Size-fractionated phytoplankton biomass, production and biogenic carbon flux in the eastern Atlantic sector of the Southern Ocean in late austral summer 1997–1998

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Abstract

Size-fractionated chlorophyll-\textalpha{} (Chl-\alpha{}) primary production and biogenic carbon flux in the vicinity of the Winter Ice-edge Zone (WIE), Spring Ice-edge Zone (SIE) and Antarctic Polar Front (APF) were investigated in the eastern Atlantic sector of the Southern Ocean during a collaborative Scandinavian/South African Antarctic cruise conducted in late austral summer (December 1997/January 1998). Microphytoplankton (>20 \textmu{}m) dominated integrated Chl-\alpha{} biomass in the SIE and at the APF, comprising >50% of the total at all stations. Within the WIE, nanophytoplankton (2–20 \textmu{}m) dominated total integrated Chl-\alpha{} biomass comprising on average 36% of the total. Total integrated primary production ranged between 316 and 729 mg C m\textsuperscript{-2} d\textsuperscript{-1} at stations occupied in the region of the SIE, and between 292 and 317 mg C m\textsuperscript{-2} d\textsuperscript{-1} within the WIE. At stations occupied in the region of the APF, total integrated production ranged between 708 and 926 mg C m\textsuperscript{-2} d\textsuperscript{-1}. The contribution of various size fractions to total productivity generally displayed the same pattern as integrated Chl-\alpha{} biomass. Microphytoplankton formed the most important contributor to total production at all stations in the SIE and at two stations in the region of the APF. Within the WIE, nanophytoplankton dominated total daily production. The elevated primary production rates in the region of the SIE and APF appear to be related to favourable light environment and the availability of iron. In the SIE, the partitioning of carbon between the microbial loop and classical food web was similar. Grazing activity by metazoans resulted in 1.5% of total daily production being transported to depth. In the region of the WIE and APF, the classical food web represented the main sink for daily primary production. Within the SIE and APF, the grazer-mediated carbon flux corresponded to 8.4% and 15.4% of the total production, respectively. The low rates of biologically mediated carbon flux resulting from grazing by zooplankton in the SIE can be related to the size structure of the phytoplankton assemblages and the absence of larger macrozooplankton in the region. As a consequence of the low grazing activity, the sinking of dead/senescent phytoplankton cells appears to be the major route for the transfer of carbon from the

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1. Introduction

The role of the oceans in the global carbon cycle is presently a leading concern in oceanographic studies (Takahashi and Azevedo, 1982; Metzl et al., 1991; Murphy et al., 1991; Legendre and Michaud, 1998). The Southern Ocean is an immense area of close to 38 million km$^2$ of open water. Due to its large geographic extent and its abundant supply of nutrients, it is expected that the Southern Ocean will have a major influence on the global carbon cycle. Although the ocean is characterised by an abundant supply of nutrients in the surface waters, total phytoplankton production in the open waters of the Southern Ocean is generally low, $<0.5$ g C m$^{-2}$ d$^{-1}$ (Allanson et al., 1981; Hayes et al., 1984; El-Sayed, 1988; Jacques, 1989; Laubscher et al., 1993; Jochem et al., 1995). As a consequence, the Southern Ocean is regarded as a high-nutrient low-chlorophyll (HNLC) region. There are, however, areas of elevated production including the vicinity of frontal regions (Laubscher et al., 1993; Bradford-Grieve et al., 1997), the Marginal Ice-edge Zone (MIZ) (Bathmann et al., 1997; Boyd et al., 1995; El-Sayed, 1988; Smith and Nelson, 1985; Whitehouse et al., 1996; Saggiomo et al., 1998) and the neritic regions of Antarctica and oceanic islands (El-Sayed, 1971; von Bodungen et al., 1981; Savidge et al., 1995; Aristegui et al., 1996; Moline and Prezlin, 1996). In these regions, total phytoplankton production may exceed 1 g C m$^{-2}$ d$^{-1}$ (Sullivan et al., 1993; de Baar et al., 1995; Bradford-Grieve et al., 1997; Saggiomo et al., 1998). The factors responsible for the increased production in these regions have been reviewed in detail in El-Sayed (1988) and Priddle et al. (1992). These include the vertical stabilisation of the water column (Holm-Hansen et al., 1977; Perissinotto et al., 1990; Sakshaug and Slagstad, 1992; Laubscher et al., 1993), seawater temperature (Jacques, 1983) and chemical processes such as trace metal availability (iron and chelators) (Martin et al., 1990; de Baar et al., 1995).

The flux of photosynthetically fixed carbon out of the photic zone is a central element in the cycling of carbon in the oceans (Broecker and Peng, 1982; Berger et al., 1989; Priddle et al., 1992; Falkowski et al., 1998). Photosynthesis and the export of organic carbon from the surface waters as dissolved or particulate organic carbon (resulting from sedimentation or grazing by zooplankton) act as a “biological pump” which lowers the partial pressure of CO$_2$ in surface waters resulting in the drawdown of atmospheric CO$_2$ (Huntley et al., 1991; Longhurst, 1991; Wefer and Fisher, 1991; Siegenthaler and Sarmiento, 1993). The efficiency of the biological pump is determined by the rate of carbon transfer to depth, which is largely a function of the partitioning of phytogenic carbon between the various size classes of the grazers (Longhurst, 1991; Fortier et al., 1994; Legendre et al., 1993; Froneman et al., 1996a, 1997). Phytoplankton production is channeled into the microbial loop or the classical food web (Longhurst, 1991; Siegenthaler and Sarmiento, 1993; Legendre and Michaud, 1998). In the microbial loop, recycling is rapid but the system is a weak exporter of organic matter to the deep layers (Longhurst and Harrison, 1989; Fahnenstiel et al., 1995). In contrast, the classical food web is generally characterised by the export of carbon to depth through the sinking of phytoplankton cells and the production of large fast-sinking faecal pellets with a high carbon content (Longhurst and Harrison, 1989; Fortier et al., 1994). The partitioning of carbon between the two food webs is largely determined by the size composition of the phytoplankton assemblages. Generally, in regions dominated by large cells, phytoplankton production is channeled into the classical food web while the microbial loop represents the sink.
for production in areas dominated by small phytoplankton (Fortier et al., 1994; Froneman et al., 1997).

The role of the Southern Ocean in the global carbon cycle is a leading concern in physical and biological oceanographic studies. Several multidisciplinary studies in different sectors of the Southern Ocean, including the Bellingshausen and Weddell Seas, have been conducted (Turner and Owens, 1995). However, the extreme variability in the physico-chemical parameters and consequently biological processes in the different sectors of the ocean suggest that to fully understand the role that frontal regions and MIZ play in the carbon cycle of the Southern Ocean, further studies in other sectors are required.

The main aims of the present study were to determine the relative importance of various factors (including physical, chemical and biological) that control primary production and to assess the consequences of these factors on the biogenic carbon flux in the eastern Atlantic sector of the Southern Ocean in austral summer 1997/1998. Within the sector, three different regions were considered, the Spring Ice-edge Zone (SIE), Antarctic Polar Front (APF) and Winter Ice-edge Zone (WIE).

2. Materials and methods

2.1. Size fractionated primary production

Water samples for chlorophyll-a (chl-a) and size-fractionated primary productivity were collected in the three zones along a south–north transect between 60°24.57′ S and 49°49.51′ S along 6°00′ E meridian aboard the S.A. Agulhas during a collaborative Scandinavian/South African Antarctic cruise conducted during December/January 1997–1998 (Fig. 1). The transect SIE was occupied from 4 to 10 January, the transect in the WIE was occupied over the period 14–16 January, while the transect in the vicinity of the APF was occupied from 28 till 31 January 1998. The APF position was defined as the northern most extent of the 2 °C isotherm (Turner et al., 2004). The SIE coincided with the ice edge which was crossed during the southbound underway transect conducted in early December 1997. Finally, the WIE represented the northern boundary of the winter ice, which coincided with the negative subsurface isotherms (Turner et al., 2004).

Conductivity, temperature and pressure measurements at each production station were made using a Neil Brown MK II CTD. Mixed layer depths were assumed to correspond to the depth where a change in ρT of 0.02 units from the stable surface value occurred (JGOFS, 1994). Daily photosynthetic active radiation (PAR, 400–700 nm) was measured using a Li-Cor 4π spherical quantum sensor (LI 1935 A) and Li-Cor data logger (LI-1000) logging 10–15 min means throughout the day. The subsurface light field was measured using the same instrument and used to calculate the sampling depths corresponding to the 100%, 50%, 25%, 10%, 5% and 1% light depths. Water samples from the corresponding depths were taken from 12L Niskin seawater bottles mounted to a teflon-coated stainless steel rosette frame carrying the CTD.

Size-fractionated primary production, defined as the uptake of inorganic carbon into particulate matter, was measured with the method adapted from Evans et al. (1987) and JGOFS Protocols (1994). Water samples (250 mL), in triplicate for the productivity measurements, were collected and incubated with 50 μCi sodium bicarbonate (NaH14CO3) for 24 h on deck in light-gradient incubators. The incubators consisted of Perspex sleeves covered with neutral density screens to simulate light intensity of depth of collection. The neutral density screens were calibrated using a Biospherical Instruments quantum metre (Model QSP-170) probe. The incubators were cooled with running surface water obtained from the scientific seawater supply. Temperatures within the incubators were maintained to within 1 °C of the sea surface temperatures.

After incubation, the water samples were gently filtered (<710 mm Hg) onto Nitex mesh (20 μm pore size) and isopore membrane (Millipore) filters (2.0 and 0.2 μm pore size). Each filter was then placed into a glass scintillation vial and 0.5 mL 3 M HCl added. The vials were then placed in a shaker under the fume hood for 2 h to ensure that...
all non-biologically precipitated labelled carbon evaporated. Time-zero controls were treated as above. Packards UltraGold XR fluor (10 mL) was added to each sample and the radioactivity was determined using a Beckman LS-133 liquid scintillation system. All counts (cpm) were converted to disintegrations per minute (dpm) by the external standard ratio method.

Total areal production at each station was estimated employing the following equation:

\[
\text{Total Areal Production} = \frac{(\text{SDPM}/V) \times (W/\text{TDPM}) \times (1.05/T)}{mg \, C \, m^{-3} \, d^{-1}}
\]

where SDPM = DPMs in filtered samples, \( V \) = volume of filtered sample (L), TDPM = total \(^{14}\)C
DPMs (in 0.05 L), \( W = \) DIC concentration in samples, 1.05 = correction for the lower uptake of \( ^{14}\text{C} \) compared to \( ^{12}\text{C} \), and \( T = \) time (days). DIC concentrations were determined using the potentiometric titration method (Almgren et al., 1983).

Size-fractionated chl-\( a \) concentrations at each light depth were determined by gently (<710 mm Hg) filtering 250 mL water samples through 20 \( \mu \)m (Nitex), 2.0 \( \mu \)m (Millipore) and Whatman GF/F filters, extraction in the dark in 90% acetone for 24 h at \( -20^\circ \)C and measuring the fluorescence before and after acidification with 10% HCl on a Turner Designs 10 AU fluorometer (Holm-Hansen and Riemann, 1978). The fluorometer was calibrated against a Chl-\( a \) standard (Sigma). Areal chl-\( a \) and productivity were obtained by trapezoidal integration (Froneman et al., 2001).

### 2.2. Biogenic carbon flux

Since the grazing impact of metazoans (meso- and macrozooplankton) was only estimated at six stations during the investigation (three in the SIE, one in the WIE and two in the APF), a single model for each region will be presented below. A summary of the grazing impact of the various size classes of zooplankton on daily primary production is presented in Table 1. A detailed description of the materials and methods employed to estimate the grazing impact of the zooplankton are presented in Froneman (2004) and Pakhomov and Froneman (2004b). The grazing impact of protozooplankton within the three regions of investigation was estimated employing the seawater dilution technique while the impact of the larger zooplankton was determined using the gut fluorescent technique (Froneman, 2004; Pakhomov and Froneman, 2004b). A carbon to chlorophyll ratio of 50 was assumed to estimate the daily production consumed by herbivorous zooplankton (Froneman et al., 1997). Grazing by protozooplankton was assumed not to contribute to the export of phytogenic carbon to depth (Longhurst, 1991; Moloney and Field, 1991; Fahnenstiel et al., 1995). An average assimilation efficiency of 70% for the entire zooplankton community was assumed (Froneman et al., 1997). No distinction was made between the sedimentation rates of meso- and macrozooplankton faecal pellets. All faecal material from the larger zooplankton (>200 \( \mu \)m) was assumed to sediment to depth. Only the role of herbivorous zooplankton in biogenic carbon flux was considered as they contributed up to 80% of the numerical abundance of the zooplankton in the region of investigation (Pakhomov and Froneman, 2004a). Carnivorous zooplankton were, therefore, unlikely to have made a substantial contribution to biogenic carbon flux. Finally, senescence and sinking of phytoplankton cells was assumed to correspond to 5% of the total daily production (Murphy et al., 1998).

### 3. Results

#### 3.1. Hydrographical conditions

The overall hydrography of the study area is discussed elsewhere (Turner et al., 2004). Here a summary of the hydrological conditions at the primary production stations is presented (Table 2). No sea-ice was encountered during the survey. Cloud cover ranged from 4/8 to 8/8 with wind speeds ranging from 4.1 to 17.8 m s\(^{-1}\) (Table 2). Sea surface temperatures in the SIE ranged between \(-0.28^\circ \)C and \( 0.09^\circ \)C, between 0.12 and \( 0.27^\circ \)C in the WIE and between 3.52 and 3.74 \( ^\circ \)C in the region of the APF. At stations occupied in the SIE, salinities displayed a distinct trend. At the four southernmost stations (D098, D126, D134

<table>
<thead>
<tr>
<th>Table 1</th>
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<tr>
<td><strong>Zooplankton group</strong></td>
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<tr>
<td>-----------------------</td>
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<tr>
<td>Protozooplankton</td>
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<tr>
<td>Metazoans</td>
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Results presented are in mg C m\(^{-2}\) d\(^{-1}\). Values in brackets are standard deviation. Standard deviation values for metazoan grazing impact in the WIE are not shown as only a single bio-station was occupied.
and D162), salinity values were 33.8 in the top 30m while at the northerly stations (D172 and D199), the values were >34.0 throughout the euphotic zone (corresponding to a depth of approx. 70m). At stations in the WIE (D233 and D258) salinities ranged between 34.2 and 34.30 in the euphotic zone (up to 90m depth). In the vicinity of the APF (stations D316, D341, D351, D368) salinity values of 33.8 were recorded throughout the euphotic zone (up to 105m).

Mixed layer depths displayed a general increase along the south–north transect (Fig. 2). With the exception of stations D233 and D258 occupied within the region of the WIE, euphotic depth exceeded the mixed layer depths (MLD) (Fig. 2).

### 3.2. Size-fractionated primary production

#### 3.2.1. Integrated chlorophyll

Total areal Chl-a concentrations in the SIE ranged from 21.2 to 55.4 mg Chl-a m⁻² (Fig. 3). Microphytoplankton formed the most important contributor to total pigments at all stations comprising between 68% and 76% of the total. Microphytoplankton integrated biomass in the SIE ranged from 15.4 to 39.7 mg Chl-a m⁻². Nanophytoplankton biomass ranged between 2.6 and 8.7 mg Chl-a m⁻² and picophytoplankton between 3.1 and 5.9 mg Chl-a m⁻² (Fig. 3). There were no distinct differences in the Chl-a profiles of the three size fractions in the euphotic depth within the three regions of investigation.

In the WIE, total integrated chlorophyll concentrations ranged from 16.7 to 23.3 mg Chl-a m⁻² (Fig. 3). A considerable shift in the size composition of the phytoplankton assemblages was evident with the smaller nano- and picophytoplankton cells contributing between 71% and 73% of the total pigment. Integrated pico- and nanophytoplankton values ranged between 6.5 and 7.8 mg Chl-a m⁻² and between 5.7 and 8.8 mg Chl-a m⁻²,

<table>
<thead>
<tr>
<th>Station</th>
<th>Sea temp. (°C)</th>
<th>Air temp. (°C)</th>
<th>Wind speed (m s⁻¹)</th>
<th>Cloud cover</th>
<th>Sea State</th>
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<tbody>
<tr>
<td>SIE</td>
<td></td>
<td></td>
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<tr>
<td>D098</td>
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<td>0.2</td>
<td>7.1</td>
<td>6/8</td>
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<tr>
<td>D126</td>
<td>0.09</td>
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<td>4.5</td>
<td>5/8</td>
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<tr>
<td>D134</td>
<td>-0.05</td>
<td>-0.5</td>
<td>13.9</td>
<td>8/8</td>
<td>5</td>
</tr>
<tr>
<td>D162</td>
<td>-0.06</td>
<td>-0.1</td>
<td>17.0</td>
<td>3/8</td>
<td>6</td>
</tr>
<tr>
<td>D172</td>
<td>0.03</td>
<td>1.4</td>
<td>10.3</td>
<td>3/8</td>
<td>2</td>
</tr>
<tr>
<td>D199</td>
<td>0.06</td>
<td>-0.2</td>
<td>16.8</td>
<td>8/8</td>
<td>6</td>
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<tr>
<td>WIE</td>
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<tr>
<td>D233</td>
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<td>1.2</td>
<td>12.3</td>
<td>8/8</td>
<td>5</td>
</tr>
<tr>
<td>D258</td>
<td>0.27</td>
<td>1.3</td>
<td>8.1</td>
<td>7/8</td>
<td>4</td>
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<tr>
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<tr>
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<td>3.2</td>
<td>14.4</td>
<td>7/8</td>
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<tr>
<td>D341</td>
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<td>2.7</td>
<td>8.7</td>
<td>8/8</td>
<td>3</td>
</tr>
<tr>
<td>D351</td>
<td>3.52</td>
<td>4.7</td>
<td>9.2</td>
<td>4/8</td>
<td>3</td>
</tr>
<tr>
<td>D378</td>
<td>3.56</td>
<td>6.4</td>
<td>17.8</td>
<td>8/8</td>
<td>7</td>
</tr>
</tbody>
</table>

SIE=Spring Ice-Edge Zone; WIE=Winter Ice Edge Zone; APF=Antarctic Polar Front.
respectively (Fig. 3). Microphytoplankton comprised <29% of the total pigment at all stations occupied within the WIE. Total integrated Chl-a biomass at stations in the vicinity of the APF ranged between 27.9 and 50.5 mg Chl-a m^-2 (Fig. 3). Microphytoplankton integrated biomass ranged between 10.8 and 23.0 mg Chl-a m^-2 or between 35% and 65% of the total pigment. Nanoprytoplankton represented the second most important fraction (Fig. 3). Integrated nanophytoplankton biomass ranged between 9.9 and 15.5 mg Chl-a m^-2. Picophytoplankton always contributed <25% of the total integrated biomass at all stations (Fig. 3).

3.2.2. Integrated primary production

Total daily integrated production within the three regions of investigation displayed the same spatial pattern as integrated biomass. Generally the highest integrated production rates were recorded at stations occupied in the vicinity of the SIE and APF (Fig. 4). Integrated primary production at stations in the SIE ranged from 317 to 887.3 mg C m^-2 d^-1 (Fig. 4). In this zone microphytoplankton were the most important contributor to total production comprising between 60% and 73% of the total. Total daily integrated microphytoplankton production ranged from 230.6 to 633.1 mg C m^-2 d^-1 (Fig. 4). Nanophytoplankton integrated production ranged between 62.3 and 246.7 mg C m^-2 d^-1, while the picophytoplankton production ranged between 24.1 and 77 mg C m^-2 d^-1 (Fig. 4).

Total integrated production in the WIE ranged between 292.8 and 317.9 mg C m^-2 d^-1 (Fig. 4). In this region, nanophytoplankton was the most important contributor to total productivity comprising between 44% and 52% of the total (Fig. 4). Picophytoplankton was the second most important contributor to total production comprising up to 26% of the total. Daily integrated picophytoplankton production values ranged between 76.5 and 83.6 mg C m^-2 d^-1 while nanophytoplankton production ranged from 141.1 to 152.7 mg C m^-2 d^-1 (Fig. 4). At stations occupied in the vicinity of the APF, total daily integrated...
production ranged from 708.5 to 926.8 mg C m$^{-2}$ d$^{-1}$ (Fig. 4). Microphytoplankton was the most important contributor to total production at stations D316 and D351, while nanophytoplankton dominated total production at stations D341 and D378 (Fig. 4). Total daily integrated microphytoplankton production ranged from 264.7 to 483.5 mg C m$^{-2}$ d$^{-1}$ while nanophytoplankton production ranged between 304.5 and 364.1 mg C m$^{-2}$ d$^{-1}$. Picophytoplankton production ranged from 84.7 to 132.3 mg C m$^{-2}$ d$^{-1}$ (Fig. 4).

### 3.3. Biogenic carbon flux

The partitioning of phytoplankton carbon between the classical food web, dominated by metazoans, and microbial loop (protozooplankton) was similar (34.9 vs. 31.7 mg C m$^{-2}$ d$^{-1}$) in the SIE (Fig. 5). Biologically mediated carbon flux resulting from the grazing by the metazoans was equivalent to 9.3 g C m$^{-2}$ d$^{-1}$ (Fig. 5). These rates correspond to a transfer of 1.5% of the total daily production to depth. The sinking of dead/senescent phytoplankton cells was equivalent to 30.1 mg C m$^{-2}$ d$^{-1}$, which accounted for 74% of the total biogenic carbon flux to depth.

Within the WIE average, total daily productivity corresponded to 305 mg C m$^{-2}$ d$^{-1}$ (Fig. 6). Microzooplankton and metazoan grazing impact was equivalent to 25.9 and 157.1 mg C m$^{-2}$ d$^{-1}$, respectively. Collectively, metazoans were responsible for the transfer of 15.4% of the total phytoplankton production to depth. The sinking of dead/senescent phytoplankton cells contributed 15.3 mg C m$^{-2}$ d$^{-1}$ or 24% of the total carbon transported to depth (Fig. 6).

Total average daily phytoplankton production at stations occupied in the region of the APF was the highest during the entire investigation corresponding to 799.9 mg C m$^{-2}$ d$^{-1}$ (Fig. 7). Protozooplankton and metazoan grazing impact was equivalent to 86.3 and 225.1 mg C m$^{-2}$ d$^{-1}$, respectively (Fig. 7). Grazing by the metazoans was responsible for the transfer of up to 67.5 mg C m$^{-2}$ d$^{-1}$ or 8.4% of the total daily production to depth. The sinking of dead/senescent cells was responsible for transferring 40 mg C m$^{-2}$ d$^{-1}$ to depth. This value corresponded to 37% of the total biogenic carbon transported to depth (Fig. 7).
4. Discussion

4.1. Size-fractionated primary production studies

Total integrated chl-α biomass and production were highest in the region of the SIE and in the vicinity of the APF (Figs. 3 and 4). The estimates of integrated primary production at stations occupied within the vicinity of these two features are in agreement with previous studies conducted in the region of the APF and MIZ in different sectors of the Southern Ocean (Weber and
El-Sayed, 1987; Laubscher et al., 1993; Boyd et al., 1995; Smetacek et al., 1997; Froneman et al., 2001). It is generally accepted that macronutrient concentrations south of the APF are above the threshold, which would limit primary production (El-Sayed, 1988; Laubscher et al., 1993; Froneman et al., 2001). As a consequence, it is unlikely that the observed pattern in primary production during this study reflects the availability of macronutrients. At stations occupied in the region of the SIE and APF, the euphotic depth (Eu) exceeded the mixed layer depth (MLD) (Fig. 2). These data suggest that high production rates recorded in the region of the SIE and APF could partially be attributed to a favourable light environment. Indeed, at stations occupied in the vicinity of these two features, the ratio of Eu to MLD accounted for up to 53% of the total variance associated with total primary production (P<0.05). The occurrence of a shallow MLD in the region of retreating ice is well documented and can be related to the release of freshwater during the ice melt, which confers local water column stability (Laubscher et al., 1993; Froneman et al., 1997). Although no sea-ice was observed at stations in the SIE, the low salinity values recorded at stations in the SIE clearly demonstrate the continual influence of the sea-ice retreat on the water column. Water column stability in the region of the retreating ice may be further enhanced by the summer capping of the colder winter waters. It is worth noting that the increase in MLD along the south–north transect in the SIE was coupled with a general decrease in total integrated primary production (Figs. 2 and 4). These facts suggest that the effect of sea-ice melt had partially been eroded at the northern stations within the SIE. Increased water column stability in the region of the APF is thought to result from the interaction of colder Antarctic surface waters with the warmer Polar Frontal zone waters, which confers localised water column stability in the region of the front (Laubscher et al., 1993). Finally, it is not impossible that the increased primary production rates recorded in the vicinity of the APF may be associated with seawater temperature (Laubscher et al., 1993). Neori and Holm-Hansen (1982) showed that the maximum assimilation rates for Antarctic phytoplankton occurred at seawater temperatures ranging between 2 and 5°C, well

![Fig. 7. Total integrated primary production and estimates of vertical carbon flux resulting from grazing activity of zooplankton and sinking of phytoplankton in the region of the APF in the eastern Atlantic sector of the Southern Ocean in austral summer (December 97–January 98). Units are mg C m⁻² d⁻¹.](image)
within the temperature range spanning the APF (Table 1). Unfortunately, the spatial resolution of this study does not allow us to test this hypothesis. Total integrated chl-a biomass and production at stations occupied in the WIE were <25 mg Chl-a m$^{-2}$ and <320 mg C m$^{-2}$ d$^{-1}$, respectively (Figs. 3 and 4). The estimates of biomass and production presented here are in the same range as those reported for open water stations in the Southern Ocean (Laubscher et al., 1993; Froneman et al., 2001). It is now generally well accepted that small nano- and picophytoplankton dominate total primary production in the open waters of the Southern Ocean (Weber and El-Sayed, 1985; Jacques, 1989; El-Sayed, 1988; Laubscher et al., 1993; Froneman et al., 2001). The predominance of small phytoplankton cells in these regions is thought to reflect the unfavourable light environment, which favours the growth of small phytoplankton cells (Fogg, 1991). The predominance of small nano- and picophytoplankton and the presence of MLD which exceeded Eu at stations occupied in the WIE suggest that this region can be considered as an open water region. It is worth noting that the production rates at stations occupied in the northern sector of the SIE are in the same range as those reported for the WIE (Fig. 4). These facts suggest that the effect of sea-ice melt on the water column had partially been eroded at the stations occupied in the northern region of the SIE. Evidence to support this hypothesis includes increased salinity values and MLD (Fig. 2).

The important role of iron (Fe) availability in limiting primary production in the Southern Ocean is now well documented (Martin et al., 1990; de Baar et al., 1995; Boyd and Law, 2001). Preliminary results of the iron study conducted in parallel to the size-fractionated primary production study indicated that Fe concentrations (10 m) were highest (up to 1.6 nM) at stations in the southern region of the SIE and lowest at the northern boundary of the APF (<0.4 nM). Intermediate concentrations, ranging between 0.4 and 1.15 nM, were recorded at the northernmost stations of the SIE, the WIE and at stations occupied at the southern boundary of the APF (Croot et al., 2004). Although the correlation between iron concentration and primary production during this study was not significant ($P<0.05$), there are several important points that require further discussion. Firstly, the decrease in total integrated primary production along the south–north transect in the SIE corresponded to the observed pattern in Fe concentration. Secondly, despite the moderately high concentrations of Fe in the WIE, total production was the lowest during the entire investigation. These facts suggest that while a favourable light environment is a prerequisite for elevated primary production in the Southern Ocean, Fe availability likely determines the magnitude of the increase.

4.2. Biogenic carbon flux

Biogenic carbon flux resulting from the grazing of zooplankton was highest at stations occupied in the region of the WIE, where up to 15.4% of the total primary production was transported to depth (Fig. 6). In contrast to the WIE, in the region of the SIE and APF, grazer-mediated carbon flux accounted for <8% of the total primary production (Figs. 5 and 7). The estimates of the contribution of zooplankton to total vertical carbon flux are in agreement with a recent study conducted in the Lazarev Sea (Pakhomov et al., 2002). The spatial variability in grazer-mediated biogenic carbon flux in the three regions of investigation appears to be related to both the phytoplankton and zooplankton community structure. A feature of the zooplankton community during the study was the virtual absence of larger macrozooplankton in the region of investigation. Indeed, mesozooplankton always accounted for >70% of the total zooplankton biomass (Pakhomov and Froneman, 2004a). In the WIE, total chl-a was dominated by nanophytoplankton, which is the optimum size particle for mesozooplankton (Fortier et al., 1994). The high rates of biogenic carbon flux resulting from grazing by zooplankton in the WIE are, therefore, not surprising. In contrast to the WIE, Pakhomov and Froneman (2004a) suggested that the grazing impact of mesozooplankton in the region of the SIE and APF was constrained by the size structure of the local phytoplankton assemblages.
APF region, microphytoplankton comprising chain forming and pennate diatom species of the genera Chaetoceros and Proboscia contributed most to phytoplankton biomass while in the region of the SIE chain forming species and the prymnesiophytes, Phaeocystis spp. dominated the phytoplankton community (Froneman, P.W., unpublished data).

The sinking of dead/senescent phytoplankton cells has been identified as an important mechanism for the transportation of carbon to depth in the region of the retreating sea-ice and oceanic frontal systems of the Southern Ocean (von Bodungen et al., 1986; Fischer et al., 1988; Murphy et al., 1998; Pakhomov et al., 2002). A recent study conducted in different oceanic provinces showed that the sinking of ungrazed large diatoms represented the key determinant of the magnitude of downward POC in the ocean (Boyd and Newton, 1999). During this study sinking of dead/senescent phytoplankton cells corresponded to 76% and 37% of the total biogenic carbon transported to depth in the SIE and APF, respectively (Figs. 5 and 7). In both regions, microphytoplankton comprising mainly diatoms contributed most to phytoplankton biomass (Froneman, P.W., unpublished data). In the region of the WIE where nanophytoplankton dominated total chl-a, the sedimentation of phytoplankton comprised only 24% of the total biogenic flux. Low rates of sedimentation of phytoplankton in the open ocean environment of the Southern Ocean have previously been documented and can be related to the predominance of small phytoplankton cells in these regions which have low sinking rates (Fischer et al., 1988).

It should be pointed out that the results presented here should be regarded with caution due to possible sources of error. For example, we have assumed an average assimilation efficiency of 70% for the entire zooplankton community. Clearly this value will vary considerably between the various groups of zooplankton. Similarly, it was assumed that grazing by protozooplankton does not contribute to the export of carbon to depth. However, a study conducted in the Weddell Sea showed that faecal pellets protozoan in origin were sampled at depths >100 m, suggesting that protozooplankton grazing may at times contribute to vertical carbon flux (Nöthig and von Bodungen, 1989). Following this, it is well documented that all the major zooplankton groups in the high Antarctic region feed on protozooplankton (Atkinson, 1996; Froneman et al., 1996b). Production originating from the microbial loop will thus be transferred to depth, increasing the local efficiency of the biological pump. The magnitude of this transfer is presently still unknown. Finally, we have not taken into account the phenomenon of coprophagy.

In conclusion, results of this study suggest that the relative efficiency of the biological pump in the three regions of investigation appeared to be related to both the size structure of the local phytoplankton assemblages and the zooplankton community structure. In both the SIE and APF regions, the local phytoplankton assemblages were too large to be efficiently grazed on by mesozooplankton which dominated the zooplankton community. As a consequence, in these regions <8% of total daily primary production was transported to depth. In contrast, in the region of the WIE, a favourable size structure of the phytoplankton community coupled with high biomass of zooplankton resulted in up to 15% of the total daily phytoplankton production being transported to depth. These facts suggest regional variability in the efficiency of the biological pump. These data are supported by pCO₂ studies conducted in parallel to this investigation, which showed that the WIE region represented a strong sink for atmospheric CO₂ while the regions of the APF and SIE were weak sinks (Chierici et al., 2004).

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