



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 ($141 \mu\text{g C l}^{-1}$ and $8.7 \mu\text{g Chl } a \text{ l}^{-1}$) and was associated with a bloom of the diatom genus *Chaetoceros*. In spite of a strong nutrient depletion that led 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. tamarensis*, *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 aquaculture production.

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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 ($\approx 55^\circ\text{S}$), the Beagle Channel is a drowned glacial valley that connects the Pacific and Atlantic oceans through 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 ($54^{\circ}52'50.01''$ S, $67^{\circ}45'21.82''$ 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. Sub-surface qualitative phytoplankton samples were additionally taken using a 20 μ m 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

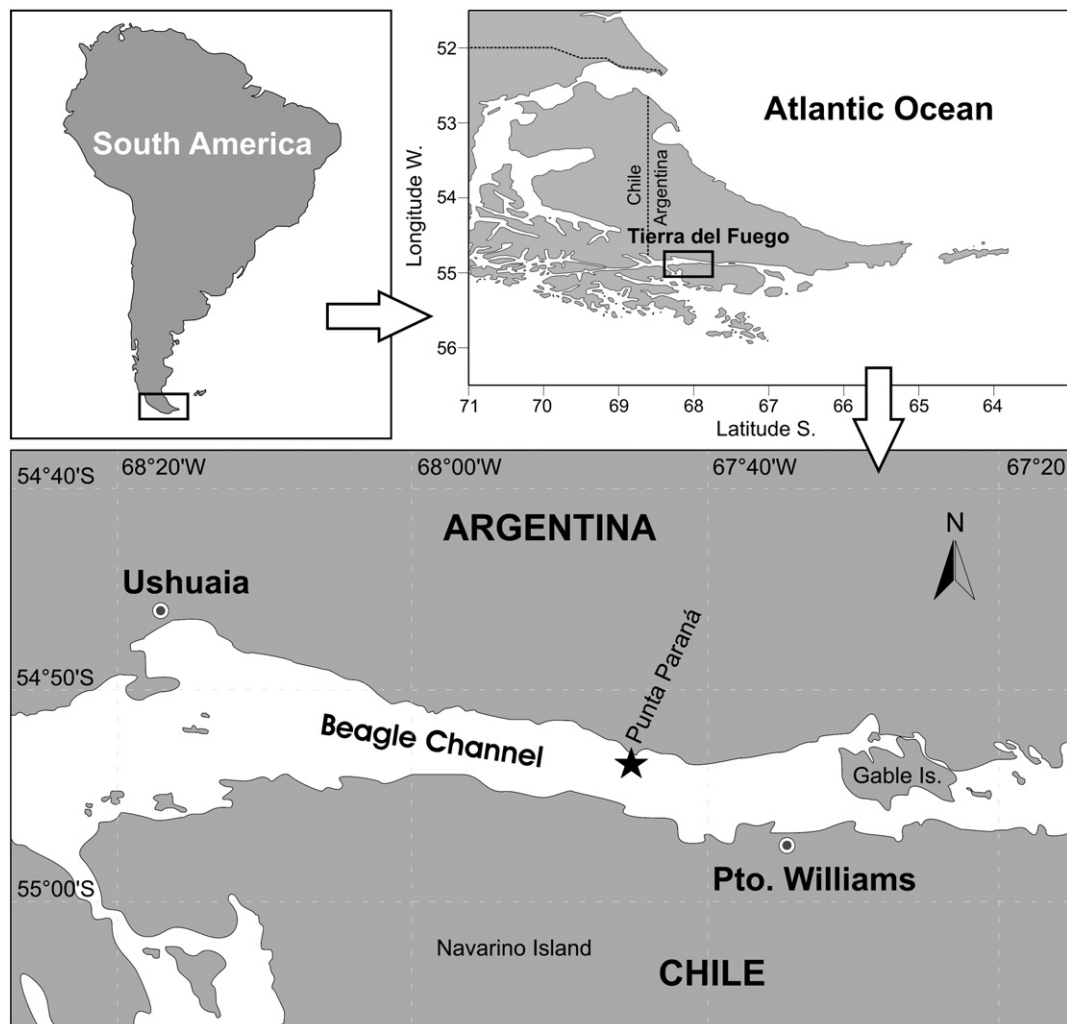


Fig. 1. Map of the study area in the Beagle Channel.

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^{-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 $\times$,

depending on their concentration and size. The whole chamber bottom was also scanned at 100 $\times$ to count large and sparse species. Since flagellates generally lose 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

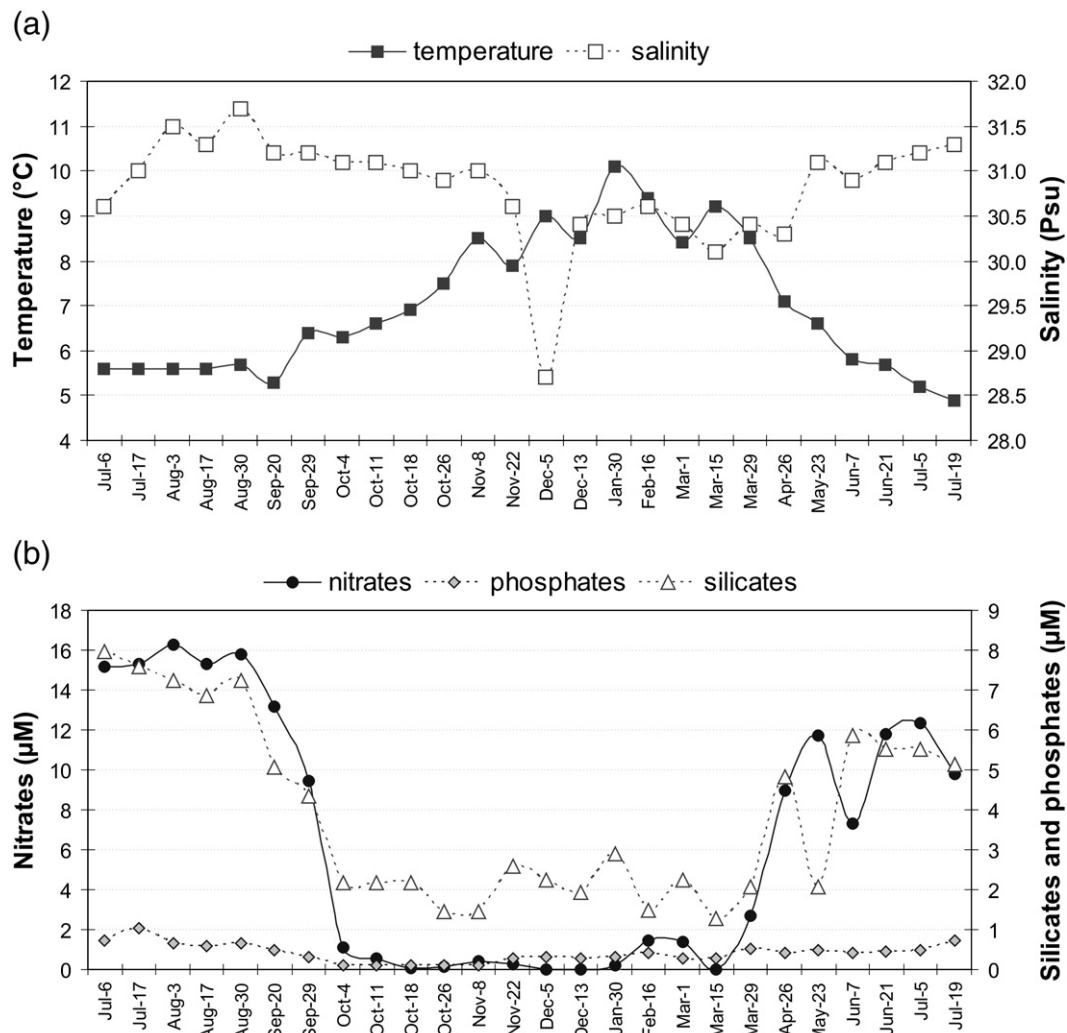


Fig. 2. Surface distribution of a) temperature and salinity and b) nitrates, phosphates and silicates concentrations during sampling period in the Beagle Channel.

Table 1

Seasonal average $\pm$ 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 $\pm$ standard deviation of phytoplankton biomass, chlorophyll *a* and cell density observed during sampling period in the Beagle Channel.

Period	Biomass ($\mu\text{g C l}^{-1}$)	Chlorophyll <i>a</i> ($\mu\text{g chl-}a \text{ l}^{-1}$)	Cell density ($\times 10^5 \text{ cells l}^{-1}$)
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 $10 \mu\text{M}$ during winter (max. $16.3 \mu\text{M}$) and were generally depleted or near the detection limit during spring–summer phytoplankton blooms. Silicate ranged from 8.0 to $1.3 \mu\text{M}$ (July 06–March 07) and phosphate varied between 2.0 and $0.2 \mu\text{M}$ (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 $0.1\text{--}7.1 \mu\text{g C l}^{-1}$ and $0.1\text{--}1.0 \mu\text{g Chl } a \text{ l}^{-1}$. In contrast, the highest values were observed during spring, in two occasions, one in

October and the other in November, reaching 141 and $121 \mu\text{g C l}^{-1}$ and 8.7 and $5 \mu\text{g Chl } a \text{ l}^{-1}$ respectively. Finally, intermediate concentrations were observed in summer, ranging between $26.6\text{--}50.8 \mu\text{g C l}^{-1}$ and $1.8\text{--}3.8 \mu\text{g Chl } a \text{ l}^{-1}$. 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 $1.5 \times 10^5 \text{ cells l}^{-1}$ were observed during fall and winter, with a minimum of $6.3 \times 10^3 \text{ cells l}^{-1}$ (July 07). In contrast, spring and summer densities were higher than $3.0 \times 10^5 \text{ cells l}^{-1}$, with a maximum of $3.5 \times 10^6 \text{ cells l}^{-1}$ 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.

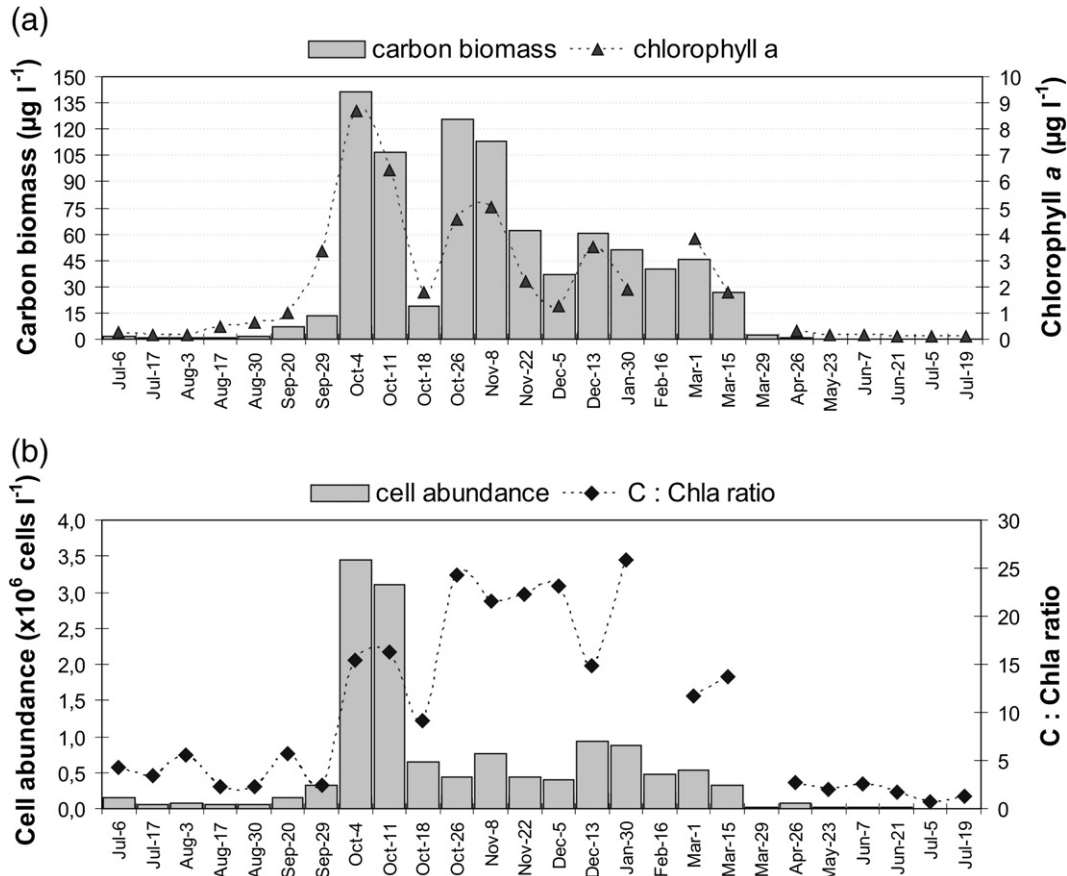


Fig. 3. Seasonal variability of phytoplankton biomass (a), abundance and C:Chl *a* ratio (b) during sampling period in the Beagle Channel.

Table 3

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

Diatoms
<i>Achnantes</i> sp.
<i>Actinocyclus curvatus</i> Janisch
<i>Actinocyclus</i> sp.
<i>Actinopterychus senarius</i> (Ehrenberg) Ehrenberg
<i>Amphora</i> spp.
<i>Asterionellopsis glacialis</i> (Castracane) Round
<i>Attheya</i> sp.
<i>Bacillaria paxillifera</i> (Müller) Hendey
<i>Cerataulina pelagica</i> (Cleve) Hendey
<i>Ceratoneis closterium</i> Ehrenberg
<i>Cocconeis convexa</i> Giffen
<i>Cocconeis krammeri</i> Lange-Bertalot & Metzeltin
<i>Cocconeis pseudocostata</i> Romero
<i>Cocconeis scutellum</i> Ehrenberg
<i>Cocconeis</i> sp.
<i>Corethron hystrix</i> Hensen
<i>Coscinodiscus janischii</i> Schmidt
<i>Coscinodiscus radiatus</i> Ehrenberg
<i>Chaetoceros affinis</i> Lauder
<i>Chaetoceros cf. concavicornis</i>
<i>Chaetoceros cf. convolutus</i>
<i>Chaetoceros criophilus</i> Castracane
<i>Chaetoceros curvatus</i> Cleve
<i>Chaetoceros debilis</i> Cleve
<i>Chaetoceros decipiens</i> Cleve
<i>Chaetoceros diadema</i> (Ehrenberg) Gran
<i>Chaetoceros didymus</i> Ehrenberg
<i>Chaetoceros lorenzianus</i> Grunow
<i>Chaetoceros radicans</i> Schütt
<i>Chaetoceros similis</i> Cleve
<i>Chaetoceros socialis</i> Lauder
<i>Chaetoceros teres</i> Cleve
<i>Chaetoceros tortissimus</i> Gran
<i>Chaetoceros</i> spp.
<i>Ctenophora pulchella</i> (Ralfs ex Kützing) Williams & Round
<i>Cyclotella</i> sp.
<i>Cymatopleura solea</i> (Brébisson) Smith
<i>Cymbella</i> sp.
<i>Dactyliosolen fragilissimus</i> (Bergon) Hasle
<i>Delphineis minutissima</i> (Hustedt) Simonsen
<i>Diploneis cf. splendida</i> (Gregory) Cleve
<i>Ditylum brightwellii</i> (West) Grunow in Van Herurck
<i>Donkinia</i> sp.
<i>Encyonopsis microcephala</i> (Grunow) Krammer
<i>Encyonema minutum</i> (Hilse in Rabenhorst) D. G. Mann
<i>Entomoneis</i> sp.
<i>Eunotia bilunaris</i> var. <i>bilunaris</i> (Ehrenberg) Mills
<i>Fallacia</i> sp.
<i>Gomphonemopsis</i> sp.
<i>Grammatophora hamulifera</i> Kützing
<i>Grammatophora cf. undulata</i>
<i>Guinardia delicatula</i> (Cleve) Hasle
<i>Gyrosigma fasciola</i> (Ehrenberg) Griffith et Henfrey
<i>Gyrosigma tenuissimum</i> (W. Smith) Griffith & Henfrey
<i>Gyrosigma macrum</i> (W. Smith) Griffith & Henfrey
<i>Hannaea arcus</i> (Ehrenberg) R.M. Patrick
<i>Haslea cf. crucigeroides</i> (Hustedt) Simonsen
<i>Hyalodiscus</i> sp.
<i>Leptocylindrus minimus</i> Gran
<i>Licmophora</i> spp.
<i>Minidiscus chilensis</i> Rivera
<i>Navicula algida</i> Grunow
<i>Navicula directa</i> (Smith) Ralfs in Pritchard
<i>Navicula perminuta</i> Grunow
<i>Navicula transitans</i> var. <i>derasa</i> f. <i>delicatula</i> Heimdal
<i>Nitzschia cf. lecontei</i> van Heurck
<i>Nitzschia cf. laevis</i> Hustedt
<i>Paralia sulcata</i> (Ehrenberg) Cleve
<i>Pleurosigma obscurum</i> W. Smith emend. Sterrenburg
<i>Pleurosigma cf. normanii</i> Ralfs in Pritchard
<i>Psammodictyon panduriforme</i> (Gregory) Mann
<i>Pseudo-nitzschia australis</i> Frenguelli
<i>Pseudo-nitzschia calliantha</i> Lundholm, Moestrup & Hasle
<i>Pseudo-nitzschia fraudulenta</i> (Cleve) Hasle
<i>Pseudo-nitzschia cf. seriata</i>

Table 3 (continued)

Diatoms
<i>Rhabdonema minutum</i> Kützing
<i>Rhizosolenia setigera</i> Brightwell f. <i>setigera</i>
<i>Rhizosolenia hebetata</i> f. <i>hebetata</i> Bailey
<i>Rhizosolenia</i> sp.
<i>Roperia tessellata</i> (Roper) Grunow ex Pelletan
<i>Skeletonema cf. costatum</i> (Greville) Cleve emend. Zingone et Sarno
<i>Stauraphora</i> sp.
<i>Staurisirella?</i> Round
<i>Stellarima stellaris</i> (Roper) Hasle & Sims
<i>Stephanopyxis turris</i> (Greville) Ralfs ex Pritchard
<i>Striatella unipunctata</i> (Lyngbye) Agardh
<i>Subsilicea fragilarioides?</i> von Stosch & Reimann
<i>Tabularia fasciculata</i> (Agardh) Williams & Round
<i>Thalassionema nitzschioides</i> (Grunow) Mereschkowsky
<i>Thalassiosira anguste-lineata</i> (Schmidt) Fryxell & Hasle
<i>Thalassiosira curviseriata</i> Takano
<i>Thalassiosira delicatula</i> Ostenfeld
<i>Thalassiosira eccentrica</i> (Ehrenberg) Cleve
<i>Thalassiosira gerloffii</i> Rivera
<i>Thalassiosira mendiolana</i>
<i>Thalassiosira cf. minima</i> Gaarder emend. Hasle
<i>Thalassiosira pacifica</i> Gran & Angst
<i>Thalassiosira rotula</i> Meunier
<i>Thalassiosira tenera</i> Proschkina-Lavrenko
<i>Thalassiosira</i> spp.
<i>Trachyneis aspera</i> var. <i>aspera</i> (Ehrenberg) Cleve
<i>Trachysphenia</i> sp.
Dinoflagellates
<i>Amphidinium</i> sp.
<i>Amphidoma acuminata</i> Stein
<i>Alexandrium catenella</i> (Whedon & Kofoid) Balech
<i>Alexandrium ostenfeldii</i> (Paulsen) Balech & Tangen
<i>Alexandrium tamarense</i> (Lebour) Balech
<i>Ceratium fusus</i> (Ehrenberg) Dujardin
<i>Ceratium lineatum</i> (Ehrenberg) Cleve
<i>Ceratium tripos</i> (Müller) Nitzsch
<i>Dinophysis acuminata</i> Claparède & Lachmann
<i>Dinophysis rotundata</i> Claparède & Lachmann
<i>Dinophysis truncata</i> Cleve
<i>Gymnodinium</i> spp.
<i>Gyrodinium</i> sp.
<i>Heterocapsa</i> sp.
<i>Oxytoxum</i> sp.
<i>Prorocentrum cf. compressum</i>
<i>Prorocentrum cordatum</i> (Ostenfeld) Dodge
<i>Prorocentrum micans</i> Ehrenberg
<i>Prorocentrum</i> sp.
<i>Protoperidinium cf. punctulatum</i>
<i>Protoperidinium joergenseni</i> var. <i>luculentum</i> Balech
<i>Protoperidinium cf. brevipes</i>
<i>Protoperidinium denticulatum</i> (Gran et Braarud) Balech
<i>Protoperidinium excentricum</i> (Paulsen) Balech
<i>Protoperidinium simulium</i> (Paulsen) Balech
<i>Protoperidinium</i> spp.
<i>Scrippsiella</i> sp.
Cryptophytes
Cryptomonads (<10 µm)
Cryptomonads (>10 µm)
Euglenophytes
<i>Eutreptia</i> sp.
Prasinophytes
<i>Pyramimonas</i> sp.
<i>Tetraselmis</i> sp.
Prymnesiophytes
<i>Chrysochromulina/Prymnesium</i> sp.
<i>Emiliania huxleyi</i> (Lohmann) Hay & Mohler
<i>Phaeocystis cf. antarctica</i> Karsten
Silicoflagellates
<i>Dictyocha speculum</i> 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 $5\text{--}11 \times 10^3 \text{ cells l}^{-1}$. 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 $200 \mu\text{m}^3 \text{ cell}^{-1}$. 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 $30\text{--}42 \mu\text{m}$; pervalvar axis $15\text{--}20 \mu\text{m}$), the dinoflagellates *Gyrodinium* sp. and *Protoperdinium joergensenii* 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 $93.6 \mu\text{g C l}^{-1}$ (74.7% of diatoms). The second bloom was mainly represented by the genus *Thalassiosira* (*T. mendiolana* and *T. anguste-lineata*), which reached $103.4 \mu\text{g C l}^{-1}$ (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

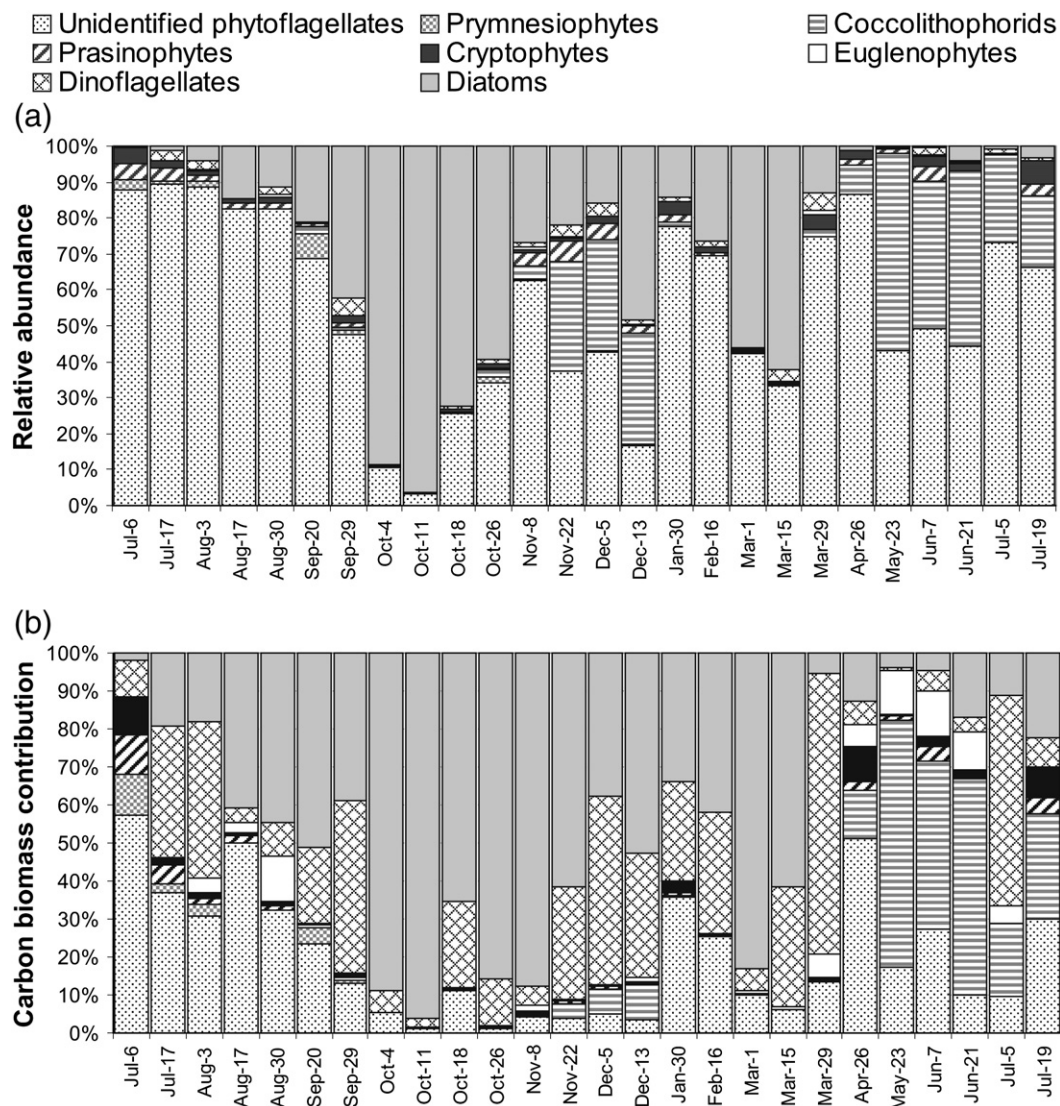


Fig. 4. Relative abundance (a) and biomass (b) of the main phytoplankton groups identified during sampling period in the Beagle Channel.

Table 4Seasonal average $\pm$ 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 $\pm$ 1.2	65.9 $\pm$ 99.8	3.4 $\pm$ 3.8	6.3 $\pm$ 4.4	3.1 $\pm$ 2.66
	Cryptophytes	1.8 $\pm$ 2.6	4.9 $\pm$ 1.5	10.8 $\pm$ 14.6	0.8 $\pm$ 0.6	0.3 $\pm$ 0.2
	Diatoms	8.5 $\pm$ 11.6	859.8 $\pm$ 1238.1	187.9 $\pm$ 83.9	1.1 $\pm$ 1.6	0.3 $\pm$ 0.2
	Dinoflagellates	0.9 $\pm$ 0.6	10.1 $\pm$ 4.9	7.7 $\pm$ 4.2	0.4 $\pm$ 0.5	0.07 $\pm$ 0.01
	Euglenophytes	0.1 $\pm$ 0.2	1.0 $\pm$ 1.7	0.4 $\pm$ 0.4	0.2 $\pm$ 0.1	0.03 $\pm$ 0.03
	Prasinophytes	2.2 $\pm$ 2.4	11.4 $\pm$ 11.3	6.2 $\pm$ 8.1	0.5 $\pm$ 0.4	0.08 $\pm$ 0.1
	Prymnesiophytes	2.6 $\pm$ 3.9	2.1 $\pm$ 2.2	–	–	–
	Unidentified phytoflagellates	75.7 $\pm$ 35.3	212.7 $\pm$ 124.5	337.4 $\pm$ 247.3	24 $\pm$ 23.1	5.12 $\pm$ 0.5
	Coccolithophorids	0.01 $\pm$ 0.02	1.25 $\pm$ 1.90	0.07 $\pm$ 0.07	0.12 $\pm$ 0.08	0.06 $\pm$ 0.05
	Cryptophytes	0.03 $\pm$ 0.04	0.08 $\pm$ 0.03	0.52 $\pm$ 0.78	0.03 $\pm$ 0.04	0.004 $\pm$ 0.004
Biomass ($\mu g C l^{-1}$)	Diatoms	0.85 $\pm$ 1.39	59.58 $\pm$ 48.10	22.06 $\pm$ 10.66	0.06 $\pm$ 0.06	0.03 $\pm$ 0.01
	Dinoflagellates	0.40 $\pm$ 0.52	11.00 $\pm$ 6.91	9.23 $\pm$ 4.90	0.42 $\pm$ 0.79	0.03 $\pm$ 0.04
	Euglenophytes	0.04 $\pm$ 0.07	0.35 $\pm$ 0.59	0.13 $\pm$ 0.15	0.07 $\pm$ 0.05	0.01 $\pm$ 0.01
	Prasinophytes	0.04 $\pm$ 0.04	0.23 $\pm$ 0.25	0.11 $\pm$ 0.14	0.01 $\pm$ 0.01	0.002 $\pm$ 0.003
	Prymnesiophytes	0.08 $\pm$ 0.13	0.07 $\pm$ 0.07	–	–	–
	Unidentified phytoflagellates	0.66 $\pm$ 0.51	2.79 $\pm$ 2.04	8.61 $\pm$ 7.29	0.22 $\pm$ 0.18	0.02 $\pm$ 0.01
	Coccolithophorids	0.01 $\pm$ 0.02	1.25 $\pm$ 1.90	0.07 $\pm$ 0.07	0.12 $\pm$ 0.08	0.06 $\pm$ 0.05
	Cryptophytes	0.03 $\pm$ 0.04	0.08 $\pm$ 0.03	0.52 $\pm$ 0.78	0.03 $\pm$ 0.04	0.004 $\pm$ 0.004

be attributed to the higher cell dimensions of dominant *Thalassiosira* species ($\approx 11,000$ – $14,000 \mu m^3 cell^{-1}$) compared to those of *Chaetoceros* ($< 2500 \mu m^3 cell^{-1}$ 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 $20 \mu g C l^{-1}$, 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 *Proto-peridinium excentricum*, followed by *Alexandrium catenella*, *Proto-peridinium joergenseni* var. *luculentum* and *Proto-peridinium cf. punctulatum*. Moreover, coccolithophorids also reached their highest densities towards the end of spring (max. $2.9 \times 10^5 cells l^{-1}$) 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 $6.8 \times 10^5 cells l^{-1}$. Likewise, cryptophytes also reached their highest densities during this season (Table 4), with a peak of $3.3 \times 10^4 cells l^{-1}$. 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 *Proto-peridinium 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

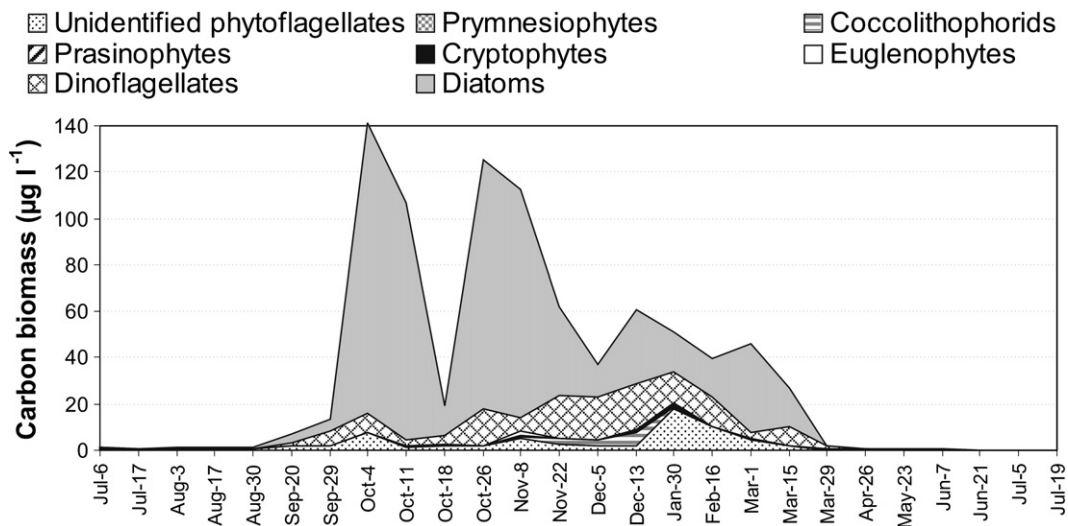


Fig. 5. Seasonal biomass variability of the main phytoplankton groups identified during sampling period in the Beagle Channel.

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		
<i>Achnantes</i> sp.	290	29
<i>Actinocyclus curvatus</i>	26,789	1123
<i>Asterionelliopsis glacialis</i>	1398	102
<i>Attheya</i> sp.	349	33
<i>Bacillaria paxillifera</i>	11,265	556
<i>Ceratoneis closterium</i>	144	16
<i>Chaetoceros cf. concavicornis</i>	1041	81
<i>Chaetoceros criophilus</i>	1605	115
<i>Chaetoceros curvisetus</i>	227	23
<i>Chaetoceros debilis</i>	403	37
<i>Chaetoceros didymus</i>	1030	80
<i>Chaetoceros lorenzianus</i>	2655	172
<i>Chaetoceros teres</i>	2359	157
<i>Chaetoceros tortissimus</i>	200	21
<i>Chaetoceros radicans</i>	1382	101
<i>Chaetoceros socialis</i>	61	8
<i>Cocconeis scutellum</i>	537	47
<i>Coscinodiscus janischii</i>	337,831	8773
<i>Coscinodiscus radiatus</i>	24,772	1054
<i>Dactyliosolen fragilissimus</i>	15,033	703
<i>Donkinia</i> sp.	27,587	1150
<i>Grammatohora cf. undulata</i>	2254	151
<i>Guinardia delicatula</i>	1199	90
<i>Haslea cf. crucigeroides</i>	43,548	1666
<i>Leptocylindrus minimus</i>	85	11
<i>Navicula transitans</i> var. <i>derasa</i> f. <i>delicatula</i>	730	60
<i>Navicula perminuta</i>	78	10
<i>Navicula directa</i>	1396	102
<i>Paralia sulcata</i>	5515	312
<i>Tabularia fasciculata</i>	236	24
<i>Pleurosigma obscurum</i>	1186	90
<i>Pleurosigma cf. normanii</i>	20,438	902
<i>Pseudo-nitzschia australis</i>	2049	140
<i>Pseudo-nitzschia fraudulenta</i>	1179	89
<i>Pseudo-nitzschia calliantha</i>	321	31
<i>Rhabdonema minutum</i>	9316	477
<i>Rhizosolenia setigera</i> f. <i>setigera</i>	7295	391
<i>Skeletonema cf. costatum</i>	321	31
<i>Stellarima stellaris</i>	10,619	530
<i>Subsilicea fragilarioides?</i>	339	32
<i>Tabularia fasciculata</i>	5944	331
<i>Thalassionema nitzschioides</i>	377	35
<i>Thalassiosira anguste-lineata</i>	11,353	560
<i>Thalassiosira delicatula</i>	2828	181
<i>Thalassiosira mendiolana</i>	14,148	669
<i>Thalassiosira minima/curviseriata</i>	207	22
<i>Thalassiosira pacifica</i>	1309	97
<i>Thalassiosira</i> sp. <30 μm	2352	156
<i>Thalassiosira</i> sp. >30 μm	20,882	918
Undetermined naviculoid <15 μm	41	6
Undetermined pennate (40–65 μm)	1048	81
Dinoflagellates		
<i>Alexandrium catenella</i>	24,089	2812
<i>Alexandrium ostenfeldii</i>	50,977	5684
<i>Amphidinium</i> sp.	1508	208
<i>Amphidoma acuminata</i>	3593	471
<i>Ceratium fusus</i>	26,471	3072
<i>Ceratium lineatum</i>	16,693	1993
<i>Dinophysis acuminata</i>	14,992	1801
<i>Heterocapsa</i> sp.	1058	149
<i>Oxytoxum</i> sp.	1684	231
<i>Prorocentrum cf. compressum</i>	1874	256
<i>Prorocentrum cordatum</i>	237	37
<i>Prorocentrum micans</i>	945	134
<i>Protoperdinium cf. brevipes</i>	833	119
<i>Protoperdinium denticulatum</i>	27,833	3220
<i>Protoperdinium joergenseni</i> var. <i>luculentum</i>	20,344	2399
<i>Protoperdinium cf. punctulatum</i>	48,328	5406
<i>Protoperdinium excentricum</i>	21,707	2550
<i>Protoperdinium simulum</i>	84,984	9185
<i>Scrippsiella</i> sp.	14,362	1730
<i>Gyrodinium</i> 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		
<i>Cryptomonads</i> <10 μm	101	17
<i>Cryptomonads</i> >10 μm	343	52
Euglenophytes		
<i>Eutreptia</i> sp.	2579	345
Prasinophytes		
<i>Pyramimonas</i> sp.	312	47
<i>Tetraselmis</i> sp.	108	18
Prymnesiophytes		
<i>Chrysochromulina/Prymnesium</i> sp.	203	32
<i>Emiliania huxleyi</i>	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 ($\approx 69^\circ\text{W}$). 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 CO₂ limits photosynthesis of other algae groups (Cloern and Dufford, 2005).

The bloom of *Chaetoceros* caused a strong nutrient depletion, with NO₃, PO₄ and SiO₃ 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 (≈ 10 – 15×10^3 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

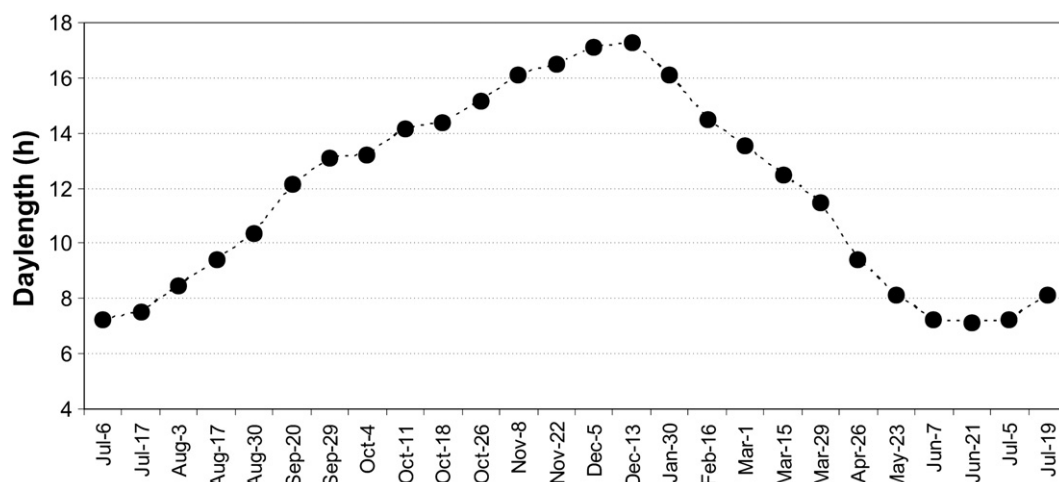


Fig. 6. Variation of day length during sampling period in the Beagle Channel. Data obtained from <http://www.webcalculator.co.uk/environmental/daycalc.htm>, using sampling location (latitude and longitude) and date (Julian day).

(*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 re-suspension 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 ($\leq 5 \mu\text{m}$) 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 ($2\text{--}5 \mu\text{m}$) 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 aquaculture 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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