Statistical relations between photosynthesis and abiotic conditions of the marine environment; an initial prognosis of the World Ocean productivity ensuing from warming up of the Earth

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Biological productivity
Photosynthesis
Nitrogen concentration
Temperature
Prognostic model

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Abstract

The article presents the relations between photosynthesis and the main abiotic factors of the marine environment. Basing on the experimental data collected in various regions of the World Ocean, the statistical correlations between the parameters of photosynthesis and temperature and the content of various forms of nitrogen have been determined. These correlations formed the background of the models forecasting the primary production of the World Ocean ensuing from the Earth warming up. The models were used to determine the possible alterations of the photosynthesis parameters in the World Ocean and also in the regions of the Polish deep-sea fishery fleet operations.

1. Introduction

The article has been inspired by the information on the increasing content of carbon dioxide in the atmosphere. This leads in consequence to the increase of the air temperature due to the changes of the optical conditions of the atmosphere and to a disturbance of the irradiance balance. It is assumed (Kellogg, 1988) that the temperature will increase by about 2.5^{o}C till the 2050 on average as regards the entire Earth and in the

[1]The investigations were carried out under the research programme CPBP 03.10, co-ordinated by the Institute of Oceanology of the Polish Academy of Sciences.

antarctic regions the increase will reach about 7^oC. This warming up will result in climatic changes of the Earth as well as in the changes of the marine ecosystems of the World Ocean. It is obvious in particular that an increase in water temperature of the euphotic zone is expected, its scale corresponding, though with a certain time lapse. to the increase of the air temperature.

The temperature of sea water belongs to the major factors limiting the functioning of the marine ecosystems and their biological productivity, because it directly influences the intensity of the marine flora and fauna biotic processes (Finenko, 1977; Vilenkin, 1977). Moreover, the temperature affects the biological productivity of the marine ecosystem by indirect impact on other biotic and abiotic factors that determine the ecosystem functioning. Thus, for example, the thermal condition of the Ocean determines its dynamices as regards the micro- and macro-scale time and spatial conditions (Kamenkovich and Monin, 1978). The latter dynamic factors determine the supply of the euphotic zone with biogenic substances, the so-called mineral feed of phytoplankton (Mordasova, 1976).

Taking into account the above problems, our studies were aimed at the determination of the influence of the temperature and other abiotic factor alterations on the biological productivity of various ecosystems of the World Ocean. This article presents the initial stage of studies concerning exclusively the primary production of phytoplankton resulting from photosynthesis. The process of photosynthesis forms the basis of the general biological productivity of marine basins (Parsons *et al.*, 1977). The number of the discussed factors affecting the intensity of primary production has been limited. For example the influence of light has been only shortly discussed because its impact on the absolute values of productivity is not the most important one (as shown in chapter 2). As regards the analysis of the nutrient effect on photosynthesis, the discussion has been limited to the derivatives of one element, *viz.* nitrogen. According to the studies of various authors (Koblentz-Mishke and Vedernikov, 1977) there is observed a deficit of nitrogen in the majority of aqueous systems as compared with other biogenic substances. That is why in most of the World Ocean regions the absolute level of primary production is regulated by nitrogen concentration.

The aim of our studies has been attained in two stages: in the I stage – the statistical correlations have been established between parameters characterizing photosynthesis of phytoplankton and sea water temperature and nitrogen content, in the II stage – the established correlations have been used to formulate the initial prognosis of photosynthesis alterations that might appear as a result of the Earth temperature increase.

2. The effect of the main abiotic factors on photosynthesis in the light of experimental data

Photosynthesis in the marine environment depends on the numerous biotic and abiotic factors. However, there are three major factors that determine the primary production and the resources of phytoplankton in the sea (Koblentz-Mishke, 1977; Bougis, 1976; Woźniak *et al.*, 1988): underwater irradiance, content of biogenic substances in water and water temperature in the euphotic zone. This chapter is devoted to the analysis of the effect of these factors, particularly the latter two, on photosynthesis.

2.1. Presentation of the physical problem

Primary production at a depth z – $P(z)$ in a sea can be expressed by the following product:

$$P(z) = AN(z) \cdot Ba(z), \tag{1}$$

where:

$Ba(z)$ – concentration of chlorophyll a at a depth z; this concentration is commonly applied as the indicator of the phytoplankton amount in unit volume of sea water,

AN(z) – intensity of photosynthesis at a depth z; so-called assimilation number (Koblentz-Mishke, 1985).

At a certain optimum depth z_{opt} (Fig. 1B) the intensity of photosynthesis attains a maximum and the assimilation number reaches the maximum value $AN_{max} = AN(z_{opt})$. Then equation (1) transforms into:

$$P(z) = A(z) \cdot AN_{max} \cdot Ba(z), \tag{2}$$

where:

$A(z) = AN(z)/AN_{max}$ – the relative photosynthesis intensity (the relative assimilation number).

Analysis of experimental data carried out by the author indicated that there are differences in the impact of the three major photosynthesis limiting factors – light, nutrient content and temperature – on the three photosynthesis factors from the right side of equation (2), *i.e.* $A(z)$, AN_{max} and $Ba(z)$. Thus, vertical distribution of the relative photosynthesis intensity $A(z)$ depends solely on the light fields in a sea (z), that is $A(z) = f[\eta(z)]$, while AN_{max} and $Ba(z)$ are practically independent on light but strongly correlated with temperature and nutrient content, particularly with nitrogen concentration (N). Hence, $AN_{max} = f(t, N)$ and $Ba(z) = f(t, N)$.

In short, light affects the vertical distributaion of primary production in the sea; especially below the optimum depth z_{opt}, the intensity of photosynthesis is proportional to the underwater irradiation $\eta(z)$ (Fig. 1). However, this factor influences only the distribution of the relative photosynthesis intensity $A(z)$. We will not proceed with the discussion on the dependence of photosynthesis on light in this article[2]. We are going

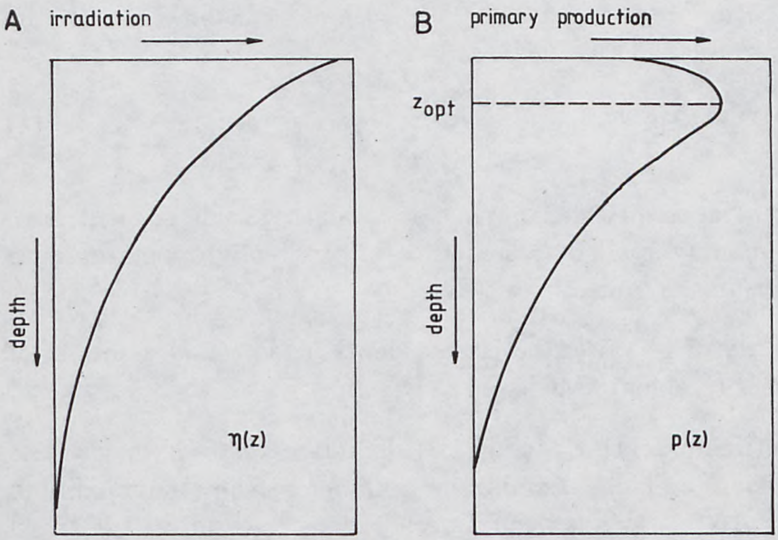


Figure 1: Examples of typical vertical distributions in sea: A – irradiation dose (z), B – primary production $P(z)$

to present the results of statistical analysis of the correlation between photosynthesis and the temperature of the euphotic zone and the nitrogen content in the sea water. These factors determine the values of AN_{max} and $Ba(z)$ and thus, considering equation (2), also determine the absolute values of primary production $P(z)$.

2.2. Characterization of the experimental data

The analysis was based on the experimental data from biologically different marine basins, collected either by the author and his collegues or found in the literature. In general, the results from over 1000 sampling stations have been analysed.

The material comprises simultaneous measurements of photosynthesis parameters, temperature and the content of inorganic nitrogen in sea water. Nitrogen concentration comprises: nitrate – $N(NO_3)$, nitrite – $N(NO_2)$ and ammonia – $N(NH_4)$. So, the sum of the inorganic forms of the bound nitrogen N_{inorg} is as follows:

$$N_{inorg} = N(NO_3) + N(NO_2) + N(NH_4). \tag{3}$$

Besides the inorganic and organic nitrogen content, the concentration of the total nitrogen N_T has been also determined:

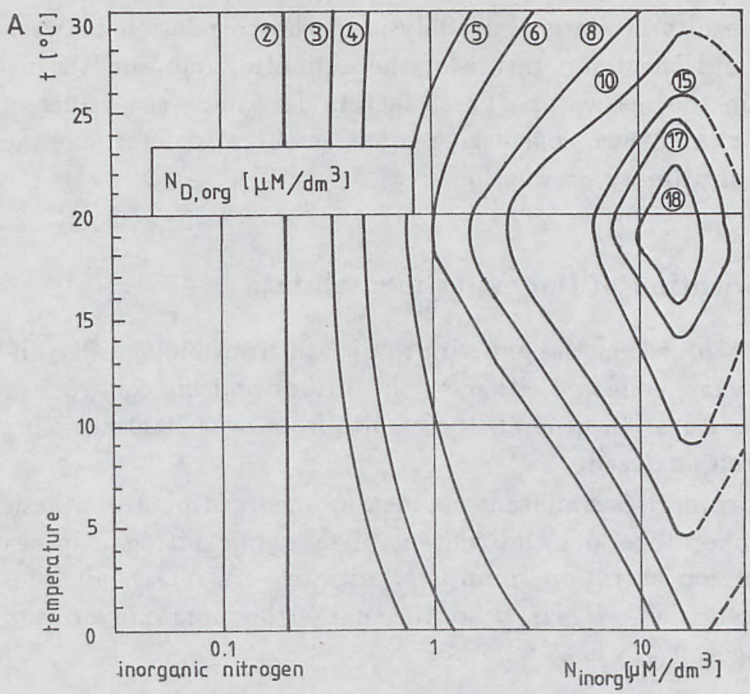
$$N_T = N_{inorg} + N_{org}, \tag{4}$$

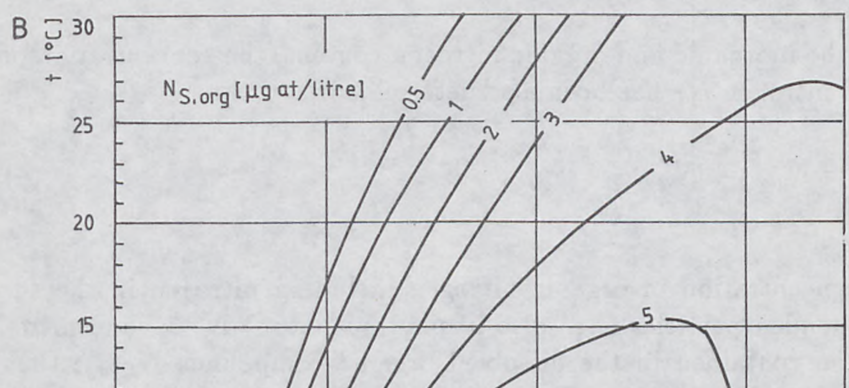
where:

N_{org} – concentration of organic nitrogen including nitrogen in the suspended particles (*i.e.* also in phytoplankton) $N_{S,org}$, and nitrogen contained in the dissolved organic compounds $N_{D,org}$; thus $N_{org} = N_{S,org} + N_{D,org}$.

The concentrations of N_T and N_{org} were determined indirectly by approximate correlations with N_{inorg} and temperature – see Figure 2. The detailed discussion of this procedure is given in the article by Woźniak (in prepared).

[2]The problem of photosynthesis dependence on light in the sea is presented in detail in articles: Woźniak, 1985, 1987 and in prepared; Woźniak *et al.*, 1988; Koblentz-Mishke *et al.*, 1985 and also in articles by other authors: Koblentz-Mishke, 1985; Platt *et al.*, 1980.


A
t [°C]
temperature
N_{D,org} [μM/dm³]
2
3
4
5
6
8
10
15
17
18
inorganic nitrogen
N inorg [μM/dm³]
0.1
1
10
0
5
10
15
20
25
30


B
t [°C]
temperature
N S,org [μg at/litre]
0.5
1
2
3
4
5
6
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inorganic nitrogen
N inorg [μM/dm³]
0.1
1
10
0
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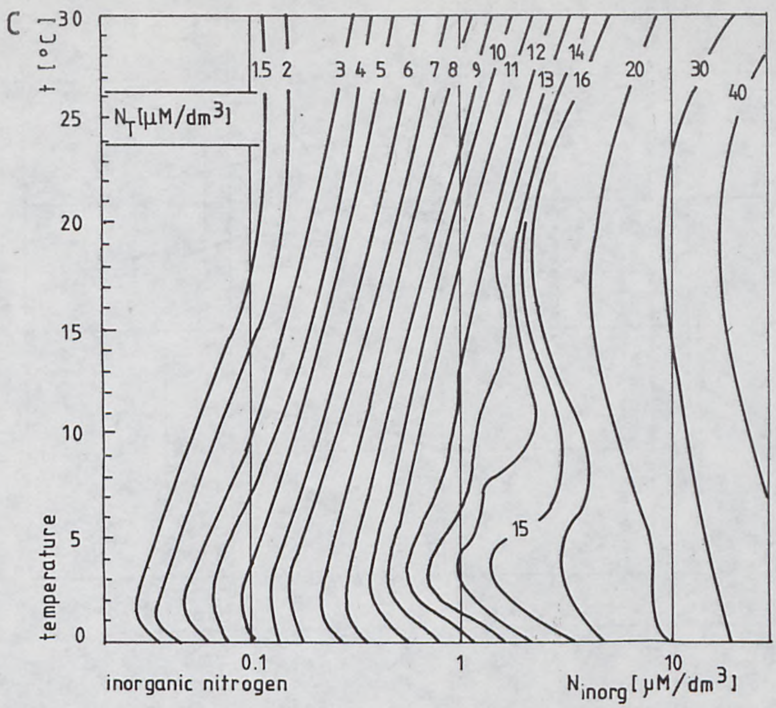


Figure 2: Statistical relations between various forms of nitrogen in the surface sea water and temperature. The relations are presented as isolines t versus N_{inorg} (inorganic nitrogen concentration): A – concentration of the organic dissolved nitrogen, $N_{D,org} = const$; B – concentration of the suspended organic nitrogen, $N_{S,org} = const$; C – concentration of the total nitrogen, $N_T = N_{inorg} + N_{org} = N_{inorg} + N_{D,org} + N_{S,org} = const$

2.3. Statistical correlation between photosynthesis and temperature, as well as the content of inorganic nitrogen compounds

The particulars of the analysed dependence of photosynthesis parameters on temperature and nitrogen concentration are given in the article by Woźniak (in prepared). The present article contains the results selected with regard to the requirements of prognosing.

The dependence of the maximum assimilation numbers AN_{max}, averaged in three temperature classes (0–10°C, 10–20°C and 20–30°C), at the optimum depth z_{opt}, on the sum of inorganic nitrogen N_{inorg} is presented in Figure 3. Similar dependences for the chlorophyll *a* concentration in the surface water layer are shown in Figure 3B. In Figure 4 the twodimensional dependences of the photosynthesis parameters on the variables N_{inorg} and t are depicted as isolines.

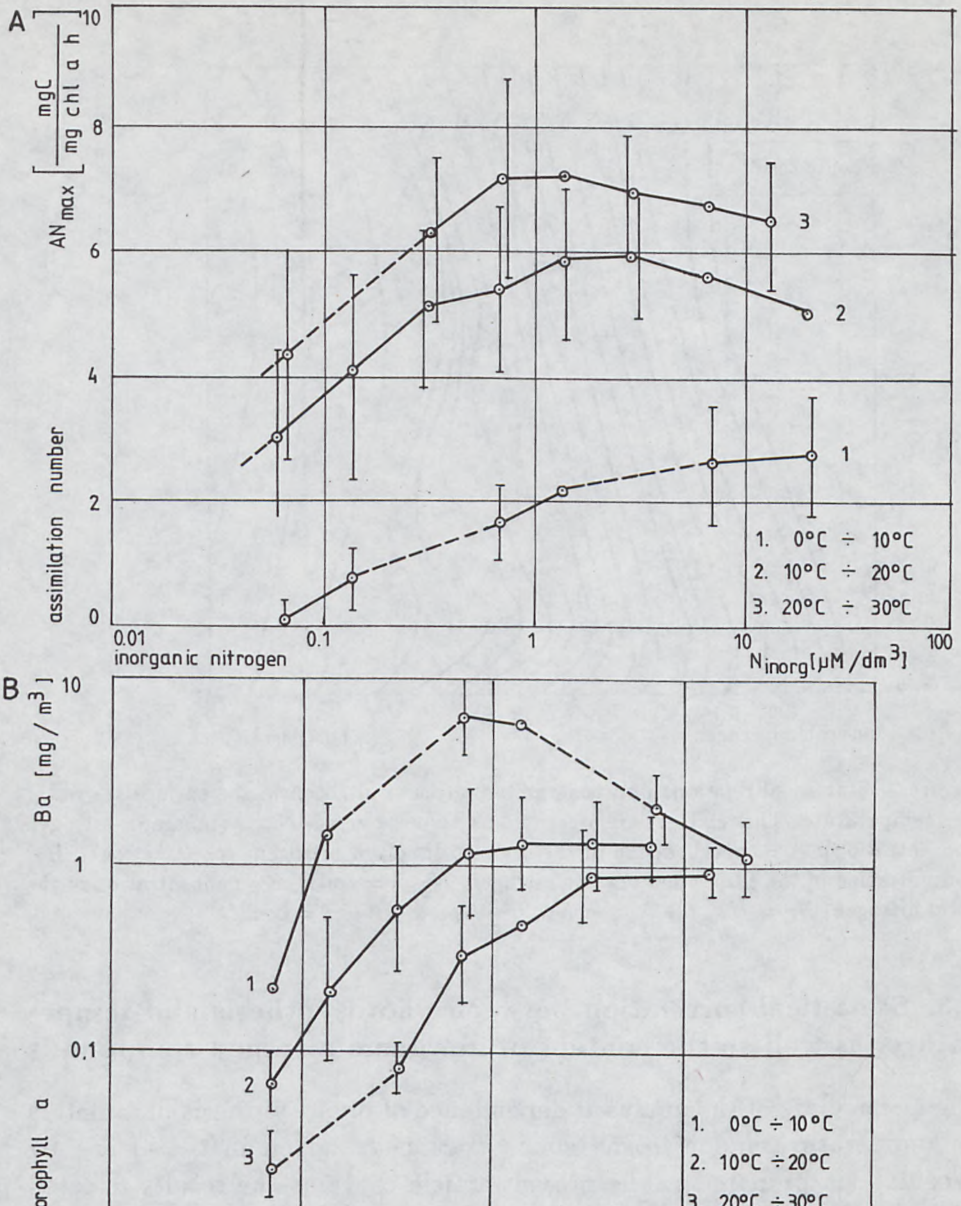


Figure 3: Relations averaged for various temperature ranges: A – maximum (*i.e.* at the optimum depth) assilimilation number AN_{max} versus inorganic nitrogen concentration N_{inorg} in the surface water layer; B – surface concentration of chlorophyll *a* Ba versus inorganic nitrogen concentration N_{inorg} in the surface water layer. Vertical segments indicate the range of standard aeviation of AN_{max} and Ba

The figures clearly indicate the fact that the intensity of photosynthesis AN_{max}, as well as chlorophyll *a* concentration Ba, in general increase consequently with an increase in nitrogen concentration N_{inorg}. This increase follows a hyperbola (compare with Fig. 3) and thus it can be described by the Michaelis-Menten law (Ketchum, 1939):

$$AN_{max} = \frac{AN_{max,M} \cdot N_{inorg}}{N_{inorg} + N'_{inorg,M}}, \tag{5}$$

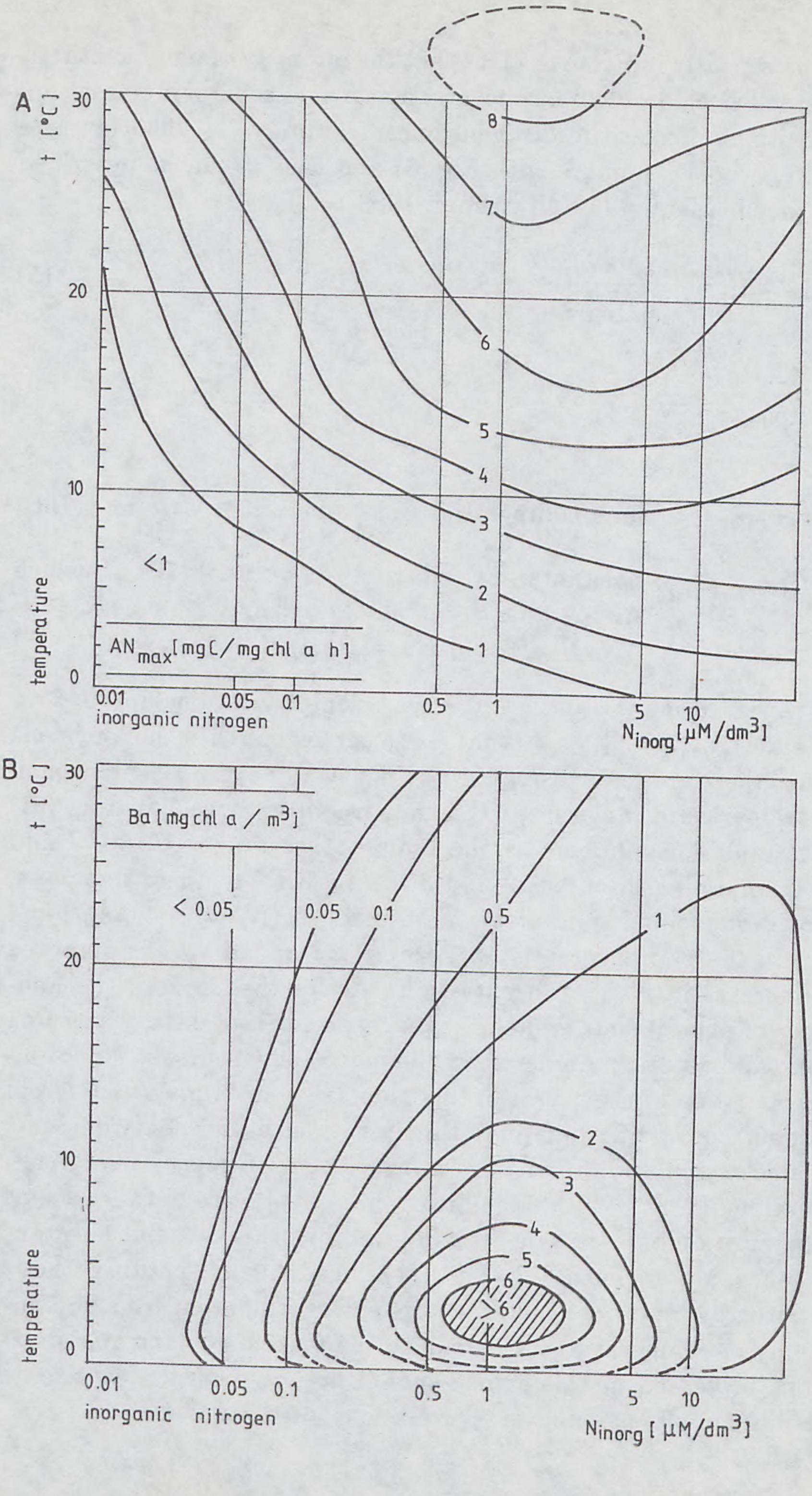
$$Ba = \frac{Ba_M \cdot N_{inorg}}{N_{inorg} + N''_{inorg,M}}, \tag{6}$$

where:

$AN_{max,M}$, Ba_M – the maximum possible values of AN_{max} and Ba,

$N'_{inorg,M}$, $N''_{inorg,M}$ – constants, *i.e.* nitrogen concentrations at which AN_{max} and Ba attain 1/2 their values: $AN_{max} = AN_{max,M}/2$ and $Ba = Ba_M/2$.

However, apart from the discussed experimental relationships $Ba = f(N_{inorg})$ and $AN_{max} = f(N_{inorg})$ that are in agreement with the Michaelis-Menten law, there are cases disregarding this law, for example chlorophyll *a* in the temperature range 0–10^{o}C (compare with curve 1 in Fig. 3B) and the assimilation numbers at the temperature ranges 10–20^{o}C and 20–30^{o}C (compare with curves 2 and 3 in Fig. 3A). In these instances, above a certain optimal concentration of nitrogen ($N_{inorg} > 1\ \mu M/dm^3$) a decrease in the photosynthesis parameters Ba and AN_{max} is observed with the increase in N_{inorg} concentration. As for the present, the limited number of experiments and the scarce experimental data concerning other biotic and abiotic parameters of the marine environment do not allow the explanation of the causes of this phenomenon. It may result from the phytoplankton species differentiation in various natural environments with variable assimilation intensities (Grand, 1967; Eppley *et al.*, 1969) towards various forms of inorganic nitrogen. Another likely cause seems to be the limitation of photosynthesis induced by other biogenic substances, *e.g.* phosphorus (Fuchs *et al.*, 1971). And finally, photosynthesis can be limited by biotic or abiotic factors entirely different from the nutrient supply or temperature. This is also the reason why the statistical correlations presented in this article should not be regarded as genetic principles but simply as empirical correlations.


A
30
20
10
0
t [°C]
temperature
8
7
6
5
4
3
2
1
<1
ANmax [mg C / mg chl a h]
0.01
0.05
0.1
0.5
1
5
10
inorganic nitrogen
Ninorg [µM/dm3]
B
Ba [mg chl a / m3]
< 0.05
0.05
0.1
0.5
1
2
3
4
5
6
>6

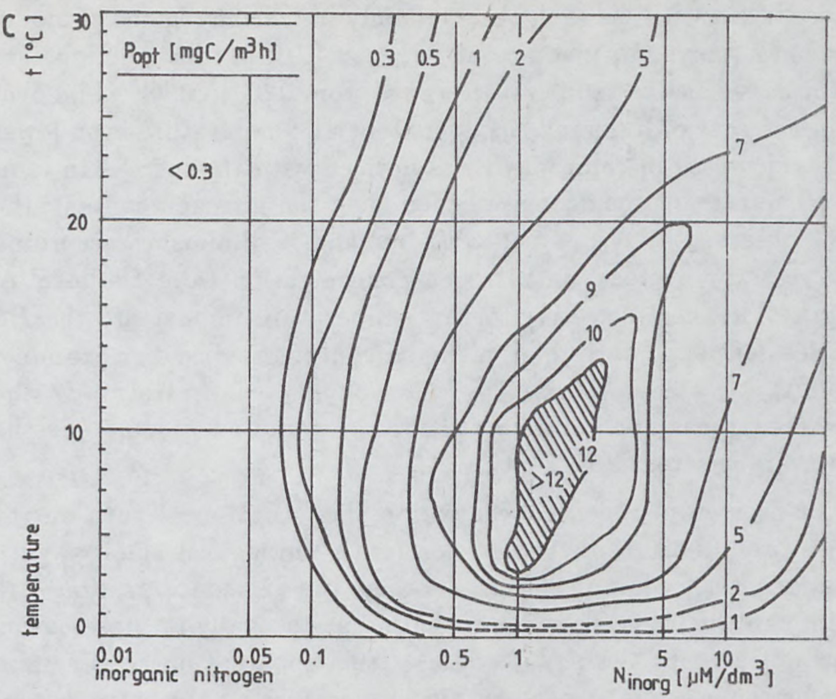


Figure 4: Approximate location of isolines: A – maximum assimilation number $AN_{max} = const$; B – chlorophyll *a* concentration $Ba = const$; C – optimum primary production $P_{opt} = const$ on diagrams t (temperature) versus N_{inorg} (inorganic nitrogen concentration)

Besides the limitation by mineral feed supply, the photosynthesis parameters are strongly correlated with sea water temperature, as indicated in Figure 3 by the curves $Ba = f(N_{inorg})$ and $AN_{max} = f(N_{inorg})$ for various temperature ranges and by isolines $Ba = const$, $AN_{max} = const$ and $P_{opt} = const$ in Figure 4. Generally, as regards the assimilation numbers AN_{max}, at the given level of mineral feed, a significant increase of AN_{max} is observed with the increasing temperature of sea water – see Figure 4A. This phenomenon is a result of the accelerating effect of temperature within the 0–30°C range, recorded in the world ocean, on the intensity of photosynthesis (Finenko, 1977; Finenko *et al.*, 1971). This accelerating effect of temperature ceases and inhibition starts probably above 30°C (broken line in Fig. 4A).

In the case of the chlorophyll Ba concentration, the indicator of the phytoplankton resources in the sea, the situation differs slightly – see Figure 4B. The positive effect of temperature on this concentration is noticeable only at a very narrow range of low temperatures, around 0°C.

An increase in Ba with t is then observed only in marine regions of moderate nitrogen supply. For instance at $N_{inorg} \approx 1.0\ \mu M/dm^3$ the increase in Ba is observed in the temperature range from 0^oC to 3^oC, while over 3^oC, or in the seas of different N_{inorg} content at temperature even lower that 3^oC, a decrease in chlorophyll a is noticed with the increasein temperature. The rate of this decrease depends on the nitrogen content; the greatest is observed at $N_{inorg} \approx 1\ \mu M/dm^3$ and it diminishes according to the increase or decrease in nitrogen concentration from the level of $1\ \mu M/dm^3$. The least sensitive to the temperature impact are the Ba values in seas of particularly high nitrogen concentrations. For example, in seas of $N_{inorg} \approx 30\ \mu M/dm^3$ the chlorophyll a concentration in the surface water layer is approximately the same – about $1\ mg/m^3$ – in the temperature range from 3 to 24^oC.

Thus, at a given nitrogen concentration the "cool" seas turn out to be the most abundant in phytoplankton (with the highest chlorophyll a concentrations Ba), while in "warm" basins the Ba concentrations are lower, although the intensity of photosynthesis is actually in those basins higher, as indicated by the AN_{max} values. This apparent paradox can be explained by the accelerating impact of temperature on the entire ecosystem, that is by the simultaneously enhanced grazing of phytoplankton by zooplankton.

In recapitulation, the relations $Ba = f(N_{inorg})$ observed in the world ocean are characterized by a certain optimum area (hatched area in Fig. 4B) of N_{inorg} and t variables (N_{inorg} approaching $1\ \mu M/dm^3$ and $t - 3^oC$). So, in the basins with the inorganic nitrogen content in the range from $0.4 - 3\ \mu M/dm^3$ and temperatures in the range from 1 to 6^oC, the maximum chlorophyll a concentrations are encountered. These basins belong to eutrophic and supereutrophic seas with chlorophyll concentrations $\sim 5\ mg/m^3$ and even greater. Similar shape to chlorophyll a relation takes the optimum primary production (*i.e.* primary production at the optimum depth) versus N_{inorg} and t. It is understandable since this parameter comes as the product of the chlorophyll a concentration Ba and the photosynthesis intensity $AN_{max}(P_{opt} = Ba \cdot AN_{max})$ [3]. However, the influence of AN_{max} – assimilation number – transferrs (in relation with the corresponding chlorophyll a area) the optimum production are of the variables N_{inorg} and t into the range of higher nitrogen concentrations and

[3]Precisely: $P_{opt} = Ba(z_{opt}) \cdot AN_{max}$, but the analysed here mean concentrations of chlorophyll a in the surface water layer Ba approximate or are proportional to $Ba(z_{opt})$.

higher temperatures – see Figure 4C. Thus, the most productive area the seas and ocean regions with temperatures $t \approx 3 - 15^oC$ and the average inorganic nitrogen concentration in the range $N_{inorg} \approx 0.75–3.5\ \mu M/dm^3$. In these basins the primary production P_{opt} attains the level of about $10\ mg \cdot C/m^4 \cdot h$ and even more.

2.4. Statistical relationship between photosynthesis and temperature and total nitrogen content

The presented above relations are useful is estimating the actual photosynthesis parameters on the basis of the measured temperature and the inorganic nitrogen concentration, but in prognosis of photosynthesis the relations between the photosynthesis parameters and the temperature and the total inorganic and organic nitrogen concentration N_T are important as well. Examples of such relations are given in Figure 5. They were obtained from the relations $Ba = f(N_{inorg}, t)$ and $P_{opt} = f(N_{inorg}, t)$ illustrated in Figure 4, after a transformation of the variable N_{inorg} to the variable N_T with the application of the diagram in Figure 2C.

The qualitative character of the relations $Ba = f(N_T, t)$ and $P_{opt} = f(N_T, t)$ is similar to that of $Ba = f(N_{inorg}, t)$ and $P_{opt} = f(N_{inorg}, t)$ and does not require separate discussion, though it has to be stressed that the accuracy of the diagrams in Figure 5 is far smaller than that in Figure 4, which results from the indirect approximation of the total nitrogen content N_T.

3. Prognosis of the effect of the Earth temperature increase on the primary production of the World Ocean

The assumption that the statistical relations presented in the predecessing chapter describe the steady or quasistatical states of the World Ocean ecosystems seems quite justified. Therefore it can be applied in forecasting the changes of these states (*i.e.* photosynthesis parameters) ensuing from alterations of any of the limiting factors, *e.g.* temperature or nitrogen content. Actually, any disturbance of the limiting factors results in a loss of the momentary dynamic equilibrium and the ecosystem becomes unstable. The processes taking place then in the ecosystem cannot be described by the relations given in Figures 4 and 5, though it is possible

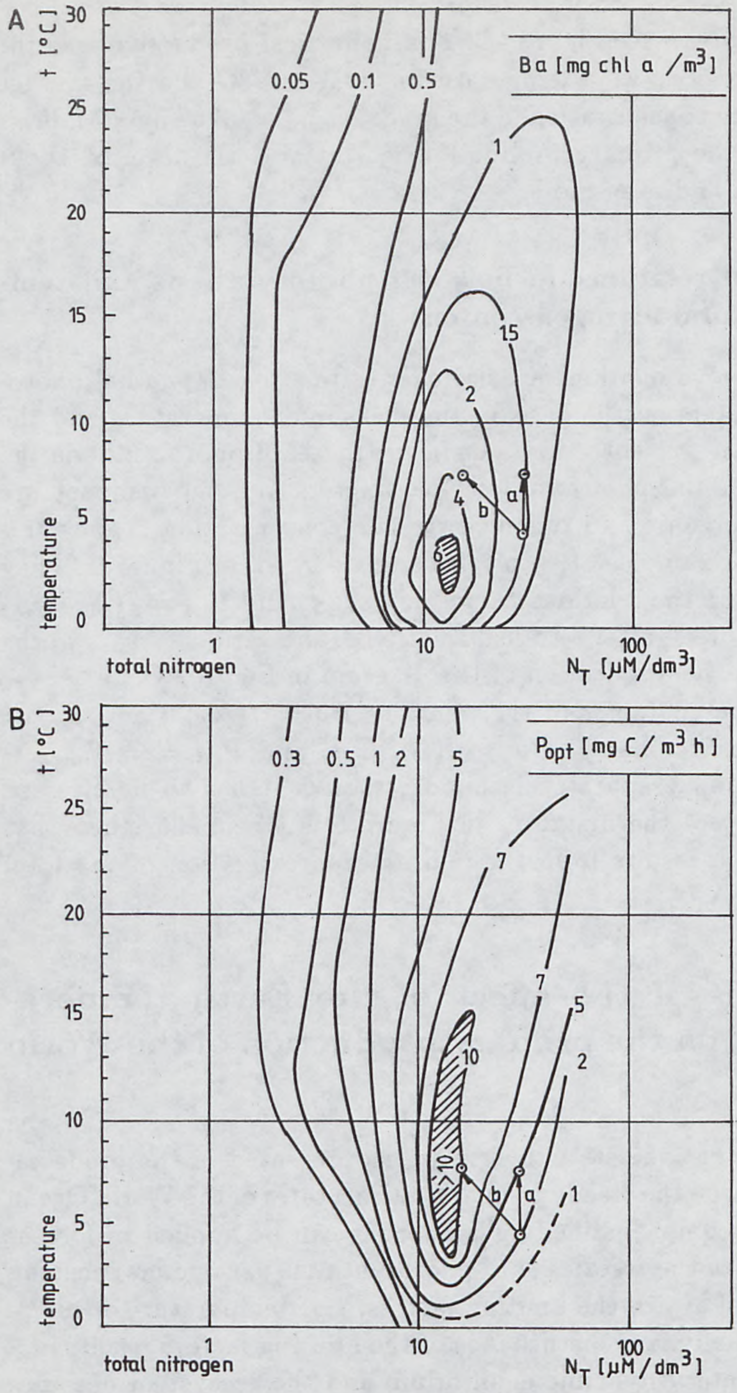


Figure 5: Approximate location of isolines: A – chlorophyll *a* concentration $Ba = const$; B – optimum primary production $P_{opt} = const$, on diagrams t (temperature) versus N_T (total nitrogen concentration)

to determine a new equilibrium that would stabilize in an appropriate time.

The presented assumption forms the basis of the two prognostic models discussed in the following chapters.

3.1. Prognostic model T ("temperature model")

The model has been constructed to asses the quantitative changes of photosynthesis parameters ensuing from the alteration of the sea water temperature at constant other factors limiting the photosynthesis. Particularly the total nitrogen concentration N_T is constant:

$$N_T = N_{inorg} + N_{org} = const \tag{7}$$

but the magnitude of the two components N_{inorg} and N_{org} may vary.

Taking into account the above assumptions and using the diagrams in Figure 5 the changes of the chlorophyll a concentration Ba and of the primary production P_{opt} are possible to assess. This is achieved by a translation of the points on these diagrams parallely to the t axis; examples are given for a shifts in Figures 5A and 5B. The situation illustrates an ecosystem which at the initial state revealed the surface chlorophyll a concentration $Ba = 1.5\ mg/m^3$ and the optimal primary production $P_{opt,S} = 2\ mg \cdot C/m^3 \cdot h$ under the nitrogen content $N_T = 30\ \mu M/dm^3$ and $t_S = 4^oC$. Due to the temperature increase by 4 ^{o}C, to the final value of $t_f = 8^oC$, the primary production is assumed to reach the final value $P_{opt,f} = 5\ mg \cdot C/m^3 \cdot h$, while the chlorophyll content would not change $Ba_s - 1.5\ mg/m^3 = Ba_f$.

Thus, to predict the change of photosynthesis parameters using the T model it is necessary to know both the initial (t_s) and the final (t_f) temperature values and the concentration of the total nitrogen. The model is also applicable when only the initial concentration of inorganic nitrogen N_{inorg} is known. In such a case the N_T content is determined from the 2C diagram.

Practical application of T model for forecasting the ecosystem alterations resulting from the rise of the Earth temperature is limited, because in such highly complex system as the World Ocean any temperature changes are followed by alterations of other factors limiting the photosynthesis, including the nitrogen content. This problem is dealt with in the subsequent prognostic model $T - N$.

3.2. Prognostic model $T - N$ ("temperature–nitrogen model")

The model has been constructed to assess the quantitative changes of the photosynthesis parameters resulting from the simultaneous changes of the sea water temperature and the total nitrogen content N_T. The prognosis is achieved by appropriate translations between the starting points $Ba_s(t_s, N_{T,s})$, $P_{opt,s}(t_s, N_{T,s})$ and the final points $Ba_f(t_f, N_{T,f})$, $P_{opt,f}(t_f, N_{T,f})$ on the diagrams in Figure 5. Exemplary translation is illustrated by segments B in Figure 5. The translation corresponds to the assumed conditions of the rise of temperature and a double decrease of nitrogen concentration N_T. Under such circumstances the final state of the ecosystem is characterized by the following photosynthesis parameters: $Ba_f \approx 3.5\ mg/m^3$, $P_{opt,f} = 10\ mg \cdot C/m^3 \cdot h$, differing from those obtained in model T.

Should the practical application of the $T - N$ model be possible, it has to include an assumption of variable nitrogen concentration.

3.3. Relation between the optimal and the global primary production of the sea

Before bringing out the problem of practical results of the forecasting it is worth to consider the relation between the optimum primary production P_{opt}, in a unit volume at the optimum depth z_{opt}, and the global primary production value P_{glob} in the entire water column under a unit area. Prognostic models T and $T - N$ render possible solely the estimation of the P_{opt} alterations. However, the statistical analysis presented in the article by Woźniak (in prepared) have pointed out the relation between both these forms of primary production as an approximate equation:

$$P_{glob} = const \cdot (P_{opt})^{1/2}. \tag{8}$$

This relation extends the results of the prognostication to the global productivity P_{glob} of the marine ecosystem. This parameter is more representative for the evaluation of the total productivity of marine ecosystem than P_{opt}.

3.4. Assumptions and extent of the prognosis

The effect of the Earth temperature alterations on marine ecosystems is complex. Besides the direct influence, temperature is related to other factors limiting photosynthesis. Quantitative definition of these relations is impossible at the present and the article does not attempt to do it.

However, it is inevitable that the irregular anticipated rise of the Earth's temperature in the future decades is going to reduce the temperature discrepancy between air and the World Ocean (smaller at the equator regions and greater at the poles). The result would be the global decrease of the dynamic activity of both the environments. Since this dynamics is responsible for nitrogen transportation to the euphotic zone of sea (Koblentz-Mishke, 1977), the subsequent decrease in nitrogen content of the World Ocean seems very probable. This effect has been included in the prognosis.

The prognosis has been carried out using both the T and the $T-N$ models. In both the cases the assumed temperature rise is $\Delta t = 3^oC$, *i.e.* the value anticipated in the middle of the next century (Kellogg, 1988). Moreover, in the case of the $T-N$ model, considering the above arguments, the decrease in nitrogen concentration is assumed. The calculations are provided for the total nitrogen concentration equal to half of the present value, *i.e.* $N_{T,f} = 0.5 \cdot N_{T,s}$. The value has been admitted á priori without any quantitative evidence. The prognosis has been prepared for a wide biological variety of natural seas. Particular attention has been drawn to the regions of the Polish deep sea fishery exploration. The most important results of the forecasting are presented in two subsequent chapters.

3.5. Results of prognosis in various regions of the World Ocean

The determination included percent change of the optimum primary production

$$\varepsilon_{opt}(\%) = \frac{P_{opt,f} - P_{opt,s}}{P_{opt,s}} \cdot 100. \tag{9}$$

Moreover, using ε_{opt} and equation (8) global primary production (P_{glob}) alterations ε_{glob} have been calculated from the equation:

$$\varepsilon_{glob}(\%) = \left[\left(\frac{\varepsilon_{opt}}{100} + 1\right)^{1/2} - 1\right] \cdot 100. \tag{10}$$

The results of ε_{opt} and ε_{glob} obtained with the application of both the models (T and $T-N$) for basins of various initial temperatures and nitrogen concentration are shown in Figures 6 and 7. The Figures illustrate

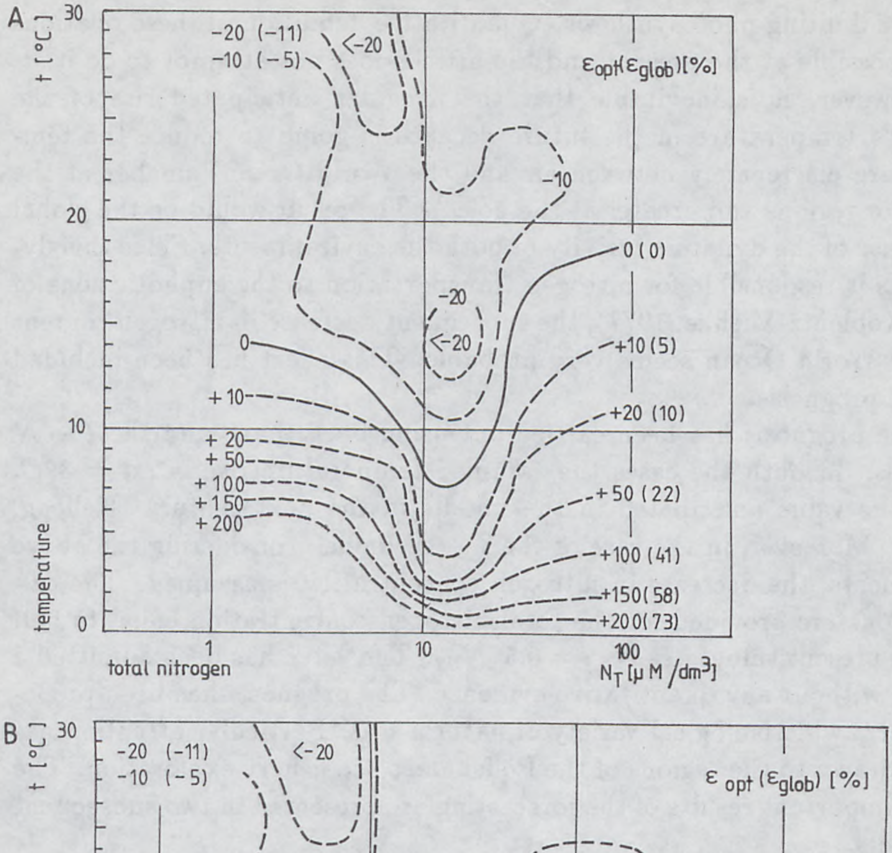
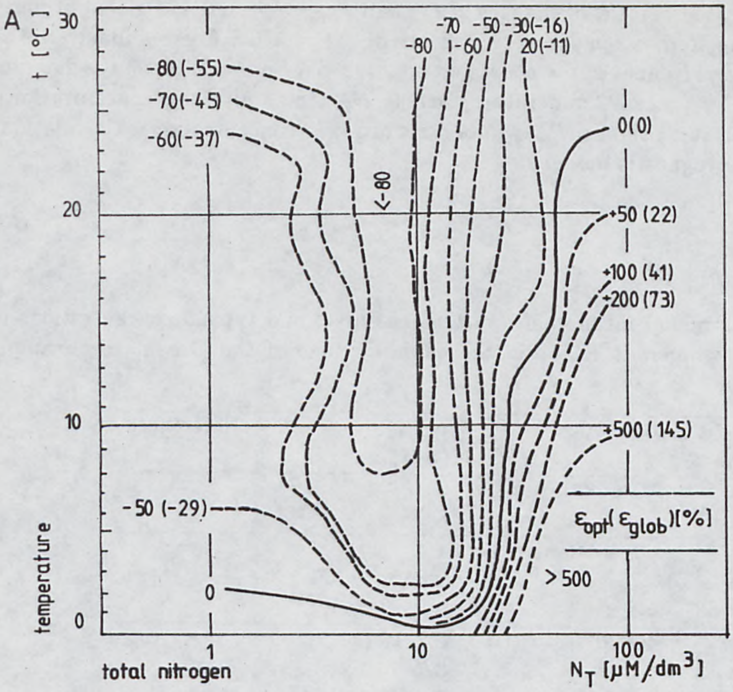

A
t [°C]
temperature
total nitrogen
N_T [μM/dm³]
$\varepsilon_{opt}(\varepsilon_{glob})$[%]
-20 (-11)
-10 (-5)
<-20
-10
0 (0)
-20
<-20
0
+10 (5)
+10
+20 (10)
+20
+50
+100
+150
+200
+50 (22)
+100 (41)
+150 (58)
+200 (73)
B
t [°C]
temperature
inorganic nitrogen
N_{inorg} [μM/dm³]
$\varepsilon_{opt}(\varepsilon_{glob})$ [%]
-20 (-11)
-10 (-5)
<-20
10
0 (0)
-20
<-20 (-11)
0
+10 (5)
+10
+20 (10)
+20
+50
+100
+150
+200
+50 (22)
+100 (41)
+150 (58)
+200 (73)

Figure 6: Prognosticated percent of changes of ε_{opt} and ε_{glob} – optimal and global primary production – ensuing from a temperature increase of $\Delta t = 3^oC$. Figures illustrate the approximate location of isolines $\varepsilon_{opt} = const$ and $\varepsilon_{glob} = const$ (in brackets) on the diagram of correlations: A – t (actual temperature) versus N_T (total nitrogen concentration); B – t (actual temperature) versus N_{inorg} (inorganic nitrogen concentration). Calculations performed with the prognostic model T

Table 1: The actual annual mean values of temperature t and typical concentrations of inorganic nitrogen compounds N_{inorg} in the euphotic zone of the Ocean, the example being the Atlantic

Region	Biologic type	Latitude	t (^{o}C)	N_{inorg} ($\mu M/dm^3$)	References
Arctic	E	70–60^{o}N	3	2	*
	M			8	
Subarctic	E	60–40^{o}N	11	1	*
	M			2	
	O			6	
Northern subtropical	E	40–20^{o}N	19	5.7–18 (11.9)	**
	M			0.7–6 (3.4)	
	O			0.48–2.25 (1.3)	
Northern tropical	E	20–10^{o}N	26	8.7–27 (17.9)	**
	M			0.7–6 (3.4)	
	O			0.35–1.25 (0.8)	
Equastorial	E	10^{o}N–10^{o}S	27	2.7–13 (7.9)	**
	M			0.7–6 (3.4)	
	O			0.31–1.25 (0.8)	
Southern tropical	E	10–20^{o}S	25	10.7–32 (21.4)	**
	M			0.7–6 (3.4)	
	O			0.31–1.25 (0.8)	
Southern subtropical	E	20–40^{o}S	20	10.6–30 (20.3)	**
	M			0.7–14 (7.4)	
	O			0.31–1.25 (0.8)	
Subarctic	O	40–50^{o}S	10	5.11–10.35 (7.75)	**
Antarctic	M/O	50–70^{o}S	1.3	20.11–25.7 (23)	**

E – eutrophic basins (of high productivity)
M – mesotrophic basins (of moderate productivity)
O – oligotrophic basins (of small productivity)
* – Burkaltseva and Ponomareva, 1976 (N_{inorg} data)
** – Ivanenkov *et al.*, 1979 (variability ranges and mean values)


A
t [°C]
temperature
30
20
10
0
-80 (-55)
-70 (-45)
-60 (-37)
-50 (-29)
0
-70 -50 -30(-16)
-80 -60 20(-11)
<-80
0(0)
+50 (22)
+100 (41)
+200 (73)
+500 (145)
$\varepsilon_{opt}(\varepsilon_{glob})$[%]
>500
1
10
100
total nitrogen
N_T [μM/dm^3]

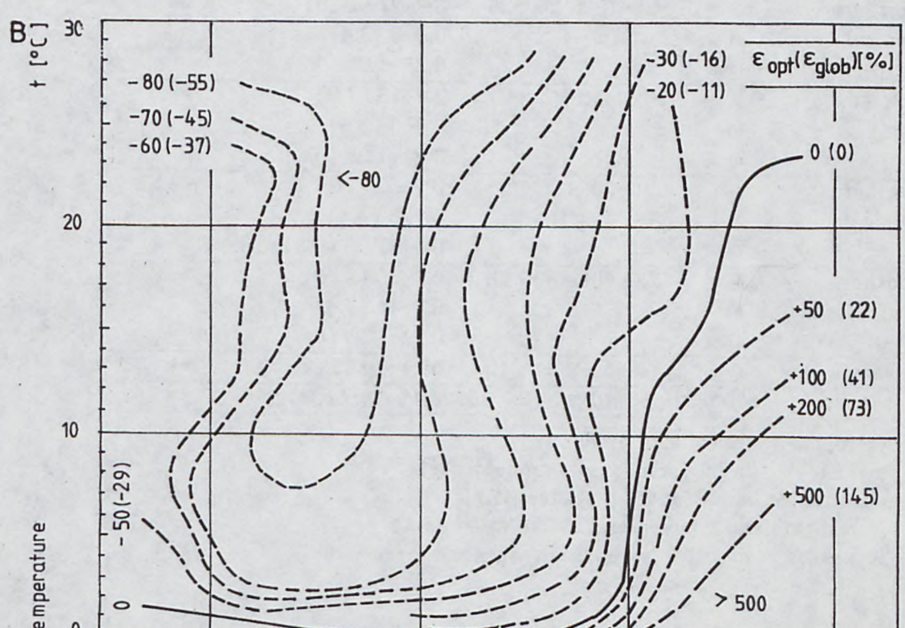

B
t [°C]
temperature
30
20
10
0
-80 (-55)
-70 (-45)
-60 (-37)
-50 (-29)
0
<-80
-30 (-16)
-20 (-11)
$\varepsilon_{opt}(\varepsilon_{glob})$[%]
0 (0)
+50 (22)
+100 (41)
+200 (73)
+500 (145)
>500
0.1
1
10
100
inorganic nitrogen
N_{inorg} [μM/dm^3]

Figure 7: Prognosticated percent of changes of ε_{opt} and ε_{glob} – optimal and global primary production – ensuing from a simultaneous temperature increase of $\Delta t = 3^oC$ and nitrogen concentration decrease to the halved level, $N_{T,f} = -0.5 N_{T,s}$: A – t (actual temperature) versus N_T (total nitrogen concentration), B – t (actual temperature) versus N_{inorg} (inorganic nitrogen concentration). Calculations performed with the prognostic model $T - N$

Table 2: Prognosticated (due to a temperature increase by 3°C) percent of ε_{opt} and ε_{glob} alterations (optimal and global primary production) in the Ocean, the example being the Altantic

Region	Biological type	Latitude	Model T		Model $T-N$	
			$\varepsilon_{opt}(\%)$	$\varepsilon_{glob}(\%)$	$\varepsilon_{opt}(\%)$	$\varepsilon_{glob}(\%)$
Arctic	E	70–60°N	+15	+8	-55	-33
	M		+40	+18	-17	-8
Subarctic	E	60–40°N	-13	-6.5	-72	-47
	M		-15	-8	-23	-40
	O		-4	-2	-25	-13.5
Northern subtropical	E	40–30°N	-7.5	-3.8	-25	-13.5
	M		-19	-8	-52	-31
	O		-15	-8	-70	-45
Northern tropical	E	20–10°N	-8	-4	-19	-10.5
	M		-4	-2	-68	-43.4
	O		-21	-12	<-80	<-55
Equatorial	E	10°N–10°S	-6	-3	-50	-29
	M		-4	-2	-72	-47
	O		-22	-12.5	<-80	<-55
Southern tropical	E	10–20°S	-9	-4.5	-18	-8
	M		-12	-6	-29	-15.5
	O		-15	-7.5	-80	-55
Southern subtropical	E	20–40°S	-8	-4	-16	-7
	M		-12	-6	-29	-15.5
	O		-15	-7.5	-80	-55
Subantarctic	O	40–50°S	+4	+2	-18	-8
Antarctic	M/O	60–70°S	+170	+64	>+500	>+145

E – eutrophical basins (of high productivity)
M – mesotrophical basins (of moderate productivity)
O – oligotrophical basins (of low productivity)

the isolines $\varepsilon_{opt} = const$, $\varepsilon_{glob} = const$ on t versus N_T and t versus N_{inorg} diagrams.

It is clearly marked that the anticipated alterations of primary production depend seriously on the initial conditions of the ecosystem and vary according to the ecosystem temperature and nitrogen concentration. The ensuing alterations can consist both in an increase of primary production (positive ε_{opt} and ε_{glob}) or in its decrease (negative ε_{opt} and ε_{glob} values).

A considerable increase of the productivity level can be expected in cool seas with high nitrogen concentration, while in the case of warm basins poor in nitrogen, that is of small productivity, a reduction of productivity to an even lower level has to be anticipated. The smallest alterations of photosynthesis (or even none) will appear in cool ecosystems with moderate nitrogen content and in warm basins of high nitrogen concentrations.

As regards the magnitude of productivity alterations assessed in the temperature model T and the temperature–nitrogen model $T - N$, the tendencies do not differ. Usually the absolute values of ε_{opt} and ε_{glob} are greater in the $T - N$ model. This is due to the assumed relatively serious, probably greater than in reality, decrease in nitrogen content in water, thus the $T - N$ model determines the upper limit of the possible productivity alterations. On the other hand, the values of ε_{opt} and ε_{glob} calculated using the T model give the lower limit.

Table 2 presents geographical location of the anticipated primary production alterations in ecosystems of various productivity, the example being the Altantic Ocean. The calculations have been carried out using literature data on temperature and nitrogen concentration listed in Table 1.

It follows from Table 2 that the increase in primary production can be anticipated in oligotrophic and mesotrophic regions of the Ocean, that is at high lattitudes (Antarctic and Arctic). The productivity level can increase by several tens or even hundred percent, while in majority of the Ocean regions, at middle and low lattitudes (40^oN – 40^oS), the decrease in productivity is very likely. This decrease will happen in various types of ecosystems – oligotrophic, mesotrophic and eutrophic as well. The estimated lower limit of the decrease (according to the T model) would be $\varepsilon_{glob} \approx -2 \div -12.5\%$, the upper one (according to the $T - N$ model) $\varepsilon_{glob} \approx -8 \div -55\%$.

3.6. Prognosis of photosynthesis alterations in regions of the Polish deep-see fishery fleet operations

The main regions of the Polish deep-see fishery fleet operations are located as follows (personal communication by Z. Russek, Sea Fisheries Institute, Gdynia):

Region I ($\varphi \approx 49^o$S – 54^oS, $\lambda \approx 56^o$W – 63^oW) – in the southern Atlantic, in the area of the Falklands.

Region II ($\varphi \approx 55^o$N – 58^oN, $\lambda \approx 173^o$E – 173^oW) – in the northern Pacific, in the Bering Sea.

Considering the chart of mean values of primary production distribution in the World Ocean and the biological classification of the seas according to Koblentz-Mishke (1977), region I – with the mean production $P_{glob} > 500\ mg \cdot C/m^3 \cdot d$ belongs to highly productive, eutrophic ecosystem, while region II classifies as a mesotrophic basin – with the mean primary production P_{glob} in the range from 150 to 250 $mg \cdot C/m^3 \cdot d$. Mean chlorophyll *a* content in the surface water layer of the regions is equal to (Mordasova, 1976) $Ba \approx 1.5 - 2\ mg/m^3$ in region I and $Ba \approx 1\ mg/m^3$ in region II. At present, both the regions meet the fishery requirements.

The prognosis of photosynthesis parameters alterations due to the rise of the Earth temperature has been carried out for both regions taking

Table 3: The determined prognosis parameters

Contents	Region I (s. Atlantic) 49°S–54°S	56°W–63°W	Region II (Bering Sea) 55°N–58°N	173°E–173°W
	model T	model $T-N$	model T	model $T-N$
Percent of primary production changes				
$\varepsilon_{opt}(\%)$	+18	+40	+57	+400
$\varepsilon_{glob}(\%)$	+9	+18	+25	+124
Present production $P_{glob,S}(mg \cdot C/m^2 \cdot d)$	> 500		~ 200	
Anticipated production $P_{glob,f}(mg \cdot C/m^2 \cdot d)$	> 541	> 590	~ 250	~ 442
Present chlorophyll *a* concentration $Ba_s(mg/m^3)$	~ 1.7		~ 1.0	
Anticipaded chlorophyll *a* concentration $Ba_f(mg/m^3)$	~ 1.45	~ 2.0	~ 1.2	~ 2.1

into account the actual values of main abiotic factors, *i.e.* sea water temperature and nitrogen content. The annual mean temperatures of the euphotic zone have been estimated after Gershanovich and Muromcev (1982), the respective values being $t \approx 7.8^oC$ in region I and $t \approx 5.4^oC$ in region II. Nitrogen concentrations $N_{inorg} \approx 12\ \mu M/dm^3$ (I) and $N_{inorg} \approx 30\ \mu M/dm^3$ (II) have been estimated after Ivanenkov *et al.* (1979). The determined prognosis parameters are given in the Table 3. In both regions an increase in productivity is anticipated, particularly marked in region II – the Bering Sea.

The presented results prognosticate good future catches in both the regions of the Polish deep-sea fishery fleet operations, provided that there does not appear a factor (*e.g.* of a local character) limiting the biological productivity that has not been taken into account in this modelling.

4. Final remarks

It is necessary to emphasize some defects and limitations in interpretation and practical use of the results presented in this article.

Statistical analysis of the relation between the photosynthesis parameters AN_{max}, Ba and P_{opt} and temperature t and inorganic nitrogen content N_{inorg} in natural environment has been carried out using the results from about 1000 measurement stations situated in various regions of the World Ocean. This number of data – considering technical difficulties in data acqusition and the complexity of the experimental data – is relatively high. Nevertheless it is far from satisfactory, especially as regards the small number of observations under particular biotic conditions – the least precise are the statistic shapes of the analysed relations in the following regions:

- in the region of low temperature ($t < 15^oC$) and small nitrogen concentration ($N_{inorg} < 0.3\ \mu M/dm^3$),
- in the region of moderate and high temperature ($t > 15^oC$) and high nitrogen concentration ($N_{inorg} > 3\ \mu M/dm^3$).

Thus, the isolines $AN_{max} = const$, $Ba = const$ and $P_{opt} = const$ on the diagrams t versus N_{inorg} (Fig. 4) should be regarded only as a qualitative description. Their quantitative credibility (generally, at the two presented ranges of t and N_{inorg}) is lower.

The relationship between the photosynthesis parameters and temperature and total nitrogen concentration N_T has been determined indirectly by shifting from the variable N_{inorg} to the variable N_T with the use of the diagram in Figure 2B. Theoretically, the credibility of the isolines Ba and P_{opt} on the diagrams t versus N_T (Fig. 5) equals, at the utmost, that of the isolines in Figure 4, but in reality it is much lower because of the rough approximation of the relation between N_{inorg} and N_T.

Needless to say, to get better precision of the results as regards the relation between the photosynthesis parameters and temperature and various forms of nitrogen (N_{inorg} and N_T) it is necessary to acquire greater number of experimental data from various regions of the World Ocean.

Since the results presented in this article, prognosticating the impact of the Earth warming up on the photosynthesis parameters in the World Ocean, have been based on statistical correlations $P_{opt} = f(t, N_T)$ and $Ba = f(t, N_T)$, the inaccuracies of these correlations are propagated to the results of prognosis. Additional errors of the forecasted photosynthesis parameters arise from adopting the inaccurate actual values of the abiotic factors (temperature and nitrogen concentration) as the initial data in the prognostic models.

Moreover, there has been a number of limitations and simplifications in both models (T and $T-N$), because in the T model only the effect of temperature has been considered, in the $T-N$ model – only the impact of temperature and nitrogen concentration, while the influence of the other biotic factors directly or indirectly limiting the marine photosynthesis has been omitted. Neither the prognosis of the nitrogen concentration change has been conducted. Instead, the magnitude of this change has been asigned á priori not having been even precisely estimated. To overcome in the models the mentioned difficulties would require additional experiments and detailed explanatory models anticipating the influence of temperature on various oceanological processes. In particular, the most important seems to be the analysis of air and water masses dynamics, that is the results determining the nitrogen and other nutrients concentration. The effect of climate changes over the continents has also to be taken into account, since they direct the inflow of various substances from land to sea. In this aspect the melting of glaciers, resulting in dislocation of the shorelines and alteration of the surface salinity of the Ocean, must be evaluated. Similarly important, though requiring different solutions, seems the prognostication of the productivity changes in regions exposed to a significant continental influence, *e.g.* in closed and semiclosed seas or bays, where photosynthesis may be limited by a variety of complex local factors.

In recapitulation, the results presented in this article of prognosing the effect of the Earth warming up on the productivity of the World Ocean are of the initiatory character.

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