ISSN 0001-4370, Oceanology, 2008, Vol. 48, No. 3, pp. 364–377. © Pleiades Publishing, Inc., 2008.
Original Russian Text © A.B. Demidov, V.I. Vedernikov, V.I. Gagarin, V.I. Burenkov, 2008, published in Okeanologiya, 2008, Vol. 48, No. 3, pp. 396–410.

MARINE BIOLOGY

Phytoplankton Production Characteristics in the Eastern Atlantic and Atlantic Sector of the Southern Ocean in October–November 2004

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Received January 23, 2007; in final form September 13, 2007

Abstract—Production parameters of surface phytoplankton were measured along three transects: La Manche–Cape Town (I); Cape Town–54°S (II); 0°–49°W (along 54°S) (III). The Canary upwelling waters were most productive along transect I, where the surface chlorophyll *a* (Chl_0) and the surface primary production (PP_0) were as high as 4.3 mg/m^3 and 173 mg C/m^3 per day, respectively. Mosaic patterns in the distribution of these parameters were recorded in the northeastern regions of the South Subtropical Anticyclonic Gyre (Chl_0 = 0.03–0.35 mg/m^3; PP_0 = 1.6–12.6 mg C/m^3 per day). Along transect II, the average twofold southward increase in Chl_0 (from 0.2 to 0.4 mg/m^3) and the concurrent decline of the phytoplankton assimilation activity (AN_0) resulted in deviations from typical latitudinal changes in PP_0. At most sites, PP_0 values varied between 6 and 15 mg C/m^3 per day. Negligible changes in Chl_0 (0.36–0.85 mg/m^3), PP_0 (8–19 mg C/m^3 per day), and AN_0 (0.7–1.6 mg C/mg chl *a* per hour) were registered for the oceanic waters along transect III. Along all the transects, PP_0 depended on Chl_0 to a greater extent than AN_0. The values of the latter parameter were largely determined by the water temperature and showed a slight correlation with the insolation. Along transect II, the integrated primary production (PP_{int}) and the layer-integrated chlorophyll *a* in the upper 200 m ($Chl_{0–200}$) generally varied from 180 to 360 mg C/m^2 per day and from 30 to 70 mg/m^2, respectively. In the Polar Front region, an increase in $Chl_{0–200}$, PP_{int}, Chl_0, and PP_0 up to respective values of 190 mg/m^2, 520 mg C/m^2 per day, 1.2 mg/m^3, and 32 mg C/m^3 per day was observed. A comparison of the water column (0–100 m) stability with the vertical distribution of the primary production and chlorophyll content along transect II implies that the thick (>100 m) upper mixed layer (UML) formed in response to the strong water cooling and wind forcing was largely responsible for the limited primary production in the Subantarctic and Antarctic regions. The large UML thickness resulted in an intense removal of plant cells from the photosynthetic layer and light starvation of a significant (up to 60%) part of the phytoplankton community.

DOI: 10.1134/S0001437008030089

INTRODUCTION

An analysis of the available maps illustrating the distribution of the primary production and chlorophyll (based on satellite data) in the World Ocean [15, 25, 47] and the results of primary production measurements along near-latitudinal profiles across the Atlantic [8, 20] reveals that the productivity in the eastern Atlantic is generally higher as compared with that in its western part. Such a difference is explained both by the confinement of the centers of northern and southern subtropical anticyclonic gyres to the western Atlantic [3, 30] and by the high productivity of the coastal waters near West Africa [24, 47]. Undoubtedly, the primary production level in the eastern Atlantic determines to a large extent the productivity of the entire Atlantic Ocean.

The primary production and chlorophyll contents were measured in the eastern Atlantic mostly in the waters located north of 20°N and in the near-equatorial zone [4, 16, 17, 25, 37, 43, 46, 53]. Variations in these parameters remain poorly studied in both subtropical waters of the Atlantic south of 20°S [4, 6, 12, 25, 44, 45] and in the Subantractic and Antarctic areas of the Southern Ocean. These areas located between Africa and Antarctica are usually attributed to the so-called high nutrient low chlorophyll (HNLC) systems [22, 49], where the primary production is not so high as could be expected from the high concentrations of the main nutrients. Meanwhile, in this region, many authors [27, 28, 35, 54] noted zones of intense phytoplankton development that were characterized by high concentrations of chlorophyll [23, 58] and primary production values [27, 38, 50, 56]. In the Southern Ocean, such zones include coastal waters, fronts between different water masses, and marginal areas near the seasonal boundaries of floating and fast ice.

The content of chlorophyll *a* in the surface layer of the ocean (Chl_0) is one of the parameters that characterize the productivity of the study area and are used in calculation algorithms for estimating primary production based on satellite data. The use of satellite data on

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† Deceased.

the Southern Ocean for such calculations meets, however, significant difficulties. More than 70% of the year [31], the sky in the high latitudes of the Southern Hemisphere is covered by clouds and the ocean surface is unobservable from satellites. Studies in marginal Antarctic seas, near the edge of fast and floating ice, and near the Antarctic barrier are complicated by another problem in addition to the above-mentioned one: the optical parameters may be inaccessible for registering from satellites because of the heavy ice conditions. Of particular interest is the vertical distribution of the phytoplankton production characteristics, the study of which is possible only during field works during marine expeditions. Systematization of vertical chlorophyll profiles is extremely important for the Southern Ocean, where they are characterized by a high diversity [40].

It should be noted that recent maps demonstrating the distribution of primary production in the Atlantic [10, 18, 43, 53] based on satellite-derived data on the chlorophyll concentrations in the surface waters provide only approximate production assessments because of the low accuracy of the calculation algorithms applied [11, 21, 26]. This is true of the productivity assessment for the entire Southern Ocean as well [19, 31]. Undoubtedly, at present, any large-scale measurements of the phytoplankton production characteristics in the Atlantic remain important.

The distribution of the surface phytoplankton production parameters (chlorophyll *a*, primary production, and assimilation number) was studied in different biogeochemical provinces located in the eastern Atlantic between La Manche and Cape Town (transect I), Cape Town and 54°S (transect II), and along 54°S between 0° and 49°W (transect III) during cruise 19 of R/V *Akademik Sergey Vavilov* (Figs. 1, 2). These works were accompanied by the assessment of integrated (for the water column) values of the phytoplankton production characteristics and by studies of the vertical distribution of the primary production and chlorophyll in different water masses. This paper is dedicated to an analysis of these data.

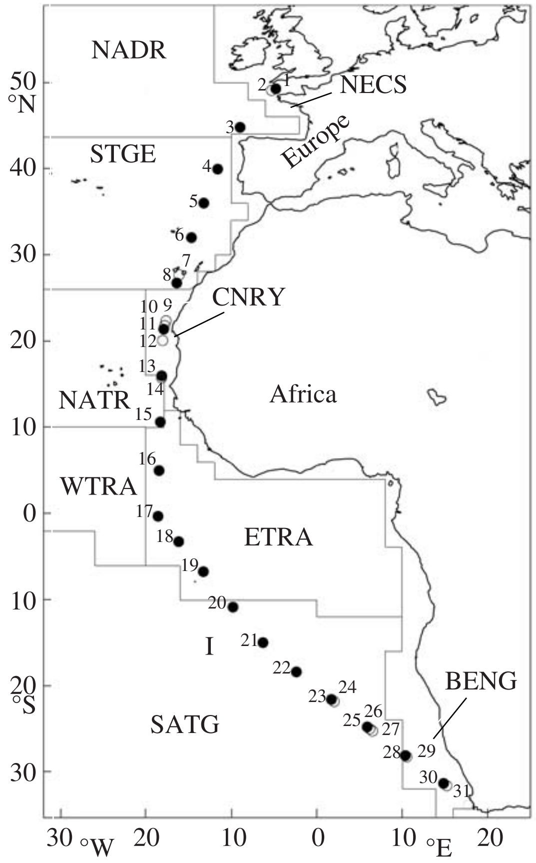

Fig. 1. Location of sampling sites for determining the productional characteristics of the surface phytoplankton along transect I. The solid circles designate the stations where the production and chlorophyll were measured; the open circles correspond to the stations where only chlorophyll was determined. Biogeochemical provinces: NESC—Northeast Atlantic Continental Shelf, NADR—North Atlantic Drift, STGE—eastern half of the Eastern Subtropical Gyre, CNRY—Canary Current Coastal, NATR—North Atlantic Tropical Gyre, WTRA—Western Tropical Atlantic, ETRA—Eastern Tropical Atlantic, SATG—South Atlantic Subtropical Gyre, BENG—Benguela Current Coastal.

MATERIALS AND METHODS

During the period from October 16 to December 2 of 2004, various phytoplankton production characteristics were estimated at stations located between 50°N and 55°S in 11 biogeochemical provinces (NESC, NADR, STGE, CNRY, NATR, ETRA, SATG, BENG, SSTC, SANT, and ANTA) (Figs. 1, 2). These provinces defined in the Atlantic for the assessment of the annual primary production values based on satellite data are used when discussing phytoplankton production parameters measured during field works [44, 45].

For estimating the chlorophyll *a* concentrations, water samples were taken at 16 stations along transect II using a Sea Bird CTD probe with a Rosette bathometric complex from seven–nine layers in the upper 200 m. Surface water samples at these stations were taken using a plastic bucket simultaneously with the bathometer closure at 10 m. At several stations and on the run of the ship (transects I and III), only surface water samples were obtained in the same manner.

The spectral photometric method was used for measuring the chlorophyll *a* concentrations. Samples 5–11 l in volume were filtered through Vladipore membrane filters 70 mm in diameter with a mesh size of 0.45 μm. Several days after filtering, the filters were extracted using a 90% solution of acetone two times during an hour. Transmissions of the extracts obtained at different wavelengths were measured in cuvettes with a working length of 2 cm using an SF-46 spectrophotometer. The chlorophyll *a* contents in the samples were calculated using the equation used for mixed phytoplankton [41].

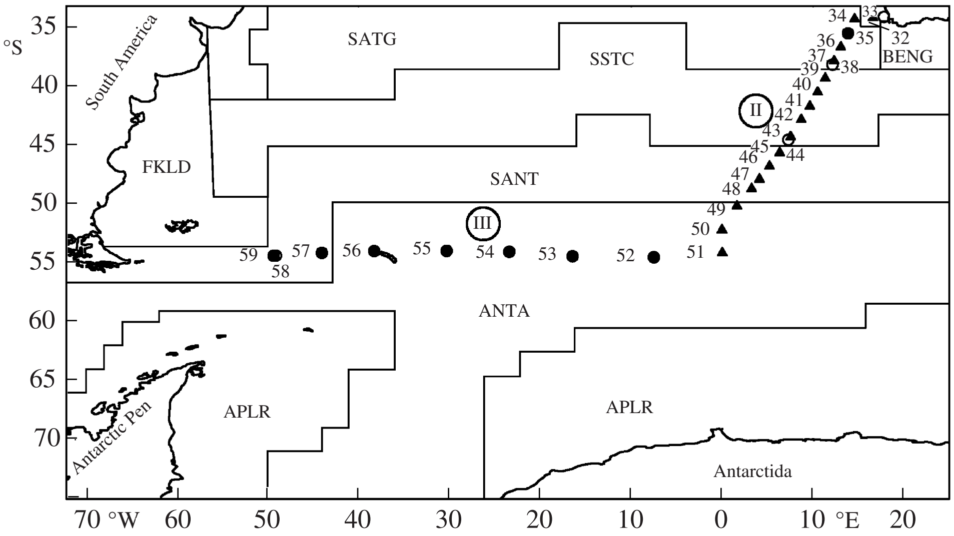

Fig. 2. Location of sampling sites for determining the productional characteristics of the surface phytoplankton along transects II and III. The solid circles designate the stations where the surface production and chlorophyll were measured, the open circles correspond to the stations where only the surface chlorophyll was determined, and the triangles mark the vertical profiles of the production and chlorophyll. Biogeochemical provinces: SATG—South Atlantic Subtropical Gyre, BENG—Benguela Current Coastal, SSTC—South Subtropical Convergence, FKLD—Southwest Atlantic Continental Shelf, SANT—Subantarctic, ANTA—Antarctic, APLR—Austral Polar.

The same surface samples that were collected for determining the chlorophyll *a* contents were used for measuring the primary production in the surface layer. The latter was estimated using the radiocarbon modification of the light-and-dark-bottle technique. After addition of carbon-labeled soda, bottles 275 ml in volume were exposed during the second half of the daylight (from the midday to sundown) in a deck incubator with frequently replaced seawater. At the end of the experiment, the contents of the bottles were filtered under vacuum through Vladipore membrane filters with a mesh size of 0.45 μm. The activity of the filters was determined with an RKS-08P oscillation radiometer. The production in the surface layer was calculated using the standard formula; the total carbon content in all the forms of carbonic acid was accepted to be 25000 mg C/m^3 [9].

For determining the production in the water column along transect II, a slightly modified method of imitated light conditions [52] was applied. Eight neutral light filters with a transmission of the photosynthetically active radiation (PAR) ranging from 0.41 to 74.2% were used for such measurements. Determinations of the primary production and chlorophyll in the surface layer and the vertical profiles of this pigment and subsurface irradiance, as well as the photosynthesis light curves determined for the surface phytoplankton at each station, were taken into account in the calculations. These calculations provided the curves of the vertical distribution of the assimilation number (*AN*) values, which served for determining the lower boundary of the layer of photosynthesis (H_f).

The relative content (%) of chlorophyll below H_f (ΔChl) was calculated as the ratio between the chlorophyll value below the layer of photosynthesis and its integrated value in the layer of 0–200 m (Chl_{0-200}). The difference between the conditional water densities ($\Delta\sigma_t$) at depths of 100 and 0 m was used as a simplified indicator of the water column stability (σ_t). The lower boundary of the upper mixed layer was determined by the waters with σ_t values exceeding by 0.01 kg/m^3 the water densities at the surface [29].

The reference photometer, which measured in absolute units the surface irradiance at a wavelength of 554 nm, was used for continuous PAR measurements during the sample exposure period. For conversion of these absolute units of the surface irradiance into PAR values, spectral measurements of the surface radiance performed by a floating spectroradiometer [1] in the range of 400–700 nm were used. These values integrated over the spectrum were used for determining the PAR values, which were then correlated with the values of the irradiance at a wavelength of 554 nm. Corresponding comparisons were performed at several stations under different weather conditions (from cloudless to entirely cloudy). Especially for estimating the influence of the sun's height, simultaneous measurements by two devices were conducted during the whole daylight. A statistical analysis of the results obtained revealed that the PAR values were correlated with the values of the irradiance at a wavelength of 554 nm and may be derived with a sufficiently high confidence degree from continuous measurements by the reference photometer.

Table 1. Production characteristics of phytoplankton in the surface layer, the water temperature at the surface, and the solar radiation in different biogeochemical provinces of the Atlantic Ocean along transect I (La Manche–Cape Town) during cruise 19 of R/V "Akademik Sergey Vavilov" (October–November of 2004)

Province*		NECS	NADR	STGE	CNRY	NATR	ETRA	SATG	BENG
Date		16.10	17.10	18–21.10	22.10	23–24.10	25–28.10	29.10–2.11 10–13.11	3–4.11 9.11
Parameter**	PP_0	9.81	14.36	5.11 ± 1.13 (4)	172.80	12.35 ± 0.20 (2)	14.30 ± 4.73 (4)	8.49 ± 4.67 (8)	11.83 ± 4.88 (3)
	Chl_0	0.36 ± 0.02 (2)	0.51	0.12 ± 0.03 (5)	2.53 ± 1.76 (4)	0.14 ± 0.004 (3)	0.19 ± 0.06 (4)	0.20 ± 0.09 (13)	0.33 ± 0.21 (5)
	AN_0	2.46	2.63	3.52 ± 0.49 (4)	3.51	7.65 ± 0.06 (2)	6.28 ± 1.48 (4)	3.57 ± 0.82 (8)	4.68 ± 2.33 (3)
	T	13.7 ± 0.4 (2)	16.7	22.4 ± 2.1 (5)	21.3 ± 1.0 (4)	29.0 ± 0.4 (3)	26.0 ± 1.7 (4)	18.9 ± 2.3 (13)	18.7 ± 1.2 (5)
	E	2654	799	2588 ± 886 (4)	3315	4533 ± 240 (2)	4665 ± 848 (4)	4976 ± 1140 (8)	4961 ± 1143 (3)

Notes: * Boundaries of biogeochemical provinces and their full names are in Figs. 1 and 2.

** Average arithmetic value and root mean square deviations are presented; the numerals in brackets are the numbers of measurements. Parameters: PP_0—primary production in the surface layer, mg C/m^3 per day; Chl_0—concentration of chlorophyll *a* in the surface layer, mg/m^3; AN_0—assimilation number of the surface phytoplankton, mg C/mg chl *a* per hour; T—temperature of the surface layer, °C; E—phothosynthetically active radiation (PAR) during the sample exposition (half of the daylight time), kJ/m^2.

The subsurface irradiance in the PAR range was measured using the measuring instrument at selected levels during one–two minutes in the rapid sounding regime. Based on these measurements, the values of the decrease in the vertical PAR (α) and the share of this radiation that reached different depths were calculated. At several stations where direct (instrumental) measurements of the subsurface irradiance were impossible because of the stormy conditions, it was calculated using the empirical dependence of the positions of the light depths with 0.1, 1.0, and 10% of the subsurface irradiance (E_0) on the relative transparency measured by a Secchi disk or on the chlorophyll content in the upper layers of the euphotic zone.

RESULTS

Seven biogeochemical provinces (STGE, CNRY, ETRA, SATG, SSTC, SANT, and ANTA) occupied by different water masses [3, 43, 53] were the main study areas of the surface layer. The northernmost of them (STGE) is located in the eastern segment of the Northern Subtropical Anticyclonic Gyre. The CNRY province corresponds to the Canary upwelling, which is crossed by the coastal branch of the cold Canary Current. The boundaries of the ETRA province pass along 4°N, 20°W, and the southern subtropical hydrological front in the north, west, and south, respectively. This province corresponds to the hydrologically active area with northern and southern tropical anticyclonic gires. The SATG province is mostly occupied by the waters of the Southern Subtropical Anticyclonic Gyre. The latter is the largest gyre in the South Atlantic, where it is formed by the Benguela, Brazil, and Circum-Antarctic currents at its northeastern, western, and southern peripheries, respectively. The SSTC province involves several hydrological fronts and represents a spacious transitional zone between the Subtropical and Subantarctic water masses. The SANT province corresponds to the water mass bordered in the south by the Antarctic Convergence (AC) zone. The areas located south of the latter are occupied by the ANTA province with the Antarctic Water Mass, the southern boundary of which coincides with that of the Antarctic Circumpolar Current. It should be noted that the boundaries between the SANT and ANTA provinces are defined by the average long-term AC position (Fig. 2) shown in the *Atlas of Antarctica* [2]. Its position appeared to be several degrees north of that in [43].

The primary production (PP_0) was also measured, in addition to the chlorophyll content (Chl_0), to characterize the productivity of the surface layer. As compared with the latter parameter, the PP_0 value is rarely used for the productivity assessment under the field conditions because of the methodical difficulties. The average Chl_0 values determined for different biogeochemical provinces along transect I varied from 0.12 (STGE) to 2.53 (CNRY) mg/m^3 (Table 1). Its lower values Chl_0 (0.03–0.06 mg/m^3) were registered in the eastern areas of the Southern Subtropical Anticyclonic Gyre (SATG) at 11 and 22°S. In contrast to the satellite-based maps of the chlorophyll distribution during the autumn season [32], the SATG province was actually characterized by greater patchiness in the distribution of both the Chl_0

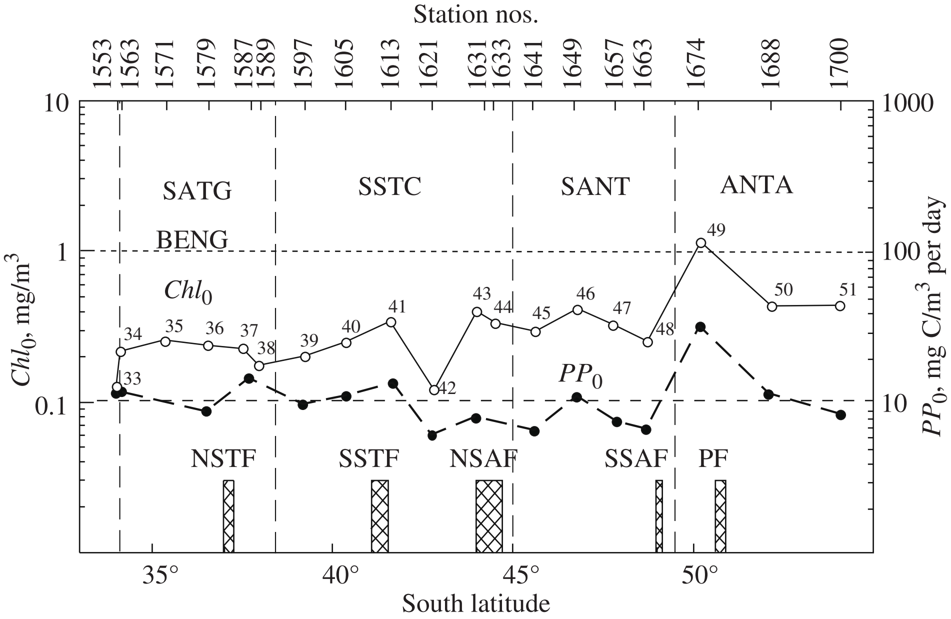

Fig. 3. Distribution of the primary production (PP_0) and the content of chlorophyll *a* in the surface layer along transect II. The numerals near the open circles designate the sampling sites shown in Fig. 2. The horizontal dashed lines show the between oligotrophic and mesotrophic waters (Chl_0 = 0.10 mg/m^3) and between mesotrophic and eutrophic waters (Chl_0 = 1.0 mg/m^3) [15, 18]. NSTF—Northern Subtropical Front; SSTF—Southern Subtropical Front; NSAF—Northern Subantarctic Front; SSAF—Southern Subantarctic Front; PF—Polar Front (Antarctic Convergence). For the literal designations of the biogeochemical provinces see Fig. 2.

and PP_0 values (from 0.03 to 0.35 mg/m^3 and from 1.6 to 12.6 mg C/m^3 per day, respectively). It should also be noted that the average Chl_0 values calculated for different biogeochemical provinces using the field measurements during the summer–autumn period [37] appeared to be close to our values of this parameter measured for the CNRY, NATR, ETRA, and SATG provinces (Table 1). Along the transect of La Manche–Cape Town, the assimilation number values (AN_0) for the surface samples (as the most popular indicator of the photosynthetic phytoplankton activity) calculated as the ratio between the hourly productivity and the chlorophyll *a* content in the samples ranged from 2.34 to 7.92 mg C/mg chl *a* per hour.

At most stations located along transect II, the Chl_0 and PP_0 values ranged from 0.2 to 0.4 mg/m^3 and from 6 to 15 mg C/m^3 per day, respectively. Higher Chl_0 and PP_0 values (1.2 mg/m^3 and 32 mg C/m^3 per day, respectively) were recorded only at station 1674 located in the Polar Front (PF) area (Fig. 3). Along transect III extending from 0° to 49°W (Fig. 2), the respective Chl_0 and PP_0 values varied from 0.36 to 0.85 mg/m^3 and from 8 to 19 mg C/m^3 per day. The Chl_0 and PP_0 values characteristic of eutrophic and transitional mesotrophic–eutrophic waters [5, 18] (3.5 mg/m^3 and 77 mg C/m^3 per day, respectively) [13] were registered only at station 56 in the coastal zone (water depth of 115 m) of South Georgia Island (Fig. 2). It should be noted that the Chl_0 and PP_0 values along 54°S, which were relatively high for this area and season, corresponded to low AN_0 values (0.68–1.64 mg C/mg chl *a* per hour), which is probably explained by the low temperatures in the surface water layer (–0.4 to +5.9°C).

The average integrated primary production value in the water column (PP_{int}), which represents one of the main trophic characteristics of the basin, varied along transect II from 206 mg C/m^2 per day in the Subantarctic (SANT) province to 446 mg C/m^2 per day in the Benguela Current (BENG) zone (Table 2). The higher PP_{int} values noted at stations 1553 and 1587 (446 and 498 mg C/m^2 per day, respectively) demonstrated no positive correlation with the integrated content of chlorophyll in the layer of photosynthesis (Chl_{f}) and were entirely determined by the increased assimilation activity of phytoplankton (AN_{av}). At station 1674, the PP_{int} value of 516 mg C/m^2 per day, the maximal one for transect II, is probably explained by the high Chl_{f} concentration (73 mg/m^2) (Figs. 4, 5).

The phytoplankton biomass (Chl_{f}) and integrated chlorophyll *a* content in the upper 200 m ($Chl_{0–200}$) at most of the stations varied from 23 to 38 mg/m3 and from 29 to 71 mg/m^2, respectively (Fig. 4). Similar Chl_{f} values were found at corresponding latitudes in the southwestern Atlantic [45]. The sharp increase in the contents of Chl_{f} (up to 73 mg/m^3) and $Chl_{0–200}$ (up to 189 mg/m^2) was observed in the Antarctic Convergence area (Fig. 4).

Figures 6 and 7 demonstrate typical curves of the vertical distribution of the primary production (*PP*) and chlorophyll concentration (*Chl*) compiled for different water masses and fronts. The particular features of the curves obtained for stations 1563 (subtropical waters)

Table 2. Production characteristics of phytoplankton and selected associated physical parameters along transect II (Cape Town–54°S) and transect III (along 54°S) in November–December of 2004

Province*		BENG	SATG	SSTC	SANT	ANTA
Date		9.11	10–13.11	14–18.11	19–22.11 1–2.12	23–30.11
Parameter**	PP_0	11.44	11.80 ± 3.06 (3)	9.26 ± 2.43 (5)	9.02 ± 3.83 (5)	13.87 ± 8.99 (7)
	PP_{int}	446	393 ± 93 (3)	270 ± 38 (5)	206 ± 31 (4)	314 ± 179 (3)
	Chl_0	0.13	0.21 ± 0.03 (5)	0.26 ± 0.10 (6)	0.40 ± 0.17 (7)	0.67 ± 0.27 (7)
	Chl_{max}	0.71	0.37 ± 0.06 (3)	0.41 ± 0.07 (5)	0.34 ± 0.06 (4)	0.75 ± 0.57 (3)
	Chl_{av}	0.27	0.27 ± 0.07 (3)	0.28 ± 0.06 (5)	0.28 ± 0.05 (4)	0.61 ± 0.47 (3)
	Chl_f	26.8	26.7 ± 2.1 (3)	29.4 ± 3.3 (5)	31.0 ± 6.5 (4)	44.3 ± 24.6 (3)
	$Chl_{0–200}$	31.5	33.7 ± 5.7 (3)	33.8 ± 3.6 (5)	41.5 ± 3.5 (4)	103.9 ± 74.4 (3)
	AN_0	7.0	3.96 ± 1.09 (3)	2.83 ± 0.82 (5)	1.54 ± 0.22 (5)	1.26 ± 0.41 (7)
	AN_{av}	1.22	1.06 ± 0.17 (3)	0.64 ± 0.04 (5)	0.45 ± 0.06 (4)	0.44 ± 0.06 (3)
	DAN	16.64	14.61 ± 2.58 (3)	19.18 ± 0.61 (5)	6.73 ± 0.94 (4)	7.07 ± 1.02 (3)
	k	211	124 ± 15 (3)	134 ± 53 (5)	103 ± 15 (4)	69 ± 5 (3)
	Q	0.217	0.149 ± 0.027 (5)	0.131 ± 0.036 (5)	0.126 ± 0.020 (4)	0.219 ± 0.157 (3)
	E	4401	5622 ± 600 (3)	4632 ± 1344 (5)	3016 ± 1426 (5)	4184 ± 1088 (8)
	E_0	4115	5256 ± 561 (3)	4331 ± 1257 (5)	2820 ± 1333 (5)	3172 ± 1156 (3)
	ψ	0.438	0.300 ± 0.032 (3)	0.245 ± 0.071 (5)	0.231 ± 0.076 (4)	0.254 ± 0.053 (3)
	H_f	100	102 ± 20 (3)	109 ± 18 (5)	106 ± 14 (4)	81 ± 15 (3)
	H_1	77	61 ± 10 (3)	79 ± 9 (5)	72 ± 5 (4)	62 ± 14 (3)
	$H_{0.1}$	130	113 ± 23 (3)	137 ± 23 (5)	129 ± 10 (4)	101 ± 24 (3)
	T	20.7	17.8 ± 2.7 (5)	10.7 ± 3.0 (6)	4.6 ± 1.6 (7)	1.1 ± 1.1 (8)

Notes: * The boundaries of the biogeochemical provinces and their full names are in Figs. 1 and 2.

** The average arithmetic value and root mean square deviation are presented; the numerals in brackets are the numbers of measurements. Parameters: PP_0 – primary production in the surface layer, mg C/m^3 per day; PP_{int} – primary production in the water column, mg C/m per day; Chl_0, Chl_{max}, and Chl_{av} – concentration of chlorophyll *a* in the surface layer, its maximal content in the water column, and its average content in the layer of photosynthesis, respectively, mg/m^3; Chl_f, $Chl_{0–200}$ – sum content of chlorophyll *a* in the layer of photosynthesis and in the upper 200 m, respectively, mg/m^2; AN_0, AN_{av} – assimilation number of phytoplankton at the surface and its value averaged over the layer of photosynthesis, respectively, mg C/mg chl *a* per hour; DAN – daily assimilation number, mg C/mg chl *a* per day; k – Chl_f/Chl_0 value; Q – efficiency in consumption of solar radiation during photosynthesis, %; E, E_0 – surface and subsurface photosynthetically active radiation (PAR) during the sample exposition (half of the daylight), kJ/m^2; ψ – productivity index, gC/g chl *a*/Einstein; H_f – thickness of the layer of photosynthesis, m; H_1, $H_{0.1}$ – depths with 1 and 0.1% of the subsurface PAR; T – temperature of the surface layer, °C.

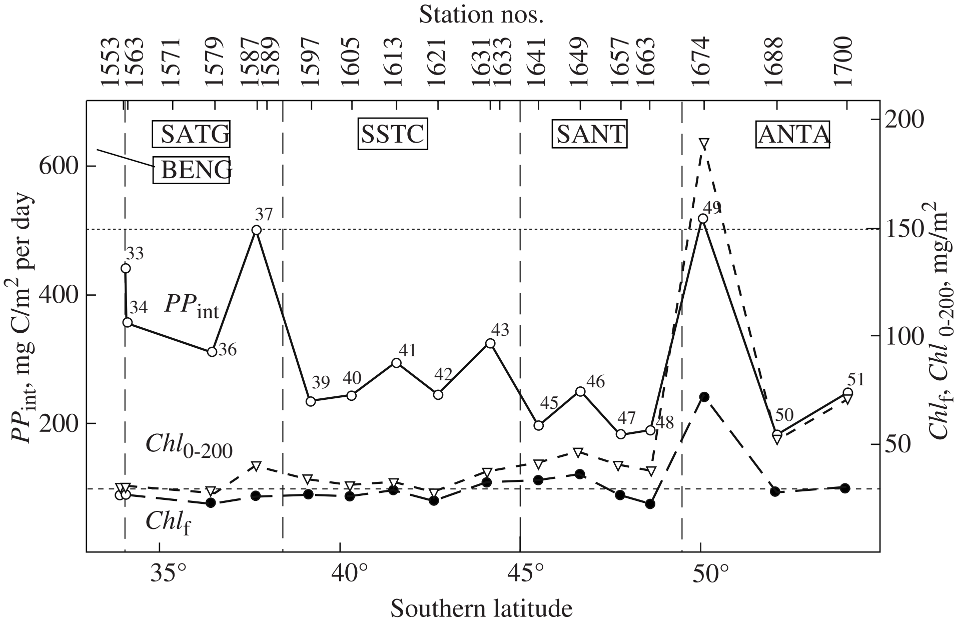

Fig. 4. Distribution of the primary production in the water column (PP_{int}) and the content of chlorophyll *a* in the layer of photosynthesis (Chl_f) and the upper 200 m (Chl_{0-200}) along transect II. The numerals near the open circles are the sampling sites shown in Fig. 2. The horizontal dashed lines show the boundaries between oligotrophic and mesotrophic waters (PP_{int} = 100 mg C/m^2 per day) and between mesotrophic and eutrophic waters (PP_{int} = 500 mg C/m^2 per day) [13]. For the literal designations of the biogeochemical provinces, see Fig. 2.

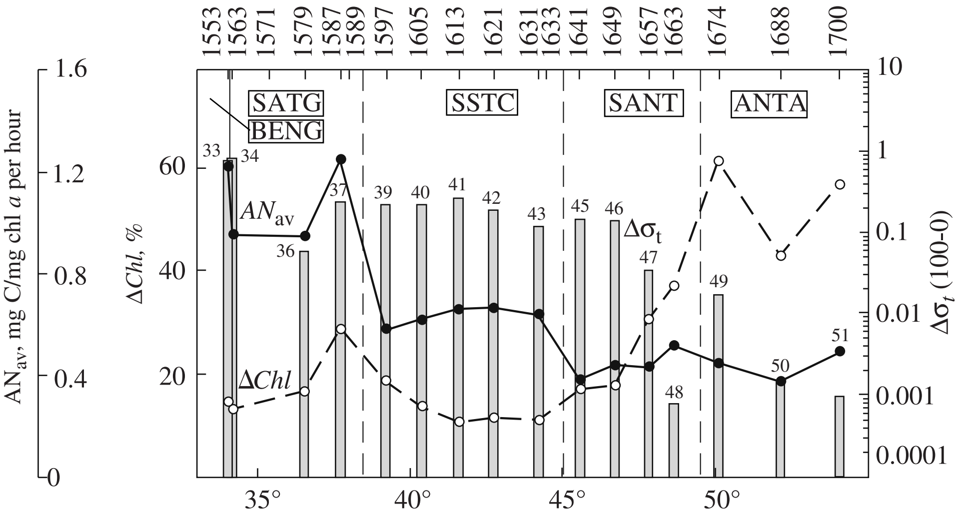

Fig. 5. Distribution of the average assimilation number value in the layer of photosynthesis (AN_{av}), the relative content of chlorophyll below the layer of photosynthesis (ΔChl), and the stability of the water column ($\Delta\sigma_t$ (100–0)) along transect II. The numerals above the columns are the sampling sites shown in Fig. 2. For literal designations of the biogeochemical provinces, see Fig. 2.

and 1605 (Subtropical Convergence) consist in the development of a distinct deep *Chl* maximum in the layer of the seasonal pycnocline in the lower part of the photosynthesis zone. The curves obtained for the Subantarctic waters (station 1641), the AC area (station 1674), and the Antarctic waters (station 1700) are

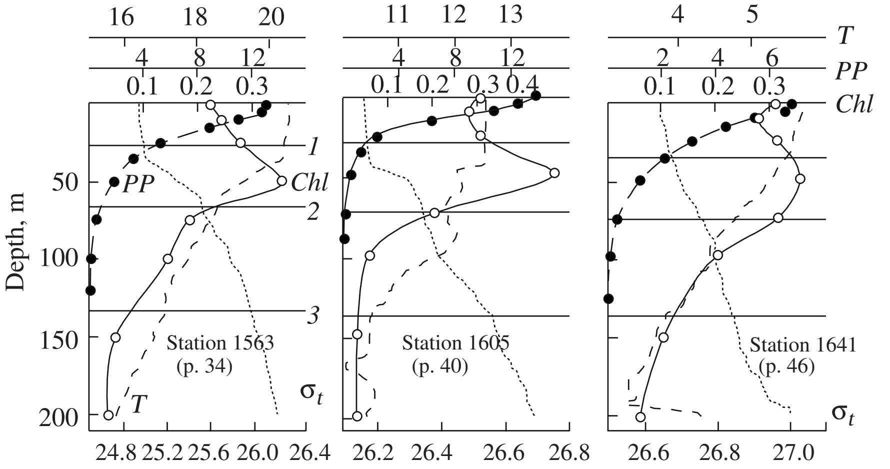

Fig. 6. Vertical distribution of the primary production (*PP*, mg C/m^3 per day), the contents of chlorophyll *a* (*Chl*, mg/m^3), the conditional density (σ_t, kg/m^3), and the temperature (*T*, °*C*) in the subtropical waters (station 1563), the Subtropical Convergence area (station 1605), and Subantarctic waters (station 1641). *1*, *2*, *3*—depths with 10, 1, and 0.1% of the subsurface PAR (E_0), respectively.

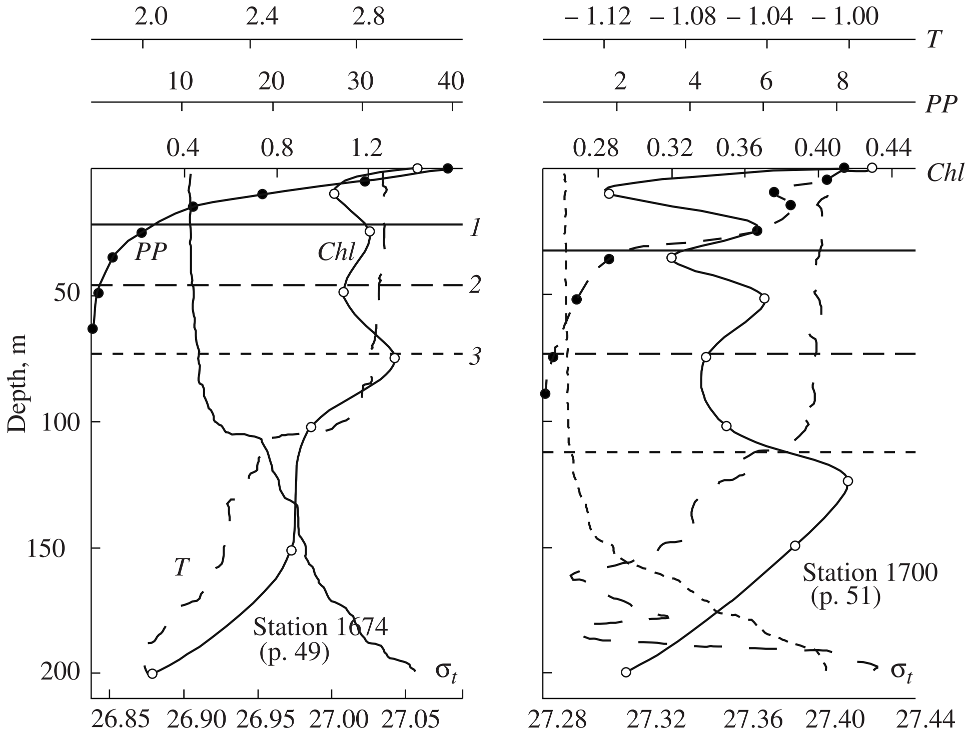

Fig. 7. Vertical distribution of the primary production (*PP*, mg C/m^3 per day), the contents of chlorophyll *a* (*Chl,* mg/m^3), the conditional density (σ_t, kg/m^3), and the temperature (*T*, °*C*) in the Antarctic Convergence area (station 1674) and Antarctic waters (station 1700). *1*, *2*, *3*—depths with 10, 1, and 0.1% of the subsurface PAR (E_0), respectively.

remarkable for the lack of a distinct chlorophyll maximum, which is explained by the low stability of the waters. Worth mentioning are the anomalously high *Chl* values below the layer of photosynthesis (H_f) registered in the AC and south of it (Fig. 7). This is particularly true for station 1700, where the *Chl* values at depths of 200 and 10 m appeared to be similar.

DISCUSSION

Table 3 presents average Chl_0 values obtained for different biogeochemical provinces obtained during cruise 19 of R/V *Akademik Sergey Vavilov* compared with the results of previous expeditions. Taking into consideration the annual variations of this parameter

Table 3. Chlorophyll *a* content in the surface layer (Chl_0, mg/m^3) in different biogeochemical provinces of the Atlantic Ocean according to the measurements conducted in the autumn (Northern Hemisphere) and spring (Southern Hemisphere) seasons of 1996–2004

Cruise	Source	Month, year	Province*							
			NECS	NADR	STGE	CNRY	NATR	WTRA	ETRA	SATG
"James Clark Ross" (AMT-3)**	[43]	IX–X 1996	–	0.38	0.06	–	0.18	0.13	–	0.19
Cruise 10 of R/V "Akademik Ioffe"***	Unpublished data	X–XI 2001	$\frac{0.45\text{–}1.19}{0.70\ (5)}$	$\frac{0.31\text{–}0.50}{0.42\ (3)}$	$\frac{0.02\text{–}0.15}{0.06\ (13)}$	–	$\frac{0.03\text{–}0.16}{0.10\ (12)}$	$\frac{0.05\text{–}0.27}{0.13\ (21)}$	–	$\frac{0.03\text{–}0.08}{0.05\ (8)}$
Cruise 11 of R/V "Akademik Ioffe"	[6]	X–XI 2002	0.47	0.25	$\frac{0.07\text{–}0.14}{0.11\ (5)}$	–	$\frac{0.07\text{–}0.42}{0.21\ (4)}$	$\frac{0.14\text{–}0.17}{0.15\ (3)}$	–	$\frac{0.02\text{–}0.23}{0.10\ (13)}$
Cruise 17 of R/V "Akademik Sergey Vavilov"	Unpublished data	X 2003	0.68	$\frac{0.12\text{–}0.89}{0.51\ (2)}$	$\frac{0.03\text{–}0.12}{0.07\ (4)}$	–	$\frac{0.05\text{–}0.17}{0.12\ (4)}$	$\frac{0.05\text{–}0.16}{0.10\ (6)}$	–	$\frac{0.03\text{–}1.44}{0.21\ (25)}$
Cruise 19 of R/V "Akademik Sergey Vavilov"	This study	X–XI 2004	$\frac{0.34\text{–}0.38}{0.36\ (2)}$	0.51	$\frac{0.09\text{–}0.18}{0.12\ (5)}$	$\frac{0.55\text{–}4.31}{2.53\ (4)}$	$\frac{0.13\text{–}0.14}{0.14\ (3)}$	–	$\frac{0.13\text{–}0.25}{0.19\ (4)}$	$\frac{0.03\text{–}0.35}{0.20\ (13)}$

Notes: * The boundaries of the biogeochemical provinces and their full names are in Figs. 1 and 2.

** Average arithmetic value.

*** For cruises 10 and 11 of R/V "Akademik Ioffe" as well as cruises 17 and 19 of R/V "Akademik Sergey Vavilov": the numerator designates variations in the Chl_0 values and the denominator corresponds to the average arithmetic value; the numerals in brackets are the numbers of measurements.

and the insufficient quantity of data, it can be stated that deviations toward lower or higher values are insignificant (Table 3). The more substantial (fourfold) differences between these values and the data obtained for the SATG province during cruise 10 of R/V *Akademik Ioffe* can be explained by the fact that they characterize the poorer western area of the gyre.

An analysis of the data obtained along transect I reveals a very high productivity of the Canary upwelling waters registered during their crossing on October 22, 2004. In the continental slope area (water depth interval of 1000–1800 m), the Chl_0 values varied from 0.55 to 4.31 mg/m^3, while the PP_0 values exceeded 100 mg C/m^3 per day. Such values agree with the satellite and field observations of high productivity in the Canary upwelling area in October–November [47], which indirectly confirms the penetration of productive Canary waters to the central areas of the Atlantic in the autumn season, which was noted during cruise 17 of R/V *Akademik Sergey Vavilov* (October–November of 2003).

A confident positive correlation between these parameters was observed at all the stations of transect I ($N = 20$), where the Chl_0 and PP_0 were simultaneously measured:

$$\ln PP_0 = 3.681 + 0.886\ 1\mathrm{n}\ Chl_0\ (r = +0.909).$$

The high correlation coefficient calculated for this pair and the lack of reliable correlation between the PP_0 values and the assimilation number (AN_0) provide grounds to conclude that the production in the surface layer mainly depended on the chlorophyll concentration rather than on the assimilation activity of the latter. The variations of the AN_0 values in the areas studied were largely determined by the water temperature ($r = +0.869$) and characterized by a low correlation with insolation ($r = +0.411$).

Such a correlation corresponds to ideas on the direct dependence of the AN_0 values on the temperature of the habitat environments of algae and their mineral feeding conditions [14]. Nevertheless, Maranon and Holligan [44] established no reliable correlation of this parameter either with the insolation level or with the water temperature along the Atlantic transect (50°N–50°S) [44]. The authors cited explain its lack by the unfavorable conditions of phytoplankton mineral feeding in the Central Atlantic characterized by the highest water temperatures. In our studies, stations with the maximal water temperatures and AN_0 values were mostly located in neritic waters off West Africa (Fig. 1) with elevated concentrations of the main nutrients. Their sufficient contents in the tropical waters explains the positive correlation between the AN_0 and temperature values.

The Chl_0 values along transect II s (Fig. 3) how a tendency to a southward increase against the background of regular latitudinal PP_0 changes. It is first established for these areas of the South Atlantic and the Southern Ocean that such a discrepancy is determined

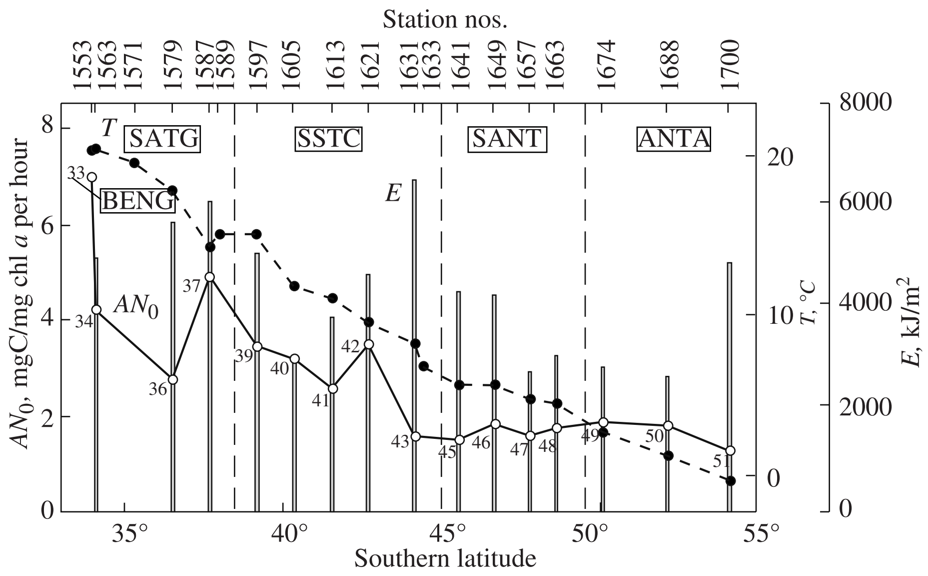

Fig. 8. Distribution of the assimilation number (AN_0) of the surface phytoplankton, the temperature (T) of the surface layer, and the radiation in the PAR range for half of the daylight (E) along transect II. The numerals near the open circles designate the sampling sites shown in Fig. 2. For the literal designations of the biogeochemical provinces, see Fig. 2.

by the southward decrease in the specific phytoplankton photosynthesis rate against the background of a sharp fall of the water temperature (Fig. 8). The southward increase in the Chl_0 values is accompanied by the AN_0 fall, which results in the lack of regular PP_0 changes in the same direction.

In general, the Subtropical, Subantarctic, and Antarctic waters along transect II, as well as more northern areas of the Atlantic, demonstrate a positive correlation between the PP_0 and Chl_0 values:

$$\ln PP_0 = 2.950 + 0.559 \ln Chl_0 \ (r = +0.742).$$

Similar to transect I, no reliable correlation between the PP_0 and AN_0 values was established, which provides grounds to consider the variability in the chlorophyll contents as the main factor responsible for the PP_0 variations in the waters studied. South of Cape Town, as well as in more northern areas, the value of the phytoplankton assimilation activity was mostly determined by the water temperature ($r = +0.869$) and was practically independent ($r = +0.209$) of the insolation (E) (Fig. 8). Thus, it should be concluded that, according to the Chl_0 [5, 18] and PP_0 values [13], practically along the entire cruise route, the waters were mostly mesotrophic (Figs. 1, 2).

Along transect II, the PP_{int} value (516 mg C/m^2 per day) at station 1674 seems to characterize a phytoplankton bloom in the AC area during the period of the studies against the background of increased chlorophyll contents (Fig. 4). It should be noted that the tendency to a southward PP_{int} decrease against the background of almost constant Chl_{f} values (Fig. 4) is determined by the AN_{av} fall (Fig. 5). The increase in both the AN_{av} and AN_0 values was most likely controlled by the water temperature fall in the southern latitudes.

Our measurements of PP_{int} values in the Antarctic Circumpolar Current areas free from ice throughout the year accord well with the data obtained during previous expeditions conducted approximately in the same season (October–November). According to [42], the primary production in the water column in the southern areas of the Antarctic Circumpolar Current averaged 251 mg C/m^2 per day. Other authors [50] report maximal PP_{int} values of 350 mg C/m^2 per day for the areas close to the Greenwich meridian. The same authors registered, however, primary production values in the Polar Front area that were 3–5 times higher as compared to ours. Such discrepancies may be explained both by the annual variability of the production processes and by significant spatial variations in the phytoplankton distribution near the front [51].

The high Chl_{f} and $Chl_{0\text{–}200}$ values (73 and 189 mg/m^2, respectively) obtained during the expedition and the published data on the chlorophyll distribution in the Atlantic sector of the Southern Ocean [23, 50] confirm the above inference on the phytoplankton bloom in the AC area during the spring season. The transport of dissolved Fe by the jets of the Antarctic Circumpolar Current from the Drake Passage, Antarctic Peninsula, and Falkland Plateau areas and its accumulation in the convergence zone near the Polar Front is now believed to be one of factors responsible for such a bloom [22, 34, 49]. Another factor is probably the enhanced density stratification in the anticyclonic eddies of the Polar Front area [55, 57]. The transport of algae into the convergence zone by Antarctic Circumpolar Current jets, their accumulation, and subsidence to greater depths cannot be ruled out as well.

Figure 4 demonstrates the divergence of the Chl_f and Chl_0 curves in the southern Subantarctic and Antarctic areas. This indicates the increased content of phytoplankton below the H_f level, which is determined by the low stability of the water column and the significant (>100 m) thickness of the upper mixed layer (Fig. 7) due to the strong surface water cooling and intense wind forcing. Figure 5 shows that, in the Antarctic (ANTA) province, ΔChl amounts to approximately 60%, which points to the light starvation of a significant part of the phytoplankton community. This fact and the negative correlation between the ΔChl and $\Delta\sigma_t$ values established for the southern Subantarctic and Antarctic areas (Fig. 5) provide grounds for considering the low stability of the water column to be one of the main factors that suppress the development of phytoplankton in these areas of the Southern Ocean.

The low insolation value may be responsible for the reduced primary production in the water column. In this connection, of great interest are the assessments of the solar radiation consumption efficiency in the photosynthesis processes (Q) [14]. The average Q values along the transect studied varied from 0.126 to 0.219% (Table 2) and were close to the upper boundary of the range characteristic of the mesotrophic waters of the World Ocean [13].

Table 2 presents the values of the productivity index (ψ), which is calculated as the ratio between the daily assimilation number (*DAN*) averaged over the layer of photosynthesis and the subsurface irradiance in the PAR range (E_0). This parameter is frequently used in algorithms for PP_{int} calculations based on satellite data [24, 36, 46]. The ψ values averaged over the biogeochemical provinces demonstrated insignificant variations: from 0.23 to 0.44 g C/g chl *a*/Einstein in the Subantactic and Benguela Current areas, respectively. In general, such ψ values are lower as compared with their counterparts (0.56–0.79 g C/g chl *a*/Einstein) previously determined in different areas of the North Atlantic [8] and the Norwegian Sea [7].

The vertical *Chl* distribution is largely determined by the water density, the concentrations of nutrients at different depths, the variability of the physiological characteristics of the algae, and their consumption rates [33, 39]. The formation of a deep chlorophyll maximum in the subtropical waters mainly results from the phytoplankton adaptation to the low illumination against the background of increased concentrations of the main nutrients [33]. In the subtropical waters and Subtropical Convergence area (stations 1563 and 1605, respectively) along transect II, the deep chlorophyll maximum was recorded in the seasonal pycnocline layer or beneath the latter under an irradiance of 1.97–2.30% E_0 (Fig. 6). Similar formation conditions of such a maximum were previously noted in the tropical and subtropical waters of the North and South Atlantic [8, 48]. The vertical profiles and the high *Chl* values below the layer of photosynthesis observed in the Polar Front area and Antarctic zone indicate an intense water downwelling in the study areas. A reorganization in the vertical structure of the phytocoenosis along transect II is evident from changes in the depth position of the layer with the maximal chlorophyll content (Fig. 9). In the

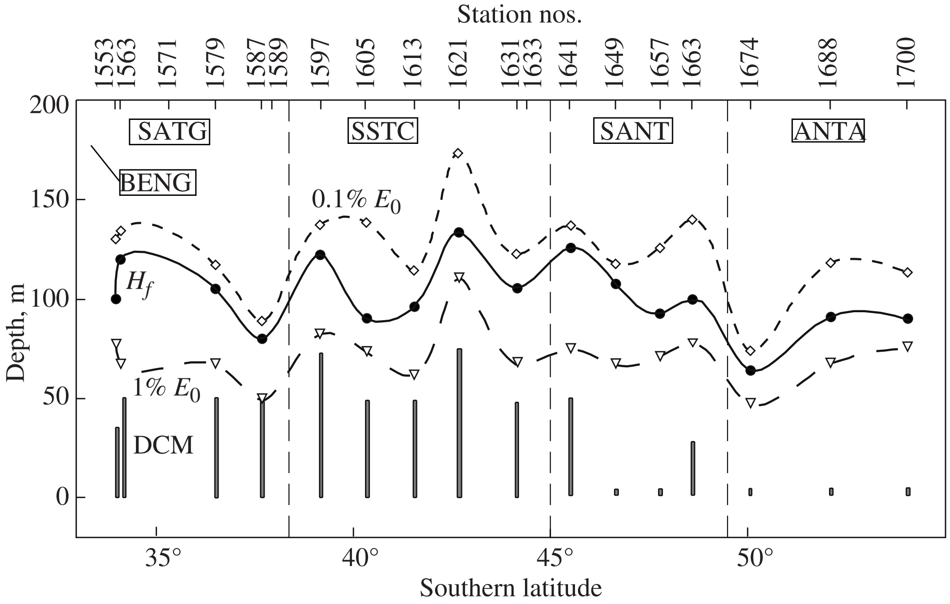

Fig. 9. Lower boundary of the photosynthetic layer (H_f), position of the light depths (1 and 0.1% of E_0), and the layer with the maximal concentration of chlorophyll *a* in the water column (DCM) along transect II. For the literal designations of the biogeochemical provinces, see Fig. 2.

subtropical waters and Subtropical Convergence area, this layer is usually recorded at depths of 50–75 m, while, in the Subantarctic and Antarctic waters, the maximal chlorophyll concentrations were registered in the surface layer.

At most stations located along the transect under consideration, the H_f values varied from 80 to 133 m (Fig. 9), which is typical of mesotrophic waters [11]. The only exception is station 1674 in the AC area, where the H_f value decreased down to 63 m against the background of high chlorophyll concentrations in the layer of photosynthesis. It should be noted that the lower boundary of this layer was usually recorded at an irradiance constituting 0.2–0.4% of the subsurface irradiance in the PAR range (Fig. 9), which is several times as low as compared with its threshold value (1% of E_0) that is usually accepted in the studies dedicated to the assessment of the productivity in the Southern Ocean.

CONCLUSIONS

The data on the primary production and chlorophyll concentration obtained for the Atlantic Ocean and the Atlantic sector of the Southern Ocean in October–December of 2004 make it possible to attribute these regions mainly to mesotrophic domains. Exceptions are the western periphery of the Canary upwelling, the Southern Polar Front, and the coastal waters around South Georgia Island, which should be considered as eutrophic or transitional mesotrophic–eutrophic areas during this season. The relatively small variations in the primary production and chlorophyll content values along the latitudinal transect in the eastern Atlantic are explained by the location of the corresponding stations at the periphery of the main gyres and neritic waters of West Africa.

The variability of the surface phytoplankton primary production was determined by changes in the chlorophyll content rather than by its assimilation activity. The intensity of photosynthesis in the surface layer was largely determined, in turn, by the water temperature being practically independent from the insolation. In the Southern Ocean, the increase in the chlorophyll concentration in the surface layer along the latitudinal transect occurred against the background of a reduced assimilation activity of phytoplankton, which resulted in the lack of regular changes in the primary production at the surface in the same direction.

The low stability of the water column represents one of the main factors responsible for the suppressed development of phytoplankton in the Subantarctic and Antarctic zones. The growth in the production parameters at the Polar Front near the Greenwich meridian in November points to a phytoplankton bloom in this region during the spring season in the Southern Hemisphere.

REFERENCES

1. V. A. Artem’ev, V. I. Burenkov, M. I. Vortman, *et al.*, “Sea-Truth Measurements of the Ocean Color: New Floating Spectroradiometert and Its Metrology,” Okeanologiya **40** (1), 148–155 (2000) [Oceanology **40** (1), 139–145 (2000)].
2. *Atlas of the Antarctic. Vol. 1* (GUGK, Moscow, 1966) [in Russian].
3. R. P. Bulatov, M. S. Barash, V. N. Ivanenkov, and Yu. Yu. Marti, *Atlantic Ocean* (Mysl’, Moscow, 1977) [in Russian].
4. M. A. Burkal’tseva, A. I. Bondarenko, N. V. Mordasova, *et al.*, *Ox, Chlorophyll, and Amino Acids as Indicators of the Winter Productivity* (Nauka, Moscow, 1986) [in Russian].
5. V. I. Vedernikov, “Dependence of the Assimilation Number and Chlorophyll *a* Concentration on the Water Productivity in Different Temperature Areas on the World Ocean,” Okeanologiya **15** (4), 703–707 (1975).
6. V. I. Vedernikov, V. I. Gagarin, A. B. Demidov, *et al.*, “Primary Production and Chlorophyll Distribution in the Subtropical and Tropical Waters of the Atlantic Ocean in the Autumn of 2002,” Okeanologiya **47** (3), 418–431 (2007) [Oceanology **47**, (3), 386–399 (2007)].
7. V. I. Vedernikov and A. B. Demidov, “Primary Production and Chlorophyll Distribution in the Northeastern Region of the Norwegian Sea in July 1995,” Okeanologiya **37** (2), 250–256 (1997) [Oceanology **37** (2), 227–232 (1997)].
8. V. I. Vedernikov and A. B. Demidov, “Primary Production and Chlorophyll in the North Atlantic in September–October 1991,” Okeanologiya **39** (6), 876–886 (1999) [Oceanology **39** (6), 796–805 (1999)].
9. G. G. Vinberg, Yu. G. Kabanova, O. I. Koblents-Mishke, *et al.*, *Methodical Manual of the Determinations of the Primary Production of Organic Matter in Basins Using Radiocarbon Techniques* (Bel. gos. un-t, Minsk, 1960) [in Russian].
10. M. E. Vinogradov, E. A. Shushkina, O. V. Kopelevich, and S. V. Sheberstov, “Photosynthetic Productivity of the World Ocean from Satellite and Expeditionary Data,” Okeanologiya **36** (4), 566–575 (1996) [Oceanology **36** (4), 531–540 (1996)].
11. M. E. Vinogradov, E. A. Shushkina, N. P. Nezlin, *et al.*, “Correlation between Different Parameters of the Ecosystem of the Epipelagic Zone of the World Ocean,” Okeanologiya **39** (1), 64–74 (1999) [Oceanology **39** (1), 54–63 (1999)].
12. Yu. G. Kabanova, V. I. Vedernikov, B. V. Konovalov, and L. N. Andreeva, “Primary Production and Chlorophyll *a*,” Tr. Inst. Okeanol. Akad. Nauk SSSR **98**, 9–29 (1974).
13. O. I. Koblents-Mishke, “Primary Production,” in *Biology of the Pacific Ocean. Vol. 1. Plankton* (Nauka, Moscow, 1967), pp. 86–97 [in Russian].
14. O. I. Koblents-Mishke and V. I. Vedernikov, “Primary Production,” in *Oceanology. Biology of the Ocean. Vol. 2. Biological Productivity of the Ocean* (Nauka, Moscow, 1977), pp. 183–209 [in Russian].
15. O. I. Koblents-Mishke, V. V. Volkovinskii, and Yu. G. Kabanova, “New Data on the Value of the Primary Production of the World Ocean,” Dokl. Akad. Nauk SSSR **183** (5), 1189–1192 (1968).

16. L. V. Stel'makh and R. A. Lobanova, "Phyto- and Bacterioplankton (Distribution of Chlorophyll *a*, Primary, and Bacterial Production)," in *Productivity of the Equatorial Atlantic* (Naukova dumka, Kiev, 1990), pp. 56–76 [in Russian].
17. Z. Z. Finenko and T. M. Kondrat'eva, "Production of Organic Matter in the Tropical Part of the Atlantic Ocean," in *Plankton and Biological Productivity of the Tropical Atlantic* (Naukova dumka, Kiev, 1971), pp. 122–162 [in Russian].
18. D. Antoine, J.-M. André, and A. Morel, "Oceanic Primary Production. 2. Estimation at Global Scale from Satellite (Coastal Zone Color Scanner) Chlorophyll," Global Biogeochem. Cycles **10** (1), 57–69 (1996).
19. K. R. Arrigo, D. Worthen, A. Schnell, *et al.*, "Primary Production in the Southern Ocean," J. Geophys. Res. **103** (C8), 15587–15600 (1998).
20. N. Bahamón, Z. Velásquez, and A. Cruzado, "Chlorophyll *a* and Nitrogen Flux in the Tropical North Atlantic Ocean," Deep-Sea Res. **50**, 1189–1203 (2003).
21. W. Balch, R. Evans, J. Brown, *et al.*, "The Remote Sensing of Ocean Primary Productivity: Use of New Data Compilation to Test Satellite Algorithms," J. Geophys. Res. **97** (C2), 2279–2293 (1992).
22. K. Banse, "Low Seasonality of Low Concentrations of Surface Chlorophyll in the Subantarctic Water Ring: Underwater Irradiance, Iron, or Grazing?" Progress in Oceanogr. **37** (3–4), 241–291 (1996).
23. U. V. Bachmann, R. Scharek, C. Klaas *et al.*, "Spring Development of Phytoplankton Biomass and Composition in Major Water Masses of the Atlantic Sector of the Southern Ocean," Deep-Sea Res. II **44** (1-2), 51–67 (1997).
24. M. J. Behrenfeld and P. G. Falkowski, "A Consumer's Guide to Phytoplankton Primary Productivity Models," Limnol. Oceanogr. **42** (7), 1479–1491 (1997).
25. W. H. Berger, "Global Maps of Ocean Productivity," in *Productivity of the Ocean: Present and Past* (John Wiley and Sons, New York, 1989), pp. 429–455.
26. B. Berthelot and P.-Y. Deschamps, "Evaluation of Bio-Optical Algorithms to Remotely Sense Marine Primary Production from Space," J. Geophys. Res. **99** (C4), 7979–7989 (1994).
27. A. U. Bracher, "Photoacclimation of Phytoplankton in Different Biogeochemical Provinces of the Southern Ocean and Its Significance for Estimating Primary Production," Ber. Polarforsch, No. 341, 1–88 (1999).
28. A. U. Bracher and M. M. Tilzer, "Underwater Light Field and Phytoplankton Absorbance in Different Surface Water Masses of the Atlantic Sector of the Southern Ocean," Polar Biology **24** (9) 687–696 (2001).
29. K. E. Brainerd and M. C. Gregg, "Surface Mixed and Mixing Layer Depths," Deep-Sea Res. I **42** (9), 1521–1543 (1995).
30. L. R. A. Capurro, "On the Mixing of Water Masses" in *Fertility of the Sea, Vol. 1* (Gordon and Breach Science Publishers, New York, 1971), pp. 71–87.
31. J. C. Comiso, C.R. Mc. Clain, C. W. Sullivan, *et al.*, "Coastal Zone Color Scanner Pigment Concentration in the Southern Ocean and Relationships to Geophysical Surface Features," J. Geophys. Res. **98**, 2419–2451 (1993).
32. M. E. Conkright, I. D. O'Brien, C. Stephens, *et al.*, *World Ocean Atlas 2001. Vol. 6: Chlorophyll*, Ed. by S. Levitus (U.S. Government Printing Office, Washington, 2002).
33. J. J. Cullen, "The Deep Chlorophyll Maximum: Comparing Vertical Profiles of Chlorophyll "a"," Canadian Journal of Fisheries and Aquatic Sciences **39** (5), 791–803 (1982).
34. H. J. W. de Baar, J. T. M. de Jong, D. C. E. Bakker, *et al.*, "Importance of Iron for Plankton Blooms and Carbon Dioxide Drawdown in the Southern Ocean," Nature, No. 373, 412–415 (1995).
35. A. E. Detmer and U. V. Bathmann, "Distribution Patterns of Autotrophic Pico- and Nanoplankton and Their Relative Contribution to algal Biomass during Spring in the Atlantic Sector of the Southern Ocean," Deep-Sea Res. II **44** (1–2) 299–320 (1997).
36. R. C. Dugdale, A. Morel, A. Bricaud, and F. P. Wilkerson, "Modeling New Production in Upwelling Centres: A Case Study of Modeling New Production from Remotely Sensed Temperature and Color," J. Geophys. Res. **94** (C12), 18119–18132 (1989).
37. Z. Z. Finenko, S. A. Piontkovski, R. Williams, and A. V. Mishonov, "Variability of Phytoplankton and Mesozooplankton Biomass in the Subtropical and Tropical Atlantic Ocean," Mar. Ecol. Progr. Ser. **250**, 125–144 (2003).
38. R. W. Froneman, E. A. Pakhomov, and M. G. Balarin, "Size-Fractionated Phytoplankton Biomass, Production and Biogenic Carbon Flux in the Eastern Atlantic Sector of the Southern Ocean in the Late Austral Summer," Deep-Sea Res. II **51** (22–24) 2715–2729 (2004).
39. W. G. Harrison, "Nitrogen Utilization in Chlorophyll and Primary Productivity Maximum Layers: An Analysis Based on f-Ratio," Mar. Ecol. Progr. Ser. **60**, 85– 90 (1990).
40. O. Holm-Hansen and C. D. Hewes, "Deep Chlorophyll *a* Maxima (DCMs) in Antarctic Waters. I. Relationship between DSMs and the Physical, Chemical, and Optical Conditions in the Upper Water Column," Polar Biology **27** (11) 699–710 (2004).
41. S. W. Jeffrey and G. F. Humphrey, "New Spectrophotometric Equations for Determing Chlorophylls a, b, c_1, and c_2 in Higher Plants, Algae, and Natural Phytoplankton," Biochem. Physiol. Pflanzen **167** (2), 191–194 (1975).
42. F. J. Jochem, S. Mathot, and B. Quéguiner, "Size-Fractionated Primary Production in the Open Southern Ocean in Austral Spring," Polar Biology **15**, 381–392 (1995).
43. A. Longhurst, S. Sathyendranath, T. Platt, and C. Caverhill, "An Estimate of Global Primary Production in the Ocean from Satellite Radiometer Data," J. Plankton Res. **17** (6), 1245–1271 (1995).
44. E. Marañón and P. M. Holligan, "Photosynthetic Parameters of Phytoplankton from 50°N to 50°S in the Atlantic Ocean," Mar. Ecol. Prog. Ser. **176**, 191–203 (1999).
45. E. Marañón, P. M. Holligan, M. Varela, *et al.*, "Basin-Scale Variability of Phytoplankton Biomass, Production, and Growth in the Atlantic Ocean," Deep-Sea Res. I **47** (5), 825–857 (2000).
46. A. Morel and J.-F. Berthon, "Surface Pigments, Algal Biomass Profiles, and Potential Production of the

Euphotic Layer: Relationships Reinvestigated in View of Remote-Sensing Applications," Limnol. Oceanogr. **34** (1), 1545–1562 (1989).

47. NASA, *Ocean color from space*, (CZCS images prepared by G.C. Feldman with text by J.A. Yoder, M.R. Lewis and P.A. Blanchard by NSF/NASA Woods Hole Oceanogr. Inst. with contributions from the Goddard Space Flight Center., Univ. of Miami, and the Univ. of Rhode Isl.), (Woods Hole, 1989).
48. V. Pérez, E. Fernández, E. Marañón *et al.*, "Vertical Distribution of Phytoplankton Biomass, Production, and Growth in the Atlantic Subtropical Gyres," Deep-Sea Res. I **53** (10), 1616–1634 (2006).
49. P. Pondaven, Ruiz-Pino., J. N. Druon, *et al.*, "Factors Controlling Silicon and Nitrogen Biogeochemical Cycles in High Nutrient, Low Chlorophyll Systems (the Southern Ocean and the North Pacific): Comparison with a Mesotrophic System (the North Atlantic)," Deep-Sea Res. I **46** (11), 1923–1968 (1999).
50. B. Quéguiner, P. Treguer, I. Peeken, and R. Scharek, "Biogeochemical Dynamics and the Silicon Cycle in the Atlantic Sector of the Southern Ocean During Austral Spring 1992," Deep-Sea Res. II **44** (1–2), 69–89 (1997).
51. J. F. Read, R. T. Pollard, and U. Bathmann, "Physical and Biological Patchiness of an Upper Ocean Transect from South Africa to the Ice Edge Near the Greenwich Meridian," Deep-Sea Res. II **49** (18), 3713–3733 (2002).
52. K. Richardson, "Comparison of ^{14}C Primary Production Determination Made by Different Laboratories," Mar. Ecol. Progr. Ser. **72**, 189–201 (1991).
53. S. Sathyendranath, A. Longhurst, C. M. Caverhill, and T. Platt, "Regionally and Seasonally Differentiated Primary Production in the North Atlantic," Deep-Sea Res. I **42** (10), 1773–1802 (1995).
54. M. H. Sosik and R. J. Olson, "Phytoplankton and Iron Limitation of Photosynthetic Efficiency in the Southern Ocean during Late Summer," Deep-Sea Res. I. **49** (7) 1195–1216 (2002).
55. V. H. Strass, A. C. Naveira Carabato, R. T. Pollard *et al.*, "Mesoscale Frontal Dynamics: Shaping the Environment of Primary Production in the Antarctic Circumpolar Current," Deep-Sea Res. II: **49** (18), 3735–3769 (2002).
56. J. E. Tremblay, M. I. Lucas, G. Kattner, *et al.*, "Significance of the Polar Frontal Zone for Large-Sized Diatoms and New Production during Summer in the Atlantic Sector of the Southern Ocean," Deep-Sea Res. II **49** (18), 3793–3811 (2002).
57. C. Veth, J. Peeken, and R. Scharek, "Physical Anatomy of Fronts and Surface Waters in the ACC Near 6°W Meridian during Austral Spring 1992," Deep-Sea Res. II **44** (1–2), 23–49 (1997).
58. A. Wulff and S.-A. Wängberg, "Spatial and Vertical Distribution of Phytoplankton Pigments in the Eastern Atlantic Sector of the Southern Ocean," Deep-Sea Res. II **51** (22–24), 2701–2713 (2004).