

## Coupling of epipelagic and mesopelagic heterotrophic picoplankton production to phytoplankton biomass in the Antarctic polar frontal region

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### Abstract

We assessed relationships between phytoplankton standing stock, measured as chlorophyll *a* (Chl *a*), primary production (PP), and heterotrophic picoplankton production (HPP), in the epipelagic zone (0–100 m) as well as in the mesopelagic zone (100–1,000 m) in the polar frontal zone of the Atlantic sector of the Southern Ocean in austral summer (late December to January) and fall (March to early May). Integrated epipelagic HPP was positively correlated to integrated PP in summer (data for fall are not available) but not to integrated Chl *a*. However, integrated mesopelagic HPP was positively correlated to Chl *a* in summer as well as fall. The mesopelagic fraction of HPP as a percentage of total HPP was also positively correlated to Chl *a*, whereas the epipelagic fraction of HPP was negatively correlated to it. These results indicate that with increasing phytoplankton standing stock, constituted mainly of highly silicified diatoms, the focus of its consumption by heterotrophic picoplankton shifts from epipelagic to mesopelagic waters. With a growth efficiency of 30%, our HPP data indicate that in both the epipelagic and mesopelagic zone heterotrophic picoplankton consume 20% of PP. Mesopelagic heterotrophic picoplankton consumed around 80% of the sinking flux, measured from depletion of <sup>234</sup>Th, which is a lower fraction than that reported from the central and subarctic Pacific. Our analysis indicates that it is important to include mesopelagic HPP in comprehensive assessments of the microbial consumption of PP, phytoplankton biomass, and particulate organic matter in cold oceanic systems with high rates of export production.

The Southern Ocean occupies around 10% of the total oceanic surface area, and variables affecting the biosphere globally such as climate warming and stratospheric ozone depletion have a special impact on this cold and sensitive biome. This is one reason why biogeochemical processes in this region have been studied extensively during the last 2 decades. Phytoplankton primary production (PP), heterotrophic picoplankton production (HPP), and respiration are quantitatively probably the most important biogeochemical processes in the carbon cycle in the pelagic zone of the Southern Ocean (e.g., Lochte et al. 1997; Ducklow et al. 2001). It has been shown that *Archaea* constitute a significant fraction of the heterotrophic picoplankton in the Southern Ocean (e.g., Murray et al. 1999). In surface waters during the growing season, however, *Archaea* do not appear to be involved in processing phytoplankton-derived organic matter with the same significance as *Bacteria* because of their inverse relationship to chlorophyll *a* (Chl *a*) concentrations. Several comprehensive investigations of dynamics of HPP and its relationship to phytoplankton biomass and PP and other controlling factors have been carried out in various regions of the Southern Ocean (e.g., Sullivan et al. 1990; Lochte et al. 1997; Bird and Karl 1999; Ducklow et al. 2000, 2001; Pedros-Alió et al. 2002). Despite all these studies, the

relative significance of the controlling factors for heterotrophic picoplankton dynamics, i.e., temperature, resource limitation, grazing, and viral lysis, is still controversial. There are also indications of a temporal decoupling between the development of phytoplankton blooms and their heterotrophic microbial consumption in the Southern Ocean and other cold marine systems, possibly because of the low temperature (Billen and Becquevort 1991; Pomeroy and Wiebe 2001).

One reason for this controversy may be that most studies were confined to the mixed layer or euphotic zone, i.e., the upper 100 m, and much fewer studies took into account heterotrophic picoplankton processes in the mesopelagic zone. Only Lochte et al. (1997), Moriarty et al. (1997), Ducklow et al. (2001), and Pedros-Alió et al. (2002) studied mesopelagic HPP in the Southern Ocean, but systematic analyses in relation to phytoplankton biomass and PP are still missing. A substantial amount of phytoplankton biomass and particulate organic carbon (POC) sinks out of the mixed layer, in particular in upwelling regions and also in the Southern Ocean (Buesseler 1998; Sweeney et al. 2000; Rutgers van der Loeff et al. 2002). Regions of a high sinking flux such as the polar front of the Southern Ocean are of special importance in this respect because they transport high amounts of organic matter to the ocean's interior and act as a sustainable sink for CO<sub>2</sub> (Falkowski et al. 1998). The significance of the polar front in this respect but also for the downward flux of biogenic silica becomes obvious from the fact that about 70% of the global oceanic sediment deposits of silica are buried in this region (Treguér et al. 1995). It has been shown that heterotrophic picoplankton in the mesopelagic zone consume major fractions of the sinking flux (Cho and Azam 1988; Simon et al. 1992), but organic matter consumption by mesopelagic picoplankton has not yet been related directly to phytoplankton biomass and PP.

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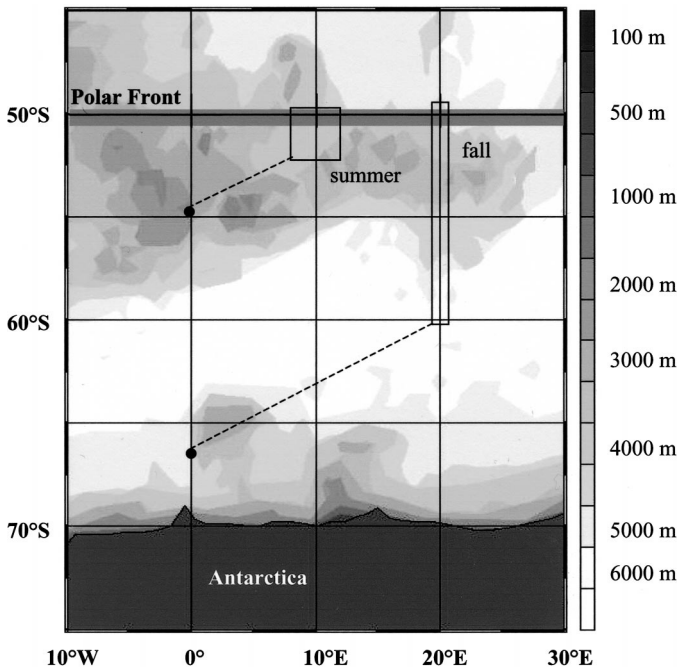


Fig. 1. Map of the investigation areas in the Atlantic sector of the Southern Ocean during cruises ANT XIII/2 in the austral summer (square at 50°S and 10°E, December 1995 and January 1996) and ANT XVI/3 during austral fall (rectangle at 50–60°S and 20°E, March–May 1999) with RV *Polarstern*. The shaded area at 50°S indicates the approximate location of the polar front. The filled circles at the end of the dashed lines indicate stations that were also visited during the investigation periods. For exact locations of the stations see Table 1. The bathymetry is provided by the shaded scale.

We studied epipelagic (0–100 m) and mesopelagic (100–1,000 m) HPP in relation to PP and Chl *a* as a proxy for phytoplankton biomass in the Atlantic sector of the Southern Ocean in the austral summer and fall. Our investigation was part of comprehensive studies of cruises of RV *Polarstern* (ANT XIII/2, Rutgers van der Loeff et al. 2002; Smetacek et al. 2002; Strass et al. 2002; Tremblay et al. 2002; ANT XVI/3, Bathmann et al. 2000), which focused on mesoscale physics and biogeochemical processes in the polar frontal region of this area. We hypothesized that export production is important in controlling heterotrophic picoplankton consumption of phytoplankton-derived organic matter and the partitioning of epipelagic and mesopelagic picoplankton in the Southern Ocean and thus helps to explain the controls of organic matter consumption by heterotrophic picoplankton in the mixed layer.

## Material and methods

**Study area and sampling**—The study was carried out on board RV *Polarstern* during cruise ANT-XIII/2 (4 December 1995 to 24 January 1996) in the austral summer and during cruise ANT-XVI/3 (18 March to 10 May 1999) in the austral fall in the Atlantic sector of the Southern Ocean (Fig. 1). In summer 10 stations were visited for collecting bacterioplankton samples between 20 and 1,000 m depth, and in fall 12

Table 1. Station numbers, latitude, longitude, region (PFZ, polar frontal zone; Wed, Weddell Sea; ACC, Antarctic circumpolar current), and date of sampling station visited during cruises ANT XIII/2 and ANT XVI/3 with RV *Polarstern*.

Station No.	Latitude (S)	Longitude (E)	Region	Date
9	53 59.9	00 06.2	PFZ	22 Dec 95
10	50 28.8	08 09.1	PFZ	25 Dec 95
13	49 49.2	11 31.6	PFZ	29 Dec 95
15	50 41.8	11 31.0	PFZ	30 Dec 95
18	40 42.0	09 34.1	PFZ	5 Jan 96
19	49 54.0	09 34.1	PFZ	5 Jan 96
25	50 18.0	10 17.5	PFZ	7 Jan 96
29	50 42.0	10 17.5	PFZ	7 Jan 96
32	49 53.8	11 33.1	PFZ	20 Jan 96
33	49 42.0	11 31.5	PFZ	20 Jan 96
153	52 00.6	20 00.0	PFZ	25 Mar 99
154	49 51.6	20 00.0	PFZ	26 Mar 99
156	48 49.8	20 00.0	PFZ	27 Mar 99
157	49 20.4	20 00.0	PFZ	28 Mar 99
169	60 00.0	20 31.8	Wed	9 Apr 99
185	66 53.4	0 00.0	Wed	21 Apr 99
190	54 01.2	19 58.2	ACC	25 Apr 99
197	51 54.0	19 58.8	PFZ	2 May 99
198	51 29.4	20 00.0	PFZ	3 May 99
200	50 00.6	20 00.0	PFZ	2 May 99
201	49 29.4	20 01.2	PFZ	4 May 99
203	48 30.6	20 00.0	PFZ	4 May 99

stations were visited (Table 1). Samples were collected with 12-liter Niskin bottles mounted on a General Oceanics Rosette sampler equipped with a Neil Brown Mark III conductivity–temperature–depth (CTD) sensor. Subsamples were withdrawn into acid-rinsed 1-liter polyethylene bottles, kept at in situ temperature ( $\pm 1^\circ\text{C}$ ), and further processed within 1 h.

**Heterotrophic picoplankton abundance**—Subsamples of 50 ml were fixed with 2% formalin and stored at 2°C until further processing within 2 d. Depending on the abundance, 3–5 ml were stained with 4,6-diamidinophenyleindole (DAPI, 1 mg 100 ml<sup>-1</sup>) for 5 min, filtered onto black 0.2- $\mu\text{m}$  Nuclepore membranes, and kept at 2°C until enumeration by epifluorescence microscopy (Porter and Feig 1980) with a Nikon microscope (Labophot 2A) on shipboard within 1 week.

**Heterotrophic picoplankton production (HPP)**—HPP was determined from the incorporation of <sup>14</sup>C-leucine according to Simon and Azam (1989). We added <sup>14</sup>C-leucine (specific activity 11.5 GBq mmol<sup>-1</sup>, Amersham [ANT-XIII/2]; 10.8 GBq mmol<sup>-1</sup>, Hartmann Analytik [ANT-XVI/3]) at a final concentration of 10 nmol L<sup>-1</sup> in triplicates and a Formalin-killed control to 10–20 ml of sample. Incubation was at in situ temperature ( $\pm 1^\circ\text{C}$ ) in the dark and stopped by adding formalin (1% final concentration) after 5 (epipelagic) to 12 h (mesopelagic). Preliminary tests at the beginning of each cruise showed that incorporation was saturated at 10 nmol L<sup>-1</sup> and still linear after the chosen incubation times. After fixation, samples were filtered onto 0.2- $\mu\text{m}$  nitrocellulose fil-

Table 2. Integrated values of heterotrophic picoplankton production, Chl *a* 0–100 m, and primary production (euphotic zone) during cruises ANT XIII/2 (Stas 9 to 33) and ANT XVI/3 (Stas. 153–203); —, not determined.

Sta.	Heterotrophic picoplankton production						Primary production			
	0–1,000 m		0–100 m		100–1,000 m		Chl <i>a</i> (mg m <sup>-2</sup> )	Primary production		
	(mg C m <sup>-2</sup> d <sup>-1</sup> )	mg C m <sup>-2</sup> d <sup>-1</sup>	% of total	mg C m <sup>-2</sup> d <sup>-1</sup>	% of total	mg C m <sup>-2</sup> d <sup>-1</sup>		%HPP 0–100 m	%HPP 0–1,000 m	
9	45.1	27.4	60.8	17.7	39.2	35.1	565	4.8	8.0	
10	75.0	38.1	50.8	36.9	49.2	49.4	503	7.6	14.9	
13	207.4	57.2	27.6	150.3	72.4	104.5	1022	5.6	20.3	
15	58.6	41.9	71.4	16.8	28.6	nd	820	5.1	7.1	
18	86.2	64.1	74.3	22.1	25.7	54.3	1018	6.3	8.5	
19	62.2	47.6	76.4	14.7	23.6	80.5	—	—	—	
25	115.8	68.3	59.0	47.5	41.0	103.4	—	—	—	
29	61.8	39.3	63.6	22.5	36.4	97.0	—	—	—	
32	75.7	35.7	47.1	40.0	52.9	139.0	603	5.9	12.5	
33	124.9	49.6	39.7	75.4	60.3	158.4	—	—	—	
mean±SD	91.2±47.9	46.9±13.0	57.1±15.1	44.4±41.6	42.9±15.8	91.3±41.1	755.2±231.3	5.9±1.0	11.9±5.1	
153	47.6	27.9	58.6	19.7	41.4	—	—	—	—	
154	39.7	18.4	46.3	21.3	53.6	32.3	—	—	—	
156	30.5	19.0	62.3	11.5	37.5	17.4	—	—	—	
157	46.9	23.4	49.9	23.5	50.1	42.7	—	—	—	
169	50.7	27.7	54.6	23.0	45.4	—	—	—	—	
185	38.5	12.0	31.0	26.6	69.1	14.9	—	—	—	
190	68.6	21.1	30.8	47.5	69.3	24.2	—	—	—	
197	34.8	18.3	52.5	16.5	47.3	31.8	—	—	—	
198	37.2	13.1	35.3	24.1	64.9	47.1	—	—	—	
200	42.0	16.9	40.2	25.1	59.8	48.7	—	—	—	
201	48.6	18.5	38.0	30.1	62.0	38.7	—	—	—	
203	24.7	10.6	42.9	14.1	57.1	22.7	—	—	—	
mean±SD	42.5±11.3	18.9±5.5	45.2±10.6	23.6±9.2	54.8±10.6	32.1±12.1	—	—	—	

ters (25 mm diameter, Sartorius), rinsed with ice-cold particle-free seawater, and extracted with ice-cold 5% trichloroacetic acid (TCA) for 5 min. After rinsing the extracted filters twice with ice-cold 5% TCA, the filters were dissolved with ethylacetate and radioassayed by liquid scintillation counting. The coefficient of variation (CV, standard deviation/mean) of the triplicate measurements was <10%. Biomass production was calculated from leucine incorporation rates by using the conversion factor of 1.5 kg C (mol leucine)<sup>-1</sup> assuming no intracellular isotope dilution (Simon and Azam 1989). Previous studies showed that this conversion factor is appropriate in the Southern Ocean (Ducklow et al. 2000; Pedros-Alió et al. 2002).

**Chlorophyll *a***—Chl *a* was determined after extraction in 90% acetone fluorometrically according to Tremblay et al. (2002). Integrated values for 0–100 m of the summer cruise are adopted from Tremblay et al. (2002).

**Primary production**—Data are only available for the summer cruise and are adopted from Tremblay et al. (2002). The <sup>14</sup>C method with two dark controls and addition of 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) was applied. Values integrated over the euphotic zone are based on samples from the surface, 50, 25, 10, 1, and 0.1% surface irradiance incubated for 24 h under simulated in situ conditions on shipboard.

## Results

During the summer cruise, temperatures in the surface layer ranged between 0°C at the southernmost station (Sta. 9) and 2.5–4.5°C at the polar frontal stations. In the temperature minimum zone at 350 m, temperatures were between 1.5 and 2.5°C (Strass et al. 2002). During the fall cruise, temperatures in the surface layer of the polar frontal region decreased from 5.9°C at the northern fringe to 1.2°C at 54°S. At 60°S (Sta. 169) and 66°53'S (Sta. 185) temperatures were 0.45 and -1.3°C.

Chlorophyll *a* concentrations in summer varied from 0.3 µg Chl *a* L<sup>-1</sup> at Sta. 9 to 1.85 µg Chl *a* L<sup>-1</sup> at Sta. 33 with an overall mean of 0.83 ± 0.55 µg Chl *a* L<sup>-1</sup>. There was a temporal build up of phytoplankton biomass at the polar front during the investigation period since highest Chl *a* concentrations were recorded at Stas. 32 and 33, which were visited at the end of the cruise (Tables 1 and 2). Enhanced Chl *a* concentrations always occurred in the size fraction >20 µm, and those in the fraction <20 µm never exceeded 0.7 µg Chl *a* L<sup>-1</sup> (Tremblay et al. 2002). In fall, Chl *a* concentrations ranged between 0.1 µg Chl *a* L<sup>-1</sup> at Stas. 156 and 185 and 0.54 µg Chl *a* L<sup>-1</sup> at Stas. 157 and 198. Concentrations were significantly lower than in summer with an overall mean of 0.35 ± 0.13 µg Chl *a* L<sup>-1</sup>. Also, values integrated over the upper 100 m were significantly lower (32.1 ± 12.1 mg Chl *a* m<sup>-2</sup>) in fall compared to summer (91.3 ± 41.1 mg Chl *a* m<sup>-2</sup>, *t*-test, *p* < 0.01).

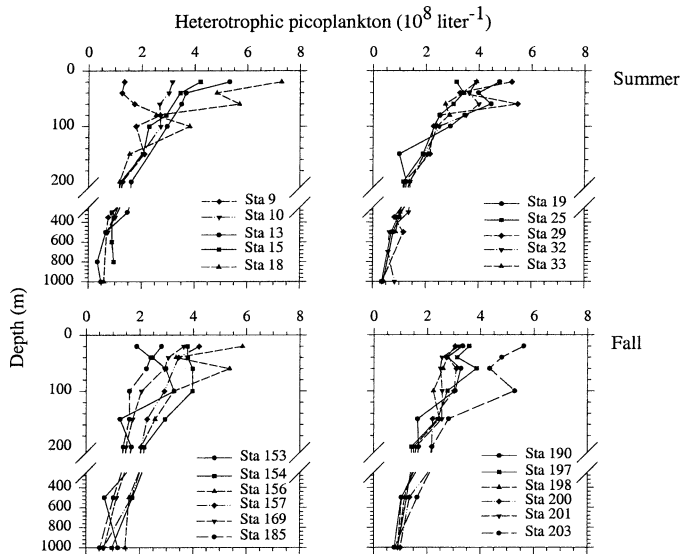


Fig. 2. Depths profiles of the abundance of heterotrophic picoplankton at indicated stations during austral summer 1995/1996 and fall 1999 in the polar frontal region of the Atlantic sector of the Southern Ocean.

The phytoplankton in summer was dominated by *Thalassiothrix* spp. and *Chaetoceros atlanticus*. *Fragillariopsis kerguelensis*, *Pseudonitzschia* cf. *lineola*, and *Rhizosolenia* spp. were also present but contributed <5% to total phytoplankton biomass each (Smetacek et al. 2002). In fall dominant species were *Fragillariopsis kerguelensis*, *Thalassiothrix* spp., and *Chaetoceros atlanticus* (Smetacek et al. unpubl. data). This analysis only includes microphytoplankton constituting the biomass build up during blooms and does not consider background nanophytoplankton.

**Heterotrophic picoplankton**—Numbers of heterotrophic picoplankton in the upper 100 m varied from  $1.2 \times 10^8$  to  $7.3 \times 10^8$  cells  $L^{-1}$  in summer and from  $1.5 \times 10^8$  to  $5.9 \times 10^8$  cells  $L^{-1}$  in fall (Fig. 2). In summer, lowest and highest numbers occurred at Stas. 9 and 18, respectively, and numbers at the other stations were fairly similar. In fall, there was little variation among the various stations except that numbers at Sta. 203 were systematically higher. Below 100 m, numbers systematically decreased with depth from  $3 \times 10^8$  to  $<1.5 \times 10^8$  cells  $L^{-1}$  at 1,000 m.

Heterotrophic picoplankton production in summer in the upper 80 m varied between 9 and  $40 \mu g C m^{-3} h^{-1}$  with lowest values at Sta. 9 and highest values at Stas. 13, 18, and 25 (Fig. 3). At 100 m and below rates of HPP decreased from 10 to  $<0.5 \mu g C m^{-3} h^{-1}$ . At quite a few stations there was no continuous vertical decrease, but elevated values occurred at various mesopelagic depths. At Sta. 13, values between 500 and 1,000 m were as high as at 100 m depth. If we assume that hourly rates are representative for 24 h and take values at a given depth as representative for half of the layer to the next value above and below, integrated values for the upper 100 m ranged from 27.4 to  $68.3 mg C m^{-2} d^{-1}$  with a mean of  $46.9 \pm 13.0 mg C m^{-2} d^{-1}$  (Table 2; Fig. 4). Integrated values for the mesopelagic zone (100–1,000

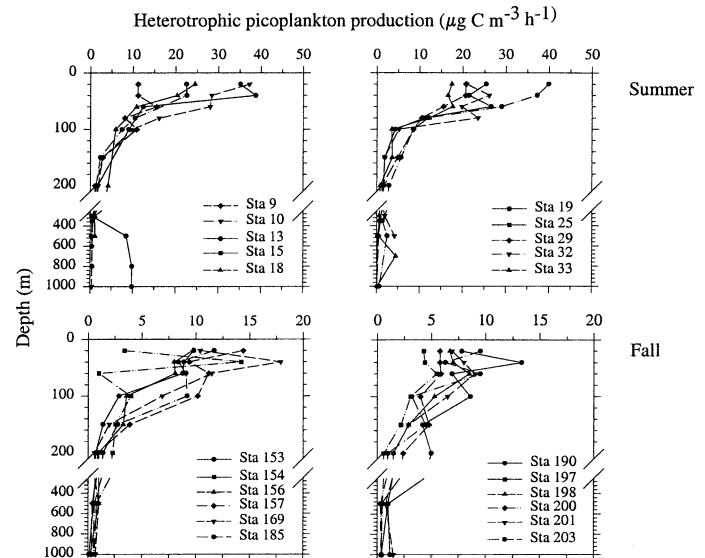


Fig. 3. Depths profiles of heterotrophic picoplankton production at indicated stations during austral summer 1995/1996 and fall 1999 in the polar frontal region of the Atlantic sector of the Southern Ocean.

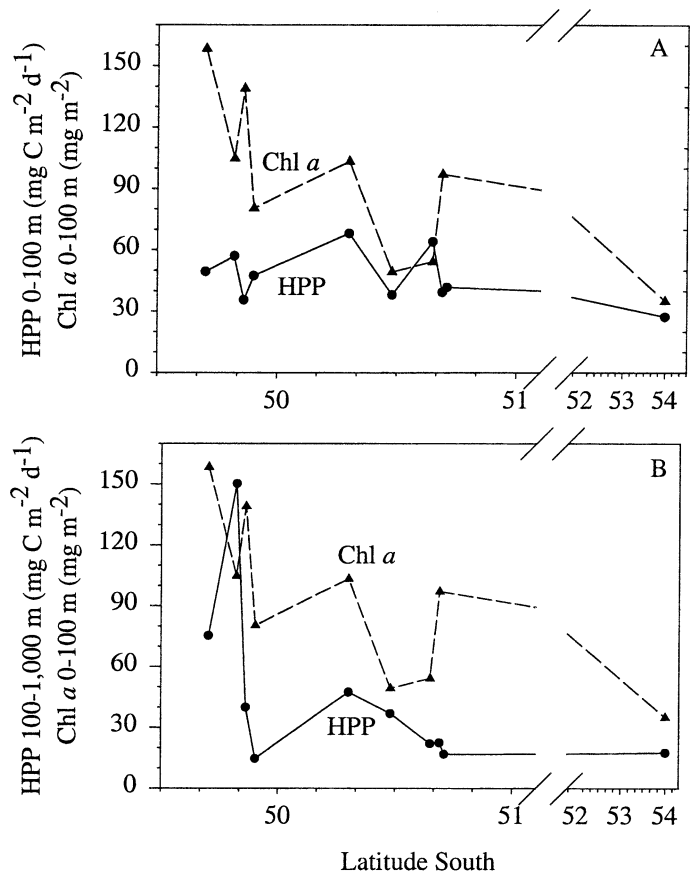


Fig. 4. Integrated rates of heterotrophic picoplankton production (HPP) and Chl *a* in the austral summer 1995/1996 in the polar frontal region of the Atlantic sector of the Southern Ocean. (A) HPP 0–100 m and Chl *a* 0–100 m; (B) HPP 100–1,000 m and Chl *a* 100–1,000 m.

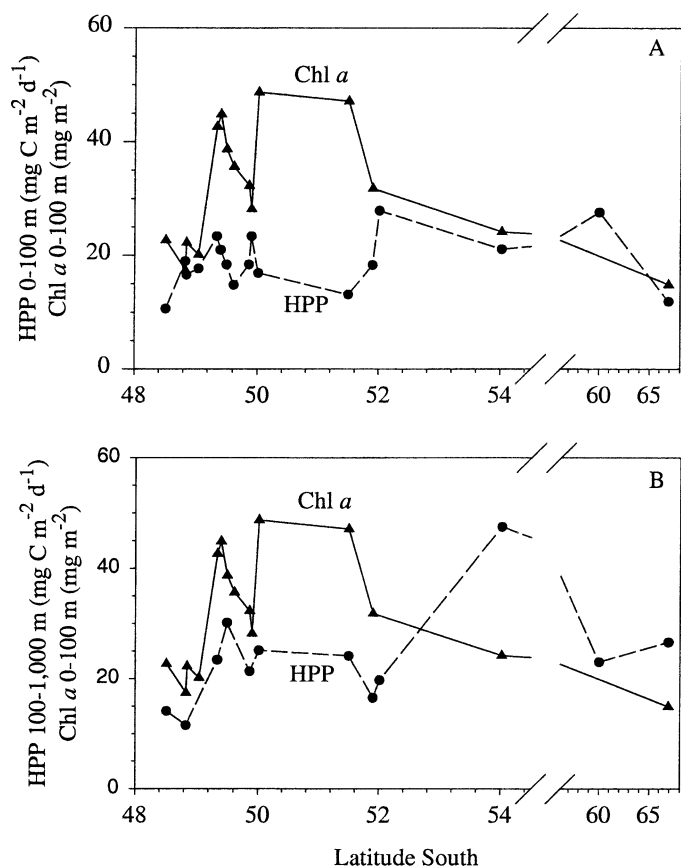


Fig. 5. Integrated rates of heterotrophic picoplankton production (HPP) and Chl *a* in the austral fall 1999 in the polar frontal region of the Atlantic sector of the Southern Ocean. (A) HPP 0–100 m and Chl *a* 0–100 m; (B) HPP 100–1,000 m and Chl *a* 0–100 m.

m) ranged between 14.7 and 150.3 mg C m<sup>-2</sup> d<sup>-1</sup> (mean: 44.4 ± 41.6 mg C m<sup>-2</sup> d<sup>-1</sup>), which is equivalent to 23.6–72.4% of total integrated HPP (mean: 42.9 ± 15.8%).

In fall, HPP in the upper 80 m was substantially lower than in summer. Volume-specific rates varied between <2.5 and 18 μg C m<sup>-3</sup> h<sup>-1</sup>, and rates integrated over the upper 100 m varied between 10.6 and 27.9 mg C m<sup>-2</sup> d<sup>-1</sup> (Table 2; Fig. 5). The mean (19.9 ± 5.5 mg C m<sup>-2</sup> d<sup>-1</sup>) was only 40% of and significantly lower than that in summer (*t*-test, *p* < 0.01). Values at 100 m and below varied between 10 and <0.5 μg C m<sup>-3</sup> h<sup>-1</sup> and, thus, in the same range as in summer. Also in fall, elevated rates of HPP were recorded at intermediate mesopelagic depths. Values integrated from 100 to 1,000 m tended to be lower than in summer (mean: 23.6 ± 9.2 mg C m<sup>-2</sup> d<sup>-1</sup>), but the overall means of the two seasons were not significantly different. The fraction of HPP in the mesopelagic zone as percentage of total HPP (mean: 54.8 ± 10.6%) was not significantly different from that in summer.

**Relation of heterotrophic picoplankton to chlorophyll and primary production**—In order to compare dynamics of heterotrophic picoplankton in the epipelagic and mesopelagic zones to Chl *a* and to PP, we made a linear regression anal-

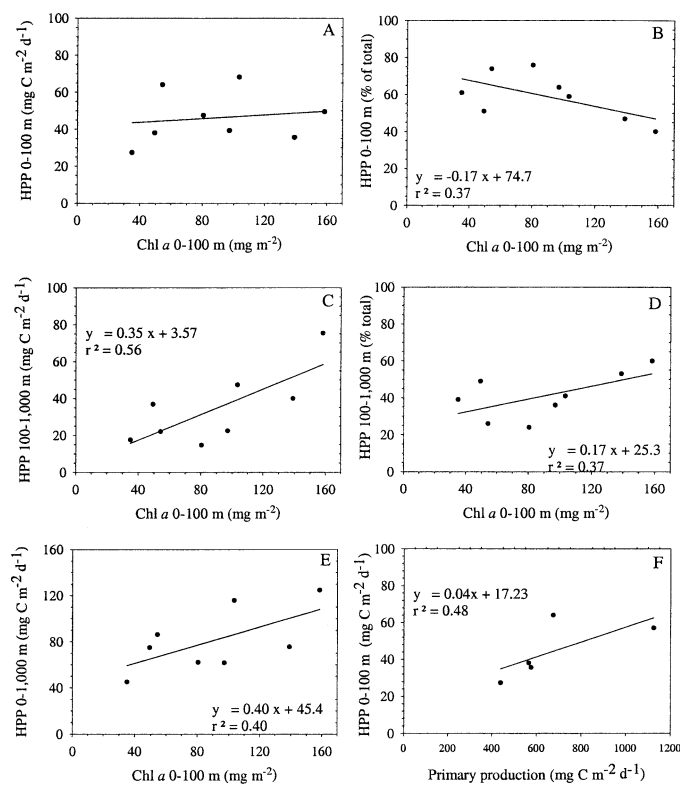


Fig. 6. Linear regression analysis of integrated rates of heterotrophic picoplankton production (HPP), Chl *a*, and primary production in the austral summer 1995/1996 (*p* < 0.01). (A) Chl *a* 0–100 m versus HPP 0–100 m; (B) Chl *a* 0–100 m versus HPP 0–100 m (percentage of total HPP); (C) Chl *a* 0–100 m versus HPP 100–1,000 m; (D) Chl *a* 0–100 m versus HPP 100–1,000 m (percentage of total HPP); (E) Chl *a* 0–100 m versus HPP 0–1,000 m; (F) Primary production versus HPP 0–100 m.

ysis of integrated values of the abundance of heterotrophic picoplankton and HPP to Chl *a* and PP (SigmaStat software). Abundance of heterotrophic picoplankton did not exhibit any significant correlation. Values of HPP integrated over the upper 100 m did not show any significant correlation to Chl *a*, either in summer or in fall (Figs. 6A and 7A). However, HPP exhibited a significant positive correlation to PP (*p* < 0.01; Fig. 6F). HPP integrated over the upper 100 m but expressed as percentage of total HPP was negatively correlated to Chl *a* (*p* < 0.01; Figs. 6B and 7B). Rates of HPP integrated from 100 to 1,000 m as absolute values but also as percentage of total HPP were significantly positively correlated to Chl *a* in summer as well as in fall (*p* < 0.01; Figs. 6C,D and 7C,D). Values from Sta. 13 of the summer cruise were excluded from this analysis. According to estimated sinking rates, enhanced rates of HPP between 500 and 1,000 m (Fig. 3) could not have been the result of phytoplankton-derived POC settled out during our cruise. The *x*-intercepts of 3.57 mg C m<sup>-2</sup> d<sup>-1</sup> and 25.2% of total HPP (summer) and of 4.39 mg C m<sup>-2</sup> d<sup>-1</sup> and 35% of total HPP (fall) are rather similar and indicate the background level of mesopelagic HPP at very low concentrations of Chl *a*. Rates of HPP integrated over the entire water column (0–1,000 m) were also positively correlated to Chl *a* but not as closely

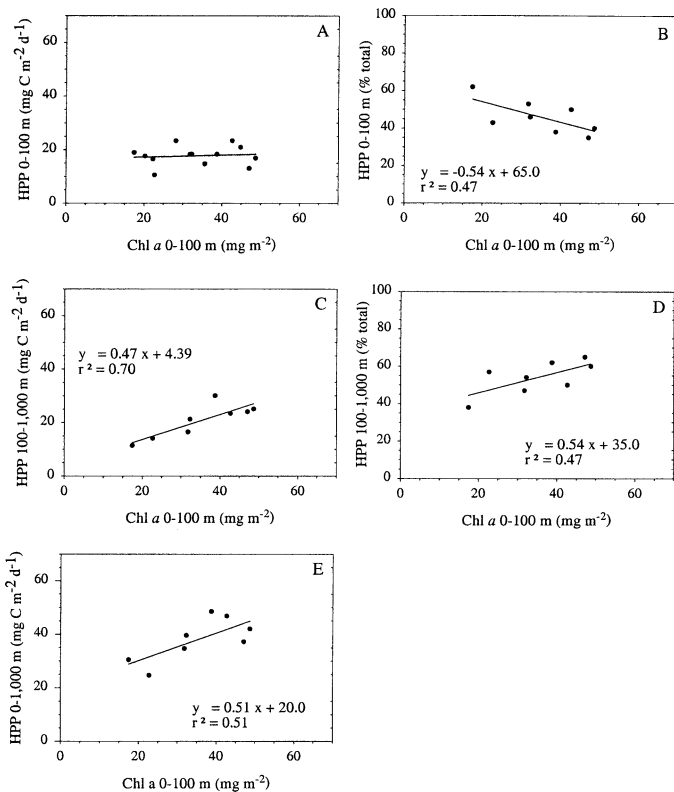


Fig. 7. Linear regression analysis of integrated rates of heterotrophic picoplankton production (HPP), Chl *a*, and primary production in the austral fall 1999 ( $p < 0.01$ ). (A) Chl *a* 0–100 m versus HPP 0–100 m; (B) Chl *a* 0–100 m versus HPP 0–100 m (percentage of total HPP); (C) Chl *a* 0–100 m versus HPP 100–1,000 m; (D) Chl *a* 0–100 m versus HPP 100–1,000 m (percentage of total HPP); (E) Chl *a* 0–100 m versus HPP 0–1,000 m.

as HPP in the mesopelagic zone ( $p < 0.01$ ; Figs. 6E and 7E). Pooling the summer and fall data sets did not yield significant correlations.

HPP as a fraction of PP varied from 4.8% to 7.6% with a mean of  $5.9 \pm 1.0\%$  for rates integrated from 0 to 100 m and from 7.1% to 20.3% with a mean of  $11.9 \pm 5.1\%$  for rates integrated from 0 to 1,000 m (Table 2). More than 75% of PP was attributed to the size fraction  $>20 \mu\text{m}$  (Tremblay et al. 2002).

## Discussion

The regression analysis shows that epipelagic and mesopelagic HPP respond differently to organic matter inputs derived from phytoplankton PP and biomass as measured by Chl *a*. Absolute rates of integrated epipelagic HPP were only positively correlated to PP, but absolute rates and the percentage of integrated mesopelagic HPP were positively correlated to Chl *a* in summer as well as in fall. In line with these results, the percentage of epipelagic HPP was negatively correlated to Chl *a*, which indicates that with increasing phytoplankton standing stock a decreasing fraction was available to epipelagic HPP as substrate source, obviously because an increasing fraction settled out into the mesope-

lagic zone. Formation of macroscopic aggregates from diatoms and fecal pellet production are potentially important processes mediating the downward transport of POC (Simon et al. 2002). Fecal pellet production may have been important during the summer cruise because grazing of mesozooplankton removed major proportions of PP (Dubischar et al. 2002). Formation of diatom aggregates presumably was also important because the mesozooplankton was unable to feed on the large diatoms, which constitute to a great extent the phytoplankton standing stock, and consumed predominantly nanoplankton and detrital material. During the fall cruise, several aggregation events took place, detected by depletion of  $^{234}\text{Th}$  in the epipelagic zone (Rutgers van der Loeff and Westernstroer 2000) and by fluorescence peaks at various depths in the upper mesopelagic zone (V. Strass and U. Bathmann unpubl. data). Therefore, we assume that in summer both fecal pellets and macroscopic aggregates and in fall mainly macroscopic aggregates dominated the sinking flux. We do not assume, however, that aggregation controlled removal of phytoplankton by zooplankton because the ambient mesozooplankton were unable to feed on the large diatoms present, at least not during the summer cruise.

The fact that in the epipelagic zone HPP was positively correlated to PP but not to Chl *a* indicates that the heterotrophic picoplankton rather rapidly reacted to the input of organic matter by PP, presumably in the form of photosynthetic extracellular products. This notion is supported by experimental work of Morán et al. (2001) carried out in the Weddell and Scotia seas, which showed that HPP was positively correlated to the release rate of photosynthetic extracellular products. Hence, release of dissolved organic matter (DOM) by decaying phytoplankton obviously contributes only little to DOM supply of epipelagic heterotrophic picoplankton but much more to that in the mesopelagic zone, presumably also by solubilizing sinking POM and diatoms (Smith et al. 1992; Bidle and Azam 1999). One reason for this delay may be that in the polar frontal region the growth of heterotrophic picoplankton is limited by temperature as shown by the great discrepancy between the ambient (4–5°C) and the optimum growth temperature ( $\geq 18^\circ\text{C}$ ) of the heterotrophic picoplankton (Simon et al. 1999). In aggregation experiments in rolling tanks during the summer cruise we observed that colonization of diatoms by bacteria remained low for up to 7 d and increased only thereafter, leading to heavily colonized algal cells and aggregates (M. Simon unpubl. data). A reduced mineralization rate of epipelagic and mesopelagic POC  $>60 \mu\text{m}$  at the polar front compared to the warmer subantarctic region in the Indian sector of the Southern Ocean was reported recently (Panagiotopoulos et al. 2002). These observations are further indications of a slow growth response of the heterotrophic picoplankton to phytoplankton growth and organic matter release, leading to a shift of the microbial decomposition of phytoplankton-derived organic matter from the epipelagic to the mesopelagic zone and eventually to a higher POC accumulation rate at the polar front (*see below*).

Positive correlations between biomass and production of heterotrophic picoplankton, often just referred to as bacteria, and Chl *a* and PP have been established, even though published data sets mainly include coastal regions and also la-

custrine systems (Bird and Kalff 1984; Cole et al. 1988). These studies indicate that PP, phytoplankton biomass, and its bacterial consumption in surface waters are closely coupled and that ratios of HPP/PP range around 0.20. Open ocean systems, and in particular from subpolar and polar regions, are underrepresented in these analyses, and several observations question whether HPP is related to PP and phytoplankton biomass in these systems in the same way as described (Billen and Becquevort 1991; Bird and Karl 1999; Pomeroy and Wiebe 2001). Ratios of HPP/PP in the subarctic Pacific and the Southern Ocean were reported to be  $<0.15$  and thus lower than in temperate regions (Kirchman et al. 1993; Lochte et al. 1997; Ducklow 1999; Ducklow et al. 2001; Pedros-Alió et al. 2002). In most of these analyses, only the epipelagic or euphotic zone was considered. Our results indicate that with increasing phytoplankton standing stock an increasing amount of the phytoplankton-derived organic matter escapes bacterial consumption in the surface layer by downward transport, thus resulting in a vertical and temporal shift of the microbial decomposition of organic matter from the epipelagic to the mesopelagic zone and, obviously, in a reduction of HPP/PP ratios in the surface layer. The correlation analysis indicates that in summer HPP in the mesopelagic zone increases twofold, and its relative proportion of total HPP increases by 15% when phytoplankton standing stock triples. Accordingly, in fall mesopelagic HPP increases 2.5-fold and its relative proportion by 10% when phytoplankton standing stock doubles. Whether fecal pellets or macroscopic aggregates dominate the sinking flux is not important because both processes can be a function of increasing phytoplankton biomass and just mediate the POC downward transport (*see above*). These processes obviously lead to an uncoupling of the microbial decomposition of phytoplankton biomass in the epipelagic zone at the polar front and link it more closely to mesopelagic HPP. Hence, export production appears to control not only heterotrophic processes in the mesopelagic zone but also consumption of phytoplankton-derived organic matter by heterotrophic picoplankton in surface waters. Whether this shift of microbial decomposition processes from the epipelagic to the mesopelagic zone is a special feature of the polar frontal region with highly silicified diatoms or also occurs in other cold oceanic regions needs to be examined and is important to better understand controlling mechanisms of the sinking flux and its significance for the draw down of atmospheric  $\text{CO}_2$ .

The general significance of mesopelagic HPP for the consumption of sinking POM was established more than a decade ago (Cho and Azam 1988; Simon et al. 1992). Our study shows that in cold environments when epipelagic HPP is limited by temperature, mesopelagic HPP becomes increasingly important, obviously because of enhanced export production. We note that during our study the phytoplankton was dominated by diatoms, partly by heavily silicified species such as *Fragillariopsis kerguelensis*. Therefore, our results should only be taken as representative for diatom-dominated situations such as in upwelling regions. When other phytoplankton dominate in cold systems, e.g., *Phaeocystis* spp., the situation may be different (Sweeney et al. 2000; Becquevort and Smith 2001; Ducklow et al. 2001).

Our data of epipelagic HPP are in the same range as other

published data from various regions in the Southern Ocean, the subarctic Pacific, and oligotrophic oceans, ranging from 3 to  $159 \text{ mg C m}^{-2} \text{ d}^{-1}$  (Kirchman et al. 1993; Lochte et al. 1997; Ducklow 1999; Ducklow et al. 2001; Pedros-Alió et al. 2002) and substantially lower than values from the North Atlantic, Equatorial Pacific, and Arabian Sea ( $257\text{--}285 \text{ mg C m}^{-2} \text{ d}^{-1}$ ; Ducklow 1999). The data of Lochte et al., who used a twofold higher conversion factor to translate leucine incorporation into HPP than we and others used, tend to be higher than ours and the other published data from the Southern Ocean. The ratio of HPP/PP for the epipelagic zone we found is at the lower end of published values of 0.01–0.28 reported from the Southern Ocean, the subarctic Pacific, and the Sargasso Sea (Kirchman et al. 1993; Lochte et al. 1997; Ducklow 1999; Ducklow et al. 2001; Pedros-Alió et al. 2002), which supports the idea that an enhanced fraction of phytoplankton-derived POC sank out of the epipelagic zone.

The mesopelagic HPP we determined is also in the same range as other data from the central and subarctic Pacific,  $22\text{--}39 \text{ mg C m}^{-2} \text{ d}^{-1}$  (Cho and Azam 1988; Simon et al. 1992), but twofold to threefold lower than mesopelagic HPP measured at the end of the growing season in the Greenland Sea (Børsheim 2000). Only 31.5% of total HPP, however, was attributed to the layer 50–500 m in the latter system, which indicates that in this system and season a completely different situation exists compared to the polar frontal zone of the Southern Ocean, with a low supply of organic matter to heterotrophic picoplankton in the mesopelagic zone. Ducklow (1993) reported much higher mesopelagic HPP from the northwestern Indian Ocean in September and October,  $173\text{--}758 \text{ mg C m}^{-2} \text{ d}^{-1}$  (100–2,000 m), which he explained partly by the consumption of accumulated organic matter from phytoplankton summer blooms and partly by other unknown sources. Also, Moriarty et al. (1997) reported elevated rates of HPP from the lower part of the mesopelagic zone in the southwestern Indian Ocean, which they explained by the advection of substrate-rich mode water and Antarctic intermediate water. These reports indicate that it is important to relate mesopelagic HPP to PP, phytoplankton biomass, and the sinking flux to examine whether other substrate sources such as advection may be important in the supply of DOM.

In order to assess the significance of mesopelagic heterotrophic picoplankton for the consumption of PP and the sinking flux, it is also important to include total carbon mineralization, i.e., the growth efficiency. Assuming a growth efficiency of 30%, which appears reasonable for Antarctic waters (Ducklow et al. 2000), mesopelagic heterotrophic picoplankton during the summer cruise consumed  $49\text{--}157$  (mean: 109)  $\text{mg C m}^{-2} \text{ d}^{-1}$ , excluding the highest value (*see above*). These values are in the same range as export production determined from depletion of  $^{234}\text{Th}$  relative to  $^{238}\text{U}$  in the upper 100–200 m,  $105\text{--}136 \text{ mg C m}^{-2} \text{ d}^{-1}$  and equivalent to 12–24% of PP (Rutgers van der Loeff et al. 2002). Mesopelagic consumption of organic matter by picoplankton during the fall cruise ranged from 38 to 158 (mean: 79)  $\text{mg C m}^{-2} \text{ d}^{-1}$ . Preliminary results indicate that export production during this cruise was in the same range as that during the summer cruise (Rutgers van der Loeff and Westernstroer

2000), which implies that a somewhat smaller fraction was consumed by mesopelagic heterotrophic picoplankton. Export production in the polar frontal zone was higher than that estimated in the central Pacific ( $79 \text{ mg C m}^{-2} \text{ d}^{-1}$ ; Cho and Azam 1988) and the subarctic Pacific ( $93\text{--}102 \text{ mg C m}^{-2} \text{ d}^{-1}$ ; Simon et al. 1992). Because mesopelagic HPP in the three systems was rather similar, our data suggest that mesopelagic picoplankton in the polar frontal zone consume a lower fraction of the sinking flux than in the other two systems, if we assume similar growth efficiencies. If these estimates are correct, they reflect that in cold oceanic regions with a high export production an enhanced draw down of atmospheric  $\text{CO}_2$  occurs because mesopelagic heterotrophic picoplankton consume a reduced fraction of the sinking flux. An even more reduced fraction of biogenic silica is mineralized in these systems because mineralization of silica is more limited by temperature than that of carbon (Bidle et al. 2002).

In conclusion, we have shown that in the polar frontal zone of the Southern Ocean with increasing standing stock of phytoplankton dominated by large diatoms an increasing fraction of phytoplankton-derived organic matter is consumed by heterotrophic picoplankton in the mesopelagic zone relative to that in the epipelagic zone. These notions have implications for a better understanding of the controls of the sinking flux and draw down of atmospheric  $\text{CO}_2$  in the polar frontal zone of the Southern Ocean and may point to differences in comparison to other oceanic systems.

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