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A Comparative Study of the Primary Production in the Norwegian Sea by Different Methods

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Abstract—The results of primary production measurements obtained by different methods are presented. These methods are the radiocarbon and oxygen modifications of the flask method, as well as fluorometric procedure with a PrimProd submersible probing fluorometer (produced at the Biological Faculty, Moscow State University). The research was carried out during a complex expedition aboard the R/V *Akademik Boris Petrov* in the Norwegian Sea in July, 1977. The distributions of the primary production values measured by different methods were correlated with other oceanographic data. Then, a comparison of the values obtained by the above-mentioned methods was performed.

INTRODUCTION

In chemical and biological oceanography, great experience has been gained and reliable techniques have been developed for the determination of the absolute values of various parameters. Up to now, the measurements of the rates of different processes have presented certain difficulties. Primary production can be referred to as one of these types of values. For this reason, when estimating it by different methods, essential discrepancies in the results are observed and a search for a more reliable and representative procedure for determining this parameter continues. The limitations of the most widespread methods for determining primary production are well known [3, 6, 8]. The chemical and radiochemical procedures for determining photosynthetic parameters are not satisfactory, nor are experiment planning and methods for processing the data obtained [3].

Recently, instrumental methods were developed for continuous probing of primary production throughout the euphotic layer and for estimating its integral value. They require the use of a PrimProd submersible pulse fluorometer produced at the Biological Faculty, Department of Biophysics, Moscow State University [4, 5] and a FASTRACKA apparatus for measuring photosynthetic parameters produced in Great Britain, etc.

During cruise 27 of R/V *Akademik Boris Petrov* in July 1977, the primary production values were measured by different methods, such as the radiocarbon and oxygen modifications of the flask method, as well as the fluorometric procedure with a submersible pulse fluorometer (PrimProd).

When examining the primary production by the oxygen and radiocarbon methods, the profiles of temperature, salinity, oxygen content, and chlorophyll *a* fluorescence distribution obtained with a Neil–Brown probing system were taken into account. Thus, we succeeded in avoiding the disadvantages arising from collecting the samples from the standard depths when the points of the maximum and minimum values of the above-listed parameters were omitted. However, in view of a certain drift of sensors and a series of other technical difficulties, no complete coincidence of the sampling points at the depths where the extrema are located can be gained. In addition, the calculation of the total value of primary production is employed through a few discrete points in profile and because of this it is an approximation.

The PrimProd submersible fluorometer makes possible the probing of fluorescent parameters with the simultaneous recording of temperature, pressure, and intensity of underwater illumination beneath the surface [1]. We expected that such an instrument would allow us to obtain the most reliable results, since the probing through all the parameters is conducted continuously and the data absolutely coinciding with respect to depth were used in the calculations.

Along with the study of the primary production values and their relation to the physical, chemical, and biological parameters, one of the aims of the cruise was to carry out a comparison of the results obtained by different methods.

MATERIALS AND METHODS

Materials for the study of the production–destruction processes were collected during cruise 27 of R/V *Akademik Boris Petrov* in July, 1997. The layout of the stations is presented in Fig. 1.

To determine the values of primary production by the oxygen [2] and radiocarbon [6] modifications of the flask method, water samples were taken from the surface and the depth with the maximum chlorophyll *a* concentration (the readings of the Sea Teach sensor) using a two-liter cassette of plastic samplers with a Neil–Brown CTD probe.

When determining primary production (PP) by the oxygen method, samples were taken in 0.35-l calibrated light bottles made of transparent plastic with a hydrophobic surface and then exposed in the experimental tanks under conditions close to those in situ with respect to illumination and temperature. To establish a light intensity of about 1% of the surface one, the tank was shaded by blue cloth of different density. The bottles were exposed for 3–7 h. Water samples were taken and incubated only during the day (6 a.m.–7 p.m.). The oxygen content was determined by the Winkler's method with the use of a Jenkons automatic burette (Great Britain) with an accuracy of ±0.01 ml per liter. To determine PP, three samples were taken from every depth level, namely, one for determination of the initial oxygen content and two others for setting the duplicate experiments. As a rule, duplicate titration of oxygen (after incubation in the experimental tank) was characterized by a good agreement. Discrepancies were not greater than 0.01–0.02 ml O_2 per liter.

In order to convert the PP per hour value to that per day, the coefficients obtained experimentally by Sorokin [3] for different periods of the day were used. From 6 a.m. to 7 p.m., the values of these coefficients changed from 14 to 19.

To determine the primary production by the radioisotopic method, 100-ml glass bottles with ground-glass stoppers were filled with water. A sterile $NaH^{14}CO_3$ solution of 0.4 ml (12.5 μc) made with sea water was added to each of the bottles. Then, they were incubated in an open tank on the ship's deck for 24 h. At every measurement, two transparent bottles and two dark ones covered with aluminum foil were used for determining the total intensity of photo- and chemosynthesis. One of the dark bottles was used to determine the intensity of chemosynthesis; another was used for reference. Prior to adding the $NaH^{14}CO_3$ solution into a reference bottle, dry merthiolate was added to reach a final concentration of 0.1 g/l. At this, all biological processes were terminated.

On completion of the exposure, the bottle content was filtered through nylon membrane filters 25 mm in diameter with a mesh size of 0.2 μm. Then, to eliminate the remaining carbonates, these filters were cleansed by passing sea water acidified by phosphoric acid to pH about 2–3 through them 3–4 times. The filters dried in the air were packed into scintillation vials for subsequent counting of their radioactivity. The radioactivity measurements of the filters were carried out at the Institute of Microbiology, Russian Academy of Sciences by means of a Rack-Beta 1219 liquid scintillation radiometer (LKB, Sweden) in a ZhS-106 toluene scintillator.

The primary production value was calculated according to the formula:

$$\text{mg C/(l day)} = \frac{r(S+A)24}{Rt},$$

where r is radioactivity of the organic matter (counts per min); $S + A$ is the content of the soluble mineral carbon in the water sample with account taken for the added $NaH^{14}CO_3$; 24 is the number of hours in a day; R is the initial radioactivity of $NaH^{14}CO_3$ added to bottles (counts per min); t is the duration of incubation (hours).

Determination of the primary production value by means of the continuous probing method using the PrimeProd fluorometer is based on the synchronous in situ measuring of the subsurface light intensity, temperature, and photosynthetic parameters, such as the fluorescence intensity of algae (F_0) and the alga photosyn-

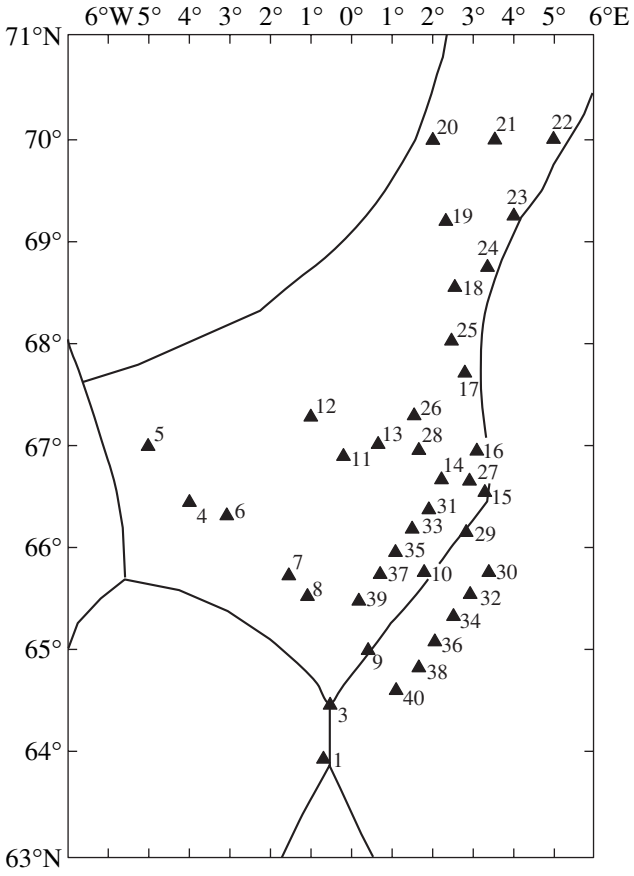

Fig. 1. Location of stations carried out during cruise 27 of R/V *Akademik Boris Petrov* (July, 1997).

thetic activity index, the so-called relative fluorescence variable (F_v/F_m).

The fluorometer consists of a submersible probe (9 kg in weight, 25 cm in diameter), an on-board power pack connected to the probe, and an IBM-compatible computer, which controls the measurement of parameters according to the program specified by the user. The registering set of the probe consists of a photodetector (photomultiplier), a pulse amplifier, an analog-to-digital converter, an interface for coupling with the computer, and two independent pulse light sources with a flash duration of 0.1 ms (spectral band 400–480 nm).

The first low-intensity probing flash with an energy of 0.01 J provides measurement of the background fluorescence (F_0), which allows us to estimate the chlorophyll *a* content in the natural phytoplankton with respect to the corresponding calibration by standard techniques. The second intensive flash with the saturating energy for photosynthesis (1 J) enables photosynthetic phytoplankton activity to be estimated. This flash precedes the probing one. The intensive illumination causes reduction of the initial acceptors of photosystem 2 and an increase of the intensity of fluorescence up to its maximum level (F_m). The fluorometer registers the extent of amplification of fluorescence intensity ($F_v = F_m - F_0$) induced by the powerful flash. This enables calculation of the efficiency of using the light by microalgae from F_v/F_m.

The employment of the sensor of the underwater light intensity in the probe permits estimation of the vertical distribution of the photosynthetic production value from the measured fluorescence variable (F_v/F_m) and the light intensity. The calculation was carried out in an automatic operation by a formula, which is based on the model of primary reactions of photosynthesis suggested by Kiefer [5]:

$$PP(d) = skI(d)F_0(d) \times \frac{F_v/F_m(d)I_{1/2}}{I(d) + I_{1/2}} \text{ (mg C/m}^{-3}\text{day}^{-1}\text{)},$$

where $PP(d)$ is the daily primary production; d is the depth; $F_0(d)$ and $F_v/F_m(d)$ are the vertical profiles of the constant and relative fluorescence variables, respectively; $I(d)$ is the vertical profile of the light intensity integrated over the spectrum in the range of PAR; $I_{1/2}$ is the light intensity, which semi-saturates the photosynthesis and was determined by us to be equal to 27 W per square meter; k is the calibrating factor found by substitution of the primary production value measured with the radiocarbon method into the left-hand side of the formula (it equals to 1.2 based on the data obtained from 9 to 12 September, 1995, during the joint Russian–Polish cruise of R/V *Oceania* belonging to the Institute of Oceanology, Polish Academy of Sciences, in the central part of the Baltic Sea); s is the coefficient for conversion of the hour's primary production into that of a day[6].

RESULTS AND DISCUSSION

Using the results of the studies of primary production by different methods, its distribution are schematically represented in Fig. 2. The absolute values of the quantifiers obtained are presented in the table.

The distribution of the primary production values measured by the oxygen method is shown in Fig. 2a. In the scheme, the area with the maximum PP values located in the northern part of the region covered is defined well where the spring–summer vegetation of diatoms lasted in relatively cold waters with temperatures in the upper 20-m layer equal to 7–8°C. The high intensity of the productive processes in this area is confirmed by the maximum values of the oxygen percentage (within the layer of the chlorophyll peak, the oxygen content reached 106%) and high concentrations of phytopigments. The mineral forms of nutrients are almost completely utilized by the developed phytoplankton and high concentrations of organic compounds and ammonia in the water are found.

This area with high PP values is well pronounced also in the schematic presenting the results of PP measurements by means of the submersible fluorometer probe (Fig. 2b). However, according to the data obtained by the radiocarbon method, in the northern part of the area studied none of the PP values exceeded the average level for this area (Fig. 2c).

All three schematics (Fig. 2) show that in the southeastern part of the region studied one more area with enhanced PP values is revealed. It is related to the waters of the western branch of the Norwegian Current (WBNC). These waters can be traced along the eastern periphery of the region by relatively high temperature and low salinity and oxygen content. In these waters, the development of juvenile forms of peridinea, nauplii, and juvenile copepods took place. Low concentrations of nitrates, phosphates, and silicon, as well as increased concentrations of the organic forms of phosphorus and nitrogen in this area point to the succession of the community into the recycling phase. The developed juvenile and small forms of phyto- and zooplankton do not have great biomass, but feature a high ability to intensive production. It is significant that according to the data obtained with the production-meter probe, in this very region the maximum F_v/F_m values were observed. As noted above, this ratio allows us to estimate the photosynthetic activity of algae and their potential ability to primary productivity. At the same time, the F_v/F_m value is a characteristic of the physiological condition of the population of phytoplankton cells under study. This fact is of considerable importance, since it is related to the prediction of the changes in the PP values in this region for the near future.

From this point of view, it is interesting to consider the nature of distribution of the average values of the F_v/F_m ratio (Fig. 3). The maximum values of this parameter are confined to the area of the spreading of

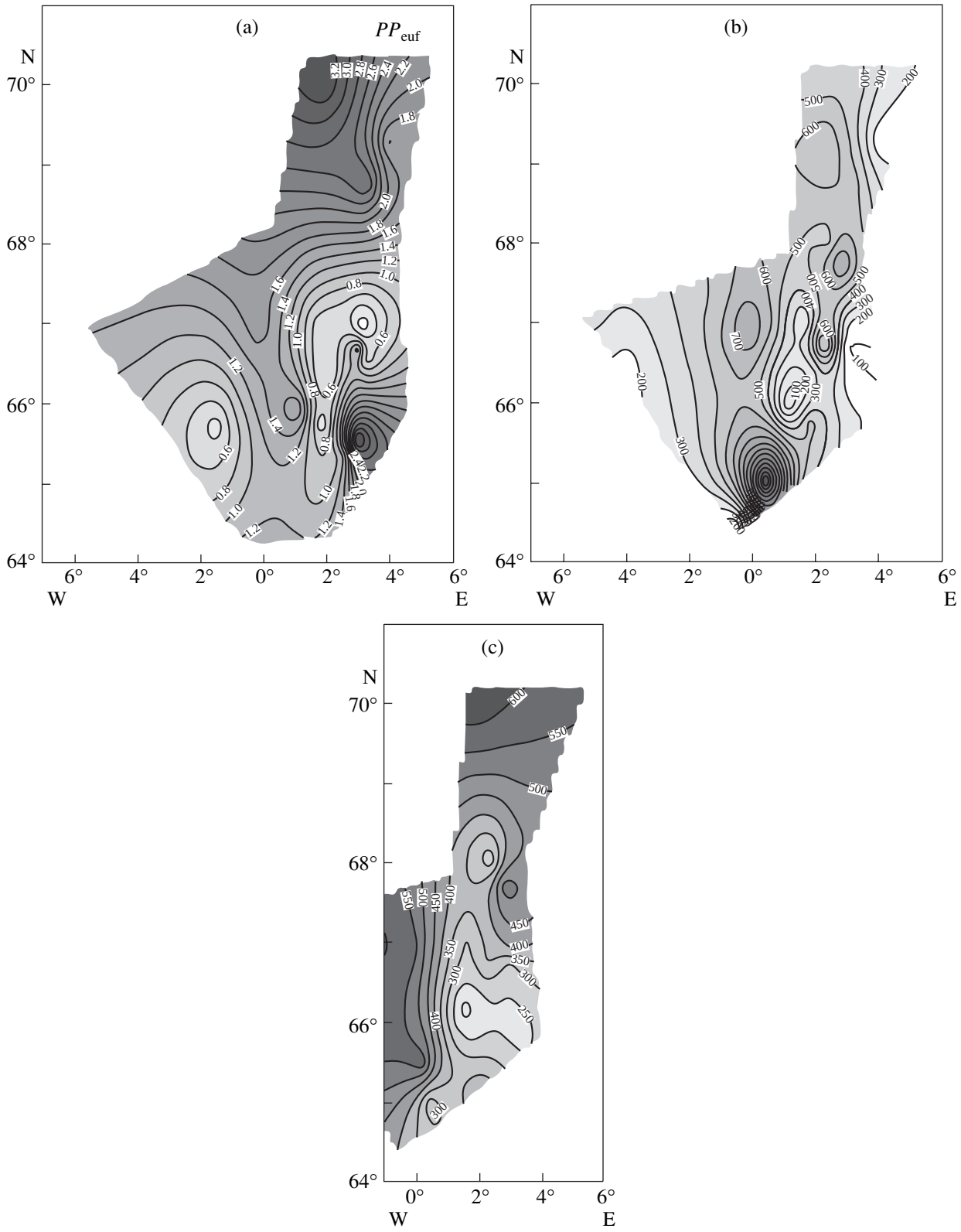

Fig. 2. Distribution of primary production values (mg/m^2), measured by (a) oxygen method, (b) ^{14}C method, and (c) submersible probe-fluorometer data.

Results of the measurements of the primary production values by different methods

Station numbers	Primary production within the euphotic layer (mg/m^2)		
	O_2	^{14}C	PrimProd
3		29.35	
4	1160	145.61	
5		320.26	
6		264.30	
7	300	439.93	
8		536.37	
9		1738.99	279
10	440	532.35	254
11	1700	814.07	583
12	1600	528.79	
13		606.02	
14		865.44	351
16	50	174.46	419
17		827.78	524
19	2730	712.28	522
20	3400	418.89	637
21		431.37	
23	1600	136.08	
24	2800	524.55	
25		457.14	271
27	1790	113.46	273
28	540	183.48	295
29		220.92	
30		205.08	232
31	240	302.04	
32	3300	256.25	
33		104.56	182
35	1180	33.93	293
36		362.50	412
38	300	345.49	
39		860.70	576
Mean	1484.38	435.24	381.44

the WBNC warm waters with the low oxygen content (Fig. 4).

In the zone of mixing of the WBNC waters with those from the deep part of the Norwegian Sea, a complicated pattern of the PP values distribution with alternating patches of enhanced and lowered values was observed. This pattern was related to the formation of meso- and microscale eddies within the frontal zone. To a certain extent, the alternating cyclonic and anticyclonic gyres are traced in the schematic presenting the results of the PP measurements by each of the methods used in this cruise (Fig. 2). The greatest differences are observed in the schematic plotted by results obtained with the oxygen method of PP measurement (Fig. 2a).

In the west of the region studied, a vast area with low PP values measured by the oxygen and ^{14}C methods was recognized. Unfortunately, no data acquired with a submersible fluorometer is available in this part of the area. This area is related to a cyclonic gyre with the center at stations 7 and 8. The low intensity of primary production in this zone is confirmed by insufficient saturation of the surface waters by oxygen (99%) and low values of chlorophyll *a* fluorescence and phytobiomass. In the area of this cyclonic gyre, at the surface, high concentrations of mineral forms of nutrients, which are not utilized by phytoplankton, are observed.

Thus, the distribution of the PP values measured by different methods has a certain similarity. The differences are related more likely to the imperfection of the methods of measurements, to the insufficient density of the network of stations, and to the differences in the location of the stations for PP studies with different methods (see table). The distribution of the PP values measured by the oxygen method correlates best with other oceanographic parameters and displays the essence of the processes taking place in the given region. But, the absolute PP values obtained by this method proved to be, on the average, 3–4 times higher than the data obtained by two other methods (see table). This fact can be readily explained, since it is known [3, 8] that the radiocarbon method underestimates the results. This method permits the measurement of only the growth of biomass based on the autothrophic CO_2 fixation, while the heterothrophic nutrition and the growth through the dissolved organic matter synthesized by algae are ignored by this method. From this it follows that the results obtained may more likely be closer to the net production than to the gross one, especially in the case of a deficiency in the mineral nutrition. In addition, the losses of small forms of plankton and bacterioplankton at the filtration and the losses of easily hydrolyzed carbohydrates and volatile compounds of acids and ketones when drying and acidificating the filters are also possible.

As to the production meter, as mentioned above, in the methodical part of the paper, the instrument was calibrated with reference to the radiocarbon method, and thus, the data obtained also appear to be mostly underestimated. Certainly, the production meter should be calibrated against the data obtained by the oxygen method and compared with the results. For technical reasons, this was not performed during the cruise, but

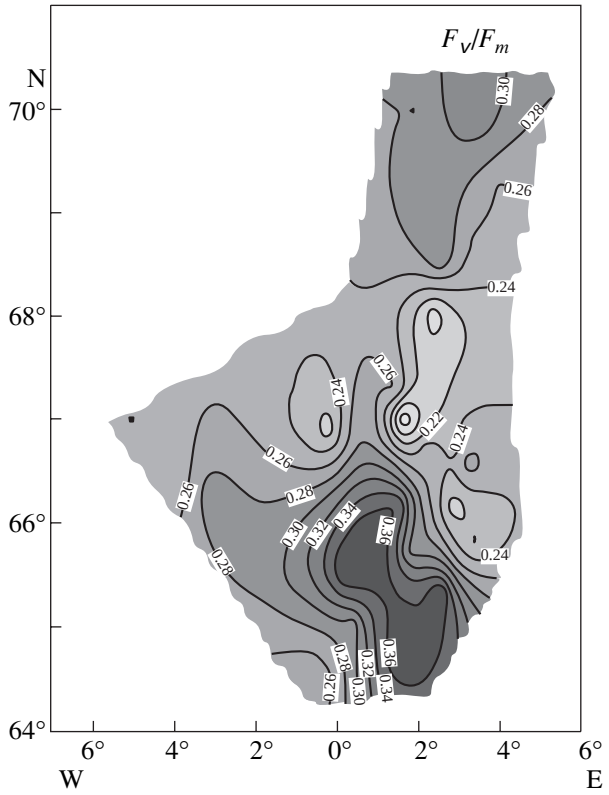

Fig. 3. Distribution of the average values of F_v/F_m.

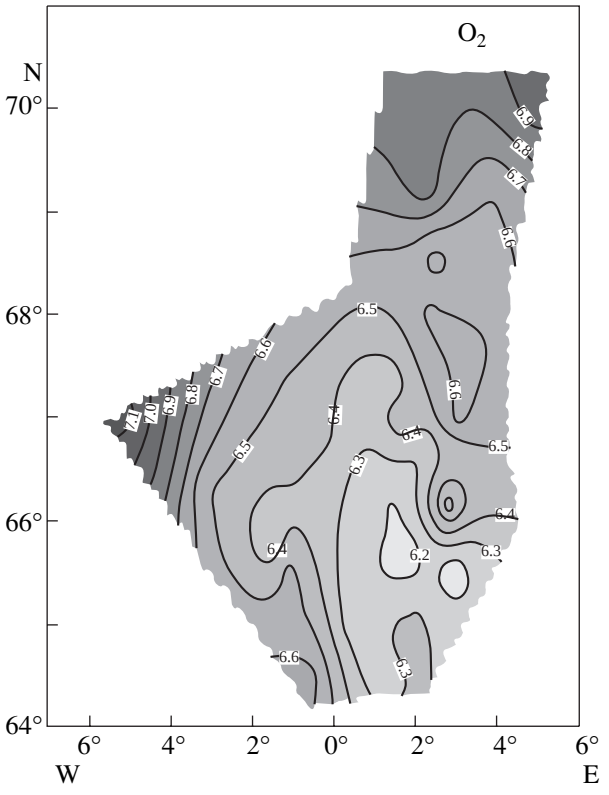

Fig. 4. Oxygen concentration in the surface layer (ml/l).

the authors are going to carry out this study in the near future.

The application of the submersible probing fluorometer in oceanographic investigations will make it possible, after proper resolution of the problems concerning the calibration of the instrument, to estimate the PP values in the oceans more exactly and objectively. The employment of the probing fluorometer will enable examination of the primary production not only at diurnal stations, but also at evening and night stations without special long ship's stops to perform the day-long experiments. The latter is very important as the ships time is extremely expensive.

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