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The FRUELA cruises. A carbon flux study in productive areas of the Antarctic Peninsula (December 1995–February 1996)

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Abstract

The FRUELA (name of an 8th century king of Asturias) project, part of the Spanish contribution to the study of biogeochemical carbon fluxes in the Southern Ocean, was based on two consecutive cruises of the B.I.O.; *Hespérides* which took place in the Bransfield and Gerlache Straits and Bellingshausen Sea between early December and early February of Austral summer 1995–1996. In addition to the cruises, data were obtained from an array of sediment traps deployed for one year in the Western Bransfield Strait Basin. The basic objectives of FRUELA were the quantification of carbon standing stocks and fluxes through the main components of the “biological pump” and the determination of carbon fluxes across different water column boundaries, including the transfer of CO₂ between the atmosphere and the ocean, the export of particulate carbon (PC) out of the euphotic zone, the vertical flux of PC in deep waters and the accumulation of carbon in sediments. The main hydrographical features found in the study region were the Southern Boundary of the Antarctic Circumpolar Current (SbyACC) and the Bransfield Front. Three major zones, with contrasting physico-chemical and biological characteristics were considered: Bellingshausen, including the Northwest Bellingshausen Sea and comprising the SbyACC, Bransfield, including the Western Bransfield Strait and the northeastern part of the Gerlache Strait, and Gerlache, with the rest of the Gerlache Strait. This paper summarizes the distribution of different properties and rate processes in these zones and discusses the major findings of the cruise concerning carbon fluxes. Our results indicate that, during the summer period, the studied area could be considered as a sink for atmospheric carbon. The amount of PC exported out of the photic layer was a moderate fraction of primary production and a low fraction of the suspended PC; high chlorophyll *a* systems dominated by microphytoplankton showed higher PC export fluxes than low chlorophyll *a* systems dominated by small flagellates and cryptomonads. The amount of PC arriving at deep waters or accumulating in the sediments was two to three orders of magnitude lower than that exported from the photic layer, probably due to biological recycling and advection out of the area. © 2001 Elsevier Science Ltd. All rights reserved.

1. Introduction

The Southern Ocean (SO) plays a key role in the control of global climate through its influence

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on atmospheric and thermohaline circulation (Webb and Sugimotohara, 2001) and through its contribution to the global carbon cycle. On the one hand, the SO is a source of intermediate and deep waters that ventilate much of the world ocean. On the other hand, the fluxes involved in the “biological pump” of the carbon cycle, and the biogeochemical processes taking place in the SO present some unusual characteristics (Turner and Owens, 1995). The role of the SO in the uptake and storage of CO₂ and its importance as a sink for anthropogenic CO₂ (Sarmiento et al., 1998) have been the subject of considerable controversy (Caldeira and Duffy, 2000). Modelling and observation results suggest that CO₂ uptake in the SO is high, but a large part of this CO₂ is exported out of the SO by isopycnal transport. These large input and output fluxes leave a wide margin for uncertainty.

Although most of its open-sea areas have low primary production, the SO also contains highly productive regions, generally associated with frontal zones or the proximity of land; these zones can be expected to be major sinks of atmospheric carbon to deep waters or sediments. The environmental and biological characteristics that distinguish the SO from other marine regions of the world include low temperatures and strong seasonal changes in light conditions, as well as other particular features. One of them is the influence of ice cover and its seasonal variability, while the other is the observation that phytoplankton growth stops before producing macronutrient depletion in a large part of this ocean, converting it to a so-called HNLC region. Several reasons have been put forward to explain this situation, including prominent Fe-limitation.

Due to the presence of high productivity areas and its importance as a transfer region, the SO is an interesting place to look for patterns and to test hypotheses concerning carbon fluxes through the food web and their relationships to environmental conditions. This interest has been recognized by the establishment of a Southern JGOFS programme, which has resulted, over the last decade, in a series of field studies addressing fluxes of biogenic materials: RACER (Huntley et al., 1991), STERNA (Turner and Owens, 1995), the cruise

ANT X/6 of R.V. *Polarstern* (Smetacek et al., 1997) among others.

2. Objectives

The FRUELA project was a part of the Spanish contribution to the study of carbon fluxes in the SO and was based on two consecutive cruises of the BIO *Hespérides*, carried out in the Bransfield Strait and Gerlache Strait during the austral summer, 1995–96. The term “FRUELA” stands for the name of an 8th century king of Asturias, a principality in northern Spain, where some of the principal investigators of the project are based. The basic objective of FRUELA was the quantification of the biogeochemical carbon fluxes in the studied area, according to the conceptual model shown in Fig. 1. A key aspect of the project was the determination of the carbon transfers across the boundaries of the water column: (a) the transfer of CO₂ between the atmosphere and the ocean, (b) the export of particulate carbon (PC) out of the euphotic zone, (c) the vertical flux of PC in deep waters and (d) the accumulation of carbon in sediments. In recognition of the fundamental role of planktonic organisms as primary or secondary producers of organic matter, regenerators of CO₂, and modulators of particulate fluxes to the sediment, special attention was paid to the measurement of the standing stocks and production of the main components of the planktonic community.

3. The study area

The western part of the Bransfield Strait and the Gerlache Strait (Fig. 2), with a strong coastal influence and extensive shelf zones, are considered as highly productive areas (Huntley et al., 1991). Wefer et al. (1988) associated these regions with episodic high production events and documented very high fluxes of settling material to the sediment in the Bransfield Strait. In addition, our study area included the eastern part of the Bellingshausen Sea because it represented a good example of a complex area with shelf and slope waters, frontal zones (the southern limit of the Antarctic Circum-

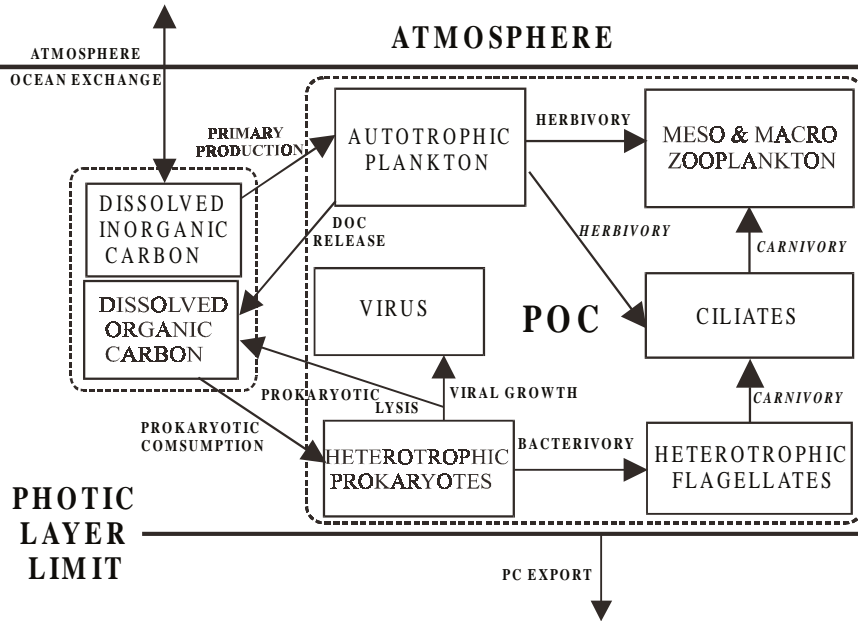


Fig. 1. Conceptual diagram used during the FRUELA project, showing the main carbon stocks and fluxes related to the “biological pump” in the photic layer, as well as the atmosphere-ocean CO₂ exchange and POC export to deep waters. Fluxes related to deep waters and sediment are not included in the diagram.

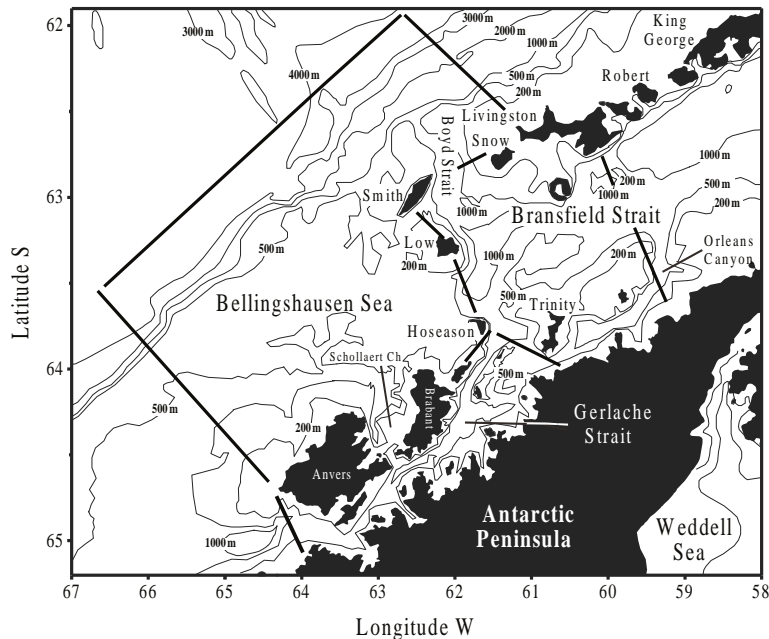


Fig. 2. FRUELA study area: bathymetry (in m) and geography of coastal zone. The areas considered for the global carbon budgets are separated by lines.

polar Current, SbyACC), and open ocean, and had been less studied than other areas (included in the LTER programme, USA).

Background information on the Bransfield and Gerlache Straits has been obtained by several research programmes, including BIOMASS-SYBEX (Grelowski et al., 1986) and RACER (Huntley et al., 1991, and other papers in the same volume). Recently, several Spanish cruises (BIOANTAR 92, BIOANTAR 93 and ECOANTAR, respectively, visited the area in the austral summers of 1991–92, 1992–93 and 1993–94) have visited them, which is closer to the Spanish Antarctic Base in Livingston Island. Basic hydrographical features of the region have been described by Gordon and Nowlin (1978), Grelowski et al. (1986) and Niiler et al. (1991). Garcia et al. (1994) and López et al. (1999) studied different aspects of the mesoscale circulation, and López et al. (1994) considered the propagation of tides.

In spite of the many surveys carried out in the Bransfield Strait region (see RACER special issue; Huntley et al., 1991), there are few data sets that allow the synoptic consideration of all the main C fluxes summarised in Fig. 1. This fact, together with its accessibility and the proximity of strong production gradients between highly productive zones (parts of the Bransfield and Gerlache Straits, the SbyACC in the Bellingshausen Sea) and oligotrophic zones (eastern part of the Bellingshausen Sea and parts of the Western Bransfield basin) made this area a good choice for the FRUELA project.

4. Workplan

The FRUELA strategy included acquisition of seasonal data by moored current meters and sediment traps (March 1995–February 1996), experiments and property measurements made at sea during two cruises of the BIO *Hespérides*, carried out during the 1995–96 austral summer. The FRUELA 95 cruise took place between 3 December 1995 and 5 January 1996, and the FRUELA 96 cruise between 17 January and 5 February 1996. The participants in the FRUELA cruises included 60 scientists and technicians from

several universities and research institutions (Table 1). Some stocks and fluxes were measured in both cruises (56 stations during FRUELA 95 and 33 stations during FRUELA 96), whereas some specific measurements were done only in one of them (see Table 1).

The FRUELA 95 cruise consisted of three legs and focused on the study of biological processes affecting the air-sea CO₂ exchanges, principally in relationship with primary production. Leg 1 was devoted to a macroscale survey of the study region and covered a sampling grid (Fig. 3A) of 47 stations separated by about 31 km (nm). Leg 2 consisted of a mesoscale survey (Fig. 3C) of 107 stations at the western Bransfield basin (sample grid of 14.5 km), as a part of an effort to characterise the coupling between mesoscale hydrographic features and biological phenomena. Also, a synoptic transect of 11 stations covering the Gerlache Strait in order to describe the spatial and temporal changes was performed. Leg 3 was mainly devoted to 5 long, 24–30 h, “biological” stations for experimentation and process studies as well as C-export measurements (five stations). The positions of these stations were defined (Fig. 3D) according to the data obtained in the previous legs. At each station, samples were taken at different times of the day, in situ incubations were carried out and drifting sediment traps were deployed.

The FRUELA 96 cruise also contained three legs and emphasized the study of processes of transformation of organic matter through the food web and the transfers between the water column and the sediments. During leg 1, 10 stations were occupied near Astrolabe Island and between the eastern mouth of the Gerlache Strait and the Bismark Strait (Fig. 3B). Leg 2 was devoted to a re-occupation of four of the five “macroscale” transects sampled during leg 1 of FRUELA 95 (Fig. 3B) (36 stations). Leg 3 included five 24–30 h “biological” stations (Fig. 3D) and sediment sampling to measure C-export and to determine the actual C burial and paleoclimatic records (13 stations). The main topics addressed during each of the FRUELA cruises are summarized in Table 1.

Table 1
Individual projects within the FRUELA cruises

Research Topic/Operation	Principal investigator	Team on board	Cruise	Reference
<i>Physics</i>				
CTD—Macro and mesoscale distribution	Marc Antoni Garcia (UPC)	Marc Antoni Garcia	F96	(Garcia et al., 2002)
	Oswaldo López (UPC)	Oswaldo López	F95	
		Julia Figa (UPC)	F95	
		Manuel González (UPC)	F95	
		Joan Puigdefabregas (UPC)	F95	
CTD—Geostrophic circulation	Damià Gomis (UIB)	María Pilar Rojas (UPC)	F96	(Gomis et al., 2002)
		Damià Gomis	F95	
<i>Chemistry</i>				
Nutrient distribution and utilization	Carmen González-Castro (IIM)	Carmen González-Castro	F95	(Castro et al., 2002)
		María José Pazo (IIM)	F96	
CO ₂ system, pH and alkalinity	Aida Fernández-Ríos (IIM)	Aida Fernández-Ríos	F96	(Álvarez et al., 2002)
		Gabriel Rosón (UV)	Gabriel Rosón	
		M ^a Victoria González (IIM)	F95	
		María Trinidad Rellán (IIM)	F96	
POC and DOC distribution	María Dolores Doval (IIM)	María Dolores Doval	F95	(Doval et al., 2002)
		Ramon Penín (IIM)	F95	
		Enrique Nogueira (IIM)	F95	
<i>Phytoplankton</i>				
Light and bio-optics	Félix López-Figueroa (UM)	Félix López-Figueroa (UM)	F95	(Figueroa, 2002) (Figueroa et al., 1997) (Lorenzo et al., 2002) (Arbones et al., 2000) (Rodríguez et al., 2002b)
		Belén Arbones (IIM)	F95	
		María Luisa Villarinos (IIM)	F96	
Flow-cytometry and size structure	Jaime Rodríguez (UM)	Jaime Rodríguez	F95	
		Francisco Jiménez (UM)	F95	
Primary production and pigments (HPLC)	Emilio Fernández (UV)	José María Blanco (UM)	F95	(Varela, et al., 2002)
		Emilio Fernández (UV)	F95	
Gross primary production and microbial respiration (oxygen)	Manuel Varela (IEO) Pablo Serret (UO)	Manuel Varela (IEO)	F96	(Rodríguez et al., 2002a) (Serret et al., 2001)
		Pablo Serret (UO)	F95	
		Emilio Marañón (UO)	F96	
DOC release Microbial ETS activity New and regenerated production(¹⁵ N)	Marta Estrada (ICM) Rosa Martínez (US) Antonio Bode (IEO)	Natalia González (UO)	F96	(Morán and Estrada, 2002) (Morán et al., 2002) (Bode et al., 2002)
		Marta Estrada	F95	
		Rosa Martínez	F95	
		Antonio Bode (IEO)	F95	

Table 1 (continued)

Research Topic/Operation	Principal investigator	Team on board	Cruise	Reference
<i>Heterotrophic microbes</i>				
Protist abundance and bacterivory	Dolors Vaqué (ICM)	Dolors Vaqué	F95	(Vaqué et al., 2002) (Pedrós-Alió et al., 2002)
		Núria Guixa-Boixereu (ICM)	F96	
Prokaryotes abundance and production, Viruses and prokaryotic lysis	Carles Pedrós-Alió (ICM)	Carles Pedrós-Alió	F96	(Guixa-Boixereu et al., 2002)
		Josep M. Gasol (ICM)	F95	
<i>Meso and macrozooplankton</i>				
Mesozooplankton composition, abundance and grazing	Florentina Álvarez-Marqués (UO) José Luis Acuña (UO)	Florentina Álvarez-Marqués	F95	(Cabal et al., 2002)
		José Luis Acuña	F96	
		Jesús Alberto Cabal (UO)	F96	
		Mario Quevedo (UO)	F96	
		Jorge Álvarez-Sostres (UO)	F96	
Copepod egg and faecal pellet production	Albert Calbet (ICM)	Ricardo Anadón	F95	(Calbet and Irigoien, 1997)
		Albert Calbet	F96	
Mesozooplankton respiration, ETS activity	Santiago Hernández-León (ULP)	Xavier Irigoien (ICM)	F96	
		Santiago Hernández-León	F96	
		Irene Lidia Montero (ULP)	F96	
Bioacoustics	Arturo Castellón (ICM)	Arturo Castellón	F96	
Macrozooplankton and fish larvae	Francesc Pagés (ICM)	Francesc Pagés	F96	
		Rafael González-Quirós (UO)	F96	
PC and PON export (drifting sediment trap)	Ricardo Anadón (UO)	Ricardo Anadón	F95- F96	(Anadón et al., 2002)
<i>Sediment</i>				
Sediment carbon burial, bioaccumulation and paleoclimatology	Jorge Guillén (ICM)	Jorge Guillén (ICM)	F96	(Masqué et al., 2002) (Bárcena et al., 2002)
		Marcelli Farran (ICM)	F96	
		Pere Masqué (UAB)	F96	
<i>Moorings</i>				
Current meters and sediment traps	Albert Palanques (ICM)	Albert Palanques Marc Garcia (UPC)		(Palanques et al., 2002) (Isla et al., 2002)
Deposition of carbon and nitrogen		Pere Puig (ICM)		
<i>Technicians</i>				
CTD, LHPR, Bioness	Pedro Jornet (UGBOIP) Mario Manríquez (UGBOIP)	Pedro Jornet	F95- F96	
		Mario Manríquez	F96	
		María Isabel Lloret (ICM)	F95	

Table 1 (continued)

Research Topic/Operation	Principal investigator	Team on board	Cruise	Reference
Computing		Fernando Uceta (UGBOIP)	F95	
		Miguel Pancorbo (UGBOIP)	F96	
		Zacarias Garcia (UGBOIP)	F95	

^aICM Institut de Ciències del Mar (CSIC)- Barcelona; IEO Instituto Español de Oceanografía, Laboratorio Costero de A Coruña - A Coruña; IIM Instituto de Investigacions Mariñas (CSIC) - Vigo; UAB Universitat Autònoma de Barcelona - Barcelona; UGBOIP Unidad de Gestión de Buques Oceanográficos e Instalaciones Polares - Barcelona; UIB Universidad de las Islas Baleares - Palma de Mallorca; ULP Universidad de Las Palmas - Las Palmas de Gran Canaria; UM Universidad de Málaga - Málaga; UO Universidad de Oviedo - Oviedo; UPC Universitat Politècnica de Catalunya (LIM) - Barcelona; US Universidad de Santander; UV Universidad de Vigo - Vigo.

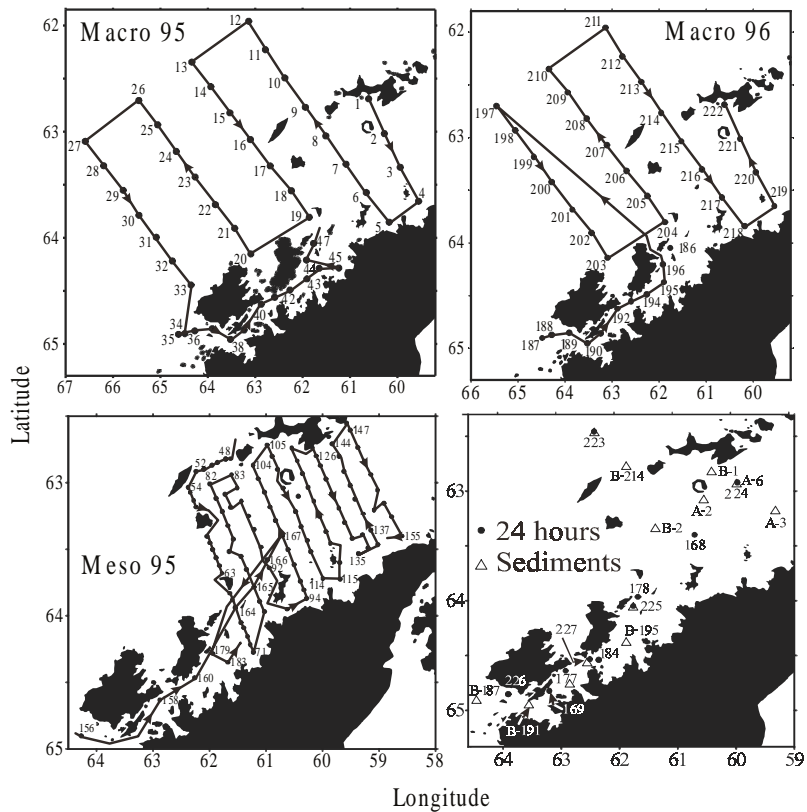


Fig. 3. Maps of the stations and trajectories during the two FRUELA cruises. Macro 95 (macroscale FRUELA 95), Mso 95 (mesoscale of FRUELA 95), Macro 96 (macroscale FRUELA 96), and 24 h (FRUELA 95 and 96) and sediment stations (FRUELA 96).

In addition to the cruise activities, moorings with current-meters and sediment traps (mid-depth and near-bottom) were deployed in the

western Bransfield Strait for one year (1 March 1995–15 February 1996) (see Palanques et al., 2002). The current meters were set up to

measure current inflows in the western Bransfield Strait. The aim of the sediment traps was to analyse the composition and annual variability of the downward and lateral fluxes of particulate matter, and to study the relative contribution of the biogenic and lithogenic particles exported vertically at different depths or transported laterally from shallower environments. One array of two sediment traps was deployed south of Livingston Island and west of Deception Island at a 1000 m depth (A6 in Fig. 3D). Five other arrays with sediment traps and current meters were deployed at other locations, but were unfortunately lost.

5. Basic findings of the FRUELA project

5.1. Hydrography

The hydrographical and dynamical features found during the FRUELA cruises were marked by several frontal areas (García et al., 2002; Gomis et al., 2002). The SbyACC, which followed the shelf-break (Figs. 4 and 5), was related to a northeastward-flowing geostrophic jet and separated Antarctic Circumpolar Current waters (Figs. 4 and 5) from those on the South Shetlands continental shelf. In the Bransfield Strait basin, the Bransfield Front (BF), associated with the Bransfield Current, represented a boundary between a

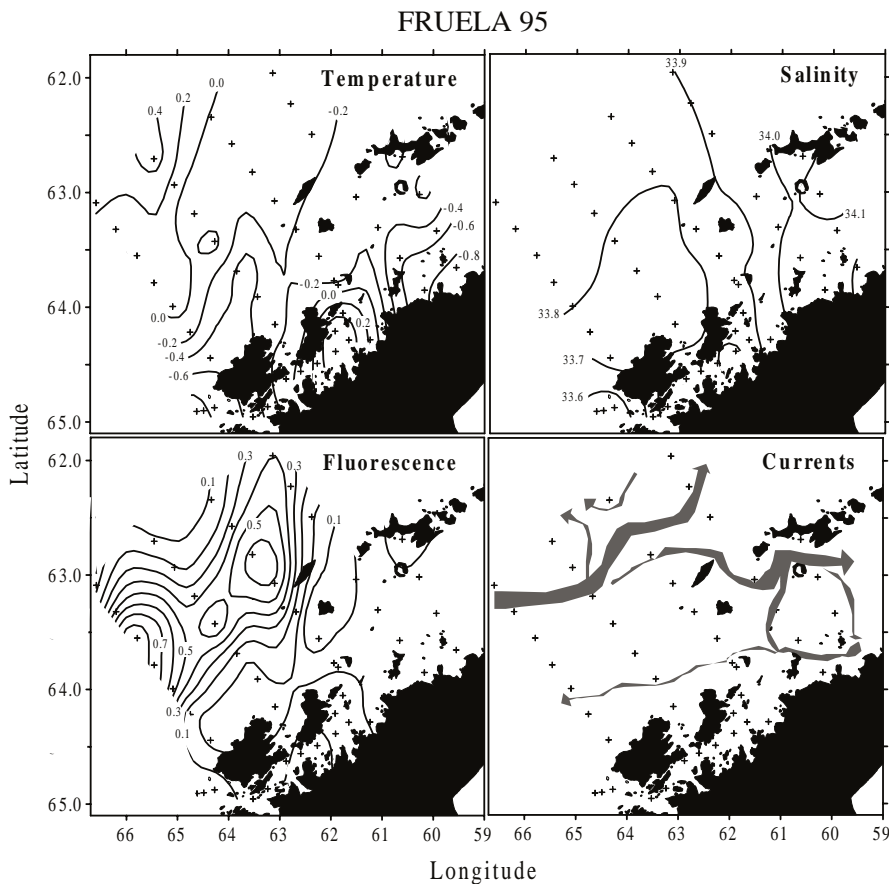


Fig. 4. Distribution of temperature, salinity, fluorescence (10m depth) and dominant currents (idealised drawing from results of Gomis et al., 2002) during the FRUELA 95 cruise.

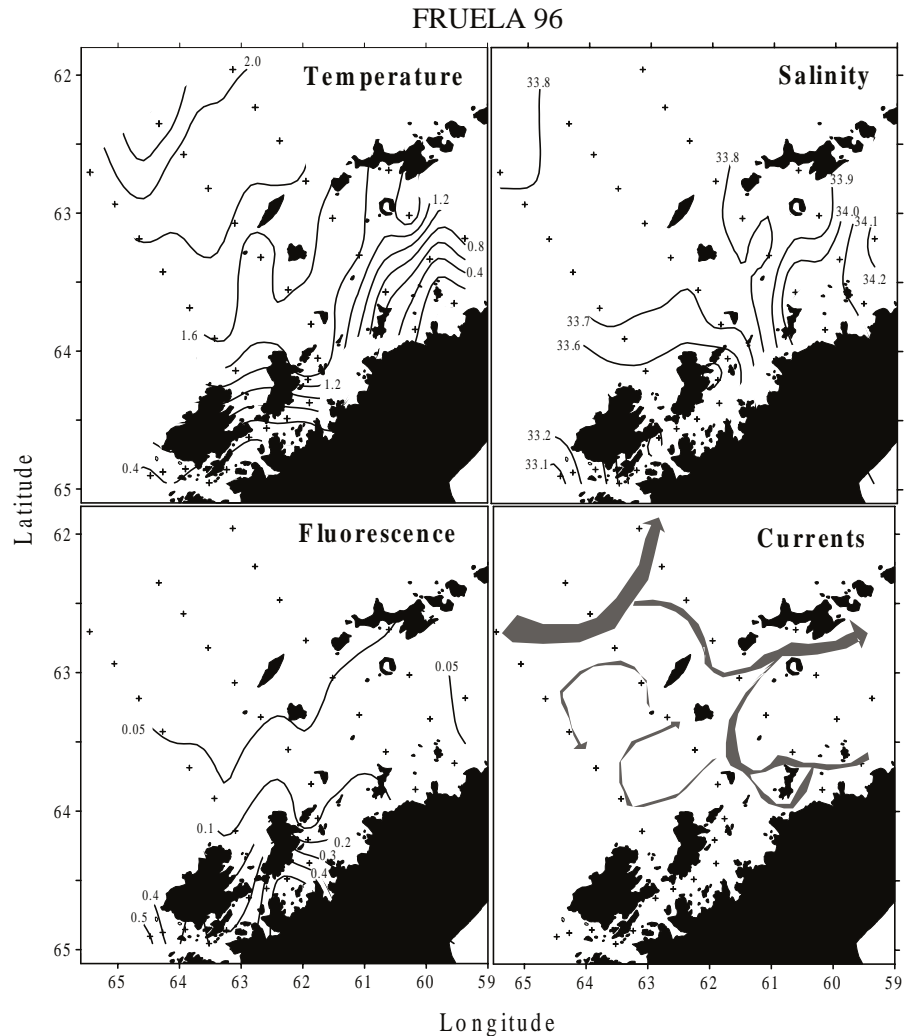


Fig. 5. Distribution of temperature, salinity, fluorescence (10m depth) and dominant currents (idealised drawing from results of Gomis et al., 2002) during the FRUELA 96 cruise.

cool and relatively salty water inflow of Weddell Sea waters, in the NE, and warmer and fresher waters of Bellingshausen Sea influence to the SW. The vertical structure of the upper part of the water column, along the transects shown in Figs. 6 and 7, showed stronger stratification in the northern part of the study area and, during FRUELA 95, presented a fluorescence maximum coinciding with the SbyACC Front (Figs. 4, 6 and 7). The disappearance of this maximum in FRUELA 96 (Figs. 5–7) has been attributed to

the advection of water bodies with low phytoplankton biomass (Cabal et al., 2002), perhaps in combination with grazing pressure (Varela et al., 2002).

At the northeastern mouth of the Gerlache Strait, another front (hereafter, the Gerlache Front) separated the cooler and relatively saline Bransfield waters from those of the central Gerlache Strait, influenced by freshwater inputs from local glacier melting (see Rodríguez et al., 2002b).

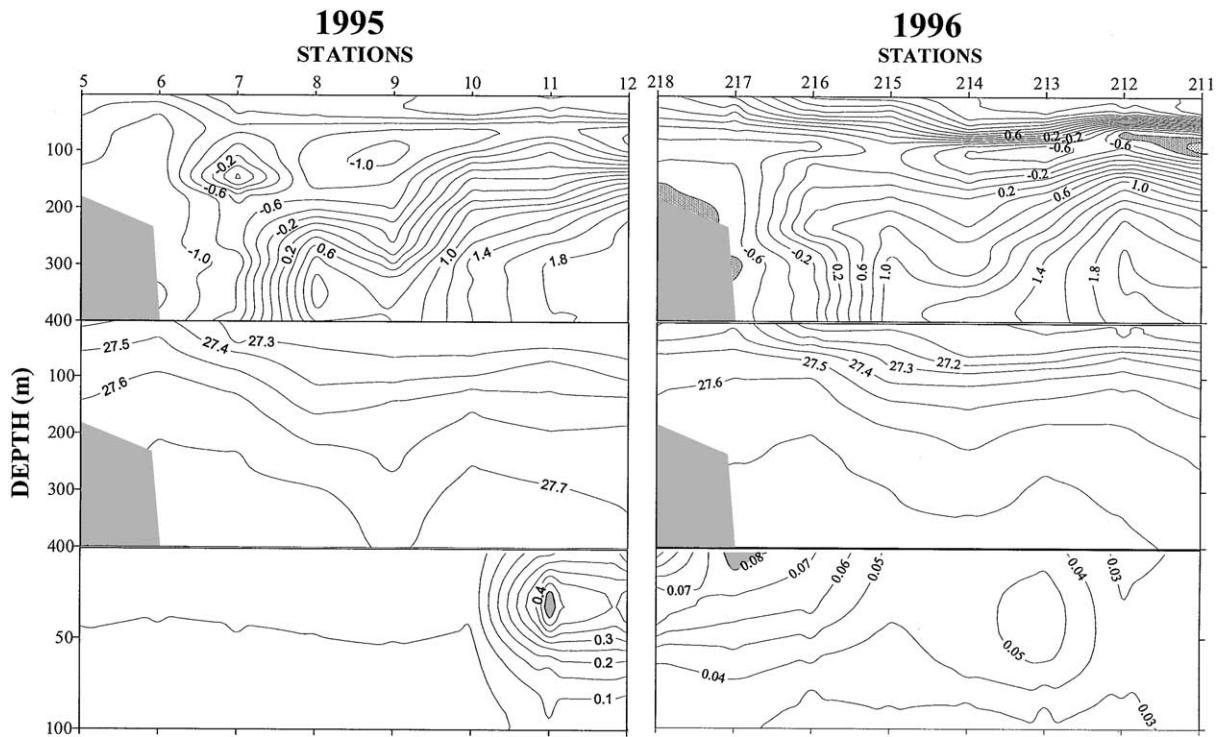


Fig. 6. Potential temperature, density (σ_t) and fluorescence along a section from Trinity Is to Boyd Strait (st. 5 to st. 12, FRUELA 95; st. 218 to st. 211, FRUELA 96) (see Fig. 3).

5.2. Main biological zones

According to topographic and hydrographical features (Garcia et al., 2002), and considering the phytoplankton composition (Bode et al., 2002; Rodríguez et al., 2002a; Varela et al., 2002), the study area could be divided into three major zones with contrasting physico-chemical and biological characteristics. With some modifications, this division was adopted to summarise the distribution of different properties and rate processes during the FRUELA cruises (see articles in this volume). The basic characteristics of each zone are described below.

The Bellingshausen zone contained the SbyACC front and the region to its northwest (Figs. 4 and 5). Chlorophyll *a* concentrations reached maximal values at the SbyACC (the maximal chlorophyll concentration 4.6 mg m^{-3} at 30 m depth at station

15) and decreased northwest of the front. During FRUELA 95, the nano- and microphytoplankton of this zone included diatoms such as *Fragilariopsis* spp., *Thalassiosira* spp., *Eucampia antarctica*, *Odontella weissflogii* and *Rhizosolenia antennata antennata*, with important contributions from *Phaeocystis* cf. *antarctica* in the high chlorophyll area of the SbyACC. The chlorophyll concentration and the abundances of large diatoms and *Phaeocystis* cf. *antarctica* colonies at the SbyACC front decreased markedly during FRUELA 96.

The Bransfield zone, southwest of the SbyACC, included the western part of the Bransfield Strait, marked by the presence of the BF, and the part of the Gerlache Strait located to the NE of the Gerlache Front. During FRUELA 95, surface chlorophyll *a* concentration in this area ranged from 0.8 to 4 mg m^{-3} and the phytoplank-

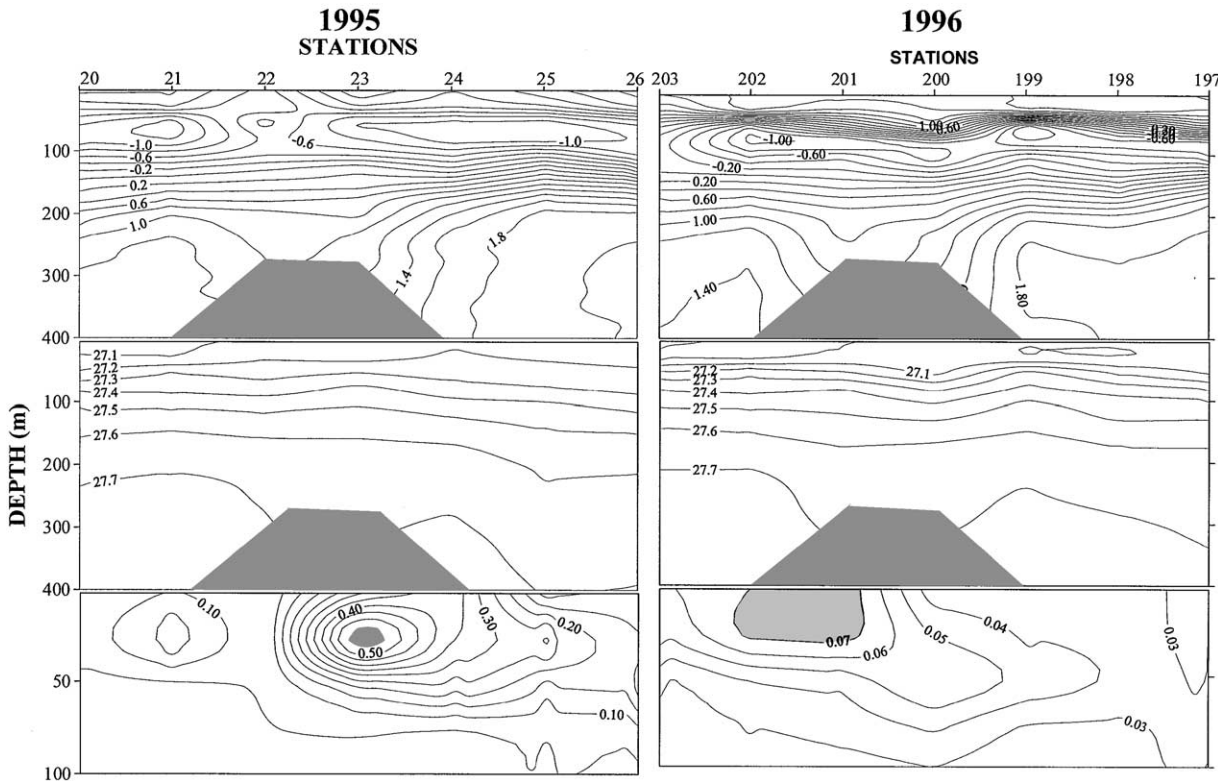


Fig. 7. Potential temperature, density (σ_t) and fluorescence along a section from Schollaert Channel to off-shore (st. 20 to st. 26, FRUELA 95; st. 203 to st. 197, FRUELA 96) (see Fig. 3).

ton was dominated by cryptomonads. Large diatoms, with *Corethron criophilum* as the main species, were scarce. During FRUELA 96, chlorophyll values decreased and cryptomonads were progressively replaced by increasing numbers of some diatoms and small flagellates, including individual cells of *Phaeocystis* cf. *antarctica*.

The Gerlache Strait zone included most of the Gerlache Strait in the vicinity of Anvers Island. Chlorophyll concentrations at surface typically exceeded 3 mg m^{-3} and reached a maximal value of 12.3 mg m^{-3} at station 187 of FRUELA 96. Phytoplankton assemblages were characterised by diatoms such as *Eucampia antarctica*, *Chaetoceros socialis*, *Odontella weissflogii*, *Rhizosolenia inermis* or *Thalassiosira* spp., accompanied by *Phaeocystis* cf. *antarctica* and *Pyramimonas* sp. During FRUELA 96 and the last part of

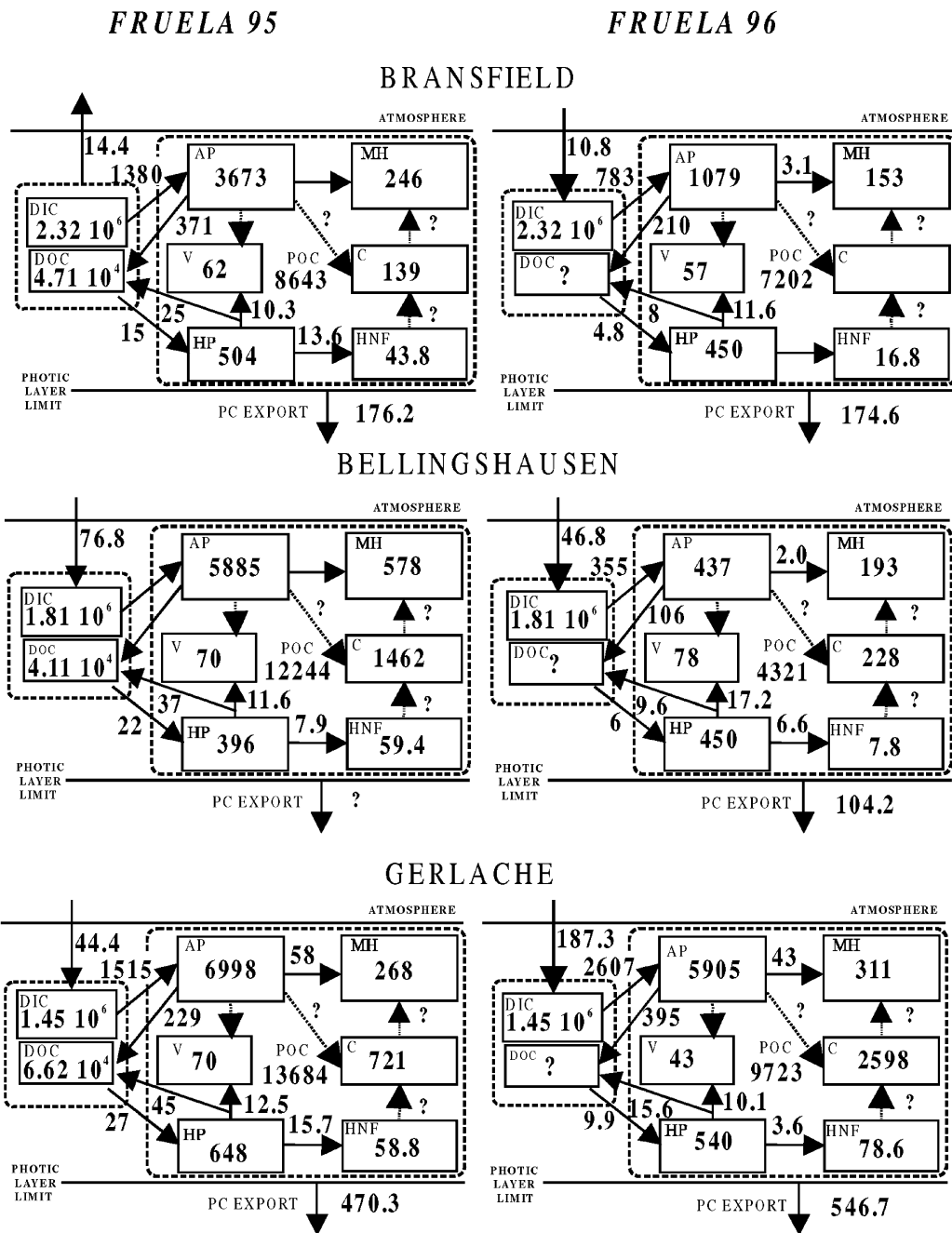
FRUELA 95, *Pyramimonas* formed a surface bloom near the southwestern boundary of the Gerlache Front.

5.3. Carbon fluxes and food web

Averages of the main standing stocks and carbon fluxes among the components of the pelagic food web, during FRUELA 95 (December 1995) and FRUELA 96 (January 1996) are represented in Fig. 8 for each of the zones considered in the study area. Although the data are based on different numbers of observations and must be interpreted with caution, some patterns can be seen. The CO_2 flow was from the air to the sea, except in Bransfield Strait during FRUELA 95. In the Bransfield and Gerlache Straits, CO_2 fluxes increased from December to January. In contrast, CO_2 fluxes decreased in the

Bellingshausen Sea, probably due to the sharp decrease of phytoplankton biomass (and presumably, of phytoplankton production) in this zone. No direct correlation could be appreciated

between CO₂ uptake by the sea (Álvarez et al., 1999) and primary production, suggesting a dissociation between the biological activity and the dissolution and transport of CO₂ into the



surface waters, from the overlying atmosphere (Follows et al., 1996). Average autotrophic biomass was relatively high in all regions during December 1995 (Varela et al., 2002). Both the Bransfield and Bellingshausen zones showed a strong decrease in the biomass of autotrophs (Varela et al., 2002), heterotrophic flagellates (Vaqué et al., 2002) and zooplankton (Cabal et al., 2002), between the December and January cruises. Primary production decreased accordingly in Bransfield zone and was very low in Bellingshausen zone during January 1996. On the other hand, in the Gerlache Strait zone, the standing stocks of the different components changed little and primary production remained at high levels throughout the study period. Some groups, such as the ciliates (Vaqué et al., 2002), showed large fluctuations, decreasing in parallel with heterotrophic flagellates in Bellingshausen Sea, but increasing in Gerlache Strait. In all zones, prokaryotic (Pedrós-Alió et al., 2002) and viral (Guixa-Bioxereu et al., 2002) biomass varied relatively little between December and January, but prokaryotic heterotrophic production and bacterial lysis decreased markedly, while viral production changed relatively little. Concerning total organic carbon, the particulate fraction varied more or less in proportion to the main biomass components, but was low compared to DOC (ranging between 18% and 29% of DOC) during FRUELA 95. Unfortunately, DOC concentrations were only available for December 1995.

The trend for a decrease in phytoplankton biomass and primary production found in the Bellingshausen and Bransfield zones from December 1995 to January 1996 is in agreement with described patterns of seasonal change in the area (Holm-Hansen and Mitchell, 1991; Smith et al., 1996). However, the findings of Bode et al. (2002), for their Bransfield Strait zone, indicate that the use of inorganic nitrogen by the phytoplankton community did not present the often observed gradual change from nitrate-based to ammonium-based production (e.g. Goeyens et al., 1998), but showed high variability, related to the appearance of secondary blooms based mainly on nitrate uptake, after the disappearance of a previous bloom. The spatial heterogeneity in environmental and biological conditions and the presence of different stages of bloom development could also explain the lack of correlation between *f* ratios (Bode et al., 2002) and carbon-based primary production values.

If the relative biomass of autotrophs and heterotrophs is considered, an overall trend of a relatively higher proportion of the heterotrophic versus the autotrophic component can be observed in all regions from December to January (Fig. 8), in agreement with the expected successional patterns (Holm-Hansen and Mitchell, 1991; Pridle et al., 1994; Schnack-Schiel and Mujica, 1994; Smith et al., 2000). Removal of phytoplankton by meso and macrozooplankton was small compared with primary production (10% on average; Cabal

Fig. 8. Carbon fluxes in the photic layer as in the conceptual diagram of Fig. 1 for three main areas studied (Bransfield and Gerlache straits and Bellingshausen Sea) during the two FRUELA cruises. STOCKS, in mg C m^{-2} integrated to photic layer (60 m), excluded zooplankton (200 m), DIC, dissolved inorganic carbon, data from (Álvarez et al., 2002) (Table 2) for FRUELA 95; we assumed the same values for FRUELA 96. DOC, dissolved organic carbon, data from (Doval et al., 2002) (Fig. 3). POC, particulate organic carbon, recalculated from data of (Castro et al., 2002). AP, autotrophic plankton, calculated from the chlorophyll *a* concentration, assuming a carbon to chlorophyll ratio of 50, HP, heterotrophic prokaryotes, data from (Pedrós-Alió et al., 2002) (Table 6B). V, viruses, recalculated from data of (Guixa-Bioxereu et al., 2002) (Table 1) as in (Bratbak et al., 1992). HNF, heterotrophic flagellates, recalculated from the data of (Vaqué et al., 2002) (Table 3). MZ, Meso- and macrozooplankton, recalculated from the data of (Cabal et al., 2002). FLUXES, in $\text{mg C m}^{-2} \text{ day}^{-1}$ integrated to photic layer (60 m), excluded zooplankton (200 m). A–O, atmosphere to ocean exchange, from (Álvarez et al., 2002) (Table 1). PP, primary production, recalculated from data of (Varela et al., 2002) with DOC-R. DOC-R, dissolved organic carbon release by the phytoplankton, calculated as a product of (Morán et al., 2002) and PP; we assumed the same PER values of FRUELA 95 for FRUELA 96. PHP, prokaryotic heterotrophic production, recalculated from data of (Pedrós-Alió et al., 2002) (Table 6B). B, bacterivory on prokaryotes by HNF, recalculated from data of (Vaqué et al., 2002) (Table 4). PL, prokaryotic lysis, calculated from data of percentage of PHP (Guixa-Bioxereu et al., 2002) (Fig. 9). VP, viral production, calculated as a product of VDR (Guixa-Bioxereu et al., 2002) (Table 3) and VR. HE, meso and macrozooplankton herbivory, recalculated from the data of (Cabal et al., 2002). PC-E, particulate carbon export, from the data of (Anadón et al., 2002) (Fig. 6).

et al., 2002) in all zones during both sampling periods, but was higher in the Gerlache Strait, where swarms of krill were detected. However, the estimates concerning macrozooplankton should be interpreted with caution, due to unreliable sampling and the patchiness of its distribution. Data on micro and nanozooplankton herbivory were not available, although these predators were probably an important component of the pelagic food web in the area, according to their biomass, which, except for Bransfield Strait, was higher than that of meso and macrozooplankton (see Fig. 8).

Carbon export from the photic layer was highest in the Gerlache Strait and varied little between December 1995 and January 1996 in this zone and in the Bransfield Strait. Only data for January 1996 are available for the Bellingshausen Sea, although, in accordance with the changes in phytoplankton biomass, it can be speculated that export values for December 1995 had been much higher. The fluxes of exported carbon were always higher and less variable than those of the air-sea exchange, which could double in the same time period (Fig. 8).

5.4. Carbon budgets

In order to understand the relative contribution of the three study zones, we estimated the total amount of carbon being transferred through different interfaces and processes: flux across the atmosphere-ocean interface, primary production (dissolved inorganic to particulate and dissolved organic phases) export out of the photic layer, inputs at 500 and 1000 m depths, and burial in the sediments (Table 2). We considered the total surface of each geographical zone for the three first fluxes, the area at 500 m for the flux at this depth, and the surface at 1000 m for the two last fluxes (except for burial in Gerlache Strait in which, due to bottom topography, we considered the area below 200 m). The Bransfield Strait, with a relatively low primary production during the studied period, had little significance in the air-sea fluxes, whereas the Bellingshausen Sea and the Gerlache Strait could be considered as a sink of atmospheric carbon. In both areas, the phytoplankton showed at least an important bloom period with the dominance of large cells.

Table 2

Main carbon fluxes (Megatons (MTn) per integrated period) in the three studied zones. Integration period from December 2 to January 10 (40 days) for FRUELA 95, and from January 12 to February 5 (25 days) for FRUELA 96. Daily averaged fluxes in Bransfield Strait at 500 m ($0.98 \text{ mg C m}^{-2} \text{ day}^{-1}$), and 1000 m ($51.03 \text{ mg C m}^{-2} \text{ day}^{-1}$) from Palanques et al., 2002), and daily averaged carbon burial ($14.52 \text{ mg C m}^{-2} \text{ day}^{-1}$) from Masqué et al., 2002). Daily averaged carbon burial in Gerlache Strait ($25.42 \text{ mg C m}^{-2} \text{ day}^{-1}$) from Isla et al., 2002)

Zone(m ⁻²)	Bransfield			Bellingshausen			Gerlache			Total
Surface	1.7×10^{10}			3.7×10^{10}			0.6×10^{10}			6×10^{10}
500 m	0.67×10^{10}						0.35×10^{10}			
1000 m	0.12×10^{10}									
Days of integration	40	25	365	40	25	40	25	365	65	
FRUELA cruise	95	96		95	96	95	96			
Atmosphere to Ocean	-0.0098	0.0046		0.114	0.043	0.011	0.028		0.190	
Primary production	0.938	0.333			0.328	0.364	0.391		1.635 ^a	
Export Photic Layer	0.120	0.074		0.293 ^b	0.096	0.113	0.082		0.682	
Sinking 500 m	0.00026	0.00016	0.0024							
Sinking 1000 m	0.0025	0.0015	0.022							
Burial	0.0007	0.00044	0.0063			0.0035	0.0022	0.056	0.0563 ^c	

^a Bellingshausen data not included due to lack of data during FRUELA 95 cruise.

^b This value was estimated from differences between POC content in the photic layer (Fig. 8), and must be considered as a minimal carbon export estimate.

^c Bellingshausen data not included due to lack of data.

Export of PC from the photic layer to deep waters could be related to the primary production (Anadón et al., 2002). In this context, the Gerlache Strait, in spite of its small surface, was as important as the Bransfield Strait (Table 2). In the Bellingshausen Sea, most of the POC in surface waters was lost—redissolved or exported—between the two cruises (averaging a minimal loss of PC of $198.1 \text{ mg C m}^{-2} \text{ day}^{-1}$), indicating that this zone can probably act as a source of PC to the deep waters.

The amount of carbon arriving at deep waters and accumulating in the sediments of the western Bransfield Basin was two to three orders of magnitude lower than that exported from the photic layer. The detected loss of PC could be due to reutilisation and recycling by macro- or mesozooplankton (i.e. coprofauna). The low prokaryotic heterotrophic activity measured (Pedrós-Alió et al., 2002) and the preferential use of DOC by prokaryotes (Kähler et al., 1997) suggest a reduced importance of this group in the recycling of PC in the water column. The export of PC out of the area by advection associated with the water flowing out of the limits of this zone (Sections 4–6, Fig. 7 in Gomis et al., 2002) cannot be excluded. The increased amount of carbon at 1000 m depth with respect to the flux at 500 m has been explained by advection due to shelf waters flowing near the bottom by Palanques et al. (2002).

6. Conclusions

The studied area could be considered as a sink of atmospheric carbon during austral summer, with a net flux from the air to the sea of 0.19 Mt of C (Table 2). This flux was not directly correlated with primary production (transformation of dissolved inorganic to particulate or dissolved organic carbon). Higher net fluxes to the sea could be appreciated in January (except for the Bellingshausen Sea), probably reflecting a time lag between primary production in the water column and the air-sea exchange.

The amount of carbon exported out of the photic layer was a moderate fraction of primary production and a low fraction of the suspended

PC. The higher fluxes corresponded to high-chlorophyll *a* systems dominated by microphytoplankton (several diatom species and *Phaeocystis*), whereas low-chlorophyll *a* systems dominated by small flagellates and cryptomonads showed lower fluxes.

A significant amount of exported carbon was not found at the deep water layers or at the sediments. The processes involved are unclear, although advective processes and biological recycling (probably by meso- and macrozooplankton) can be suggested.

Research on the links between air-sea exchange and biological activity (“biological pump”), the mechanisms of particulate carbon disappearance in deep waters, the role of meso and macroplankton, and the transport of particulate carbon by near-bottom currents could be of major interest to complete our knowledge of the processes relating productivity in the upper water layers to burial of carbon in the sediments. Further insight should also be obtained on the mechanisms of blooming and disappearance of phytoplankton in the SbyACC of the Bellingshausen Sea and the associated carbon sink.

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