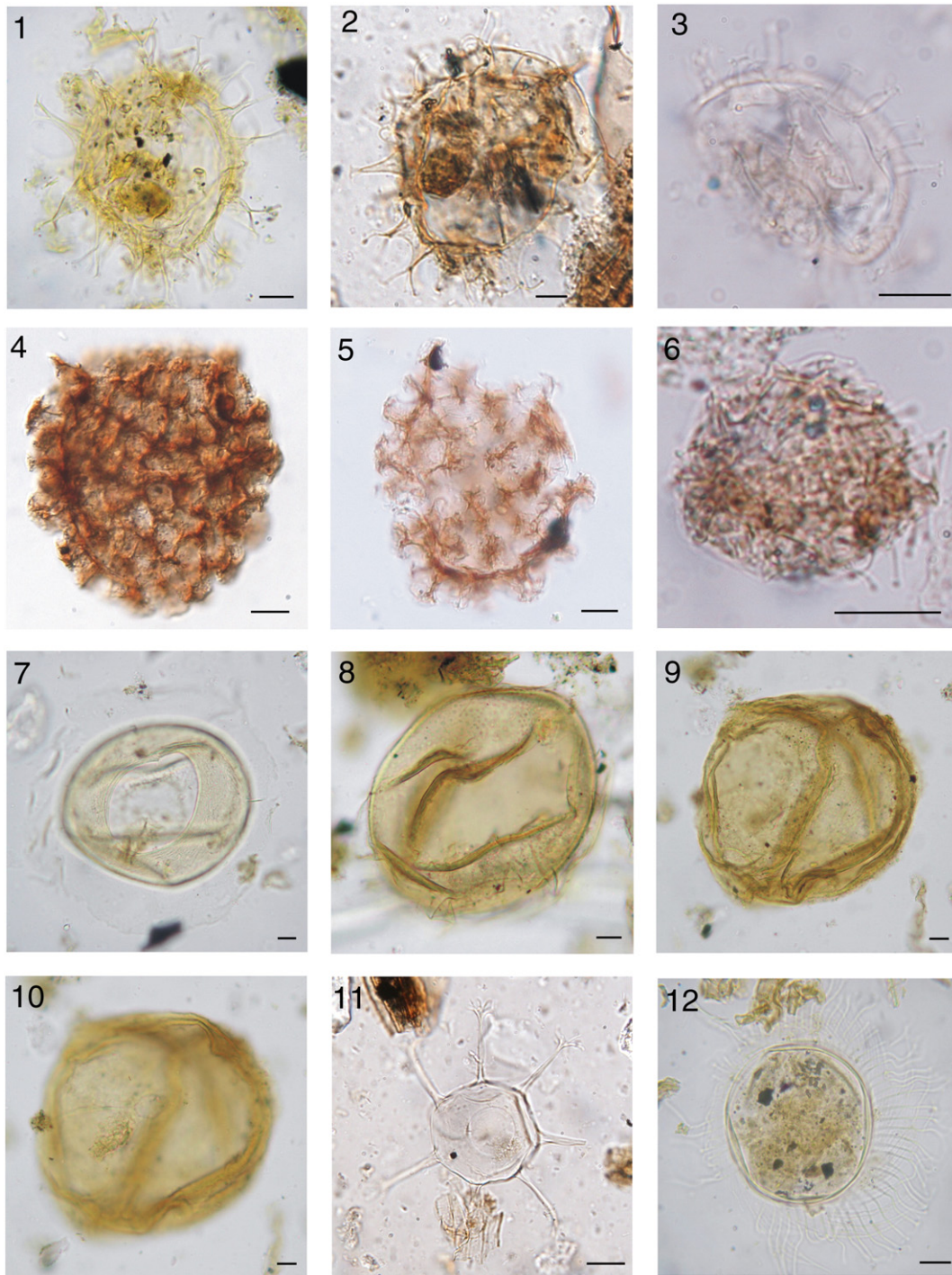
Fig. 3. Scale bar is 10 μm. Sample number followed by England Finder coordinates. 1, *Spiniferites lazus* FCB2347-4: M26/2. 2, *Spiniferites* sp. FCB2347-5: R16. 3, *Pentapharsodinium dalei* FCB2347-1: L44. 4, *Polykrikos kofoidii* FCB2347-2: J40/4. 5, *Polykrikos schwartzii* FCB2347-2: S34/4. 6, Dinocyst sp. 1. FCB2347-1b: S11/4. 7, Acritarch sp. 1 FCB3166: U29/2. 8, Acritarch sp. 2 FCB3166: H33/1. 9–10, ? *Cyclopsiella* sp. FCB3166: P41/2. 11, *Polyasterias* sp. FCB 2347-5: E35. 12, *Radiosperma corbiferum* FCB2349-1: M20/4.

4. Results

4.1. Western sector of Beagle Channel

The most abundant aquatic component in the western sector (BL, BG and BU localities; Fig. 1) is *Halodinium* sp. (up to 77.6%). The dinocysts reach up to 60.3%, and the most abundant taxa are *Brigantedinium* spp., *Selenopemphix quanta*, *Selenopemphix* cf. *S. quanta* and *Pentapharsodinium dalei*. They are accompanied by *Echinidinium granulatum*, *Echinidinium* cf. *E. delicatum*, *Echinidinium* spp., *Islandinium minutum*, *Selenopemphix nephroides*, *Trinovantedinium* cf. *T. applanatum*, *Votadinium calvum*, *Votadinium spinosum*, *Quinquecuspis concreta*, *Dubridinium* cf. *D.* sp., *Spiniferites ramosus*, *Spiniferites lazus*, *Polykrikos kofoidii*, *Polykrikos schwartzii* and Dinocyst sp. 1 (Table 2). Copepod eggs and organic foraminiferal linings are also present reaching up to 8.8% and 43.9%, respectively. Algae such as *Botryococcus*, Zygnemataceae, Tasmanaceae and *Polyasterias* sp. occur occasionally and represent less than 4%. Total aquatic palynomorph concentrations ranged between 581 and 21,157 palynomorphs/g (Fig. 4).

Table 2
List of identified aquatic palynomorphs in surface sediments from the Beagle Channel area.

Sector	Western	Central	Eastern
Dinocysts			
Brigantedinium cariacoense (Wall, 1967) Lentin and Williams, 1993		x	x
Brigantedinium simplex Wall, 1965 ex Lentin and Williams, 1993	x	x	x
Brigantedinium spp.	x	x	x
Dinocyst sp. 1	x	x	x
Dubridinium cf. *D.* sp. Reid, 1977	x		x
Echinidinium cf. *E delicatum* Zonneveld, 1997	x	x	x
Echinidinium granulatum Zonneveld, 1997	x	x	x
Echinidinium cf. *E. granulatum* Zonneveld, 1997	x	x	x
Echinidinium spp.	x	x	x
Islandinium? *cezare* (de Vernal et al., 1989 ex de Vernal in Rochon et al., 1999) Head et al., 2001	x	x	x
Islandinium minutum (Harland and Reid in Harland et al., 1998) Head et al., 2001	x	x	x
Pentapharsodinium dalei Indelicato and Loeblich III, 1986	x	x	x
Polykrikos kofoidii Chatton, 1914	x	x	x
Polykrikos schwartzii Bütschli, 1873	x	x	x
Protoperidinioids	x	x	x
Quinquecuspis concreta (Reid, 1977) Harland, 1977	x	x	x
Selenopemphix nephroides (Benedek, 1972) Benedek and Sarjeant, 1981	x	x	x
Selenopemphix quanta (Bradford, 1975) Matsuoka, 1985	x	x	x
Selenopemphix cf. *S. quanta* (Bradford, 1975) Matsuoka, 1985	x	x	x
Spiniferites lazus Reid, 1974	x		
Spiniferites ramosus (Ehrenberg, 1838) Mantell, 1854 sensu lato	x	x	x
Spiniferites cf. *S. mirabilis* (Rossignol 1964) Sarjeant, 1970			x
Spiniferites sp.	x		
Spiniferites spp.	x	x	x
Trinovantedinium cf. *T. applanatum* (Bradford, 1977) Bujak and Davies, 1983	x	x	
Votadinium calvum Reid, 1977	x	x	x
Votadinium spinosum Reid, 1977	x	x	x
Dinocyst species diversity	17	16	17
Acritarchs			
Acritarch sp. 1		x	x
Acritarch sp. 2		x	
?*Cyclopsiella* sp.		x	
Halodinium sp.	x	x	x
Zoomorphs			
Copepod eggs	x	x	x
Foraminiferal linings	x	x	x
Other algae			
Botryococcus braunii Kützing, 1849	x		
Botryococcus sp.	x	x	x
Zygnemataceae	x		x
Spirogyra sp.		x	
Tasmanaceae	x		
Radiosperma corbiferum Meunier, 1910	x	x	x
Polyasterias sp.	x	x	x

4.2. Central sector of Beagle Channel

This sector comprises the Punta Remolino (PR) and Punta Paraná (PP) localities (Fig. 1). It has a moderate number of fluvial streams that come from smaller interior basins than those of the western part of the Beagle Channel.

The aquatic palynomorphs record a high abundance in this area, and the dinocysts dominate the assemblages with percentages reaching up to 57.1% and with a relatively low species diversity (16 identified taxa, Table 2). The foraminiferal linings and *Halodinium* sp. represent up to 40% and 21.1%, respectively. The dinocyst assemblages are characterized

by *Brigantedinium* spp., *Selenopemphix* cf. *S. quanta*, *Echinidinium* spp., *Selenopemphix quanta*, *Spiniferites* spp., *Pentapharsodinium dalei*, *Polykrikos kofoidii*, *Polykrikos schwartzii*, *Islandinium minutum*, *Votadinium spinosum*, *Selenopemphix nephroides*, *Quinquecuspis concreta*, *Votadinium calvum*, *Trinovantedinium* cf. *T. applanatum*, *Islandinium*? *cezare*, *Brigantedinium simplex*, *Brigantedinium cariacoense* and *Echinidinium* cf. *E. delicatum*. Other marine palynomorphs are represented by copepod eggs (up to 18.5%) and acritarchs (up to 2.2%). The marine to brackish algae (*Radiosperma corbiferum* and *Polyasterias* sp.) together with the freshwater algae (*Botryococcus* sp. and *Spirogyra* sp.) represent less than 1.3%. The aquatic palynomorph concentration ranges between 2198 and 7654 palynomorphs/g (Fig. 4).

4.3. Eastern sector of Beagle Channel

The foraminiferal linings are the most abundant palynomorphs reaching up to 46.8% of the aquatic palynomorph assemblages, along with dinocysts (up to 54.6%). The dominant dinocyst taxa are *Brigantedinium* spp., cyst of *Pentapharsodinium dalei*, *Spiniferites* spp. and *Islandinium minutum*. They are accompanied by *Echinidinium* spp., *Echinidinium* cf. *E. delicatum*, *Echinidinium granulatum*, *Selenopemphix nephroides*, *Selenopemphix quanta*, *Selenopemphix* cf. *S. quanta*, *Votadinium spinosum*, cysts of *Polykrikos kofoidii*, cysts of *Polykrikos schwartzii* and Dinocyst sp. 1. Other marine palynomorphs include copepod eggs (up to 11.2%). *Halodinium* sp. records low percentages between 3 and 28.3%, whereas freshwater algae and brackish-marine algae (*Botryococcus* sp., Zygnemataceae, *Radiosperma corbiferum* and *Polyasterias* sp.) record percentages ranging between 1.6 and 18%. The total aquatic palynomorph concentration ranges from 3217 to 10,965 palynomorphs/g (Fig. 4).

5. Discussion

5.1. Dinoflagellate cyst assemblages and concentrations

The palynological analysis of surface sediments from the Beagle Channel shows the predominance of terrestrial palynomorphs (pollen and spores) over aquatic palynomorphs (dinocysts, acritarchs and zoomorphs) (Candel, 2010). The dinocyst assemblages are characterized by relatively low species diversity and Peridiniales taxa dominate over Gonyaulacales, which is often the case in inner neritic environments (e.g. de Vernal and Giroux, 1991; Grøsfjeld et al., 2009). The assemblages dominated by Protoperidiniaceae along with foraminiferal linings and copepod eggs suggest the proximity of a terrestrial source with a high input of organic matter in the marginal-marine environment under restricted circulation conditions. The record of *Halodinium* sp., *Radiosperma corbiferum*, *Polyasterias* sp., *Botryococcus braunii* and *Botryococcus* sp. suggests low to moderate salinity and high nutrient content in surface waters due to river inputs. In the western sector of the channel, the high percentages of *Halodinium* sp. are related to the high input of freshwater and nutrients by rivers in a transitional environment from brackish to marine (de Vernal et al., 1989; Mudie, 1992; Head, 1993). This sector has a high number of freshwater streams that come from cirque glaciers located in the high Andean valleys (Isla et al., 1999). In the eastern sector (IG and EIG localities) of the channel, high percentages of the genus *Spiniferites* and abundant foraminiferal linings, point to fully marine conditions related to the influence of the Atlantic Ocean waters.

The analysis reveals dinocyst assemblages characterized by low concentrations (253–5568 dinocyst/g), which could result from the dilution of marine microfossils because of the high sedimentation rate, low cyst fluxes related to low productivity, or unfavorable conditions for preservation such as exposition of material, and sediment grain sizes. Also, an important point to remember about dinoflagellates is that approximately 15% of living species are known to produce resting cysts with walls of organic, calcareous or siliceous composition, although the latter cyst types are subject to dissolution problems

Table 3

Main morphological differences of some identified dinocysts in relation to the type species described by different authors from sediments in the Northern and Southern Hemispheres.

Dinocyst	Central body			Processes			Archeopyle	Specimens measured
	Diameter (μm)	Shape	Cyst wall	Length (μm)	Form	Characteristics		
Echinidinium cf. *E. granulatum*	21 (28.3) 43	Spherical to sub-spherical	Granulate	4 (5) 9	Acuminate	Hollow and solid with circular expanded bases	Split along suture	15
Echinidinium cf. *E. delicatum*	19 (23.2) 28	Spherical	Smooth	2 (4.1) 5	Acuminate	Hollow with sub-circular bases	Split along suture	15
Selenopemphix quanta	30 (45.1) 66	Sub-spherical to reniform	Smooth	4 (10.5) 14.4	Sharp and blunt	Solid with expanded bases	Intercalary	30
Selenopemphix cf. *S. quanta*	30 (38.4) 48.8	Sub-spherical	Smooth	5-(9.8) 13	Sharp and blunt	Solid, without expanded bases	Intercalary, not clearly observable	22
Trinovantedinium cf. *T. applanatum*	65 (65.7) 75.4	Pentagonal to rounded	Smooth to microgranulate	2.4 (3.8) 5	Acuminate	Short processes or spines with intratabular distribution	Intercalary, not clearly observable	6
Pentapharsodinium dalei	19 (26) 33.8	Spherical	smooth	3 (4.6) 6.5	Branched	Solid with expanded bases	Split (chasmic)	25
Polykrikos kofoidii	31.5 (54.8) 75	Elongate	Outer fibrous membrane forming an irregular reticulum	4 (11) 20	Fibrous ridges	Distally open defined by an irregular reticulum	Apical	13
Polykrikos schwartzii	42.4 (58.2) 83	Sub-elongate	Fibrous and coarsely wrinkled	4.8 (8.3) 14.7	Cylindrical	Isolated, fibrous and thick, distally open	Apical	25
Dinocyst sp. 1	18 (22.4) 28	Spheroidal	Smooth	3 (3.8) 4.8	Commonly capitate	Solid, thin and flexible, circular and unexpanded bases	Unknown	10

(Mudie et al., 2001). The species producing fossilizable organic-walled cysts constitute a relatively small percentage of the overall living dinoflagellate population (de Vernal et al., 1997).

In the present case, preservation cannot be invoked because the dominant taxa, which are cysts of the *Protoperidinium* species (*Brigantedinium* spp. and species of the genera *Echinidinium* and *Selenopemphix*) are also those which are the most sensitive to oxidation (e.g. Zonneveld et al., 2008). Moreover, the presence of pyrite associated with phytoclasts and palynomorphs suggests reducing conditions in the surface sediment (Candel, 2010), thus favorable to the good preservation of palynomorphs. On the other hand, the sediment grain size is an important factor influencing the dinocyst concentrations. Low concentration values might be related to the poor preservation of palynomorphs in coarse lithologies (coarse sands). In the BG locality, low concentrations and species diversity of dinocysts might be related to coarse-grained sediments, in addition to the dilution of biogenic remains by high terrigenous inputs in a marine environment under stress due to low and fluctuating salinities (24–31; Aguirre and Lovrich, pers. comm., 2010). Low productivity is also unlikely in view of the occurrence of copepod eggs and because the Protoperidiniacean taxa usually characterize high productivity environments (e.g. Radi and de Vernal, 2008). The occurrence of copepod eggs could be related to high productivity under a high continental input regime (van Waveren, 1994). Thus, the low concentrations are probably due to dilution by high inputs of terrigenous matter, which is normal given the nearshore location of all sites. According to Isla et al. (1999), the Beagle Channel has a high number of freshwater streams that come from the cirque glaciers located in the high Andean valleys. Thus the contribution of detritus is important and forms plumes of suspended sediment several hundred meters into the channel. This is consistent with palynofacies analyses showing the dominance of translucent phytoclasts accompanied by amorphous organic matter (Candel, 2010).

5.2. Distribution of the main dinoflagellate cyst taxa

Among the Peridiniales, the *Brigantedinium simplex* has an inner neritic distribution in the North Atlantic (Harland, 1983) and occurs in cold temperate zones to Arctic zones (e.g. Dale, 1983; Edwards and Andrle, 1992; Rochon et al., 1999). Its occurrence in the Beagle Channel is thus compatible with the known distribution of the species. This is not the case with *Votadinium spinosum*, which has been recorded for the Northern Hemisphere in temperate to subtropical regions (e.g. Marret and Zonneveld, 2003; Radi and de Vernal, 2004, 2008; Limoges et al., 2010). Thus, the occurrence of *V. spinosum* in the surface samples from the Beagle Channel extends its known distribution to cool temperate regions. Similarly, *Echinidinium delicatum* and *Echinidinium granulatum* have been reported mostly from subtropical to tropical regions characterized by meso/eutrophic conditions where temperatures range from 13.4 to 29.6 °C (winter–summer) and salinities range from 26.5 to 36.6 (Zonneveld, 1997; Marret and Zonneveld, 2003; Vásquez-Bedoya et al., 2008; Limoges et al, 2010). *Echinidinium granulatum* has also been documented in the North Pacific (Radi and de Vernal, 2004; Radi et al., 2007; Radi and de Vernal, 2008). The occurrence of *E. granulatum*, *E.* cf. *E. delicatum* and *Echinidinium* spp. in the Beagle Channel, suggests that their distribution may extend to subpolar regions and that the primary factor in their distribution is not sea-surface temperature.

The taxon *Islandinium minutum* shows a bipolar distribution in coastal areas north of 30°N and south of 30°S. The distribution maps of Rochon et al. (1999) and de Vernal et al. (2001), indicate a wide distribution in the Arctic and cool temperate regions of the North Atlantic Ocean. In addition, Harland et al. (1998) and Harland and Pudsey (1999) indicate its presence in modern polar regions of the Southern Hemisphere (Southern Ocean). *Islandinium minutum* has been observed in a wide range of temperatures and salinities, between freezing point and 27 °C (winter–summer) and 21.3 and 35.3 (spring–summer) respectively. However, maximum abundances and high percentages have been found in regions with sea-surface temperatures below 5 °C. Its tolerance to variable salinities probably explains its abundance in estuarine environments (Head et al., 2001). These conditions are consistent with those prevailing in the Beagle Channel and could explain its occurrence in surface sediments from this area. Similarly, *Islandinium*? *cezare* is characteristic of cold, polar and subpolar regions with seasonal sea-ice cover. This taxon is found in a wide range of salinities and nutrient conditions in areas marked by seasonal fluctuations in physical parameters (Marret and Zonneveld, 2003).

Protoperidiniacean taxa such as *Quinquecuspis* sp., *Selenopemphix nephroides*, *Votadinium calvum* and Diplopsalidae such as *Dubridinium*
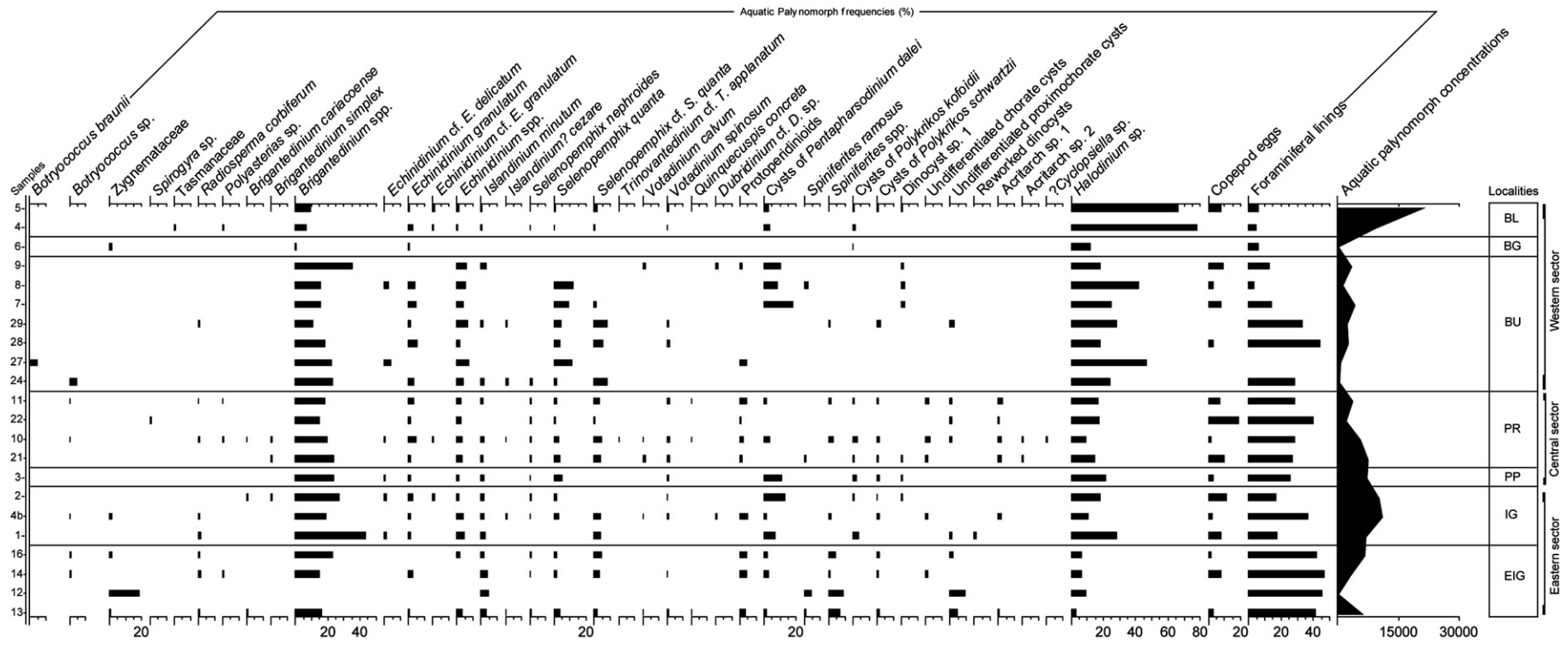
Fig. 4. Percentages and concentrations of aquatic palynomorphs in surface sediment samples from the Beagle Channel.

sp., among others, are often documented in low latitude marine environments (Lewis et al., 1990; Marret, 1994) and are usually associated with relatively warm (16°–21 °C) and high salinity conditions. Their ecological affinity for warm water might explain their rarity at middle to high latitudes. However, these species were reported from colder environments of the North Pacific Ocean (Radi et al., 2001) and in the Beagle Channel (this study), suggesting that their distribution is probably not primarily determined by temperature. On the other hand, *Selenopemphix quanta* has mainly been documented in coastal sites from the Northern Hemisphere to the Southern Hemisphere Subtropical Front (roughly north of 45°S). It is distributed in a broad range of temperatures between freezing point and 29.6 °C (winter–summer) and salinities between 16.9 and 36.7 (winter–summer) (Marret and Zonneveld, 2003). According to Rochon et al. (1999) and de Vernal et al. (2001) this species shows greater adaptability to temperatures varying between 8 and 14 °C and salinities between 23 and 31. Thus, the presence of *S. quanta* in sediments from the Beagle Channel extends its known distribution to cool temperate regions to south of 45°S.

Cysts of *Pentapharsodinium dalei* are found from temperate to Arctic regions. This taxon occurs in a wide range of temperatures, from freezing point to 29.6 °C, and salinities ranging from 21.3 to 36.7, but it clearly shows a preference for cool temperate conditions to subpolar conditions (Marret and Zonneveld, 2003; Radi and de Vernal, 2008). It tolerates dense sea-ice cover throughout most of the year (de Vernal et al., 1997; Harland et al., 1998; de Vernal et al., 2001, 2005; Matthiessen et al., 2005). Its maximum abundance is reported in cold environments. Harland et al. (2004) suggested that it is an opportunistic species in areas with high anthropogenic activity and high nutrient inputs from local runoff during spring, thus favoring phytoplankton blooms. According to Radi et al. (2007), this species occurs in stratified waters marked by continental runoff and seems to be characteristic of coastal areas near urban centers. In the surface sediments of the Beagle Channel, the cysts of *P. dalei* show morphological differences when compared to those described from the North Atlantic, especially regarding the central body size and process length. They occur in relatively high percentages (up to 17%), near the port of Ushuaia City (Bahia Ushuaia) and the Isla Gable area, which are characterized by cold and stratified surface waters due to abundant freshwater runoff and meltwater discharge through the rivers during spring and summer. At these locations, the proximity of urban areas could also result in high nutrient input.

Polykrikos schwartzii has been previously reported as *Polykrikos kofoidii* (e.g., Matsuoka, 1985, 1987; Marret and Zonneveld, 2003; Radi and de Vernal, 2004). Here, the identification of *Polykrikos schwartzii* and *Polykrikos kofoidii* conforms to that of Matsuoka et al. (2009). For this reason, the environmental conditions previously associated with each species of *Polykrikos* have to be carefully considered. In the Beagle Channel, *P. schwartzii* and *P. kofoidii* are both smaller than those described in Rochon et al. (1999), Matsuoka (1985, 1987) and Matsuoka and Cho (2000). *P. schwartzii* is a tropical to temperate species and seems to be more adapted to temperatures and salinities ranging between 25 and 29 °C and between 31.6 and 36.6, respectively. It has been described (as *P. kofoidii*) in Japanese coastal waters (Matsuoka, 1985) and is also frequently reported in coastal regions and upwelling areas, between 45° N and 45°S. Radi et al. (2001) documented *P. schwartzii* (also under the name of *P. kofoidii*) from the northern Pacific (Bering and Chukchi seas). Its occurrence in samples from the Beagle Channel suggests that this species can tolerate cold temperatures.

Selenopemphix antarctica was not found in the surface sediments from the Beagle Channel. This species characterizes the high latitudes of the Southern Ocean and is considered to be an endemic species of the Antarctic region (cf. Marret and de Vernal, 1997; Marret et al., 2001). This taxon is distributed in sediments from cold/polar, fully marine, mesotrophic to extreme eutrophic environments where sea ice develops seasonally (cf. Marret and de Vernal, 1997; Marret et al., 2001; Marret and Zonneveld, 2003). Its absence from the Beagle Channel assemblages suggests that this species is exclusive to Antarctic oceanic areas where there is a seasonal sea-ice cover (cf. Marret and de Vernal, 1997; Marret et al., 2001).

6. Conclusions

The present study provides the first record of dinocyst assemblages from recent sediments off the coast of southern South America. The dinocyst assemblages are dominated by Protoperidiniales and could be associated with estuarine environments affected by glacier meltwater discharge resulting in low sea-surface salinities. They are comparable with the assemblages from the continental shelf of the Arctic Ocean, which is also strongly influenced by freshwater inputs from rivers. However, the modern assemblages of the Beagle Channel include taxa previously reported in temperate to warm climatic domains. These taxa include *Echinidinium granulatum*, *Echinidinium delicatum*, *Polykrikos kofoidii*, *Quinquecuspis concreta*, *Votadinium calvum* and *Votadinium spinosum*. This finding suggests that surface water temperature and salinity may not be the most determinant parameters controlling the distribution of these species. Hence, this study extends the known ecological range of some dinocyst species as published in the literature (e.g. Marret and Zonneveld, 2003; Radi and de Vernal, 2008). Finally, it is noteworthy that specimens recovered from the Beagle Channel show morphological differences from the type of species described for the Northern Hemisphere, suggesting the existence of sub-species and possibly cryptic species in the Northern and Southern Hemispheres. Further palynological studies of samples collected along the coasts of Tierra del Fuego could help to obtain a more comprehensive view of the dinocyst distribution in subpolar regions of the Southern Hemisphere.

Appendix A. Systematic descriptions

Division Dinoflagellata (Bütschli, 1885) Fensome et al., 1993
Subdivision Dinokaryota Fensome et al., 1993
Class Dinophyceae Pascher, 1914
Subclass Peridiniphycidae Fensome et al., 1993
Order Peridiniales Haeckel, 1894
Suborder Peridiniineae (autonym)
Family Protoperidiniaceae Balech, 1988
Subfamily Protoperidinioidae Balech, 1988

Genus ***Echinidinium*** Zonneveld, 1997 ex Head et al., 2001
Type species. *Echinidinium granulatum* Zonneveld, 1997
Echinidinium* cf. *E. granulatum Zonneveld, 1997
(Fig. 2.11)
Description. Spherical spiny cysts with numerous randomly distributed processes. Cyst wall granulate and pale brown. Processes

are acuminate, hollow and solid with a circular transverse section at base. Archeopyle indicated by a single split along one or more sutures.

Dimensions. Central body diameter, 21 (28.3) 43 μm. Process length, 4 (5) 9 μm. Diameter process base, 1.5 (2.7) 4 μm, (15 specimens measured).

Remarks. Differs from *E. granulatum* by having shorter processes than the range given by Zonneveld (1997) and shows both hollow and solid processes (Table 3). For this reason, these specimens of *Echinidinium* are compared but not assigned to *E. granulatum* and referred to here as *Echinidinium* cf. *E. granulatum*.

Echinidinium cf. E. delicatum Zonneveld, 1997
(Fig. 2.12)
Description. Proximochorate spherical cysts with numerous slender processes. The periphragm surface is smooth and pale brown. The processes are non-tabular, hollow and acuminate with sub-circular bases at the cross-section. Archeopyle indicated by split along one or more sutures.

Dimensions. Body diameter, 19 (23.2) 28 μm. Process length, 2 (4.1) 5 μm, (15 specimens measured).

Remarks. Specimens referred to here as *Echinidinium* cf. *E. delicatum* are characterized by hollow and acuminate processes but the cyst wall is often not clearly seen unlike the specimens described by Zonneveld (1997) (Fig. 2, Table 3), and for this reason the specimens found in the Beagle Channel are compared with *E. delicatum*.

Dinocyst sp. 1
(Fig. 3.6)
Description. Proximochorate, spheroidal and brown cysts. The cyst wall is smooth with numerous non-tabular, solid, thin and flexible processes. The processes are mostly capitate, although a few specimens show acuminate process tips. Process bases are circular and not expanded. The distance between two processes is about 2 μm. The archeopyle is unknown.

Dimensions. Central body diameter, 18 (22.4) 28 μm. Length of the processes, 3 (3.8) 4.8 μm, (10 specimens measured).

Remarks. The specimens studied show certain morphological features coincident with dinocysts belonging to the family Protoperidiniaceae and for this reason are included here. These specimens were not included in the genus *Echinidinium* because they have capitate processes. In addition, they differ from *Islandinium cezare* by having a central body of a relatively smaller size (Table 3).

Genus Selenopemphix Benedek, 1972 emend. Head, 1993
Type species. *Selenopemphix nephroides* Benedek, 1972 emend. Benedeck and Sarjeant, 1981

Selenopemphix quanta (Bradford, 1975) Matsuoka, 1985
(Fig. 2.4)
Description. Proximochorate cysts with polar compression and subcircular to reniform outline. The wall cyst is smooth, pale to medium brown, ornamented with numerous processes. The processes are solid with sharp terminations, in some cases truncated ("blunt") and hollow expanded bases, homogeneously distributed except in the sulcus where they are absent. Archeopyle is intercalary (2a).

Dimensions. Central body (width), 30 (45.1) 66 μm. Process length, 4 (10.5) 14.4 μm, (30 specimens measured).

Remarks. Specimens of *Selenopemphix quanta* were identified, but some of them had a smaller central body and greater variability range of the processes than those from the North Atlantic Ocean (body width: 40–83 μm; process length: 10–16 μm, Rochon et al., 1999).

Selenopemphix cf. S. quanta (Bradford, 1975) Matsuoka, 1985
(Fig. 2.5)
Description. Cysts have a sub-spherical body and polar compression. The wall cyst is smooth and light brown in color. Processes are solid, acuminate and truncated, with slightly expanded bases and

are homogeneously distributed. The archeopyle intercalary (2a) was not clearly observed in some studied specimens.

Dimensions. Central body (width), 30 (38.4) 48.8 μm. Process length, 5 (9.8) 13 μm, (22 specimens measured).

Remarks. These specimens are compared and are not assigned to *Selenopemphix quanta*. The cysts with smaller central bodies, lower density and shorter processes having narrower bases are grouped as *Selenopemphix* cf. *S. quanta* (Fig. 2, Table 3).

Genus Trinovantedinium Reid, 1977 emend. De Verteuil and Norris, 1992
Type species. *Trinovantedinium capitatum* Reid, 1977

Trinovantedinium cf. *T. applanatum* (Bradford, 1977) Bujak and Davies, 1983
(Fig. 2.6)
Description. Cysts compressed dorsoventrally with pentagonal to rounded outline. Wall surface is smooth to microgranulate, hyaline, ornamented by short and acuminate processes or spines with intratabular distribution. The cingulum is defined by the alignment of processes along each margin. The antapical horns are short and rounded. Archeopyle is intercalary (2a).

Dimensions. Central body (length), 65 (65.7) 75.4 μm. Central body (width), 60 (66) 72 μm. Process length, 2.4 (3.8) 5 μm, (6 specimens measured).

Remarks. Specimens that we refer to as *Trinovantedinium* cf. *T. applanatum* differ from type ones illustrated in Rochon et al. (1999) by having short horns and a central body with a rounded shape (Fig. 2, Table 3).

Family Peridiniaceae Ehrenberg, 1831
Subfamily Calciodinelloideae Fensome et al., 1993
Genus *Pentapharsodinium* Indelicato and Loeblich III, 1986 emend. Montresor et al., 1993
Type species. *Pentapharsodinium dalei* Indelicato and Loeblich III, 1986
Pentapharsodinium dalei Indelicato and Loeblich III, 1986
(Fig. 3.3)
Description. Proximochorate cysts with spherical central body. Wall surface is smooth and hyaline with a variable density of non-tabular processes. The processes are solid, branched and have expanded bases. Archeopyle indicated by a split (chasmic type).

Dimensions. Cyst body diameter, 19 (26) 33.8 μm. Length of processes, 3 (4.6) 6.5 um, (25 specimens measured).

Remarks. Cysts of *Pentapharsodinium dalei* recovered from the Beagle Channel shows morphological differences from the Northern Hemisphere specimens presented in Rochon et al. (1999), especially the relationship between the central body size and length of processes (Table 3). *Pentapharsodinium dalei* shows a similar morphology to cysts belonging to *Ensiculifera imariense* Kobayashi et Matsuoka, but differs from the latter because the cysts of *P. dalei* are colorless, the processes are narrower than those of *E. imariense* and the absence of membranous proximal bases.

Subclass Gymnodiniphycidae Fensome et al., 1993
Order Gymnodiniales Apstein, 1909
Suborder Gymnodiniineae (autonym)
Family Polykrikaceae Kofoid and Swezy, 1921
Genus *Polykrikos* Bütschli, 1873
Comments. A motile-based genus
Polykrikos kofoidii Chatton, 1914
(Fig. 3.4)
Description. Cysts with an elongated body, medium to dark brown in color. The outer layer or periphragm is fibrous with crests that have a distally expanded, coarse reticulum. The archeopyle, probably apical, is observed at one end of the cyst.

Dimensions. Cyst body (length), 31.5 (54.8) 75 μm. Length of ornaments, 4 (11) 20 μm, (13 specimens measured).

Remarks. These specimens differ from typical cysts of *Polykrikos kofoidii* (described as *P. schwartzii*, Matsuoka, 1985) by having a smaller body size (body length: 50.5 to 108.4 μm; length of ornamentation: 6.6 to 10.3 μm, Matsuoka, 1985) (Fig. 3, Table 3).

Polykrikos schwartzii Bütschli, 1873

(Fig. 3.5)

Description. Proximochorate cyst with a sub-elongated body and dark brown wall. The periphragm is ornamented by isolated, fibrous and thick processes expanded distally. Apical archeopyle.

Dimensions. Cyst body length, 42.4 (58.2) 83 μm. Process length, 4.8 (8.3) 14.7 μm, (25 specimens measured).

Remarks. Some specimens differ from typical cysts of *Polykrikos schwartzii* by having a smaller size (length: 52.5 to 74.9 μm, length of processes: 11.8 to 17.9 μm, as *P. kofoidii* in Matsuoka, 1985). *Polykrikos schwartzii* and *P. kofoidii* observed in this study were smaller in size than those described in Rochon et al. (1999), Matsuoka (1985, 1987) and Matsuoka and Cho (2000) (Fig. 3, Table 3).

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