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Seasonal phytoplankton dynamics in extreme southern South America (Beagle Channel, Argentina)

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ABSTRACT

The phytoplankton biomass and composition dynamics in relation with environmental factors were explored during an annual cycle (July 2006–2007) for the first time in the Beagle Channel. Samples were examined by light and scanning electron microscopy and carbon biomass was estimated using measured cell biovolumes. The annual cycle was characterized by a sharp contrast between low density and biomass during the autumn–winter period and a significant increase during spring and summer. The maximum biomass peak was observed during early spring ($141\ \mu g\ C\ l^{-1}$ and $8.7\ \mu g$ Chl $a\ l^{-1}$) and was associated with a bloom of the diatom genus *Chaetoceros*. In spite of a strong nutrient depletion that lead to the subsequent bloom decline, a second peak of biomass was observed after 2 weeks, mainly represented by the diatoms *T. mendiolana* and *T. anguste-lineata.* Towards the end of spring and during summer diatom density decreased and assemblages were enriched by unidentified tiny phytoflagellates and dinoflagellates. A total of 138 taxa were identified during the study period. From these, 10 are known as potentially toxic species: *Alexandrium catenella*, *A. ostenfeldii*, *A. tamarense*, *Dinophysis acuminata*, *D. rotundata*, *Prorocentrum cordatum*, *Pseudo-nitzschia australis*, *P. calliantha*, *P. fraudulenta* and *P. cf. seriata*. Their presence is noteworthy since the area sustains a growing aquiculture production.

1. Introduction

Phytoplankton plays a key role in marine environments, forming the base of the food web and having a substantial function in nutrient dynamics and in the carbon biogeochemical cycle (Graham and Wilcox, 2000; Sarmiento and Gruber, 2006). Patterns of seasonal phytoplankton succession have been extensively investigated around the world. Long term monitoring programs allowed a comprehensive knowledge of phytoplankton dynamics in selected areas (*e.g.* Cloern, 1996; Ribera d'Alcalà et al., 2004; Silva et al., 2009). These dynamics can be generally ascribed to changes in environmental variables, such as water column stability, light and nutrient availability or grazing pressure. However, much work is still needed to unravel phytoplankton patterns and composition in many remote areas that remain largely unexplored, like southern Argentina.

Located at the southern extreme of South America (≈55°S), the Beagle Channel is a drowned glacial valley that connects the Pacific and Atlantic oceans trough the islands of Tierra del Fuego Archipelago. Due to its particular location, it is considered a key environment for the study of interactions between the sub-Antarctic and the Antarctic regions (Pérez-Barros et al., 2004). Ushuaia city, the biggest settlement on the channel with about 50,000 inhabitants, exerts an increasing anthropogenic pressure by discharges of urban and industrial effluents (Torres et al., 2009). Likewise, an incipient mussel aquaculture (*Mytilus edulis chilensis*) has developed in the area in the last years, representing an important commercial resource for local populations.

Studies on the ecology and dynamics of phytoplankton in the Beagle Channel are scarce and usually limited to observations during spring oceanographic cruises covering the area between the Strait of Magellan and Cape Horn (Hamamé and Antezana, 1999; Avaria et al., 2003; Pizarro et al., 2005). These studies reveal a high spatial variability in phytoplankton biomass and composition, with diatoms as the dominant group during the blooms observed in October (Avaria et al., 2003; Pizarro et al., 2005) and November (Hamamé and Antezana, 1999).

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In the light of the thinning of the stratospheric ozone layer problem observed on occasions in this high latitude zone (the so-called ozone "hole"), some studies have been carried out concerning the effects of ultraviolet radiation on phytoplankton growth (Hernando and San Roman, 1999; Hernando et al., 2006). In addition, some investigations have focused on the occurrence of toxic dinoflagellate *Alexandrium catenella* blooms, which have caused severe damage to public health in this area and economic losses to aquaculture (Benavides et al., 1995; Guzmán et al., 2002). By contrast, there is no information regarding phytoplankton seasonal patterns and the associated forcing factors.

In this study we explore for the first time phytoplankton biomass and composition dynamics during an annual cycle in the Beagle Channel, in relation with environmental factors. It is expected that the present results provide a reference for future research in this little known sub-Antarctic area, as well as a basis for the study of long-term comparison in a global climate change scenario.

2. Materials and methods

2.1. Study area and sampling strategy

Field sampling was carried out between July 6, 2006 and July 19, 2007, at a fixed station located in the Beagle Channel (54°52′50.01″ S, 67°45′21.82″ W) (Fig. 1). Previous studies (Hernando, 2006; Hernando and San Roman, 1999; Hernando et al., 2006) suggest that phytoplankton assemblages in this sampling station are representative of the Beagle Channel. The station, which is the control site of a monitoring program of toxic algae carried out since 2005 in the eastern sector of the Beagle Channel, was situated at a distance of approximately 300 m from the coast (~15 m depth). Sampling frequency was biweekly most of the year and weekly during the phytoplankton spring bloom.

Water temperature and salinity were measured *in situ* with a Horiba U-10 multi-parametric sensor (Horiba Ltd., Kyoto, Japan). Seawater was sampled at 2 m depth using a 5 l Niskin bottle lowered from a boat. Aliquots of 250 ml were preserved with 4% borax buffered formalin for quantitative phytoplankton analyses. Subsurface qualitative phytoplankton samples were additionally taken using a 20 μm mesh net and fixed as previously described. All samples were kept in the dark at room temperature until analysis.

For chlorophyll *a* determination, 0.5–2 l of seawater were filtered onto Whatman GF/F filters and kept frozen until analysis, which was performed within one week of sampling. Pigment extracts were read in a Turner 450 Beckman spectrofluorometer and corrected for phaeopigments, following Holm-Hansen and Riemann (1978). The spectrofluorometer was calibrated using a standard of Chl *a* (Sigma). Concentrations were calculated according to Holm-Hansen et al. (1965).

Samples for nutrient analyses were filtered through Whatman GF/F filters and kept frozen (−20 °C) until analysis, which was done within 3 months after sampling. Nitrates, phosphates and silicates

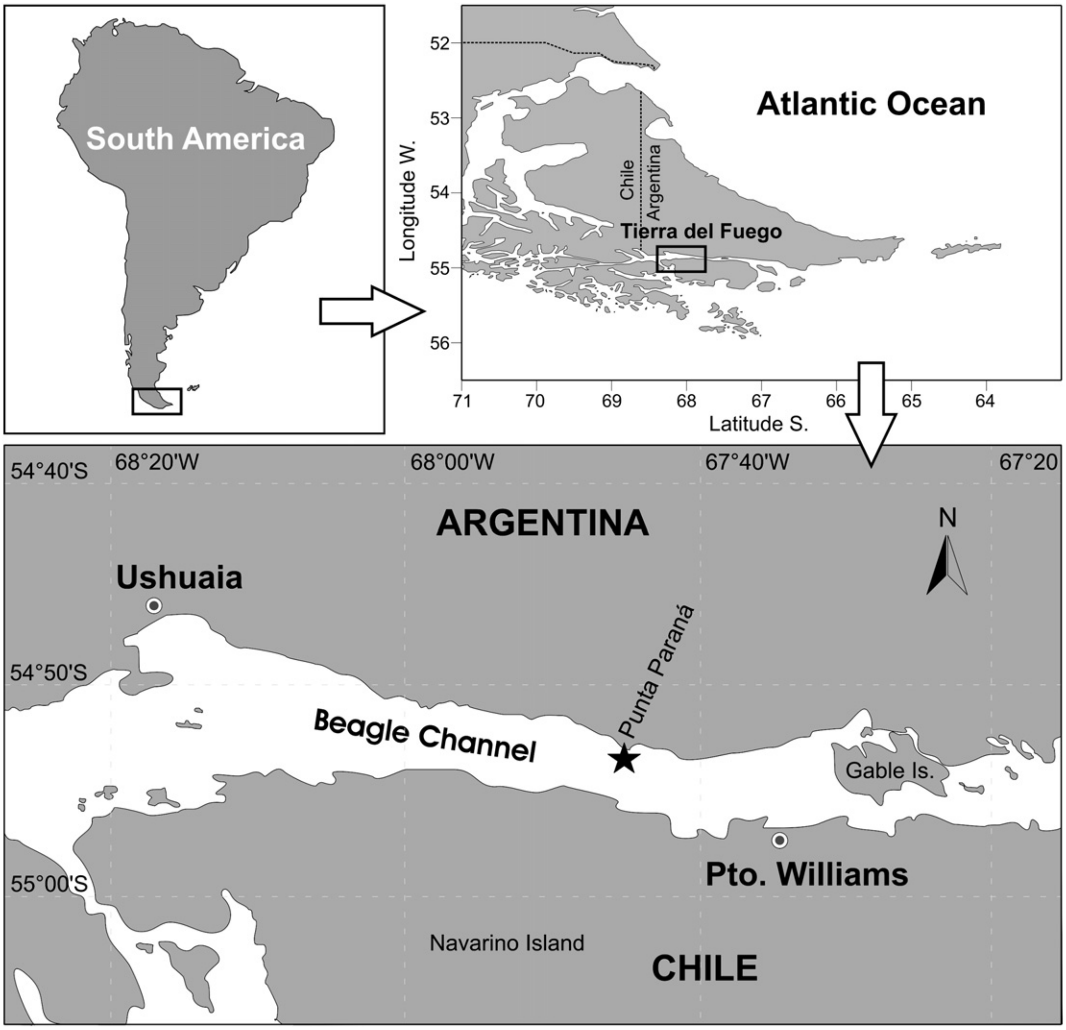

Fig. 1. Map of the study area in the Beagle Channel.

were measured with an automated analyzer (Autoanalyzer Technicon II), following the methods described in Grasshoff (1969), Grasshoff et al. (1983), Technicon (1977) and Eberlein and Kattner (1987).

2.2. Phytoplankton analyses

Qualitative samples were examined using phase contrast, differential interference contrast (DIC) and UV epifluorescence microscopy under two Leica DM 2500 microscopes. In order to analyze the presence of colonies, delicate organisms, plastids, *etc*., qualitative analyses began with the examination of water mounts. For diatom frustules observation, organic material was routinely removed from net subsamples using sodium hypochlorite (NaClO, 55 g Cl l^{-1}). One to three drops of NaClO were added to 3–6 ml sample, allowed to stand for 2–6 min and washed 4 to 6 times with distilled water. Clean material was then dried onto cover glasses for mounting in Naphrax following Ferrario et al. (1995). For dinoflagellates identification, thecal plates were stained with Calcofluor according to Fritz and Triemer (1985). Further scanning electron microscopy observations of selected samples were made with a Jeol JSM-6360 LV (SEM).

For quantitative estimations, cells were enumerated with a phase contrast Iroscope SI-PH inverted microscope according to the procedures described by Utermöhl (1958). Subsamples of 50 or 100 ml were left to settle for 24 or 48 h respectively in a composite sedimentation chamber. At least 100 cells of the dominant taxa were counted in one or more strips of the chamber at 250 or 400×, depending on their concentration and size. The whole chamber bottom was also scanned at 100× to count large and sparse species. Since flagellates generally loose their flagella by the addition of fixatives, unidentified phytoflagellates and round-shaped organisms with or without flagella were included in a single group as "phytoflagellates" during cell counting and classified according to their size.

Cell dimensions were measured throughout the sampling period using an ocular micrometer. At least 25 randomly selected cells were measured for each of the most abundant species, while 10–15 specimens were generally considered for the rest. Cell biovolumes were calculated by approximation to the nearest geometric shapes proposed by Hillebrand et al. (1999). Cell carbon content (C) was estimated with two different carbon-to-volume ratios, one for diatoms and one for all the other algae groups (Menden-Deuer and Lessard, 2000). Biovolume was only estimated and considered in further carbon estimations for species present in the quantitative samples.

3. Results

3.1. Physical and chemical characteristics

Water temperature ranged from 4.9 °C (July) to 10.1 °C (January) (Fig. 2a; Table 1). Salinity showed a contrasting pattern, with highest values in winter (max. = 31.7 in August) and a progressive decrease

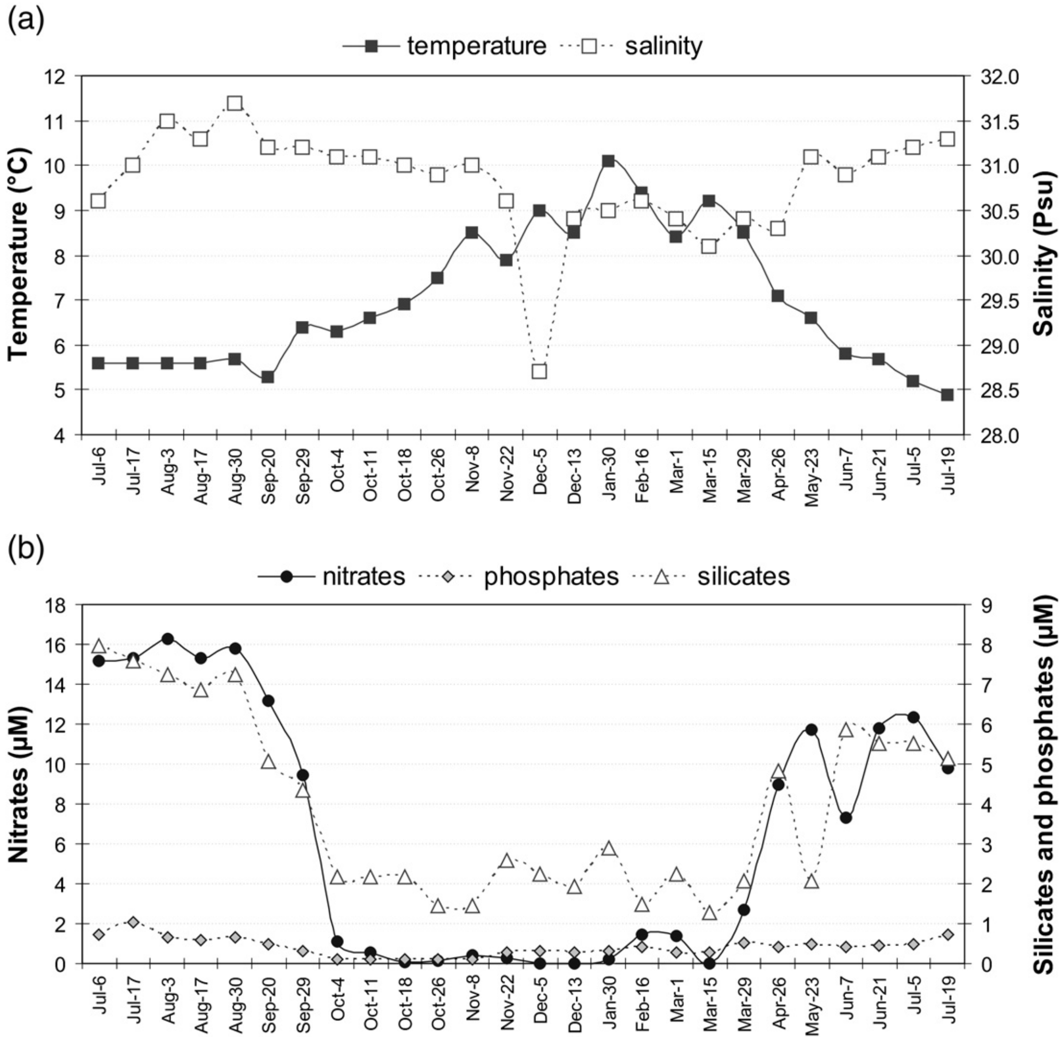

Fig. 2. Surface distribution of a) temperature and salinity and b) nitrates, phosphates and silicates concentrations during sampling period in the Beagle Channel.

Table 1
Seasonal average ± standard deviation of temperature, salinity and dissolved nutrients concentration observed during sampling period in the Beagle Channel.

Period	Temperature (°C)	Salinity (Psu)	Nitrates (μM)	Phosphates (μM)	Silicates (μM)
Winter 2006	5.6 ± 0.1	31.2 ± 0.4	15.2 ± 1.1	1.4 ± 0.4	7.0 ± 1.0
Spring 2006	7.5 ± 1.0	30.7 ± 0.8	1.3 ± 3.1	0.4 ± 0.2	2.3 ± 0.9
Summer 2007	9.3 ± 0.7	30.4 ± 0.2	0.8 ± 0.8	0.6 ± 0.1	2.0 ± 0.7
Fall 2007	7.0 ± 1.1	30.7 ± 0.4	7.7 ± 3.8	0.9 ± 0.1	3.7 ± 1.9
Winter 2007	5.3 ± 0.4	31.2 ± 0.1	11.3 ± 1.4	1.1 ± 0.3	5.4 ± 0.2

Table 2
Seasonal average ± standard deviation of phytoplankton biomass, chlorophyll *a* and cell density observed during sampling period in the Beagle Channel.

Period	Biomass (μg C l^{-1})	Chlorophyll *a* (μg chl-*a* l^{-1})	Cell density (×10^5 cells l^{-1})
Winter 2006	2.1 ± 2.5	0.5 ± 0.3	0.9 ± 0.5
Spring 2006	75.3 ± 47.6	4.1 ± 2.4	11.7 ± 12.2
Summer 2007	40.7 ± 10.4	2.5 ± 1.2	5.5 ± 2.3
Fall 2007	0.9 ± 0.9	0.2 ± 0.1	0.3 ± 0.2
Winter 2007	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0

during spring and summer, with the lowest value of 28.7 observed in December 2006 (Fig. 2a; Table 1).

Nutrient concentrations were highest during winter, showing a sharp decrease during spring and summer (Fig. 2b, Table 1). The lowest values, observed from October to March, coincided with phytoplankton maxima (see below). Nitrate showed values higher than 10 μM during winter (max. 16.3 μM) and were generally depleted or near the detection limit during spring–summer phytoplankton blooms. Silicate ranged from 8.0 to 1.3 μM (July 06–March 07) and phosphate varied between 2.0 and 0.2 μM (July 07–October 06).

3.2. Phytoplankton biomass and abundance

Phytoplankton biomass estimated in terms of carbon (C) and chlorophyll *a* (Chl *a*) showed similar patterns ($r = 0.92$; $p < 0.0001$), with a high seasonal variability (Fig. 3a). During fall and winter, biomass presented very low concentrations (Table 2), ranging between 0.1–7.1 μg C l^{-1} and 0.1–1.0 μg Chl *a* l^{-1}. In contrast, the highest values were observed during spring, in two occasions, one in October and the other in November, reaching 141 and 121 μg C l^{-1} and 8.7 and 5 μg Chl *a* l^{-1} respectively. Finally, intermediate concentrations were observed in summer, ranging between 26.6–50.8 μg C l^{-1} and 1.8–3.8 μg Chl *a* l^{-1}. The C:Chl *a* ratio (excluding heterotrophic dinoflagellates in its calculation) varied through the year from 0.7 to 25.8 (mean 9.8), showing higher values during spring and summer and lower values during autumn and winter (Fig. 3b).

Cell density distribution was similar to that observed for biomass (Fig. 3b). Densities lower than 1.5 × 10^5 cells l^{-1} were observed during fall and winter, with a minimum of 6.3 × 10^3 cells l^{-1} (July 07). In contrast, spring and summer densities were higher than 3.0 × 10^5 cells l^{-1}, with a maximum of 3.5 × 10^6 cells l^{-1} reached in October 2006.

3.3. Phytoplankton composition

A total of 138 taxa were identified during the study period (Table 3). Most of them were diatoms (102), predominantly marine planktonic species such as *Chaetoceros* spp. and *Thalassiosira* spp. However, the presence of some benthic species was also observed (*e.g.*

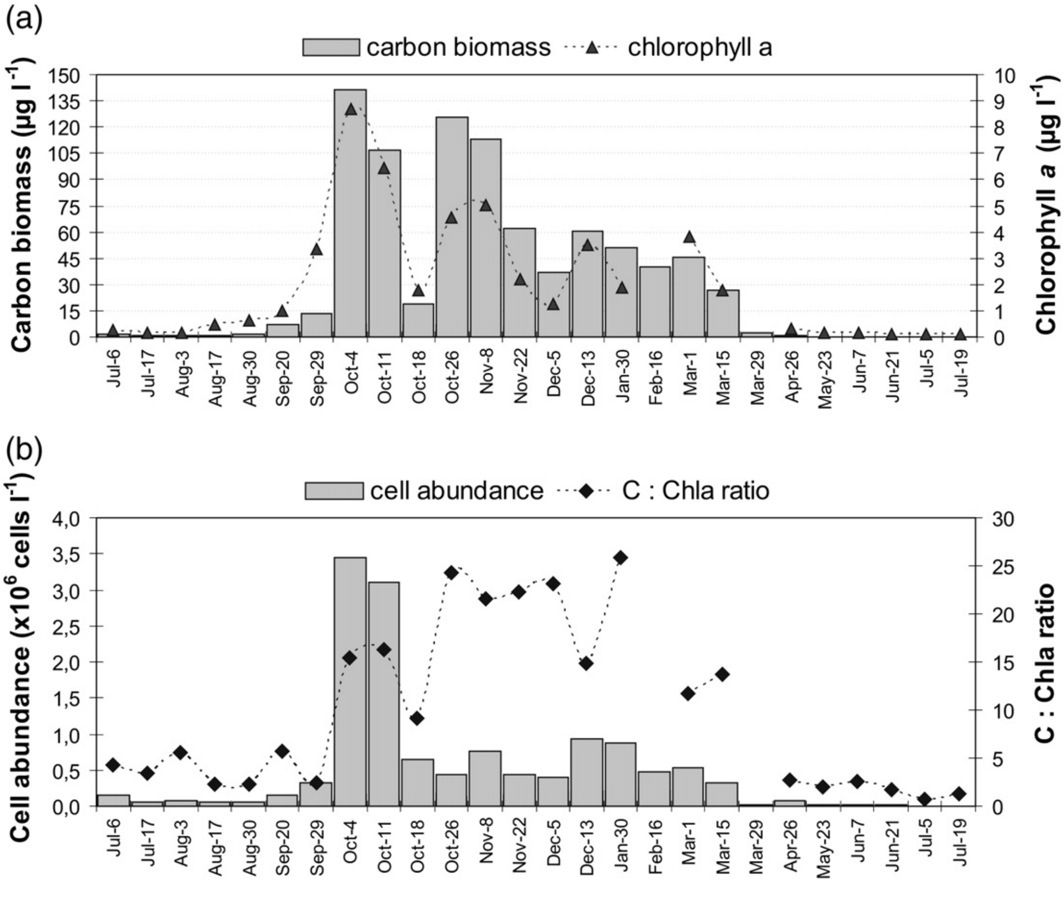

Fig. 3. Seasonal variability of phytoplankton biomass (a), abundance and C:Chl *a* ratio (b) during sampling period in the Beagle Channel.

Table 3
List of taxa identified during sampling period in the Beagle Channel.

Diatoms
Achnantes sp.
Actinocyclus curvatulus Janisch
Actinocyclus sp.
Actinoptychus senarius (Ehrenberg) Ehrenberg
Amphora spp.
Asterionellopsis glacialis (Castracane) Round
Attheya sp.
Bacillaria paxillifera (Müller) Hendey
Cerataulina pelagica (Cleve) Hendey
Ceratoneis closterium Ehrenberg
Cocconeis convexa Giffen
Cocconeis krammeri Lange-Bertalot & Metzeltin
Cocconeis pseudocostata Romero
Cocconeis scutellum Ehrenberg
Cocconeis sp.
Corethron hystrix Hensen
Coscinodiscus janischii Schmidt
Coscinodiscus radiatus Ehrenberg
Chaetoceros affinis Lauder
Chatoceros cf. concavicornis
Chaetoceros cf. convolutus
Chaetoceros criophilus Castracane
Chaetoceros curvisetus Cleve
Chaetoceros debilis Cleve
Chaetoceros decipiens Cleve
Chaetoceros diadema (Ehrenmberg) Gran
Chaetoceros didymus Ehrenberg
Chaetoceros lorenzianus Grunow
Chaetoceros radicans Schütt
Chaetoceros similis Cleve
Chaetoceros socialis Lauder
Chaetoceros teres Cleve
Chaetoceros tortissimus Gran
Chaetoceros spp.
Ctenophora pulchella (Ralfs ex Kützing) Williams & Round
Cyclotella sp.
Cymatopleura solea (Brébisson) Smith
Cymbella sp.
Dactyliosolen fragilissimus (Bergon) Hasle
Delphineis minutissima (Hustedt) Simonsen
Diploneis cf. splendida (Gregory) Cleve
Ditylum brightwellii (West) Grunow in Van Herurck
Donkinia sp.
Encyonopsis microcephala (Grunow) Krammer
Encyonema minutum (Hilse in Rabenhorst) D. G. Mann
Entomoneis sp.
Eunotia bilunaris var. *bilunaris* (Ehrenberg) Mills
Fallacia sp.
Gomphonemopsis sp.
Grammatophora hamulifera Kützing
Grammatophora cf. undulata
Guinardia delicatula (Cleve) Hasle
Gyrosigma fasciola (Ehrenberg) Griffith et Henfrey
Gyrosigma tenuissimum (W. Smith) Griffith & Henfrey
Gyrosigma macrum (W. Smith) Griffith & Henfrey
Hannaea arcus (Ehrenberg) R.M. Patrick
Haslea cf. crucigeroides (Hustedt) Simonsen
Hyalodiscus sp.
Leptocylindrus minimus Gran
Licmophora spp.
Minidiscus chilensis Rivera
Navicula algida Grunow
Navicula directa (Smith) Ralfs in Pritchard
Navicula perminuta Grunow
Navicula transitans var. *derasa* f. *delicatula* Heimdal
Nitzschia cf. lecontei van Heurck
Nitzschia cf. laevis Hustedt
Paralia sulcata (Ehrenberg) Cleve
Pleurosigma obscurum W. Smith emend. Sterrrenburg
Pleurosigma cf. normanii Ralfs in Pritchard
Psammodictyon panduriforme (Gregory) Mann
Pseudo-nitzschia australis Frenguelli
Pseudo-nitzschia calliantha Lundholm, Moestrup & Hasle
Pseudo-nitzschia fraudulenta (Cleve) Hasle
Pseudo-nitzschia cf. seriata
Rhabdonema minutum Kützing
Rhizosolenia setigera Brightwell f. *setigera*
Rhizosolenia hebetata f. *hebetata* Bailey
Rhizosolenia sp.
Roperia tesselata (Roper) Grunow ex Pelletan
Skeletonema cf. costatum (Greville) Cleve emend. Zingone et Sarno
Staurophora sp.
Staurosirella? Round
Stellarima stellaris (Roper) Hasle & Sims
Stephanopyxis turris (Greville) Ralfs ex Pritchard
Striatella unipunctata (Lyngbye) Agardh
Subsilicea fragilarioides? von Stosch & Reimann
Tabularia fasciculata (Agardh) Williams & Round
Thalassionema nitzschioides (Grunow) Mereschkowsky
Thalassiosira anguste-lineata (Schmidt) Fryxell & Hasle
Thalassiosira curviseriata Takano
Thalassiosira delicatula Ostenfeld
Thalassiosira eccentrica (Ehrenberg) Cleve
Thalassiosira gerloffii Rivera
Thalassiosira mendiolana
Thalassiosira cf. minima Gaarder emend. Hasle
Thalassiosira pacifica Gran & Angst
Thalassiosira rotula Meunier
Thalassiosira tenera Proschkina-Lavrenko
Thalassiosira spp.
Trachyneis aspera var. *aspera* (Ehrenberg) Cleve
Trachysphenia sp.
Dinoflagellates
Amphidinium sp.
Amphidoma acuminata Stein
Alexandrium catenella (Whedon & Kofoid) Balech
Alexandrium ostenfeldii (Paulsen) Balech & Tangen
Alexandrium tamarense (Lebour) Balech
Ceratium fusus (Ehrenberg) Dujardin
Ceratium lineatum (Ehrenberg) Cleve
Ceratium tripos (Müller) Nitzsch
Dinophysis acuminata Claparède & Lachmann
Dinophysis rotundata Claparède & Lachmann
Dinophysis truncata Cleve
Gymnodinium spp.
Gyrodinium sp.
Heterocapsa sp.
Oxytoxum sp.
Prorocentrum cf. compressum
Prorocentrum cordatum (Ostenfeld) Dodge
Prorocentrum micans Ehrenberg
Prorocentrum sp.
Protoperidinium cf. punctulatum
Protoperidinium joergenseni var. *luculentum* Balech
Protoperidinium cf. brevipes
Protoperidinium denticulatum (Gran et Braarud) Balech
Protoperidinium excentricum (Paulsen) Balech
Protoperidinium simulum (Paulsen) Balech
Protoperidinium spp.
Scrippsiella sp.
Cryptophytes
Cryptomonads (<10 μm)
Cryptomonads (>10 μm)
Euglenophytes
Eutreptia sp.
Prasinophytes
Pyramimonas sp.
Tetraselmis sp.
Prymnesiophytes
Chrysochromulina/Prymnesium sp.
Emiliania huxleyi (Lohmann) Hay & Mohler
Phaeocystis cf. antarctica Karsten
Silicoflagellates
Dictyocha speculum Ehrenberg

Bacillaria paxillifera, *Donkinia* sp., *Trachyneis aspera*, *Psammodictyon panduriforme*), as well as species typical of estuarine or freshwater environments (*e.g. Ctenophora pulchella*, *Cymatopleura solea*, *Eunotia bilunaris*, *Encyonopsis microcephala*, and *Cymbella* sp.).

The most abundant phytoplankton groups observed throughout the year were, in decreasing order, unidentified tiny phytoflagellates, diatoms and coccolithophorids, which collectively represent more than 85% of total phytoplankton density in all samples analyzed (Fig. 4a). Prasinophytes ($\bar{x}=1.7\%$), cryptophytes ($\bar{x}=1.6\%$), dinoflagellates ($\bar{x}=1.6\%$), other prymnesiophytes ($\bar{x}=0.6\%$) and euglenophytes ($\bar{x}=0.2\%$) were found in much lower concentrations. The presence of the silicoflagellate *Dictyocha speculum* was just recorded in concentrated qualitative samples.

In terms of the relative contribution of the different groups to phytoplankton biomass, diatoms, dinoflagellates and unidentified tiny phytoflagellates were the most important, representing an average of 42, 22 and 19% of total carbon year round (Fig. 4b). Coccolithophorids ($\bar{x}=9.6\%$), euglenophytes ($\bar{x}=2.9\%$), cryptophytes ($\bar{x}=1.7\%$), prasinophytes ($\bar{x}=1.4\%$) and other prymnesiophytes ($\bar{x}=0.8\%$) followed in order of decreasing mean relative contribution.

3.4. Phytoplankton seasonality

Low densities observed during fall and winter, were mainly represented by unidentified tiny phytoflagellates, which dominated in 75 and 89% of samples during each season (Fig. 4a). Likewise, the coccolithophorid *Emiliania huxleyi* dominated in May and June 2007, with densities reaching $5–11\times10^3$ cells l^{-1}. In contrast with the large numerical predominance of these groups, their contribution to total biomass was moderate (Fig. 4b.) This relates with their relative small cell size, which varied between ≈5 and 200 μm^3 $cell^{-1}$.The other phytoplankton groups were generally observed at very low densities during this period (Table 4), except for diatoms which showed a slight increase in their abundance towards the end of winter 2006 (Fig. 4a), with an assemblage mainly composed by *Thalassiosira minima/curviseriata*, *Chaetoceros debilis*, *C. socialis* and *Thalassionema nitzschioides*. Other important taxa in terms of contribution to biomass were the diatoms *Thalassiosira cf. pacifica/angulata* and an unidentified *Thalassiosira* (diameter 30–42 μm; pervalvar axis 15–20 μm), the dinoflagellates *Gyrodinium* sp. and *Protoperidinium joergenseni* var. *luculentum* and the euglenophyte *Eutreptia* sp., which together accounted for 21% of biomass during this period.

The two conspicuous maxima of phytoplankton biomass observed during spring were composed by more than 85% of diatoms (Fig. 5). However, the specific composition of both blooms showed important differences. The first one was dominated by the genus *Chaetoceros* (mainly represented by *C. teres*, *C. debilis*, *C. socialis* and *C. tortissimus*), which reached 93.6 μg C l^{-1} (74.7% of diatoms). The second bloom was mainly represented by the genus *Thalassiosira* (*T. mendiolana* and *T. anguste-lineata*), which reached 103.4 μg C l^{-1} (96.1% of diatoms). In spite of the similar biomass values reached in both blooms, the cell density of the first one was eight fold higher than the second. This can

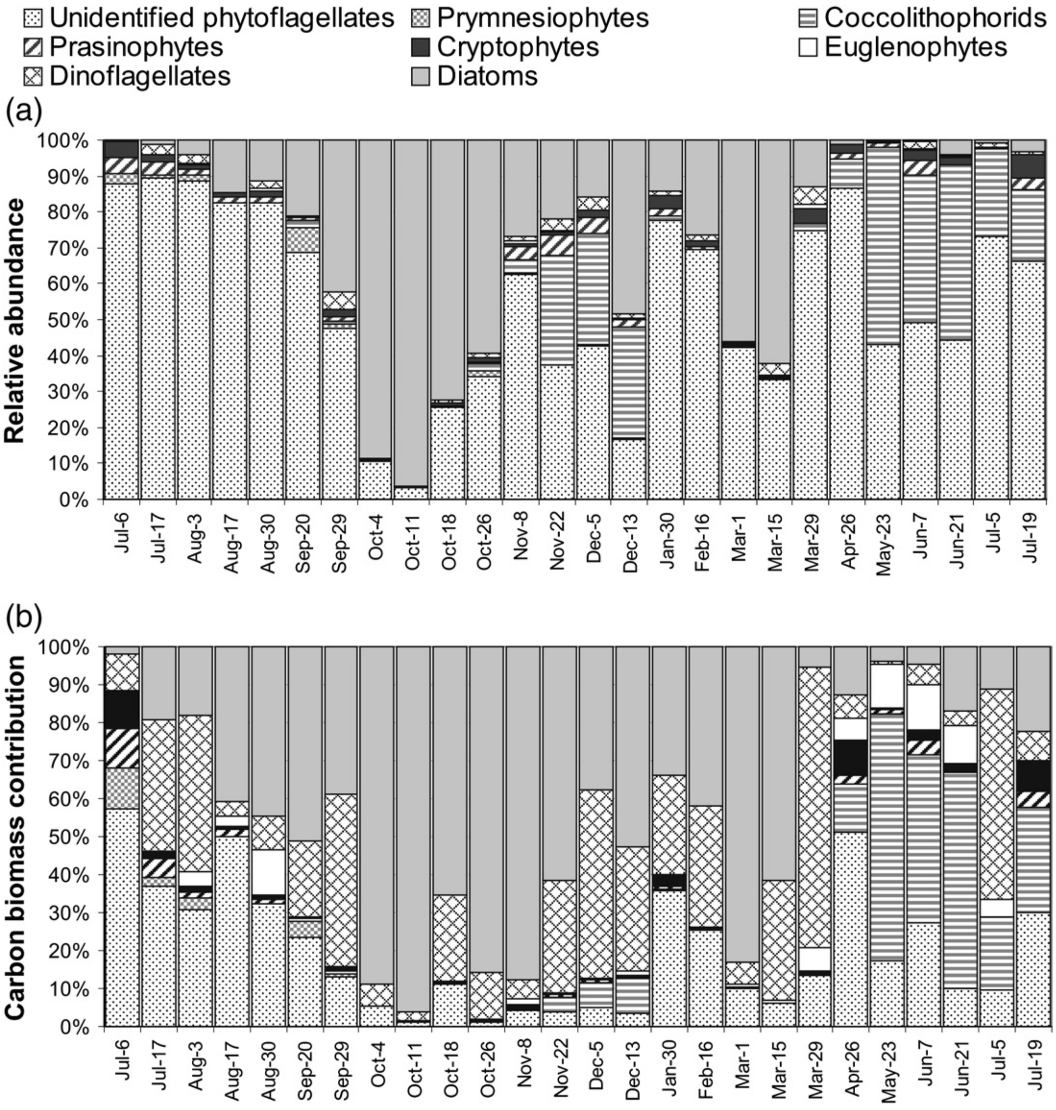

Fig. 4. Relative abundance (a) and biomass (b) of the main phytoplankton groups identified during sampling period in the Beagle Channel.

Table 4
Seasonal average ± standard deviation of cell density and biomass of the main phytoplankton groups identified during sampling period in the Beagle Channel.

		Group	Winter '06	Spring '06	Summer '07	Fall '07	Winter '07
Cell density	($\times 10^3$ cells l^{-1})	Coccolithophorids	0.5 ± 1.2	65.9 ± 99.8	3.4 ± 3.8	6.3 ± 4.4	3.1 ± 2.66
		Cryptophytes	1.8 ± 2.6	4.9 ± 1.5	10.8 ± 14.6	0.8 ± 0.6	0.3 ± 0.2
		Diatoms	8.5 ± 11.6	859.8 ± 1238.1	187.9 ± 83.9	1.1 ± 1.6	0.3 ± 0.2
		Dinoflagellates	0.9 ± 0.6	10.1 ± 4.9	7.7 ± 4.2	0.4 ± 0.5	0.07 ± 0.01
		Euglenophytes	0.1 ± 0.2	1.0 ± 1.7	0.4 ± 0.4	0.2 ± 0.1	0.03 ± 0.03
		Prasinophytes	2.2 ± 2.4	11.4 ± 11.3	6.2 ± 8.1	0.5 ± 0.4	0.08 ± 0.1
		Prymnesiophytes	2.6 ± 3.9	2.1 ± 2.2	–	–	–
		Unidentified phytoflagellates	75.7 ± 35.3	212.7 ± 124.5	337.4 ± 247.3	24 ± 23.1	5.12 ± 0.5
Biomass	(μg C l^{-1})	Coccolithophorids	0.01 ± 0.02	1.25 ± 1.90	0.07 ± 0.07	0.12 ± 0.08	0.06 ± 0.05
		Cryptophytes	0.03 ± 0.04	0.08 ± 0.03	0.52 ± 0.78	0.03 ± 0.04	0.004 ± 0.004
		Diatoms	0.85 ± 1.39	59.58 ± 48.10	22.06 ± 10.66	0.06 ± 0.06	0.03 ± 0.01
		Dinoflagellates	0.40 ± 0.52	11.00 ± 6.91	9.23 ± 4.90	0.42 ± 0.79	0.03 ± 0.04
		Euglenophytes	0.04 ± 0.07	0.35 ± 0.59	0.13 ± 0.15	0.07 ± 0.05	0.01 ± 0.01
		Prasinophytes	0.04 ± 0.04	0.23 ± 0.25	0.11 ± 0.14	0.01 ± 0.01	0.002 ± 0.003
		Prymnesiophytes	0.08 ± 0.13	0.07 ± 0.07	–	–	–
		Unidentified phytoflagellates	0.66 ± 0.51	2.79 ± 2.04	8.61 ± 7.29	0.22 ± 0.18	0.02 ± 0.01

be attributed to the higher cell dimensions of dominant *Thalassiosira* species (≈11,000–14,000 μm^3 $cell^{-1}$) compared to those of *Chaetoceros* (<2500 μm^3 $cell^{-1}$ Table 5).

By late spring, there was a decline in the importance of diatoms, with a simultaneous increase in the biomass of dinoflagellates. Dinoflagellates reached carbon concentrations close to 20 μg C l^{-1}, representing about 50% of total phytoplankton biomass in December (Fig. 5). This increase was related to the presence, in relative low densities (≈250–3000 cells l^{-1}) of large species, like *Ceratium lineatum* and *Protoperidinium excentricum*, followed by *Alexandrium catenella*, *Protoperidinium joergenseni* var. *luculentum* and *Protoperidinium cf. punctulatum*. Moreover, coccolithophorids also reached their highest densities towards the end of spring (max. 2.9×10^5 cells l^{-1}) and accounted for 6.5 to 9.1% of total biomass.

During summer, the highest abundances of unidentified flagellates were observed (Table 4), with a maximum of 6.8×10^5 cells l^{-1}. Likewise, cryptophytes also reached their highest densities during this season (Table 4), with a peak of 3.3×10^4 cells l^{-1}. In terms of the relative contribution to biomass, the most important groups during summer were diatoms, dinoflagellates and unidentified tiny phytoflagellates (Fig. 5; Table 4), representing average values of 55, 24 and 19% respectively. A wide prevalence of *Thalassiosira cf. delicatula* was observed among diatoms in all samples analyzed, whereas a noticeable increase of the genus *Pseudo-nitzschia* was detected in mid-March. The most conspicuous dinoflagellates during this period were mainly *Scrippsiella* sp., followed by *Gonyaulax* sp. and *Protoperidinium joergenseni* var. *luculentum*.

4. Discussion and conclusions

One of the most conspicuous features of the annual phytoplankton dynamics in the Beagle Channel was the sharp contrast between the low density and biomass concentration during the autumn–winter period and its marked increase during spring and summer. In fact, mean cell density, Chl *a* and C concentrations were 18, 12 and 50 fold higher in spring–summer than autumn–winter periods respectively. This seasonal pattern is consistent with the annual biomass cycle described in adjacent areas of the southern Argentine Sea (Romero et al., 2006) and the fjord area in southern Chile (Iriarte et al., 2007).

As it is well known, the reduced radiation available during winter and autumn, limits phytoplankton productivity in temperate waters (Sverdrup, 1953). In this context, very low cell densities and biomass concentrations were observed in the Beagle Channel during this period, with phytoplankton assemblages mainly dominated by unidentified tiny phytoflagellates. Irradiance could also be responsible of the lower C:Chl *a* ratio values observed during autumn and winter, since it is well known that the ratio decreases from high light to low light under nutrient-replete conditions as part of cell's photoacclimation mechanisms (Wang et al., 2009). Probably due to low consumption, advection and regeneration, nutrient concentration

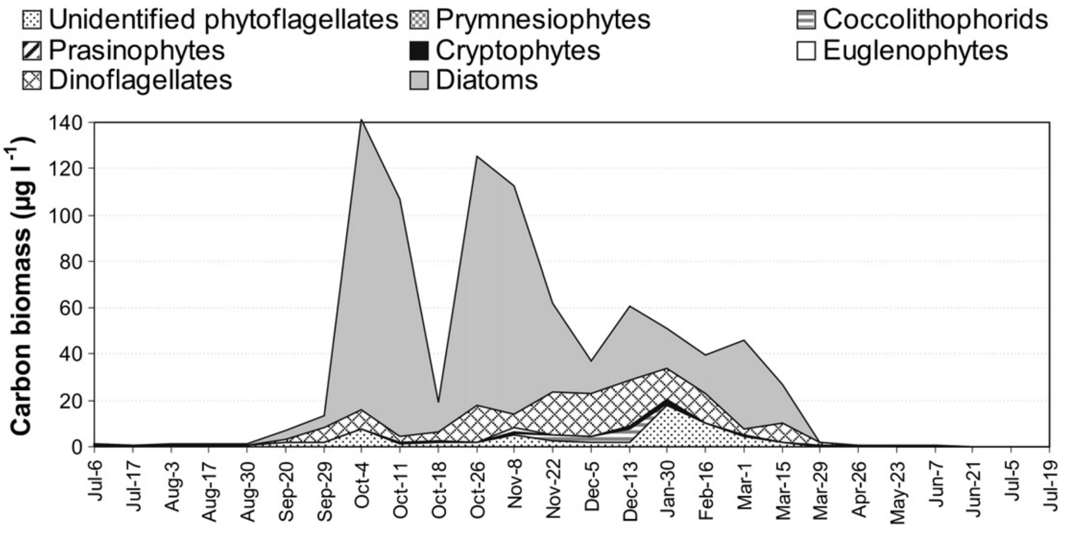

Fig. 5. Seasonal biomass variability of the main phytoplankton groups identified during sampling period in the Beagle Channel.

Table 5
Volume and carbon content of the most abundant taxa observed in the Beagle Channel.

Taxa	Volume (μm^3)	Cell carbon (pg C cell^{-1})
Diatoms		
Achnantes sp.	290	29
Actinocyclus curvatulus	26,789	1123
Asterionelliopsis glacialis	1398	102
Attheya sp.	349	33
Bacillaria paxillifera	11,265	556
Ceratoneis closterium	144	16
Chatoceros cf. concavicornis	1041	81
Chaetoceros criophilus	1605	115
Chaetoceros curvisetus	227	23
Chaetoceros debilis	403	37
Chaetoceros didymus	1030	80
Chaetoceros lorenzianus	2655	172
Chaetoceros teres	2359	157
Chaetoceros tortissimus	200	21
Chaetoceros radicans	1382	101
Chaetoceros socialis	61	8
Cocconeis scutellum	537	47
Coscinodiscus janischii	337,831	8773
Coscinodiscus radiatus	24,772	1054
Dactyliosolen fragilissimus	15,033	703
Donkinia sp.	27,587	1150
Grammatohora cf. undulata	2254	151
Guinardia delicatula	1199	90
Haslea cf. crucigeroides	43,548	1666
Leptocylindrus minimus	85	11
Navicula transitans var. *derasa* f. *delicatula*	730	60
Navicula perminuta	78	10
Navicula directa	1396	102
Paralia sulcata	5515	312
Tabularia fasciculata	236	24
Pleurosigma obscurum	1186	90
Pleurosigma cf. normanii	20,438	902
Pseudo-nitzschia australis	2049	140
Pseudo-nitzschia fraudulenta	1179	89
Pseudo-nitzschia calliantha	321	31
Rhabdonema minutum	9316	477
Rhizosolenia setigera f. setigera	7295	391
Skeletonema cf. costatum	321	31
Stellarima stellaris	10,619	530
Subsilicea fragilarioides?	339	32
Tabularia fasciculata	5944	331
Thalassionema nitzschioides	377	35
Thalassiosira anguste-lineata	11,353	560
Thalassiosira delicatula	2828	181
Thalassiosira mendiolana	14,148	669
Thalassiosira minima/curviseriata	207	22
Thalassiosira pacifica	1309	97
Thalassiosira sp. <30 μm	2352	156
Thalassiosira sp. >30 μm	20,882	918
Undetermined naviculoid <15 μm	41	6
Undetermined pennate (40–65 μm)	1048	81
Dinoflagellates		
Alexandrium catenella	24,089	2812
Alexandrium ostenfeldii	50,977	5684
Amphidinium sp.	1508	208
Amphidoma acuminata	3593	471
Ceratium fusus	26,471	3072
Ceratium lineatum	16,693	1993
Dinophisis acuminata	14,992	1801
Heterocapsa sp.	1058	149
Oxytoxum sp.	1684	231
Prorocentrum cf. compressum	1874	256
Prorocentrum cordatum	237	37
Prorocentrum micans	945	134
Protoperidinium cf. brevipes	833	119
Protoperidinium denticulatum	27,833	3220
Protoperidinium joergenseni var. *luculentum*	20,344	2399
Protoperidinium cf. punctulatum	48,328	5406
Protoperidinium excentricum	21,707	2550
Protoperidinium simulum	84,984	9185
Scrippsiella sp.	14,362	1730
Gyrodinium sp.	36,390	4142

Table 5 (*continued*)

Taxa	Volume (μm^3)	Cell carbon (pg C cell^{-1})
Dinoflagellates		
Undetermined Gymnodinoids <15 μm	392	59
Undetermined Gymnodinoids >15 μm	1381	192
Cryptophytes		
Cryptomonads <10 μm	101	17
Cryptomonads >10um	343	52
Euglenophytes		
Eutreptia sp.	2579	345
Prasinophytes		
Pyramimonas sp.	312	47
Tetraselmis sp.	108	18
Prymnesiophytes		
Chrysochromulina/Prymnesium sp.	203	32
Emiliania huxleyi	118	19
Others		
Unidentified phytoflagellates 2 μm	4	1
Unidentified phytoflagellates 3–5 μm	24	4
Unidentified phytoflagellates 6–10 μm	184	29
Unidentified phytoflagellates 10–15 μm	836	120

reached their highest values during July and August, which is considered as the initial or winter stock observed during pre-bloom periods (Cloern, 1996). Winter nitrate and phosphate concentrations observed in our study are much lower than those observed in Ushuaia Bay, where a strong nutrient enrichment in the coastal zone is related to anthropogenic sources and riverine sources that discharge nitrate originating from dense woods and very large peatlands (Amin et al., 2011).

The increase in biomass and cell density observed during early spring was associated with an intense bloom of the diatom genus *Chaetoceros*, with a peak of 3×10^6 cells l^{-1}. Spring diatom blooms are recurrent phenomena in temperate coastal environments (Cloern, 1996; Gentien et al., 2005) and blooms of *Chaetoceros* spp. have been previously observed in the Beagle Channel during spring (Hamamé and Antezana, 1999; Avaria et al., 2003; Pizarro et al., 2005), suggesting that this genus is a key phytoplankton component in this area.

Phytoplankton blooms are events of rapid production and accumulation of biomass, resulting from the balance between gains and losses in response to environmental factors operating at different time scales such as solar radiation, water column stability, nutrient availability, grazing pressure, *etc.* (Cloern, 1996). Of these, the availability of solar radiation in the water column appears as the main factor limiting the development of phytoplankton blooms in the fjord and channel areas of Tierra del Fuego (Pizarro et al., 2005). By contrast, water column stability, usually considered a prerequisite for spring blooms in temperate zones, seems not to be essential for this study area, since waters west of Gable Island show a vertical homogeneity during most of the year in the Beagle Channel (Bujalesky, 2007). This agrees with Hamamé and Antezana (1999) observations, who reported a peak of chlorophyll during spring, in vertically homogeneous waters of the western part of the Beagle Channel (≈69°W). It has been additionally hypothesized that the onset of blooms in thoroughly mixed water columns may be controlled by daylength-dependent germination of entrained spores from the bottom sediment (Eilertsen et al., 1995; Eilertsen and Wyatt, 2000). During culture experiments, spore germination of *C. teres*, *C. socialis* and *C. debilis* occurred only when daylength exceeded 11 h and the highest number of viable cells was found with a photoperiod of 13 h (Eilertsen et al., 1995). In coincidence, the onset of the

Chaetoceros bloom in the Beagle Channel was observed during October, when day length reached 13 h (Fig. 6). Although diatom resting spores were not counted in the present study, their presence was usually detected during sample examination.

Several hypotheses have been proposed to explain why diatoms efficiently exploit the conditions of high solar radiation and elevated concentration of nutrients observed during spring. These include the high cell rate division resulting from rapid nitrate uptake and assimilation in nitrogen rich waters, their high growth efficiency at low light levels and the use of bicarbonate during blooms, when the concentration of dissolved CO_2 limits photosynthesis of other algae groups (Cloern and Dufford, 2005).

The bloom of *Chaetoceros* caused a strong nutrient depletion, with NO_3, PO_4 and SiO_3 concentrations decreasing to 0.10, 0.18 and 2.17 µM, respectively, which lead to the subsequent bloom decline, observed after 2 weeks (October 18). In addition, phytoplankton abundance could also have been controlled by top-down biological processes, like zooplankton grazing. In this sense, previous studies have shown an increase in the abundance of invertebrate larvae (Hamamé and Antezana, 1999) and copepods (Torres et al., 2006) in response to the spring phytoplankton proliferation in the Beagle Channel, suggesting the presence of a strong coupling between phyto- and zooplankton.

A second peak of biomass was observed 2 weeks after the first bloom, represented mainly by diatoms of the genus *Thalassiosira*. Only two species *T. mendiolana* and *T. anguste-lineata*, accounted for more than 90% of total carbon biomass. The low nutrient concentrations observed before and during this bloom do not evidence river runoff as a potential source of nutrient replenishment, which is known to intensify during November and December (Hernando, 2006). In contrast, the observed low nitrate concentration (0.11 µM) suggests that ammonium could have been the main source of nitrogen supporting this second bloom, as observed in the Strait of Magellan (Antezana, 1999) and Bahía Blanca estuary (Popovich et al., 2008). Unfortunately, no data on ammonium concentrations are available for the Beagle Channel neither from previous studies nor from the present one to support this hypothesis. An alternative explanation for the presence of the second biomass peak could be advection rather than local growth and biomass accumulation. In this sense, Benavides et al. (1995) observed an intense summer bloom of the dinoflagellate *Alexandrium catenella* to spread south and eastwards in the Beagle Channel and suggested that the bloom likely originated from northern waters of the Strait of Magellan. Although no causality can be established, it is noteworthy that during an oceanographic cruise carried out in October 1998 along and extensive area between the Strait of Magellan and Cape Horn, a bloom of *T. cf. mendiolana* was observed in waters of the Strait of Magellan whereas a bloom of *C. radicans*, *C. didymus* and *C. socialis* was found in southern waters of Beagle Channel (Avaria et al., 2003). The advection hypothesis can be tested once water mass circulation data in this area are available.

Towards the end of spring and during summer, diatoms density decreased and assemblages were enriched by unidentified tiny phytoflagellates and dinoflagellates. The first ones reached densities up to 6.8×10^5 cells l^{-1}, but accounted only for a small percentage of total biomass ($\bar{x}=12\%$) due to their relative small dimensions. By contrast, in spite of their relative low densities ($\approx 10–15\times10^3$ cells l^{-1}), big sized dinoflagellates represented a considerable amount of total biomass during this period ($\bar{x}=30\%$). This is in accordance with the classic pattern of seasonal diatom-dinoflagellates succession described by Margalef (1978) and observed in many temperate ecosystems (Baretta-Bekker et al., 2009; Bresnan et al., 2009). In this general sequence of species succession, diatoms dominate in periods of mixing and high nutrient concentrations and dinoflagellates prevail under oligotrophic and more stratified waters. Due to the rainfall regime and riverine runoff in the study area, maximum freshwater inputs are observed during November and December (Hernando, 2006). Thus, the decrease in salinity observed during December 2006, could have lead to certain degree of stabilization of the water column through salinity stratification, favoring the development of flagellates. Despite the clearly defined numerical dominance of the different phytoplankton groups observed throughout species succession, it should be noted that diatoms constituted a significant portion of the biomass during much of this study. Since this particular group is characterized by rapid sinking in the water column, its contribution to coastal pelagic–benthic coupling may be highly significant for the energy support in the bottom ecosystem in the Beagle Channel area (Ambrust, 2009).

Phytoplankton species richness in the Beagle Channel was larger than observed in previous studies carried out in Tierra del Fuego Archipelago (Avaria et al., 2003; Zingone et al., in press), which could be related to the fact that these earlier studies were based only on summer oceanographic cruises. In spite of the rich phytoplankton assemblages observed in the qualitative samples, it is remarkable that only a few taxa dominated the phytoplankton. Among diatoms, the most abundant species were *C. socialis*, *C. tortissimus*, *C. debilis*, *C. teres*, *T. mendiolana*, *T. anguste-lineata* and *T. delicatula*. All these species have a cosmopolitan or temperate distribution (Hasle and Syvertsen, 1997) and have been previously observed in Argentinean waters (Vouilloud, 2003). Their presence in the Beagle Channel was observed all year-round, although they reached peak abundances during early October (*C. socialis*, *C. tortissimus*, *C. debilis*, and *C. teres*), late October

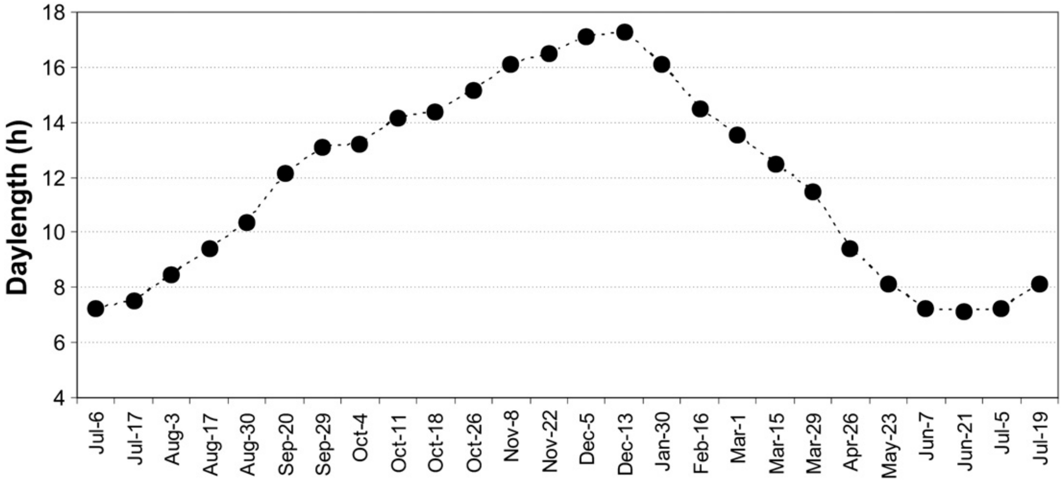

Fig. 6. Variation of day length during sampling period in the Beagle Channel. Data obtained from http://www.webcalculator.co.uk/environmental/daycalc.htm, using sampling location (latitude and longitude) and date (Julian day).

(*T. mendiolana*), November (*T. anguste-lineata*) and March (*T. delicatula*). The presence of some benthic species as well as some typical estuarine or freshwater species suggests the influence of resuspension processes and the contribution of inland waters to the water column in the studied station, further increasing the species richness. By contrast, it is worth signaling the absence of typical cold water species, like *Fragilariopsis* spp., which are broadly distributed in Antarctic waters but may also extend northwards to Argentinean shelf and slope subantarctic waters through the Malvinas Current (Cefarelli et al., 2010; Olguín and Alder, 2011).

In a recent study in the neighbor Strait of Magellan, Zingone et al. (in press) highlighted the presence of some small-sized (≤5 μm) taxa, such as the coccoid prasinophyte *Pycnococcus provasolii* and the diatoms *Lennoxia faveolata* and *Minidiscus trioculatus* during summer. Some of the tiny unidentified coccoid specimens (2–5 μm) and some small specimens of *Ceratoneis* (*Cylindrotheca*) *closterium* found in our study in the Beagle Channel could correspond to *P. provasolii* and *L. faveolata* respectively, as electronic transmission microscopy was not used in our study. By contrast, the finding of *Minidiscus chilensis* (instead of *Minidiscus trioculatus*) and some other differences in species composition between these two environments (see Table 1 in Zingone et al., in press), could be linked either to hydrological differences or to inter-annual variability and/or the more than 15 years passed between both sampling periods (1991–2006/2007).

At least 10 potential toxic species were identified during the study period, including *Alexandrium catenella*, *A. ostenfeldii*, *A. tamarense*, *Dinophysis acuminata*, *D. rotundata*, *Prorocentrum cordatum*, *Pseudo-nitzschia australis*, *P. calliantha*, *P. fraudulenta* and *P. cf. seriata* (Table 3). These species, with the exception of *P. cf. seriata*, are commonly observed in southern South America coasts and some of them have been related with regional toxic events (Sar et al., 2002). Given the scarcity of taxonomic studies in the area, the presence of *P. cordatum*, *A. tamarense*, *P. calliantha* and *P. fraudulenta* are new records for the Beagle Channel, although they have all been previously observed in the Argentine Sea (Balech, 2002; Ferrario et al., 2002; Almandoz et al., 2007; Carreto et al., 2008). *P. pungens*, a worldwide distributed species usually observed in northern coastal environments of Argentina (Sunesen et al., 2009), was not detected in the Beagle Channel, which could support its southward distribution limit to around 54°S in the Argentine Sea (Almandoz et al., 2007). Observed specimens of *P. cf. seriata* are in conflict with classical descriptions of both *P. seriata* and *P. australis*. However, SEM analyses revealed they were strikingly similar to unusual specimens of *P. seriata* isolated from Scottish waters, which prompts new questions about the worldwide distribution of *P. seriata* and its morphological differentiation with *P. australis* (Almandoz et al., 2009). The presence of potential toxic species is noteworthy since the area sustains rich aquiculture activities. A detailed description of these toxigenic species will be presented elsewhere (Almandoz et al., in prep.).

Different future scenarios proposed in the context of the global climate warming predict a series of impacts over marine ecosystems, such as a temperature increase in the surface water layer of the oceans, acidification, changes in the vertical structure of the water column and changes in the seasonality and volume of freshwater discharges from inland bodies in coastal waters (Riebesell, 2004; Moore et al., 2008). The potential consequences of these changes, coupled with other anthropogenic processes such as the transport of ballast water and eutrophication, on phytoplankton growth and composition are difficult to predict. The investigation of these impacts will require the implementation of long term multidisciplinary studies in different geographical areas, combining the simultaneous observation of physico-chemical and biological parameters (Moore et al., 2008). In this sense, although one year observations are not sufficient to trace accurate temporal phytoplankton trends, the present field research provides for the first time a description of the annual phytoplankton cycle in the Beagle Channel.

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