43

ECOPHYSIOLOGY OF PHYTO- AND BACTERIOPLANKTON GROWTH IN THE PRYDZ BAY AREA DURING THE AUSTRAL SUMMER 1987

Part I : Modelling phytoplankton growth

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ABSTRACT

A model of phytoplankton growth based on the knowledge of phytoplankton physiology and vertical mixing of surface waters was applied in the Prydz Bay during end-summer 1987. Physiological parameters of the model were experimentally estimated by means of kinetics of phytoplanktonic activities, measurements combining radiotracer technology and classical biochemical methods. Their control by temperature was outlined. It was found that phytoplankton cells of the Prydz Bay were able to grow at their maximal rate between + 2°C and 12°C. An exponential dependence on temperature was however observed in the range -1.8°-+ 2°C. Comparison between field data and predictions of the model run for the different growing conditions encountered by the cells during end-summer in the Prydz Bay indicated that growth and physiological death of phytoplankton were well balanced resulting in no net increase of biomass at this end-summer period. Finally additional runs of the model under the extreme growing conditions of Antarctic phytoplankton has shown that the major trends of variations in phytoplankton biomasses could be predicted by the model.

INTRODUCTION

Among the potential resources of Antarctica its marine living resources are generally considered as those which could possibly lend themselves the best to economic exploitation. The proverbial richness of the Southern Ocean originates from the observation of tremendous biomasses of krill, whales, seals and birds. This *richness* seems however paradoxical since primary production and phytoplankton biomasses as low as in oligotrophic oceanic

regions were generally reported in the Southern Ocean in spite of high macronutrients concentrations (see the review by El-Sayed, 1987). It seems therefore difficult to explain how biomass of higher trophic levels can be sustained by oceanic primary production without appealing to other source of phytoplankton biomasses. Indeed some spectacular phytoplankton blooms were occasionally located within the marginal ice zone (El-Sayed, 1971, Smith and Nelson, 1986) and in sea ice microhabitats (Whitaker, 1977, Garrison et al, 1986, Mc Grath Grossi et al, 1987). The enhanced vertical stability of the surface layer resulting from the physical properties of both these particular phytoplankton habitats provides a stable environment with light levels favorable for phytoplankton growth in such a way that biomasses, as high as 190 and 200 μg Chla.l^{-1}, were occasionally recorded within the marginal zone (El-Sayed, 1971) and sea ice (Whitaker, 1977) respectively.

Impact of ice edge blooms could be very important as the extent of the marginal zone covers a wide area. Its contribution to overall primary production is still difficult to evaluate because these blooms are space and time-limited, depending on meteorological conditions. However, preliminary estimates based on occasional primary production field data and on rates of ice retreat indicate that ice edge primary production would increase of more than 60 % the present estimate of Antarctic primary production (Smith and Nelson, 1986).

Also, how much is the contribution of sea ice phytoplankton production is an important question that cannot be answered presently because both the physical and chemical ice habitat and the physiology of ice phytoplankton are still not well known (Garrison et al, 1986).

Because of the variety of habitats in Antarctica (ice, melting ice, oceanic water), accurate estimate of overall primary production should only be provided by means of predictive mathematical model which would take into account the physiology of phytoplankton and its interaction with its habitat. Such a model was developed for temperate coastal waters (Lancelot et al, 1986, submitted). Its applicability to Antarctic environments was tested during an end-summer cruise conducted in the Prydz Bay where the physiological parameters of the above model were experimentally determined.

MATERIAL AND METHODS

Studied area

Sampling stations were visited in the Prydz Bay from February the 14th to March the 23th, 1987. Bathymetry and hydrography of the Prydz Bay are well described in Smith et al (1984). Samples were collected at sunrise at each station from 5 m. depth with a pump. Samples for phytoplankton measurements were stored in the dark at *in situ* temperature until being used. In addition, at those stations where C.T.D. drops were carried out, samples were collected with polyethylene Niskins bottles at 0, 25, 50, 75, 100, 125 and 150 m.

Physical measurements

Vertical structure of the water column was determined for each station from the continuous record of temperature and salinity down to 600 m or the the bottom when shallower. Light profiles were determined by means of an underwater cosine quantum Li-Cor. The vertical light attenuation coefficient was calculated following the Beer Lambert's law. Incident photosynthetically active radiation (P.A.R.) was measured by means of another Li-Cor sensor set up on the superior deck of the ship. Relative losses occuring at sea surface were determined by measurements of incident P.A.R. just above and below the sea surface.

Phytoplankton cellular constituants and activities

Phytoplankton cellular constituants were estimated by regression analysis of measurements of particulate protein, carbohydrates and lipids on chlorophyll a concentrations. Experimental procedures are described in Lancelot-Van Beveren (1980).

Phytoplankton activities -photosynthesis, growth, respiration, excretion- were determined by means of a mathematical model based on elementary cellular biochemistry. This model assumes that synthesis of functional cellular constituants (F)(composed or 80 % of proteins) constitutes the best index of cellular growth. Theoretical basis and experiments supporting it are

described in Lancelot et al (1986, submitted).

The structure of the model is illustrated by the diagram of Fig. 1. Three pools of cellular constituants were considered on basis of their biological function : the functional and structural macromolecules F, the reserve products R, composed of lipids and polysaccharides and the small metabolites S, precursors for macromolecules synthesis. Mathematical equations that describe the metabolic processes of their synthesis and catabolism, symbols and units of parameters and variables involved in the equations are listed on Table I.

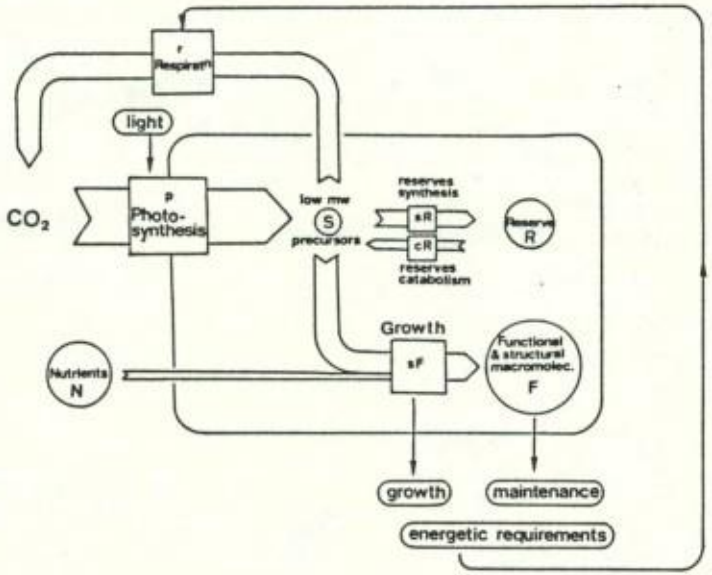

Figure 1 : Diagrammatic representation of phytoplankton cellular constituants and metabolic activities.

Experimental determination of the parameters was carried out based on two kinds of experiments combining radiotracer technology and classical biochemical procedures.

Table I : Mathematical model of phytoplankton growth.

Equations

$$sF = \mu max \cdot \frac{N}{KN + N} \cdot \frac{S}{KS + S} \cdot F \qquad (1)$$

$$p = kmax \cdot \left(1 - \frac{\alpha I}{kmax}\right) \cdot e^{\frac{-\beta I}{kmax}} \cdot B \qquad (2)$$

$$e = P.E.R. \cdot p \qquad (3)$$

$$sR = \ell max \cdot \frac{S}{KS + S} \cdot R \qquad (4)$$

$$cR = KR \cdot R \qquad (5)$$

$$r = (MAINT \cdot F) + (CESP \cdot sF) \qquad (6)$$

Variables and parameters : symbols and units

Variables	Symbols	Unit
Cellular biomass	B	$\mu gC.l^{-1}$
Functional macromolecules	F	$\mu gC.l^{-1}$
Reserve macromolecules	R	$\mu gC.l^{-1}$
Precursors	S	$\mu gC.l^{-1}$
External nutrients	N	$\mu mole.l^{-1}$

Parameters

Photosynthetic capacity	α	$h^{-1}\ (\mu E.m^{-2}.sec^{-1})^{-1}$
Maximal specific rate of photosynthesis	kmax	h^{-1}
Index of photoinhibition	β	$h^{-1}\ (\mu E.m^{-2}.sec^{-1})^{-1}$
Percentage of excretion	P.E.R.	dimensionless
Maximal specific rate of R synthesis	ℓmax	h^{-1}
Constant of R catabolism	KR	h^{-1}
Maximal specific rate of F synthesis	μmax	h^{-1}
Half-saturation constant of N assimilation	KN	$\mu mole.l^{-1}$
Half-saturation constant of S assimilation	KS	$\mu gC.l^{-1}$
Constant of maintenance of basal metabolism	MAINT	h^{-1}
Energetic costs for F synthesis	CESP	dimensionless

(i) the experimental determination of photosynthetic parameters involved short-term ^{14}C incubation - Steemann-Nielsen standard method - performed at different light intensities. Photosynthetic parameters kmax, α, β were then statistically estimated by means of Platt et al (1980)'s equation.

(ii) the experimental determination of growth parameters was performed by mathematical adjustment based on the results of long-term kinetics of ^{14}C assimilation into 4 pools of cellular constituants easily separable by simple biochemical procedures: lipids, small metabolites, polysaccharides and proteins (see below).
^{14}C incubation were carried out in a thermostatic growth cabinet illuminated by artificial light (maximal P.A.R. = 135 $\mu E.m^{-2}.sec.^{-1}$). Experimental procedure and biochemical fractionation are those described in Lancelot and Mathot (1985).

RESULTS AND DISCUSSION

End-summer phytoplankton in the Prydz Bay : level and growing conditions

Chlorophyll a concentrations measured during February-March 1987 in the Prydz Bay and in the northern open waters are reported on Fig.2a. Significantly higher concentrations were measured in shelf waters although chlorophyll a concentrations were very low offshore in agreement with data generally reported for this area (Painting et al, 1985; Fukui et al,1986). On the other hand vertical mixing (Fig 2b) was less intense in the coastal area suggesting an inverse correlation between the two variables. Temperature was found to range between -1.8° and + 2°C and nutrients concentrations were far above saturation.

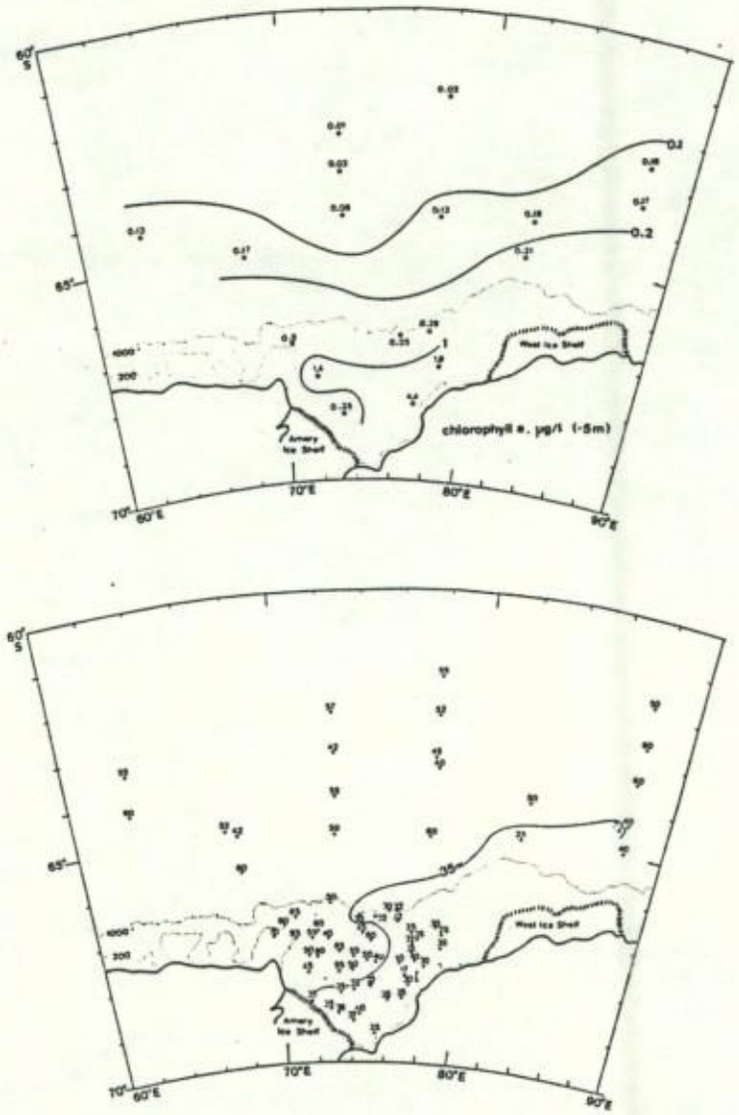

Figure 2 : Spatial distribution of a) chlorophyll a concentrations and b) depths of the mixed layer in the Prydz Bay during February-March 1987.

Physiological parameters of the model and their control by temperature

Fig. 3ab shows an example of the experimental determination of the parameters that characterize respectively photosynthesis and phytoplankton growth processes. Values of parameters and initial conditions are reported on Table II.

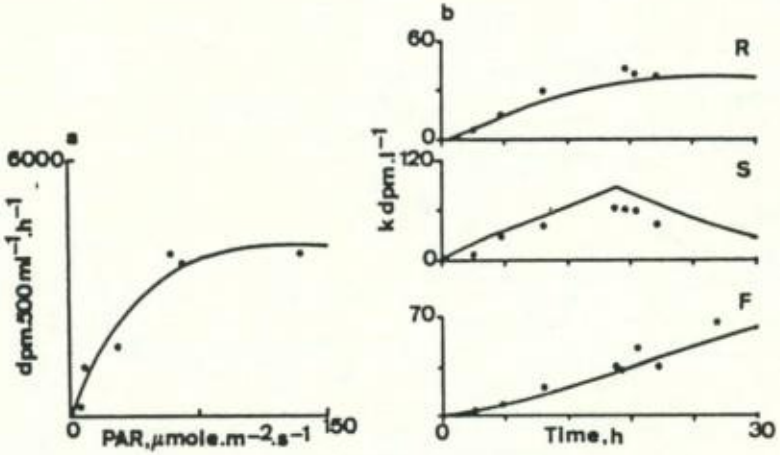

Figure 3 : Physiological characteristics of a phytoplanktonic community sampled at 64°04S, 91°29E on February 15th 1987 :
a. Relationship between photosynthesis and light
b. Kinetics of ^{14}C assimilation into R, S and F cellular phytoplanktonic constituants during a 17 : 7 light:dark cycle : prediction curves and experimental data.

Examination of Fig.3 indicates good agreement between the prediction of the model and the experimental data relative to the assimilation of ^{14}C into R, S and F cellular constituants. Validation of the model used for calculating phytoplankton daily growth was provided by Fig. 4 which shows results from several runs of the model using identical sets of parameters for different photoperiods along with the corresponding experimental data.

Table II : Initial conditions and physiological parameters characteristical of a phytoplankton community sampled in February 1987 at station 64°04S, 91°29E.

Initial conditions			Parameters	
F	311	µgC.l⁻¹	α	1.6.10⁻⁴ h⁻¹.(µE.m⁻².sec⁻¹)⁻¹
R	0.5	"	kmax	9.10⁻³ h⁻¹
S	16	"	ρ	10⁻³ h⁻¹ (µE.m⁻².sec⁻¹)⁻¹
N	13	µmole.l⁻¹	P.E.R.	0.05
			KR	0.12 h⁻¹
			µmax	8.10⁻³ h⁻¹
			KN	4 µmole.l⁻¹
			KS	15 µgC.l⁻¹
			MAINT	10⁻³ h⁻¹
			CESP	0.32

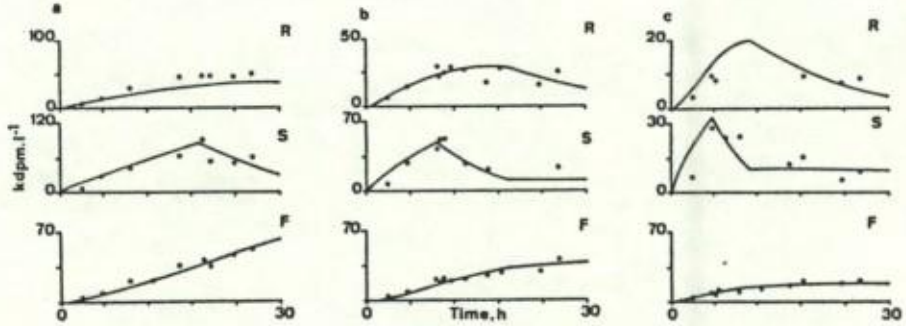

Figure 4 : Kinetics of ^{14}C assimilation into R, S and F cellular constituants during
a. 19: 5 light:dark cycle
b. 10:14 light:dark cycle
c. 6:18 light:dark cycle

Parameters of the model were determined for different stations in the Prydz Bay and their control by temperature was investigated. This environ-

mental variable controls mostly three parameters : the maximum specific photosynthesis kmax, the maximum specific growth rate μmax and the maintenance constant MAINT.

Two types of adaptations to temperature were considered as recommended by Precht (1958) : Resistance adaptation, on one hand, which refers to mechanisms that determine the upper and lower temperature extremes limiting growth, and capacity adaptation, on the other, which occurs at temperature between the extremes and is described by a particular kinetics.

Resistance adaptation to temperature of end-summer phytoplankton of the Prydz Bay can be seen on Fig. 5ab which shows the dependence of kmax and μmax respectively for a range of temperature between -2 and + 21°C.

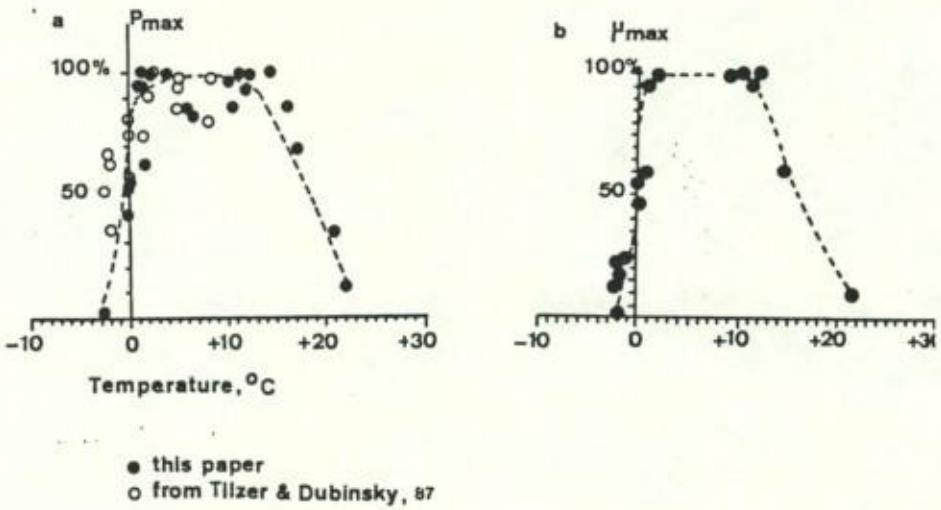

Figure 5 : Relationship between a) kmax and b) μmax and temperature : results expressed in % of maximal rate.

This figure shows clearly that end-summer Antarctic phytoplankton is able to photo-synthetize and grow at its maximal rate when temperature ranges between + 1 and 11°C, in agreement with Tilzer and Dubinsky's (1987) results. Below

and above these temperatures, kmax values decrease very sharply in agreement with similar data obtained by Neori and Holm-Hansen (1982) in the western Scotia Sea and Bransfield Strait.

Capacity adaptation to temperature on the other hand can be seen on Fig.6 which suggests an exponential dependence of kmax on *in situ* temperature.

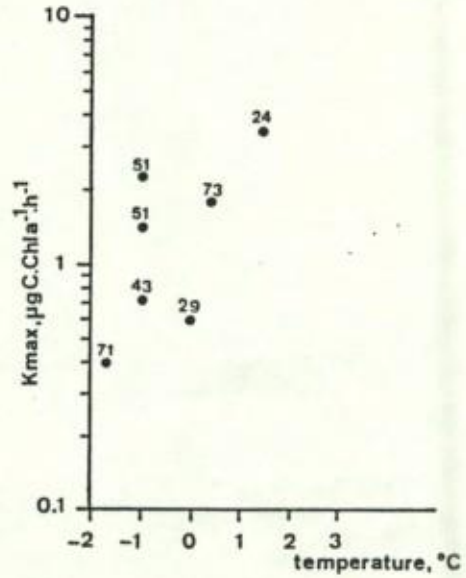

Figure 6 : Relationship between kmax and *in situ* temperature.

The maintenance constant is mostly determined by adjustement of experimental data as illustrated by Fig.3. Its dependence on temperature is therefore not obvious. However, under extreme temperature of - 1.8°C, maintenance could be estimated from the catabolism rate of storage products as deduced from data reported on Fig. 7. Indeed dark protein synthesis does not proceed at this low temperature and respiration ensures the only maintenance of basal metabolism.

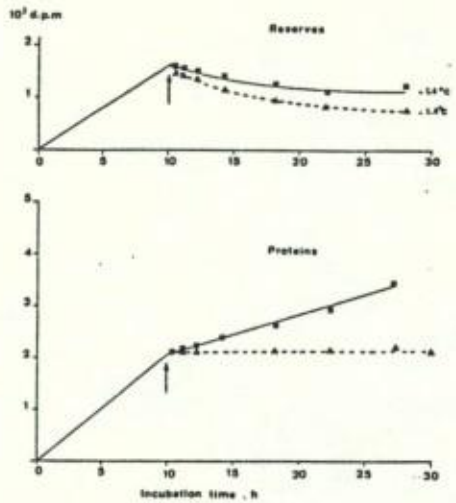

Figure 7 : Kinetics of ^{14}C dark assimilation into storage products and proteins by Prydz Bay phytoplankton incubated at + 1.6° and -1.8°C (dotted line). Previous photoperiod = 10 h.

Phytoplankton growth in the Antarctic environment

Vertical mixing is known to have an important impact on the environment experienced by phytoplankton cells (Lewis et al, 1984) and numerous authors now claim that extreme conditions of turbulence together with low temperature are at origin of the phytoplanktonic scarcity of Southern Ocean (Whitaker, 1977, El-Sayed and Taguchi, 1981, El-Sayed, 1984, 1987, Priddle et al, 1986). Inversely, the high vertical stability induced by melting waters contributes to provide high biomasses of phytoplankton in the marginal ice zone. Indeed following values of δ, the ratio between euphotic and mixing depth, phytoplankton will spend more or less time in the aphotic layer. Depending on its own physiology, phytoplankton will therefore grow, maintain, autocatabolize or ultimately die depending on the size of photosynthetized storage products i.e. the previous light history of the cells.

The control of phytoplankton growth by variations in intensity of

vertical mixing was established for an end-summer phytoplanktonic community of the Prydz Bay by means of the mathematical model previously described. Daily specific rates of growth and physiological death by phytoplankton were calculated by integration of equations gathered on table I on the variations of P.A.R. and on the depth down to the depth of the mixed layer. Values of parameters are those reported on table II. The model assumes in addition that vertical motion within the mixed layer is very fast, ensuring an identical light history to the whole phytoplanktonic community (cf. Lewis et al, 1984). Results of these calculations are illustrated by Fig. 8a.

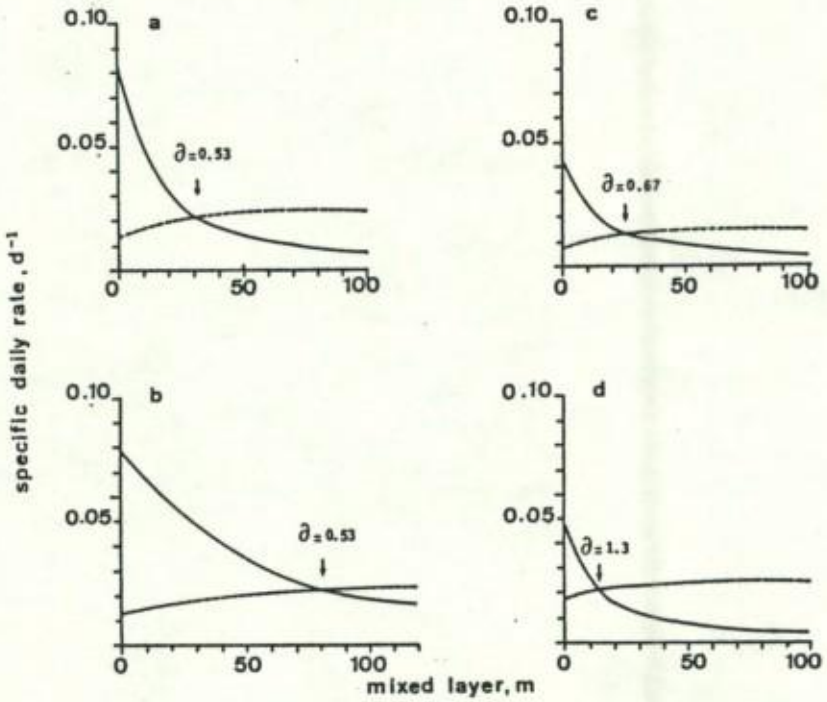

Figure 8 : Daily specific growth rate and physiological death (dotted line) calculated for different depths of the mixed layer under different growing condition

a) η = 0.29 m^{-1} photoperiod ϕ = 17 h T° 1°C.
b) η = 0.1 m^{-1} ϕ = 17 h T° 1°C
c) η = 0.29 m^{-1} ϕ = 13 h T° 1°C
d) η = 0.29 m^{-1} ϕ = 17 h T° -1.8°C

It shows that specific daily growth decreases exponentially when mixed layer becomes deeper, although specific daily physiological death increases slowly with depth and stabilizes as a consequence of the simultaneous decrease in phytoplankton biomass. The critical depth, i.e. the depth where growth compensates exactly physiological death on a daily average, occurs under these particular growing conditions at -30 m corresponding to a δ value of 0.53. Results from several runs of the model under different growing conditions as change in optical properties of the water column (Fig. 8b), changes in daily P.A.R. (Fig. 8c), decrease in temperature corresponding to decrease in kmax, μmax, MAINT (Fig. 8d) show that critical depth is determined by both the depth of the mixed layer, the optical properties of the water column and the physiology of phytoplankton. This constrasts with Sverdrup's (1953) hypothesis assuming a single control by vertical stability.

From these predictions and assuming that optical properties of the water column are mostly dependent on the biomass of phytoplankton and that the physiological characteristics of the phytoplanktonic community remain identical, it is possible to calculate the steady-state biomass of the phytoplankton community growing in a large range of mixed layers reproducing ice edge system on the one hand and oceanic one on the other. Results of these calculations as illustrated by Fig.9 show an asymptotical dependence of steady-state phytoplankton biomass on the depth of the mixed layer.

At shallow mixed layer as in marginal zone, steady-state biomass tends to fabulous concentrations of chl.a, in perfect agreement with the concentration of 190 μgChl.l^{-1} recorded by El-Sayed (1971) in surface waters of the Weddell Sea. Inversely at high depth of mixed layer, steady-state biomass tends to undetectable concentrations of chl.a as usually recorded in the oceanic area (cf. El-Sayed, 1987).

Validation of the mathematical model developed for prediction of phytoplankton growth was finally supported by Fig. 9b which shows comparison between prediction curves of steady-state biomass calculated for extreme conditions of temperature and light encountered by phytoplankton cells during end-summer in the Prydz Bay and the field data reported on Fig.2a. Perfect agreement between prediction curves and field data indicates that from a

physiological point of view growth and death of phytoplankton are well-balanced in the Prydz Bay during this end-summer period. No net increase of phytoplankton biomass should therefore be observed at this period.

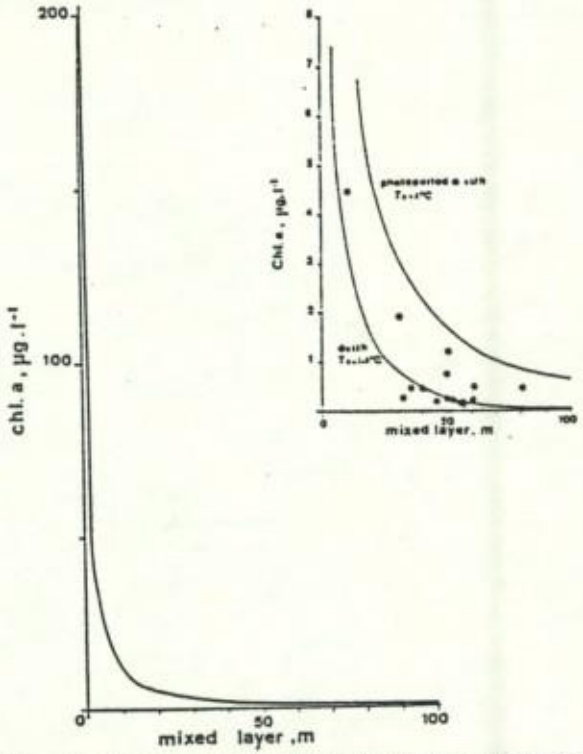

Figure 9 : Relationship between steady-state phytoplankton biomass and depth of the mixed layer.

CONCLUSIONS

Simulation experiments of phytoplankton growth described above indicate that we have developed a conceptual mathematical model of phytoplankton growth able to predict the major trends of the variations in Antarctic phytoplankton,

on basis of the knowledge of the growth physiology of phytoplankton and the vertical mixing of surface waters.

This model represents therefore an important tool for the overall estimate of primary production of the Antarctic ecosystems. Better knowledge of phytoplankton physiology in the different antarctic habitats (water, ice melting, ice) together with development of hydrodynamical models for the prediction of vertical mixing of surface waters and ice progression and retreating rates would allow to further refine this model. It will then permit a priori calculation of primary production in the different habitats, an information essential for the understanding of the ecological functioning of the Antarctic ecosystem. This will be the purpose of our future work on Antarctica phytoplankton.

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