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BELGIAN SCIENTIFIC
RESEARCH PROGRAMME
ON ANTARCTICA

SCIENTIFIC RESULTS OF PHASE ONE (OCT 85 - JAN 89)

edited by
S. CASCHETTO

VOLUME I

PLANKTON ECOLOGY

This volume presents the scientific results of researches in Plankton Ecology that were carried out from January 1986 to January 1989 in the framework of **Phase One** of the **Belgian Scientific Research Programme on Antarctica.**

Studies conducted in other fields addressed by the Programme form the subject of two additional volumes issued by the Science Policy Office (Vol. II: Marine Geochemistry and Marine Geophysics and Vol. III: Glaciology-Climatology).

The Programme was implemented through the decision of the Council of Ministers of 29 July 1985 with the aim at contributing to the betterment of the knowledge of the functioning of the Antarctic's marine ecosystems and of the role played by Antarctica and the Southern Ocean in global changes.

The studies are being carried on within **Phase Two** of the Programme that will ensure the pursuing and the development until December 1991 of the Belgian research effort.

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ECOPHYSIOLOGY OF PHYTO- AND BACTERIOPLANKTON GROWTH IN THE SOUTHERN OCEAN

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SUMMARY

Understanding the overall functionning of the Antarctic marine ecosystem at the first levels of the trophic web is required to evaluate the potential primary resources available for herbivores grazing and thus to assess the potential for krill exploitation.

An experimental approach has been developped for studying phyto– and bacterioplankton dynamics at a rather fine physiological level.

The control of phytoplankton photosynthesis and growth by light and temperature has been studied in details for the open sea and marginal ice communities. A conceptual model has been developped which is able to predict the major trends of variations of phytoplankton biomass and activity in Antarctic waters from the knowledge of the physical characteristics of the environment among which the stability of the water column was shown to be the most important factor. Application of this model to the different habitats of the Southern Ocean during late summer yields net primary production (phytoplankton growth) rates ranging between 20–25 $mgC.m^{-2}.d^{-1}$ in the open sea areas, and between 30–250 $mgC.m^{-2}.d^{-1}$ in the marginal ice zone. These are the first available estimations of net primary production in this ecosystem.

The dynamics of the microbial loop has been experimentally studied according to a similar approach, and a model of bacterioplankton development in response to phytoplankton has been elaborated. Although a much longer delay (about one month) exists between phytoplanktonic and bacterial development, the role of bacterial activity in utilizing primary produced organic matter was proven quantitatively as important in the Southern Ocean as it is in temperate marine systems.

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1. INTRODUCTION

1.1. GENERAL OBJECTIVES

Microbial processes at the first trophic levels largely determine the overall functioning of aquatic ecosystems, i.e. the way organic matter and biogenic elements flow through its main biological constituents.

Understanding the ecological functioning of the antarctic marine system (hence the microbiological processes involved) is important for both basic and applied purposes.

From a basic research point of view, the study of the Southern Ocean offers a unique opportunity for the ***validation of the methods and concepts developed in the study of temperate marine systems.*** The unique climatic and hydrological conditions prevailing under high latitudes indeed result in basic differences in the environmental control exerted on the biota. Nutrient limitation, for instance – a most important regulation mechanism governing the dynamics of temperate marine ecosystems – is seldom of application in the nutrient rich waters of Antarctica. Temperature is very low and does only vary within a narrow range. The light regime is very pecular, because seasonally episodic. Indeed, long dark period in winter contrasts with long summer period characterized with high light intensities. Moreover, even during summer period light limitation may sometimes result either from sea ice covering or from deep vertical mixing induced by storms prevailing most of the time at these high latitudes. Understanding the controls of organic matter circulation at the first trophic levels of the antarctic marine system is therefore a challenge for any general theory of the functioning of aquatic ecosystems. Conversely, insights into this peculiar ecosystem can help understanding some features of temperate ecosystems, particularly those receiving large inputs of nutrient.

From an applied point of view, on the other hand, understanding the functioning of the antarctic marine system is urgently required for allowing a rational management of its possible resources. Among these, the living ones are generally considered as those which lend themselves the best to economic exploitation. Since the late 18th century, intensive exploitation indeed took place. The first target was the large populations of seals, mainly hunted for the oil, which resulted, within about 50 years, to the quasi complete disappearance of seals from all accessible sites. Similarly, the development of whaling in the early 20th century led to the extinction of most big cetaceans in the Southern Ocean. It is now frequently claimed that the potential for krill fishing exceeds the total volume of the world fisheries (about 80 10^6T.yr^{-1} (fresh weight)). However, several basic features of the working of the antarctic marine ecosystem are still largely not understood, depriving such affirmations from any serious grounds. Owing to the fragility of the ecosystem, attested by the examples cited above, a carefull assessment of the potential resources of organic matter provided by the basis of the trophic web to herbivores, is required before starting any economic exploitation of these biological resources.

1.2. SPECIFIC OBJECTIVES AND STATE OF THE ART

Among the aspects of the ecological functioning of the antarctic marine ecosystem which are presently not well understood, three interrelated topics are particularly important :

(i) Primary production, although locally very high, is generally as low as in nutrient depleted open ocean areas, in spite of high macro–nutrients concentrations and sufficient light intensities. The factors controlling phytoplankton growth in the Southern Ocean are far from being completely understood.

(ii) The microbial loop, which, in most temperate marine systems, rapidly recycles a significant part of primary production, has not been intensively studied in the Antarctic seas. Some authors (Pomeroy & Deibel, 1986) claimed that bacterial activity in permanently cold environments is strongly reduced, leaving a larger part of primary production available for grazing by herbivores.

(iii) The surprisingly high biomass of secondary and tertiary consumers, quite noticeable even for the occasional observer, is at the origin of the proverbial richness of the Southern Ocean. According to the standards derived from our knowledge of temperate marine systems, it is presently difficult to explain how this biomass can be sustained on the primary production occurring in the antarctic ecosystem.

We address the first two of these questions with an approach based on *in situ* study of the processes controlling ***growth*** of phyto– and bacterioplankton, at a rather fine physiological level, trying to identify the mechanisms governing the rate of these processes. We will show in the conclusion of this report how the third question could be partly answered as a result of the combined answers to the two others.

1.2.1. Phytoplankton photosynthesis and growth

1.2.1.1. *The marine environment*

The very peculiar climatic and hydrological conditions prevailing in the antarctic ecosystem provide a unique physical and chemical environment for phytoplankton, affecting strongly its biology, distribution and abundance.

It is now well recognized that neither major nutrients (Franceschini, 1978; Hayes *et al.*, 1984; Koike *et al.*, 1986; Jacques, 1983; Maeda *et al.*, 1985) nor incident light intensity (El–Sayed, 1970, 1987; Aruga *et al.*, 1985) are limitant for phytoplankton growth in the Southern Ocean.

Examination of geographical distribution of phytoplankton biomass in the antarctic ecosystem (El–Sayed, 1987; Priddle *et al.*, 1986) indicates however that light regime resulting from the vertical stability of the water or ice column is the dominant factor controlling photosynthesis. It appears therefore that vertical stability, i.e. the hydrodynamic properties of the water column, plays a key rôle in determining phytoplankton activity and distribution.

From the point of view of phytoplankton dynamics, four distinct but interdependent habitats, largely variable in time and space, have to be considered in the antarctic marine system, as illustrated on Fig. 1. Biological activity and dominant phytoplankton species widely differ within these habitats.

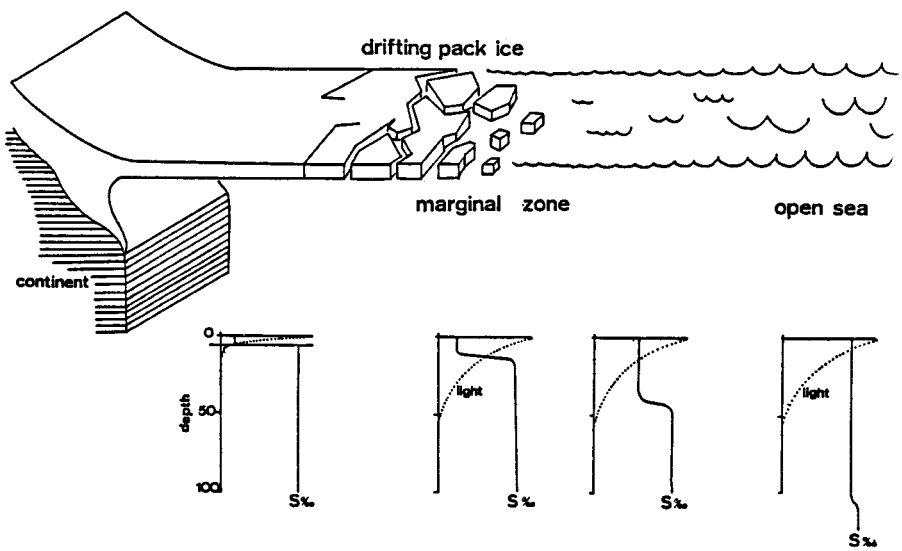


Figure 1 : *Schematic picture of antarctic phytoplankton habitats, showing the relationship between light penetration and vertical stability.*

(i) The **open sea areas** are submitted to violent winds and are characterized by a low stability of the water column. As a result, phytoplankton cells undergo important light fluctuations within a time scale of seconds to hours, according to the strength of the wind. The physiological adaptation of phytoplankton to this fluctuating light regime is still not very well known, in spite of several works (Marra, 1980; Lewis *et al.*, 1984; Neale & Marra, 1985).

However, as a major trend, the mixed upper layer is most of the time deeper than the photic layer preventing phytoplankton developments in spite of high nutrients concentrations, according to Sverdrup's theory of compensation depth. In

agreement with this are the low daily primary production and phytoplankton biomass, respectively 100–450 mgC.m^{-2}d^{-1} and 0.1–1 mgChla.m^{-3} observed by different authors (Holm–Hansen *et al.* 1977; Franceschini, 1978; El–Sayed, 1987).

At the boundary of these areas, frontal structures like the polar front or the Weddell/Scotia confluence represent zones of higher stability. Accordingly, biomasses as high as 5 mgChl.m^{-3} were observed in these frontal zone (Allanson *et al.*, 1981; El–Sayed & Weber, 1982; Yamaguchi & Shibata, 1982; Lurjehams *et al.*, 1985; Bidigare *et al.*, 1986).

(ii) The **inshore waters** are characterized by shallow wind mixing resulting in a higher vertical stability. Phytoplankton biomasses ranging between 2 and 25 mg Chl.m^{-3} were reported for these areas (El–Sayed, 1987).

(iii) The **marginal ice areas** represent the transition areas between completely ice covered zones and waters uninfluenced by effects of pack ice. These areas are characterized in early summer by the presence of a shallow upper mixed layer induced by melt water. Melting of ice enhances ice–edge phytoplankton developments both by providing a constant high illumination for phytoplankton and a large source of seed population, particularly if the volume in which the algae are distributed is small.

Consequently the level of primary production within the stabilized region of an ice edge depends on the importance of vertical stability which in turn depends on both the rate of receeding pack ice and the interannual variability in the ice extent.

According to this, greatest primary production and accumulation of phytoplankton biomass were found in regions with strongest vertical stability. As an example, Wilson *et al.* (1986) determined the mean primary production within the stabilized region of an ice edge in the Ross Sea to be 962 mgC.m^{-2}d^{-1} with minimum and maximum values of 31 to 1750 mgC.m^{-2}d^{-1}. The contribution of ice edge blooms to overall primary production of the Southern Ocean is still difficult to evaluate because these blooms are highly variable in time and space, depending on meteorological conditions. However, preliminary estimates based on occasional primary production field data and on rates of ice retreat indicate that taking into account ice edge primary production would increase by more than 60 % the present estimate of antarctic primary production (Smith & Nelson, 1986).

(iv) The **sea ice microhabitats** offer to phytoplankton conditions of high hydrodynamic stability but of low light intensity because of the high albedo of the ice cover. In response to this, specific algae like some pennates (Horner, 1985) have developed well adapted physiological properties (Bunt, 1963,; Grossi *et al.*, 1987; Kottmeier & Sullivan, 1987; Rivkin & Voytek, 1987; Palmisano *et al.*, 1985, 1987). Accordingly, high concentrations of ice algae (*brown ice*) reaching 300 mg Chla.m^{-2} were occasionally recorded within the pack ice (Palmisano & Sullivan, 1983). Summer meltback of sea ice constitutes an important source of seed population for ice edge plankton blooms. This indicates how sea ice extent and ice dynamics may have a direct influence on the location and magnitude of primary production in the antarctic ecosystem.

Superimposed to the effect of vertical structure and sea ice dynamics, *temperature*, *trace elements* and *grazing pressure* were also considered as important in controlling phytoplankton growth in the different habitats of the antarctic ecosystem.

The response of antarctic phytoplankton to low temperature has been intensively studied. Neori & Holm-Hansen (1982) showed that antarctic phytoplankton species are obligate psychrophiles with optimal growth rate around 7° C and decreased growth rate for decreasing temperatures in the range 5 to –1.8° C.

Manganese and iron were recently studied as possible limiting element of phytoplankton growth in non productive offshore waters of Northeast Pacific Subarctic (Martin & Fitzwater, 1988) and of Scotia Sea (De Baar *et al.* submitted) and in marginal zone of Antarctic (Davidson & Marchant, 1987). Data relative to open seawaters present contradictory conclusions calling for a careful reexamination of data in terms of change in the phytoplankton community during the course of the bioassay. Conversely data of Davidson & Marchant (1987) show clearly that *Phaeocystis* blooms exhaust available manganese in the marginal zone, thus controlling indirectly species succession.

Biological control of phytoplankton growth by grazing pressure is still difficult to estimate despite the recent development of acoustical technology (Hampton, 1985; El-Sayed, 1987). This is to be related to the highly efficient feeding strategy of krill – the most important herbivorous zooplankton in the Southern Ocean – which can swim

very fast in the water column and over long distances. More statistical data on phytoplankton and krill distributions are therefore required on a finer spatial, vertical and temporal scale to assess the rôle of zooplankton on phytoplankton distribution.

As well as affecting biomass distribution of phytoplankton, grazing by zooplankton would influence the size composition of phytoplankton. Intense grazing would result in the preponderance of nanoplankton forms (Kawamura, 1981; Meyer & El–Sayed, 1983; Kawamura & Ichikawa,1984; Weber & El–Sayed, 1985; Priddle *et al.*, 1986).

1.2.1.2. *The phytoplankton model*

Regarding the importance of the physical properties of phytoplankton habitats in determining its growth, regarding the great spatial and temporal variabilities of these microhabitats and the present lack of predictability, accurate estimate of year to year overall primary production in the antarctic ecosystem should only be provided by means of a predictive mathematical model which would take into account the physiology of phytoplankton and its interaction with its fluctuating habitat. This model would consist therefore in a coupling between an hydrodynamical and a biological model.

The hydrodynamical model should be able to predict the main physical trends of the antarctic ecosystem as considered as important for phytoplankton growth :

(i) The depth of the upper mixed layer in areas free of ice and the mixing velocity as a function of wind.

(ii) The spatial and temporal ice edge localisation and its vertical stability.

(iii) The extent of sea ice and its cycle of production and meltback.

The biological model should take explicitely into account the relationship between phytoplankton and the particular light regime it encounters as a consequence of the physics of the antarctic ecosystem. The models available in the literature for calculating daily primary production, on the basis of the experimental response of photosynthesis to constant light intensity, do not take these particular light regimes into account. The estimations they provide are therefore, in Antarctica more than elsewhere, largely uncertain. We developed for the case of the coastal North Sea a quite different approach for the estimation of phytoplankton growth (Lancelot *et al.*, 1986). It is based on the knowledge of the control mechanisms of protein synthesis instead of total photosynthesis. The former process is indeed under indirect control of light intensity, through the size of the pool of precursor metabolites. It is much less dependent on the fluctuations of light intensity, and depends only on the integrated light received.

Our purpose is to check the applicability of this model to the different microhabitats that characterize the antarctic ecosystem and to better understand the control of photosynthesis and growth under these extreme conditions. The summer cruise in the Prydz Bay in 1987 gave us the opportunity to test our concepts by measuring biological activities of phytoplankton sampled in open sea areas, antarctic divergence, inshore waters and marginal zone.

1.2.2 Bacterioplankton activity.

The recent development of powerful methods for measuring the activity of heterotrophic micro–organisms on the one hand, the discovery of the occurrence of significant extracellular release of dissolved organic matter by primary producers on the other hand, dramatically changed our view of the relationships at the first trophic levels of aquatic ecosystems (see e.g. Pomeroy, 1974; Williams, 1981; Azam *et al.*, 1983). It is now recognized that, in temperate marine systems, a large fraction of primary production flows through the pool of dissolved organic matter, either after direct excretion by phytoplankton or by lysis of ungrazed phytoplankton cells. This

part of primary production is unavailable for herbivorous zooplankton and is mainly utilized by bacteria, able to take up organic substrates at nanomolar concentration. Planktonic bacteria thus appear as key organisms, the activity of which represents both a *shunt* of the classical food chain leading to fish production, and a *link* between dissolved primary production and production at higher trophic levels. A shunt, because heterotrophic microbial activity can result in the rapid mineralization of a significant part of primary production which then does not flows to zooplankton; a link, because microbial activity converts a part of dissolved primary production into particles which are susceptible to grazing by protozoans, thus possibly initiating a new trophic chain reentering the zooplankton–fish food chain.

This microbial loop has not been intensively studied in the Southern Ocean and its rôle in the overall function of the antarctic marine ecosystem is still a matter of controversy.

Some authors (Kriss *et al.*, 1969; Sorokin, 1971; Pomeroy & Deibel, 1986) suggested that a dramatic decrease of bacterial activity occurs below 2° C, while algae continue to be active at these temperatures. This could explain the preservation of dissolved organic matter, which has sometimes been found in high concentration in Antarctic waters (Bolter & Dawson, 1982). This organic matter would then be exported to lower latitudes by the deep oceanic circulation (Sorokin, 1971). On the other hand, this reduced activity of the microbial loop, leaving a larger part of primary production available to grazers than in temperate or tropical marine systems, would contribute to explain the surprisingly high secondary production often reported for permanently cold waters.

Other authors (Hodson *et al.*, 1981; Hanson & Lowery, 1983) reported measurements of microbiological activities in the Antarctic Ocean of the same order of magnitude as those observed in temperate areas. They conclude that the microbial loop plays a similarly important rôle in the antarctic marine system as it does in temperate systems. This conclusion has even been extended to the case of sea–ice microbial communities (Grossi *et al.*, 1984).

It was shown, on the other hand, that the dependency of bacterial activity toward temperature is very complex (Li & Dickie, 1984), according to the coexistence within arctic and antarctic communities of several thermic types, from eurytherms to obligate psychrophiles.

We developed a general methodology for measuring and understanding the control of bacterial activity in aquatic environments. Our approach is based on the direct measurement of some basic processes involved in bacterial organic matter utilization (the HSB model – Servais, 1986; Billen & Fontigny, 1987; Billen & Servais, 1988). Our purpose is to check the applicability of this approach to antarctic waters and to try to resolve the present controversy regarding the rôle of bacterial activity in antarctic waters.

2. BIOTOPE : THE PRYDZ BAY AREA.

Our team was kindly invited to take part to the ***Marine Science Voyage*** 7 cruise, organized by the Australian ***Antarctic Division*** (Kingston, Tasmania), in the Prydz Bay area, on board of the M.V. *Nella Dan.* Departure was from Hobart, Tasmania, on February 5, 1987, return to Hobart on April 2, 1987. The ships track and the sampling stations during the travel to and within the Prydz Bay area are represented in Fig. 2.

From 19th to 21st of January 1987, the French ship *Marion Dufresne* made a short visit to the same area. The observations carried out at this occasion by our Belgian colleagues on board of this ship offered useful points of reference. Their stations are also indicated on Fig. 2.

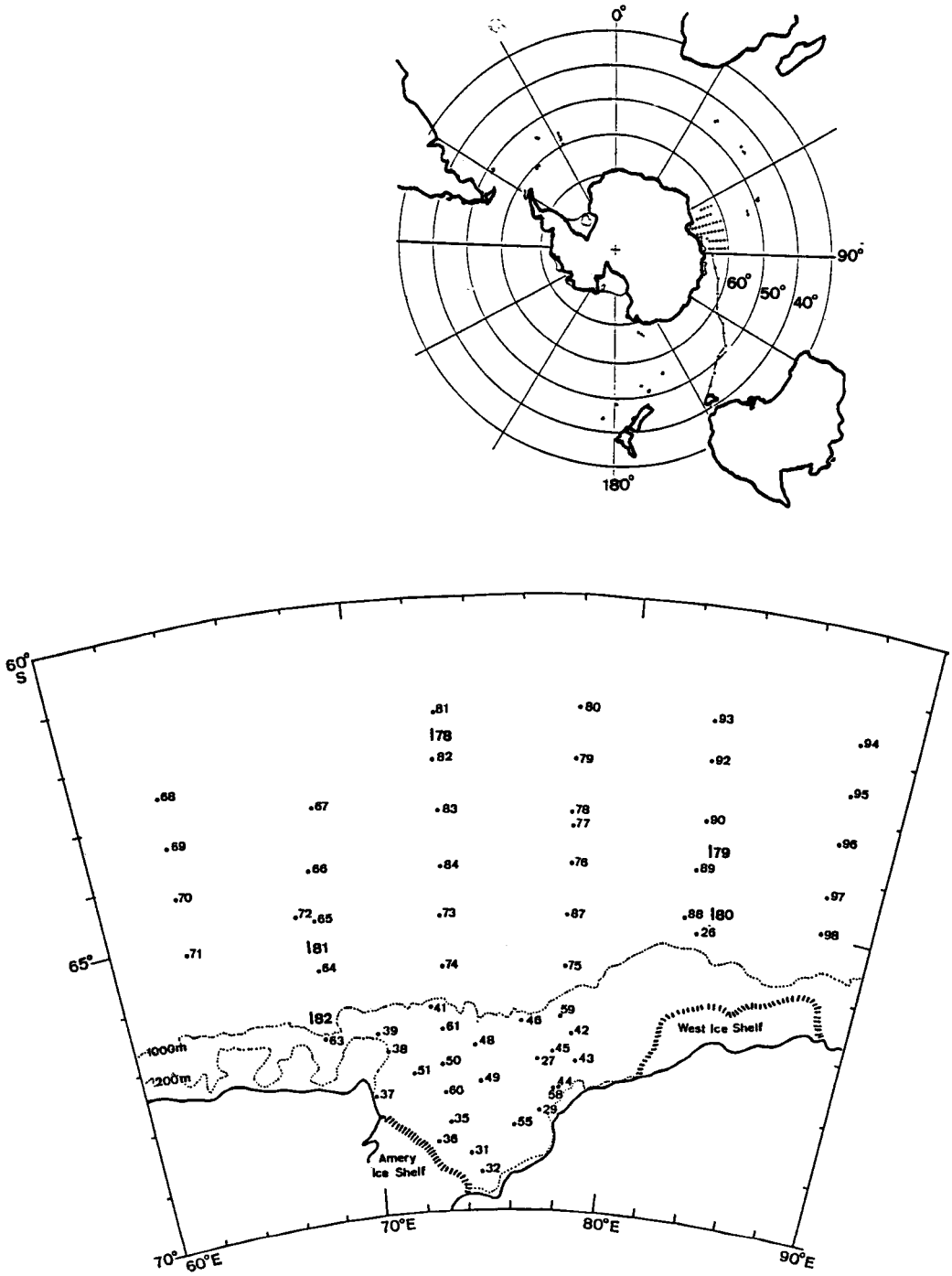


***Figure 2** : Track and sampling web of the M.V. Nella Dan during Voyage 7 cruise of the Australian Antarctic Division, to the Prydz Bay area.*

2.1. GENERAL DESCRIPTION OF THE AREA

2.1.1. Bathymetry

The bathymetry of Prydz Bay is represented in Fig. 3.

The continental plate is situated south of 65–66°S. All stations visited were deeper than 200 m.

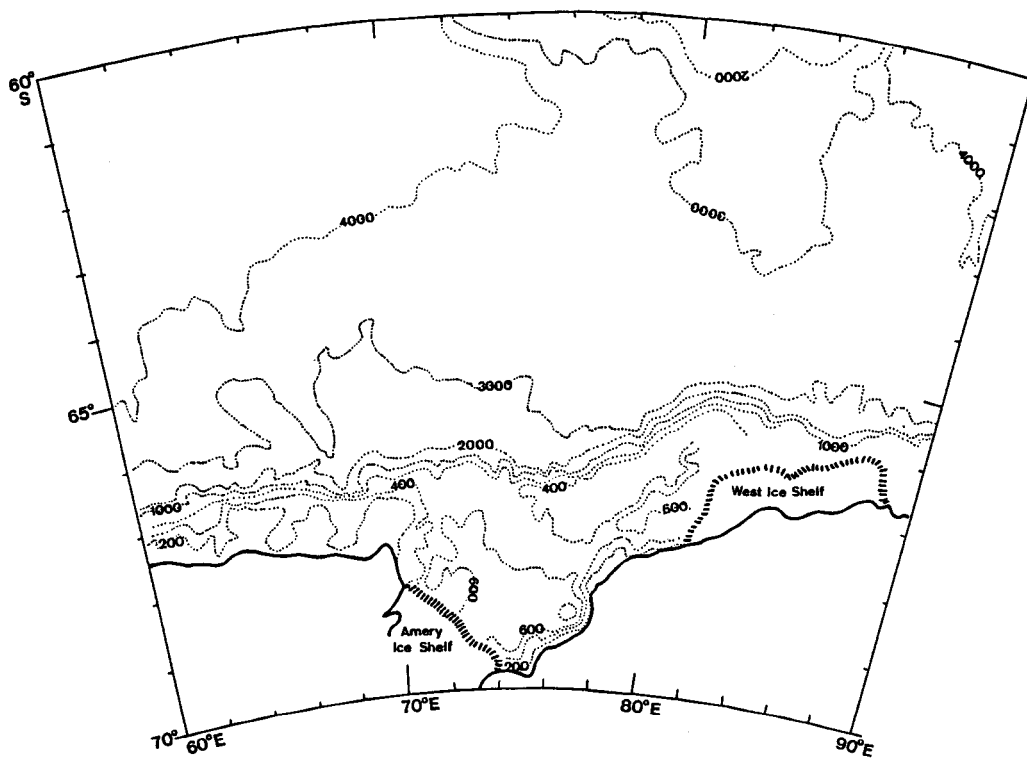


Figure 3 : *Bathymetry of the Prydz Bay area. After Smith* et al., 1984.

2.1.2. Horizontal water mass circulation

A good description of the water masses and water circulation in the Prydz Bay area has been recently published (Smith *et al.*, 1984). Figure 4, summarizing informations contained in this publication, represents the general horizontal circulation of the surface water masses. A low atmospheric pressure belt encircles the continent at about 64°–66° latitude S. North of this, the principal flow is associated with the Antarctic Circumpolar Current, driven eastwards by the prevailing westerlies. South, eastwinds prevail and drive a westward circulation. A zone of divergence therefore exists around 65° S. The whole horizontal circulation pattern is rendered more complex by the presence of a gyre within Prydz Bay.

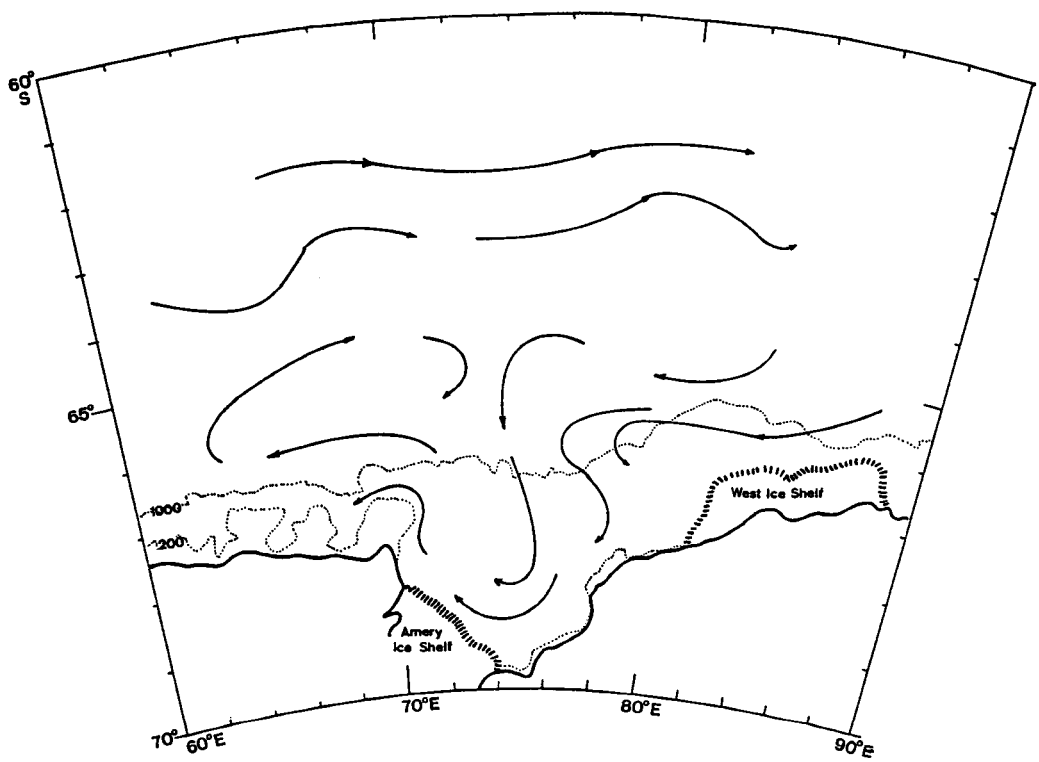


Figure 4 : *General surface watermasses circulation in the Prydz Bay area. After Smith* et al., 1984.

2.2. DYNAMICS OF THE MARINE HABITATS IN PRYDZ BAY

As explained in section 1.2.1. above, three major habitats have to be distinguished in the antarctic marine system, with respect to the conditions of planktonic development : ice covered zones, marginal and open sea areas including frontal zones. The geographic distribution of these three habitats varies seasonally as a result of ice cover dynamics and wind induced turbulence. The purpose of this section is to describe and understand the changes which occurred from this respect during the period of observation in the Prydz Bay area.

2.2.1. Ice cover dynamics of the area

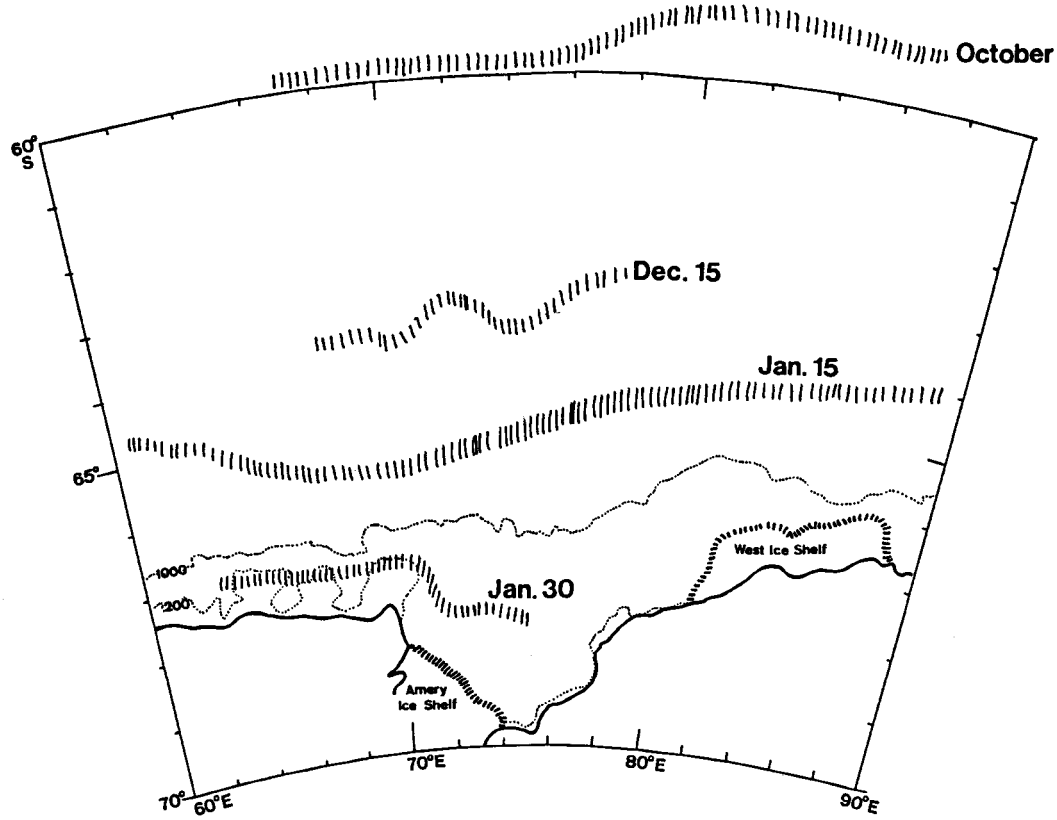


Figure 5 : *Positions of the ice edge at different periods off Prydz Bay. Data compiled from Hellmer & Bersch*, 1985.

Figure 5 summarizes a compilation of data concerning the seasonal variations of the extent of the ice–cover off Prydz Bay. The continental shelf area of the bay is only free of ice by the end of January. Dense pack ice areas remain until March west of West Ice Shelf.

2.2.2. Enhanced water column stability resulting from sea ice melting

2.2.2.1. *A general theory*

The mean winter surface water salinity **Ss** in open ocean areas (winter antarctic surface water) is about 34.50 $^{0}/_{00}$. The mixed layer extends down to 60–80 m depth (Hellmer & Bersch, 1985).

The salinity of annual sea ice **Si** depends somewhat on its rate of freezing but generally ranges between 2–6 $^{0}/_{00}$ (e.g. Tison & Haren, in press) as a mean for its 1–1.5 m thickness **th** (Untersteiner, 1966). On melting of this ice, fresh water is produced, forming an upper water layer of lower density. Its progressive mixing with the underlaying salt water results both in increasing the upper water salinity and in increasing the depth of the pycnocline. An ideal relationship between salinity **Sm** and depth **Dm** of the upper mixed layer can therefore be derived. The mass balance of salinity during the process of mixing can be written :

$$Sm \cdot Dm = Si \cdot th + Ss \cdot (Dm - th)$$

hence,

$$Sm = Ss - \frac{(Ss - Si)}{Dm} \cdot th$$

Figure 6 shows this relationship between Sm and Dm, for a set of values of annual sea ice salinity and thickness.

2.2.2.2. *Application to the Prydz Bay area*

The depth of the upper pycnocline, observed during the *Nella Dan* and *Marion Dufresne* cruises in Prydz Bay, varies from 10 to 80 m. The relationship observed between the depth of the upper mixed layer and its salinity, shown in Fig. 6, fits nicely that predicted by the idealized melting sea ice theory developed above, giving support to the idea that the shallow upper mixed layer (< 40 m) found in the offshore areas in January and in the inshore areas in February, indeed correspond to the position of the marginal zone at those periods.

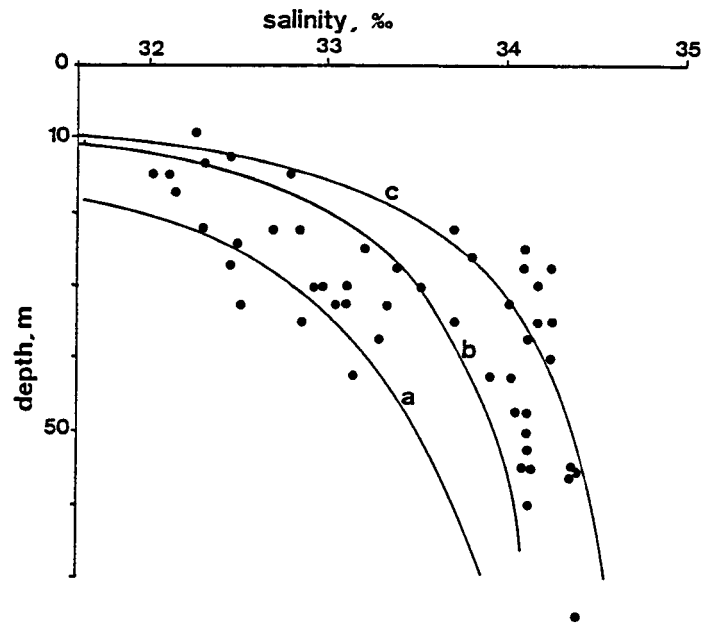


Figure 6 : *Relationship between upper mixed layer depth and salinity. Theoretical curves calculated according to the model described in the text for the following values of the parameters:*
a. Si=2%.; th=1.5m; Ss=34.5%. **b.** Si=5%.; th=5m; Ss=34.5%.
c. Si=3.5%. th=1m; Ss=35%.
Observed values in Prydz Bay during the Austral summer 1987.

2.2.3. Frontal structure within the open sea area at the antarctic divergence

Off the continental plate, a further pycnocline, below the upper pycnocline, is observed between 100 and 300 m. depth, indicating the transition with warmer, more saline, subantarctic deep water. Upwelling of these water masses at the divergence, interrupting the tongue of cold winter antarctic surface water, was clearly demonstrated by the temperature profiles measured along North–South transects off Prydz Bay in March during the *Nella Dan* cruise (Fig. 7). Unfortunately, due to a failure of the CTD probe, no salinity data are available for these profiles.

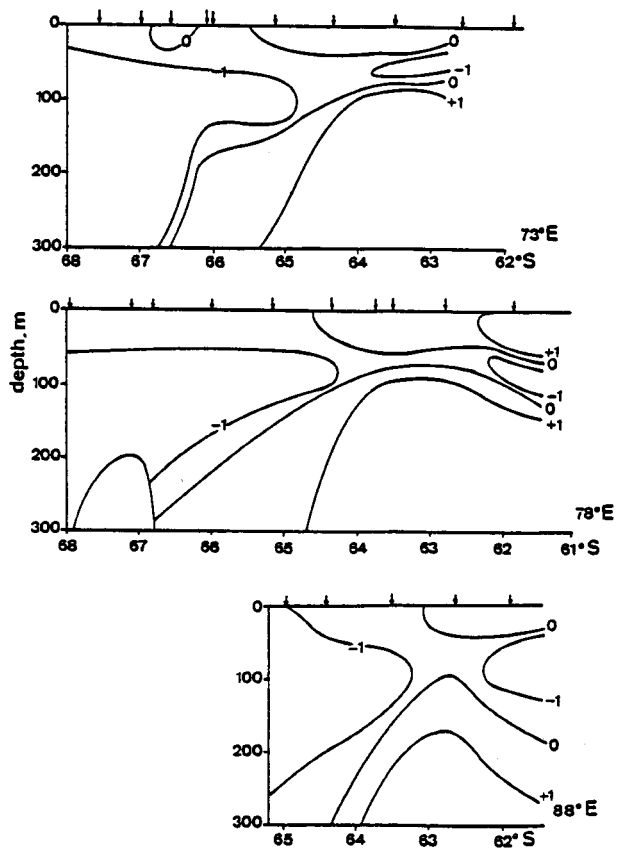


Figure 7 : North-South transects of the temperature structure of the water column off Prydz Bay in March 1987.

Apparently, the divergence results in a somewhat shallower upper mixing layer.

2.2.4. Distribution of the marine habitats and its seasonal variations in Prydz Bay.

Figures 8a, b and c summarize the above discussions by presenting the distribution of ice, marginal and open sea areas in mid-January, February and March.

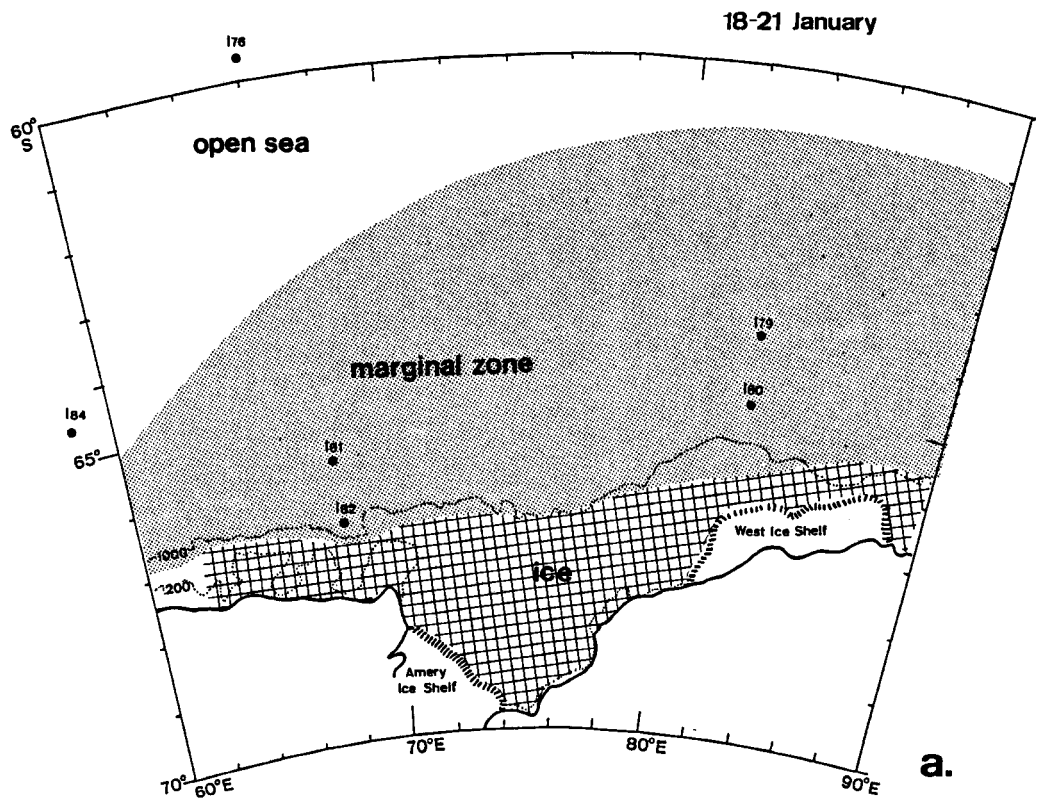
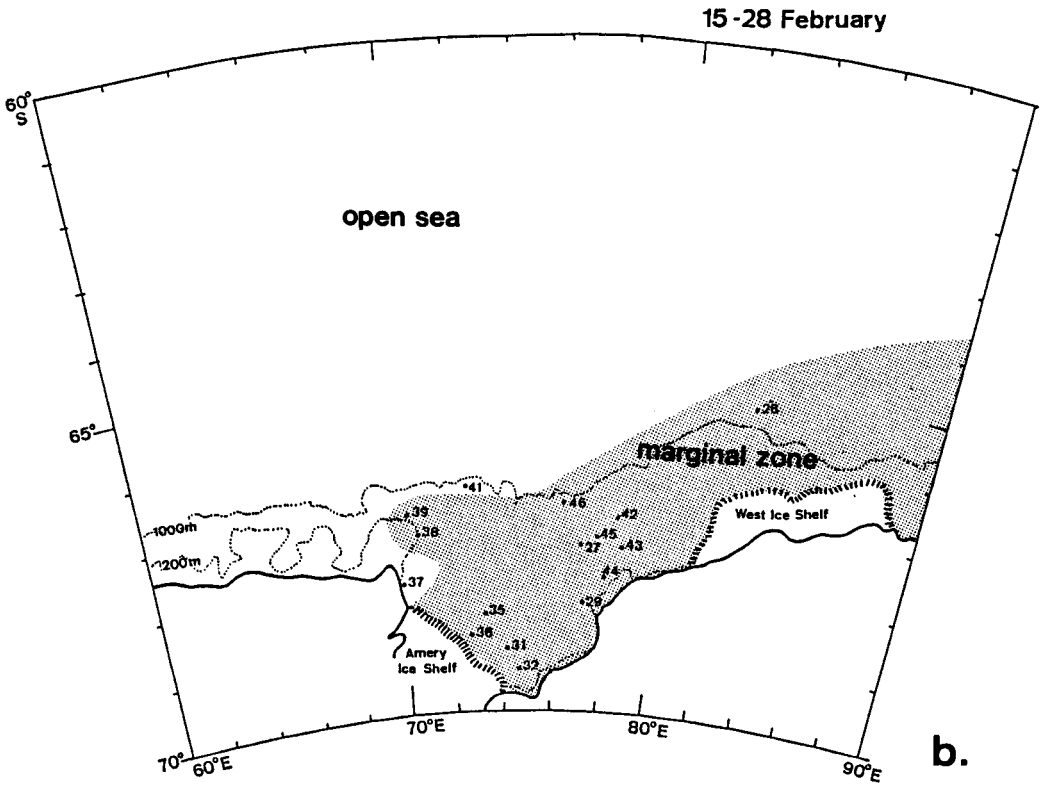
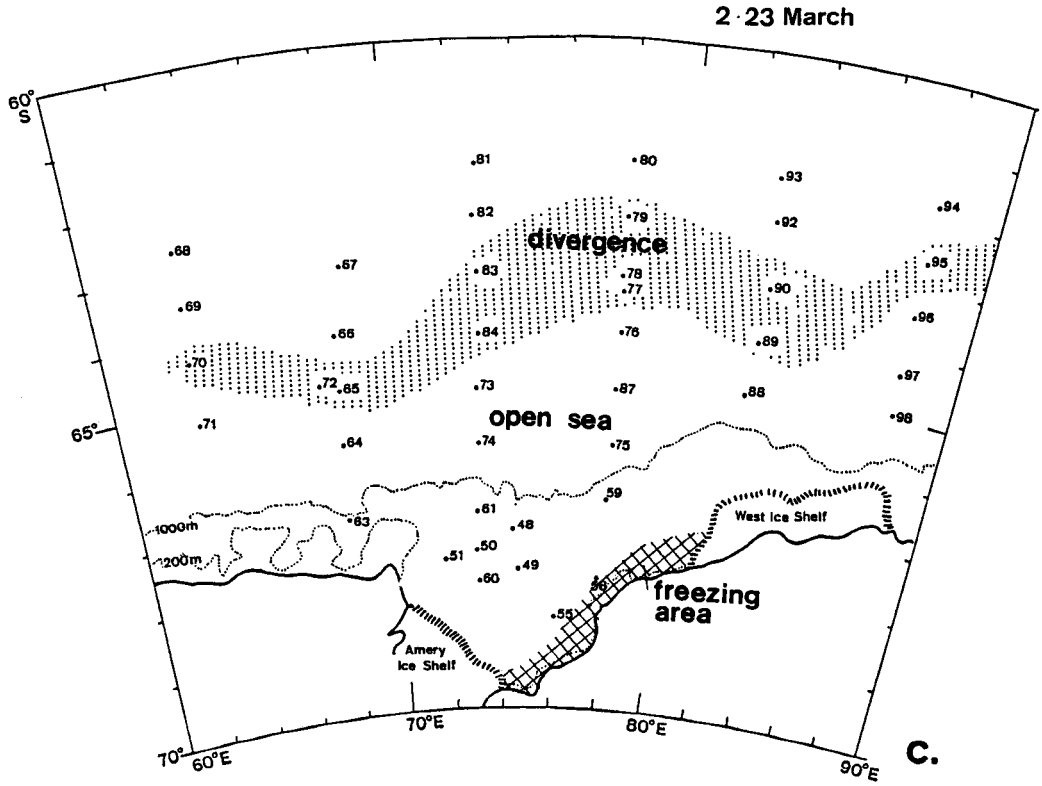


Figure 8 : *Geographical distribution of the major phytoplanktonic habitats in Prydz Bay at three periods of observation during the austral summer* 1987.
a. *Early summer situation* (18–21 January 1987)
b. *End summer situation* (15–28 February 1987)
c. *Early winter situation* (2–23 March 1987)


15-28 February
60° S
open sea
65°
marginal zone
West Ice Shelf
1000m
200m
Amery
Ice Shelf
70°
60°E
70°E
80°E
90°E
b.


2-23 March
60° S
divergence
open sea
65°
West Ice Shelf
freezing
area
1000m
200m
Amery
Ice Shelf
70°
60°E
70°E
80°E
90°E
c.

3. PHYTOPLANKTON

3.1. ECOPHYSIOLOGICAL MODEL OF PHYTOPLANKTON GROWTH

3.1.1. Motivation

Numerous models have been described for phytoplankton developments since the last 30 years. Their capabilities are related to their conceptual structure and to the technical procedures used to determine their parameters.

The first models were developed on the basis of the mathematical description of one essential biological process always departed from its cellular context. Among them, the most popular are those describing the photosynthetic process on the one hand, and the nutrient uptake on the other hand. The formers are based on the mathematical description of the photosynthesis–light relationship as developed by Vollenweider (1965) for lacustrian phytoplankton and by Platt & colleagues (see e.g. the review by Platt & Gallegos, 1980) for marine phytoplankters. The latters postulate that growth can be expressed by the product of uptake kinetics and a constant yield, as first developed by Dugdale (1967) and improved by Droop's (1973, 1979) cell–quota model that postulates a threshold cell quota.

Since the introduction of these models – which surprisingly were published at the same period, but were never linked to each other – many changes were brought to improve both the mathematical equations and integrate calculus and the experimental determination of the parameters and their control by environmental factors. However, at this stage of model development, even sophisticated refinements would never improve the description and the prediction of phytoplanktonic activity in natural environments, because these models reduce phytoplankton metabolism to the kinetic of one single process without considering phytoplankton cell as a biological entity.

Indeed, as previously described, phytoplankton cells growing in a fluid or sea ice environment are submitted to many stresses, the nature, the intensity and the time scale of which are very variable. It is now well known that phytoplankton cells have developed specific physiological adaptative behaviour in response to these stresses. The models described above were not devised to take into consideration these metabolic changes. The predictive capacities of these models are therefore very limited.

Explanatory models, based on the fundamental biochemistry associated to growth and division of phytoplankton cells, are therefore required for interpreting the growth patterns in natural environments and for a reliable prediction of changes in growth rate and species dominance in response to environmental stress. In a previous study (Lancelot & Billen, 1985), we recommended to divide cellular constituant on basis of their cellular function. This subdivision was inspired from Cohen & Parna's (1976) theory on the storage of reserve materials according to growth requirements. Three subclasses of molecules were considered : the monomeric precursors for macromolecular synthesis, including the Calvin and TCA intermediates, the reserve products composed of polysaccharides and lipids and the functional (enzymes, DNA, ATP) and structural (eg.membranes) products composed for 85% of proteins (Mayzaud & Martin, 1973; Dorsey *et al.*, 1978).

This conceptual model was chosen because it takes explicitely into account the light history of the cells as reflected by the pool size of the storage products.

In view of the importance of light fluctuactions in the antarctic ecosystem, we develop in this section a theoretical model of phytoplankton growth based on the mathematical formulation of the control by light and inorganic nutrients of the metabolic activities described above.

3.1.2. Structure of the model

The structure of the model is illustrated by Fig. 9, which shows a diagrammatic representation of the internal metabolism of phytoplankton cells together with its exchanges with the external medium. The most important biochemical cellular constituents involved in these processes are indicated too. These are the pool of very active small metabolites **S**, including monomers and oligomers precursors for macromolecular synthesis, the pool of reserve products **R** composed of polysaccharides and/or lipids and the pool of functional and structural products **F**. These latters are composed of about 85 % as protein and contain the major part of inorganic nutrient taken up by the cell. Because of their biological function and because of their slow turnover rate, the synthesis of these macromolecules constitutes a good index of cellular growth. Growth model of phytoplankton is therefore based on the mathematical description of **F** synthesis.

Examination of Fig. 9 shows that synthesis of macromolecules **F** is regulated by the availability of both inorganic nutrients **N** and internal precursors **S**. These latters are provided either directly by the photosynthetic process **p** or indirectly by the catabolism of reserve macromolecules **cR**. Also the energetic requirements in ATP and reductants for transfer of nutrients inside the cell, biosynthesis of macromolecules and maintenance of cellular structures are provided either directly by the photosynthetic process or by the catabolism of reserve products. As a consequence and contrarily to the photosynthetic process, cellular growth can proceed during dark periods on condition that the pool size of reserve material is high enough to insure the requirements in energy and precursors (Fig. 9b). However, during periods of prolonged darkness, as illustrated by Fig. 9c, reserve products are getting exhausted. Energetic requirements for maintenance of basal metabolism are then provided by the catabolism of **F**. Depending on the time scale of this light stress, physiological adaptation of the cells leads to the apparition of dormancy forms, encystments, resting spores.... A final stage being obviously the *natural* death of the cell.

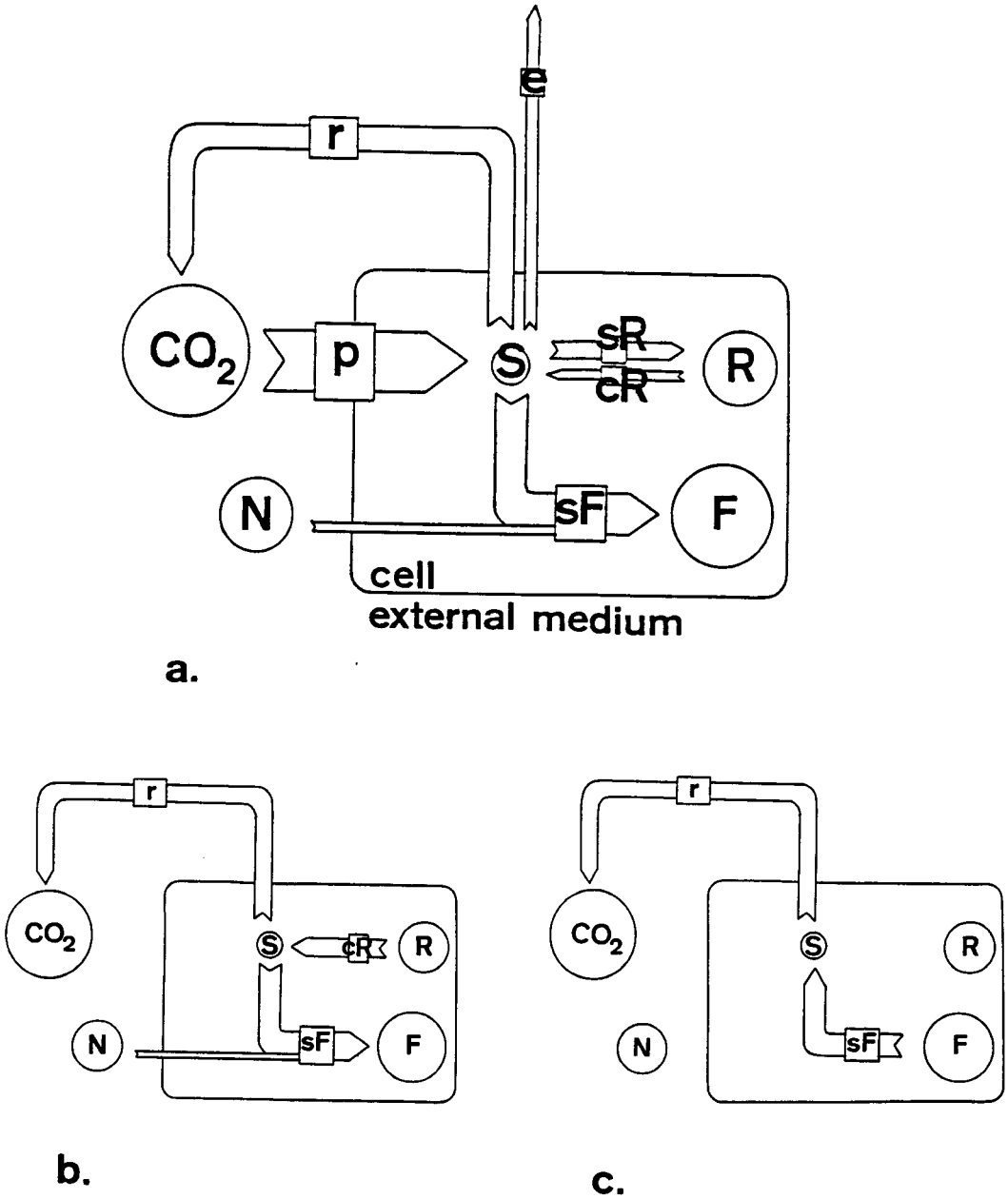


Figure 9 : *Diagrammatic representation of phytoplankton metabolism under* **a.** *Full illumination;* **b.** *Short stay in the dark;* **c.** *Prolonged stay in the dark. See text for explanation.*

In this conceptual model, environmental factors controlling the growth of phytoplankton in antarctic ecosystem are explicitely :

- temperature directly controlling the synthesis of new biomass and the maintenance of basal cellular structure.
- light indirectly controlling growth by acting on photosynthesis and the size of the storage products pool.
- trace metals, controlling growth both through their direct action in enzymatic reactions and because they are important element for the synthesis of some structural and functional macromolecules like e.g. chlorohyll a.

3.1.3. Mathematical formulation

Figure 9 shows that photosynthesis **p**, respiration **r**, reserve products synthesis **sR** and their catabolism **cR** and nutrients uptake **u**, are the main processes involved in the cellular growth **sF**. The kinetics of each processes were determined on the basis of experiments conducted both on natural phytoplankton (Lancelot, 1983; Lancelot *et al.*, 1986) and on batch cultures as described in the literature. The environmental control of the processes was studied according to Blackmann's theory, which is an extension of the Liebig law of minimum. This means that only one factor was considered as limiting at any time, another one taking eventually over beyond a defined threshold level of the first one. Mathematical formulation and the parameters that characterize equations are described below. Symbols and units are explained in Table 2.

The rate of growth is given by the product of two Michaelis–Menten functions governing respectively **N** uptake and **S** assimilation by a temperature dependent growth constant :

$$sF = \mu max \frac{N}{K_N+N} \frac{S}{K_S+S} F \qquad (1)$$

The photosynthetic process **p** is controlled by available light **I** following a

kinetics described by Platt *et al.* (1980) :

$$p = kmax \ (1 - \exp(\alpha I/kmax)) \ \exp(-\beta I/kmax) \ B \qquad (2)$$

where I is the photosynthetically active radiation P.A.R., expressed in $\mu E.m^{-2}.sec^{-1}$.

Synthesis of storage products sR is assumed to be governed by the size of S followings a Michaelis–Menten function :

$$sR = \rho max \ \frac{S}{K_S + S} \ R \qquad (3)$$

Catabolism cR of storage products R is postulated to obey a lst order kinetics :

$$cR = K_R \ R \qquad (4)$$

Metabolic costs, in terms of a demand for ATP and reductants, are primarily met by cellular respiration (Cook, 1966). Following Shuter (1979), cellular respiration r is then expressed by the sum of 2 terms associated respectively with maintenance processes **maint** and with the synthesis of new cellular material ξ

$$r = maint \ F + \xi \ sF \qquad (5)$$

In addition, under unfavorable growth conditions, some phytoplankters do excrete in the external medium large quantities of organic molecules that are lost for the cell (see the review by Lancelot & Billen, 1985). When this process occurs, the model assumes that it is governed by the same laws as the photosynthetic process itself :

$$e = \epsilon \ p \qquad (6)$$

Table 2 : Variables and parameters of the phytoplankton model : 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	ϵ	dimensionless
Maximal specific rate of R synthesis	ρmax	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	ξ	dimensionless

3.2. EXPERIMENTS AND CALCULATIONS

3.2.1. Experimental determination of parameters

The above described formulation of the basic processes involved in phytoplankton metabolism is admittedly idealized. Its operational value lies in the fact that powerful experimental procedures have been developed for assessing most of the parameters involved.

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

(i) The experimental determination of ***photosynthetic parameters*** involved short–term ^{14}C incubation – Steeman–Nielsen standard method – performed at different light intensities (P/I curves).
Bottles (Cel–Cult) tissue culture flasks of 250 and 700 ml were generally incubated in a thermostatic growth cabinet illuminated by artificial light. Maximal light intensity reached 135 $\mu E\ m^{-2}sec^{-1}$ i.e. very close to the light saturation constant characteristic of antarctic phytoplankton. At some occasions, additional simulated *in situ* incubations were run at incident solar radiation in deck incubators with running seawater. ^{14}C incubation were conducted at *in situ* temperature for different fractions of light intensity (0, 1, 4, 6, 15, 20, 40, 50, 100 %). Incubation times of 6–9 h were chosen after a preliminary study of P/I curves for different incubation times. This choice minimizes losses by respiration and increases accuracy of the experimental measure. After incubation, samples were filtered on GF/C filters. Radioactivity was measured on the filter (photosynthetic carbon fixation) and in the dissolved organic matter (excretion). Radioactivity of the latter was, however, never significantly different from that of the background. Excretion was therefore assumed to represent a maximum of 5 % of total photosynthesis. 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 (eq. 1–6) of data relative to 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.

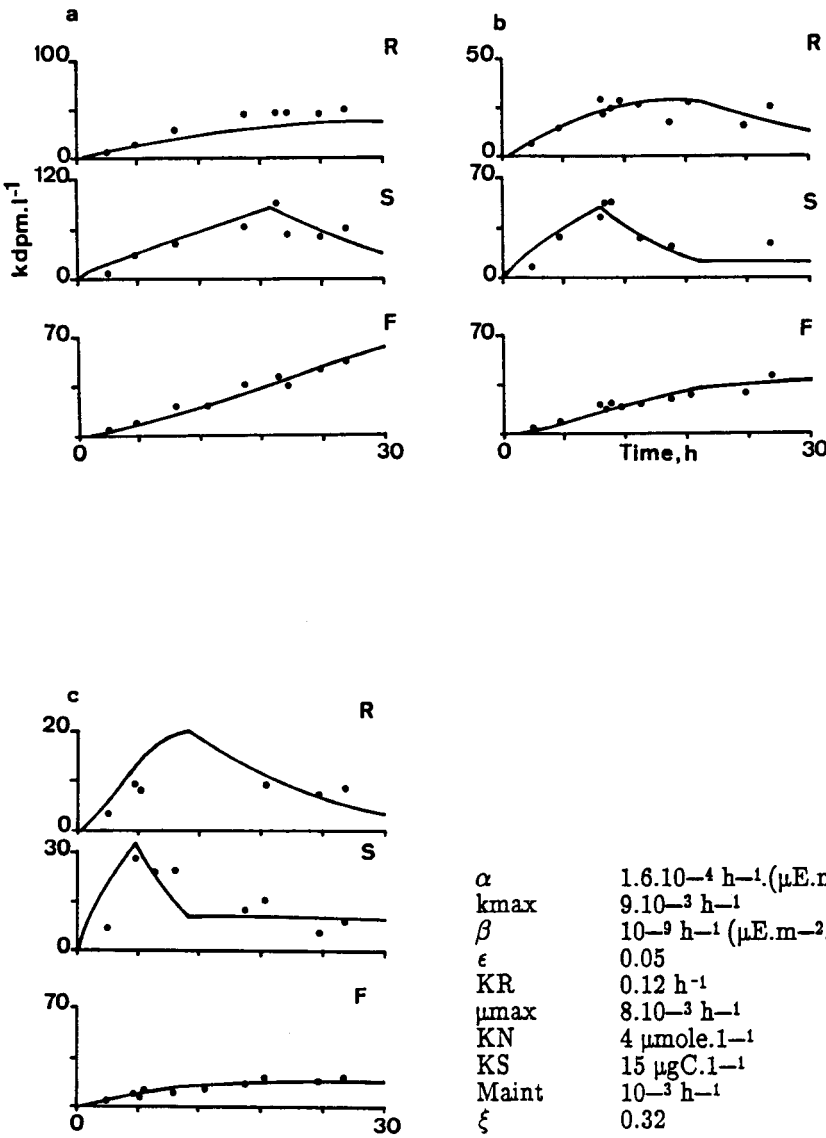
^{14}C incubation were carried out in a thermostatic growth cabinet illuminated by artificial light (maximal P.A.R. = 135 $\mu E.m^{-2}.sec^{-1}$). Experimental procedure and biochemical fractionation are those described in Lancelot & Mathot (1985).

Basic values of parameters for mathematical adjustment of data were estimated either on the basis of independent physiological experiments conducted on *in situ* phytoplankton communities or relative to natural phytoplankton growing under comparable nutrients conditions. For some parameters, experimental determination was not possible because of the interdependence of biological processes. In this case, basic values were estimated from literature data relative to physiological experiments on pure phytoplankton. Values of parameters and their environmental control are discussed in § 3.3.2.. The high prediction level of our methodology is illustrated by Fig. 10 which shows, for a same set of parameters, good agreement between prediction curves of ^{14}C assimilation in the main metabolites of antarctic phytoplankton undergoing different photoperiods and corresponding experimental data. Values of parameters are indicated too.

3.2.2. Daily rates

Daily integrated photosynthesis rates were calculated by depth and time integration of eq. 1 , taking into account the variations of solar radiation, P.A.R., with depth and during the day, recorded with a LICOR cosine quantum sensor.

Daily specific rates of growth were calculated by integration of eq. 1–6 on the variations of P.A.R. and on the depth down to the depth of the mixed layer. 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 of the upper mixed layer (cf. Lewis *et al.*, 1984).



α	$1.6.10^{-4}$ h^{-1}.(µE.m^{-2}.sec^{-1})
kmax	9.10^{-3} h^{-1}
β	10^{-9} h^{-1} (µE.m^{-2}.sec^{-1})$^{-1}$
ϵ	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}
ξ	0.32

Figure 10 : *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.*

3.3 PHYTOPLANKTON GROWTH IN PRYDZ BAY DURING SUMMER 1987

3.3.1. Phytoplankton biomass and the physico-chemical characteristics of its environment

The antarctic sector under study was divided in different subareas corresponding to the basic habitats previously defined as important for phytoplankton growth : ***open sea, frontal structure*** and ***marginal ice zone***. On the basis of this subdivision, marginal phytoplankton was studied in the Prydz Bay in February although phytoplankton sampled in the northern part of the Prydz Bay in early March should be representative of more mature open sea communities as a consequence of both geographical position and advance in season. Qualitative and quantitative differences are indeed apparent in the phytoplankton communities of these habitats. Preliminary data on chlorophyll a concentrations measured for different size particles (Wright, unpublished data) indicate that open sea waters should be dominated by small species (< 8 μm), suggesting the predominance of flagellates over diatoms. This should however be confirmed by data on species composition when they will be available (David Thomas, University of Hobart, Tasmania, in preparation). Phytoplankton of the marginal zone, on the other hand, seems to be composed in more than 80 % of species larger than 8 μm (Wright, unpublished data).

Average and extreme values of total phytoplankton biomass as expressed in chlorophyll a unit were calculated for the 3 habitats of phytoplankton. Values are reported on Table 3. This table shows that phytoplankton biomass of the marginal zone is one order of magnitude higher than that characteristical of open sea. Chlorophyll a ranges are in perfect agreement with those reported in El Sayed's revue (1987) for similar marginal areas. Also in agreement with this paper are the extremely low mean value of 0.14 $\mu gChla.l^{-1}$ calculated for the open sea sector. Phytoplankton biomasses measured in the divergence band, on the other hand, were particularly low and not significantly different from those typical of the open sea.

Table 3 : Characterization of phytoplankton biomass[1] in its habitats.

Phytoplankton habitats	Chlorophyll a($\mu g l^{-1}$) Minimum	mean	Maximum
Open sea	0.01	0.14	0.50
Divergence band	0.06	0.25	0.50
Marginal ice zone	0.4	2.1	4.5

[1] *calculated from Lancelot* et al., 1988 *and unpublished data of Wright* (*Antarctic Division, Hobart, Australia*).

The **light environment** of phytoplankton is determined from the conjugated effect of surface incident PAR (Photosynthetically Active Radiation) with optical and hydrodynamical properties of the water/ice column. Incident PAR is itself defined by the maximal intensity at noon and the length of the photoperiod. The latter varies according to the season and the latitude. The former is in addition strongly dependent on the cloud cover.
Table 4a summarizes means and extreme values of light parameters as calculated from daily curves of incident PAR continuously recorded by means of a LICOR cosine light sensor situated at the superior deck of the ship. Examination of Table 4a indicates that cloud cover more than latitude is the factor determining the level of daily incident PAR. Surface incident PAR was estimated from air incident PAR using a mean daylight reflection coefficient of 0.82. This latter was shown to vary between 0.60 and 0.94 according to water motion and cloud cover.

The optical properties of the water column are defined by the transparency of the water column itself dependent on dissolved and detrital particulate matter together with phytoplankton biomass. Figure 11 suggests however an empirical relationship between the vertical light attenuation coefficient η, as calculated from vertical light profiles performed at several stations of the studied area, by means of an underwater LICOR sensor, and the corresponding chlorophyll a measured in the upper mixing layer.

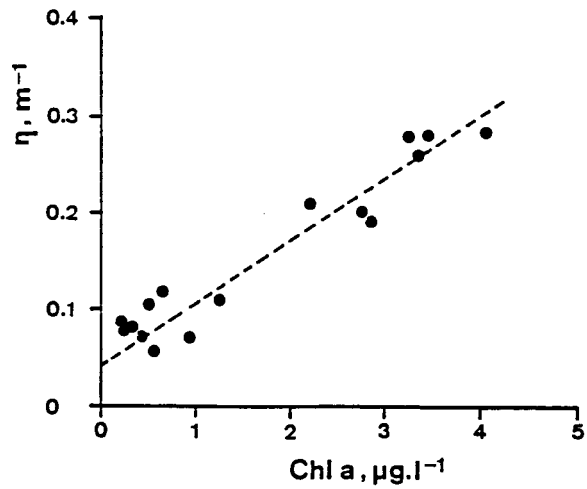


Figure 11 : *Empirical relationship between the vertical light attenuation coefficient and phytoplankton biomass.*

Average and extreme values of η were calculated for the different habitats of phytoplankton and are gathered on Table 4b. From these, mean euphotic depths of 22 m and 50 m were calculated respectively for the marginal and the open sea – frontal area. These differences mainly reflect the higher phytoplankton biomasses in the marginal with respect to the open sea area.

The **light environment** of phytoplankton cells was therefore calculated by the mathematical formulation of Riley (1957), which combines optical and hydrodynamical properties of the water column. Average and extreme values of mean light intensities in the upper mixed layer of the three phytoplankton habitats are reported on Table 4b.

Comparison of the average light intensities indicates surprisingly that the light environment is very similar for the three habitats considered. However, the range of values characteristic of the marginal zone is significantly wider as an illustration of the transient property of the melting upper waters. This indicates that the marginal ice zone cannot be studied on a broad scale and that the hydrodynamics

of ice melting must be considered carefully in strong relation with phytoplankton developments.

Nutrient conditions of phytoplankton growth were determined by the level of major inorganic nutrients NO^-_3, PO^-_4 and $Si(OH)_4$. Average and extreme values of these elements as calculated for the 3 phytoplankton habitats are reported on Table 5.

Although nutrient depletion was never observed, as usual for the Southern Ocean (Priddle *et al.*, 1987), Table 5 shows clearly a significant reduction of all nutrients in each habitats, if compared with the maximal values of 28, 2, 50 measured for N, P and Si respectively.

The importance of nutrient reduction increases from open sea to the marginal ice zone. Moreover, nutrient reduction was much higher in the shallower part of the marginal zone, where nitrates concentrations were at some occasions lower than half–saturation constant reported for inorganic nitrogen uptake in similar rich area (Lancelot *et al.*, 1986). This indicates that intense phytoplankton activities were proceeding in this particular marginal ice area in agreement with the concept of higher stability previously developed. However, maximal chlorophyll a concentrations measured in this area (Table 3) do not reflect the high decrease observed in nutrient concentrations, indicating important phytoplankton losses by physical or biological process like sedimentation and grazing.

Table 4 : Light environment of phytoplankton during end–summer 1987.

a. Light parameters of incident PAR

Phyto–plankton	Period	Lat. sud	photo–period (hours)		max light intensity at noon ($\mu E.m^{-2}sec^{-1}$)			daily incident PAR ($E.m^{-2}$)		
			min	max	min	mean	max	min	mean	max
Marginal zone	21–28.02	64–69	15	18	522	694	857	10	14	19.5
Open sea & Divergence	2–23.03	61–66	12.5	13.5	249	559	985	4.5	10	18.2

b. Available light in the water column

	η (m^{-1})			Mean PAR in the upper mixed layer		
	min.	mean	max	min.	mean	max.
Marginal zone	0.11	0.21	0.28	21	44	104
Open sea & divergence	0.05	0.07	0.08	25	47	75

Table 5 : Major nutrients concentrations in the upper mixed layer of the Prydz Bay sector during end–summer 1987.

Phyto–plankton habitats	NO^-_3 ($\mu mole.l^{-1}$)			PO_4^{3-} ($\mu mole.l^{-1}$)			Si ($\mu mole.l^{-1}$)		
	min.	mean	max.	min.	mean	max.	min.	mean	max.
Open sea	18	21	28	1	1.6	2	25	38	5O
Divergence band	13	17	25	1.3	1.5	1.4	22	27	29
Marginal zone	3.2	13	22	0.2	0.9	1.5	5	21	40

sources: Goffard & Hecq, 1988
Antarctic Division (Australia), unpublished data.

3.3.2. Physiological parameters of the model of phytoplankton growth and their environmental control

Parameters of the equations that describe the physiological model of phytoplankton growth were determined by mathematical adjustment of data relative to tracer experiments, conducted on several natural communities growing in the three phytoplankton habitats. *Light* mediated by hydrodynamics and *temperature* were considered as main environmental factors controlling phytoplankton growth in the Southern Ocean. We report in the following paragraphs range of parameters values specific to antarctic phytoplankton of end–summer and their environmental control.

3.3.2.1. *Photosynthetic parameters*

Photosynthetic parameters **Kmax**, α and β and their derived parameters Km, Im and Ik were statistically determined on the basis of experimental photosynthesis versus irradiance curves using Platt *et al.* (1980,1982) equations. The physiological significance of photosynthetic parameters and derived ones is summarized below.

Kmax	Potential maximum photosynthetic capacity.
α	Photosynthetic efficiency (= initial slope of the light saturation curve).
β	Index of photoinhibition (negative slope of the light saturation curve).
Km	Maximum relative photosynthesis realized.
Im	Light intensity at which photosynthesis is maximal.
Ik	Light adaptation parameter (Talling, 1957). $= Km/\alpha$.

Temperature control on photosynthesis parameters was deduced from data on experimental photosynthesis–light relationships, conducted at different temperatures. Figure 12 shows typical photosynthesis–light curves for two natural phytoplankton communities, sampled in the studied area. Examination of Fig. 12 indicates that only light–saturated photosynthesis is temperature–dependent whereas temperature effect is absent under limiting light in agreement with general physiology of photosynthesis (Talling, 1957), which indicates that light–limited photosynthesis rate depends only on photochemical reactions which are temperature independent. Contrasting with this, the recent data of Tilzer *et al.* (1986) on antarctic phytoplankton suggests that under extremely low temperature light–limited photosynthesis rates become temperature dependent due to changes in maximum quantum yields. Photosynthesis rates reported by these authors at extremely low light and temperature could have been underestimated, however, because of the very short incubation time used (2 hours).

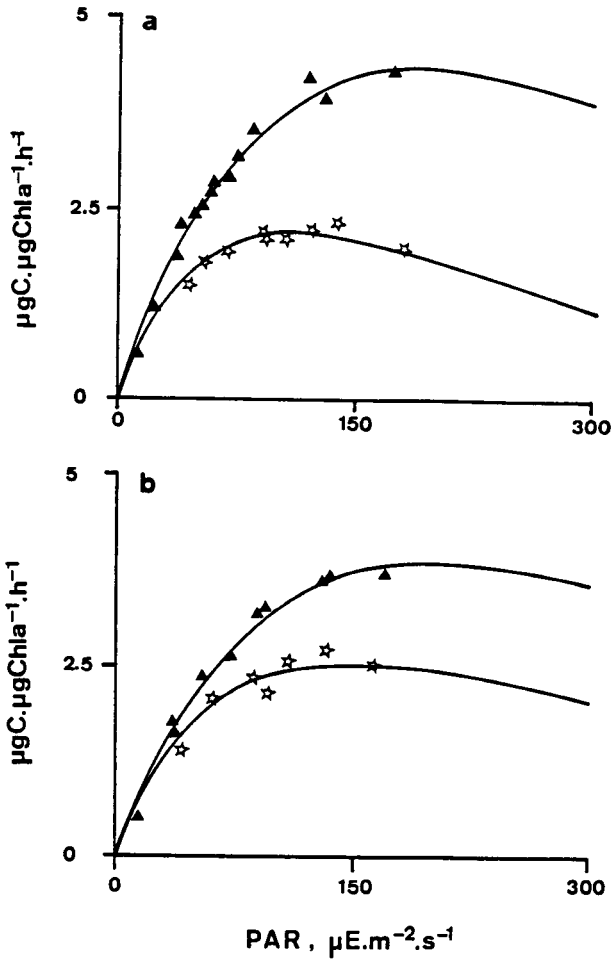


Figure 12 : *Temperature dependence of the photosynthesis–irradiance relationship characteristic of phytoplankton communities of* a. *divergence* and b. *open sea areas*
Ambient temperature: ▲ +6°C; ☆ +1°C.

Summarizing the results of Fig. 12, Table 6 gathers the photosynthetic parameters calculated from these data. It shows clearly the high dependence on temperature of maximal capacity Kmax and the independence to temperature of the photosynthetic efficiency, according to the physiological significance of these parameters. Also the so–called photoinhibition index β appreciably increases with temperature.

Table 6 : Temperature dependence of photosynthetic parameters calculated for two typical stations.

Station	Temperature ^0C	α (1)	kmax (2)	β (1)
Divergence				
93	1.5	0.060	6	0.032
	6	0.064	13.6	0.044
Open sea				
78	1	0.054	4.2	0.010
	6.5	0.056	8	0.018

(1) : $\mu gC.\mu gChla^{-1}.h^{-1}.(\mu E.m^{-2}.s^{-1})^{-1}$
(2) : $\mu gC.\mu gChla^{-1}.h^{-1}$.

Table 7 gathers calculated photosynthetic parameters available from our experiments.

Table 7 : Photosynthetic coefficients and derived parameters.

Station n°	Lat.S	Long.E	date 1987	T(°C) *in situ*	α (1)	kmax (2)	β (1)	Im (3)	Km (2)	Ik (3)
Marginal zone										
29	68°20	77°07	02.18	−0.58	0.016	0.42	0.0002	115	0.39	25
39	67°12	69°16	02.22	−0.49	0.072	1.26	0.0005	87	1.21	16.8
43	67°34	78°44	02.26	−1.11	0.041	1.11	0.0041	65	0.8	19.5
46	66°53	76°16	02.28	−0.45	0.098	3.52	0.0090	89	2.57	26
51	67°44	71°51	03.04	−1.00	0.058	1.18	0.0042	55	0.91	16
Divergence band										
71	65°05	67°53	03.10	−0.08	0.053	2.78	0.009	101	1.71	32
73	64°19	62°57	03.13	+0.42	0.085	3.95	0.001	207	3.7	44
86	64°21	72°57	03.19	+0.57	0.067	6.62	0.012	186	4	60
91	64°19	82°58	03.21	−0.28	0.110	4.81	0.018	86	3	27
93	62°40	87°57	03.23	+0.01	0.060	3.94	0.032	69	1.46	24
24	64°04	91°29	02.15	+1.40	0.060	3.10	0.038	49	1.04	17
Open sea										
78	64°19	77°58	03.16	+0.48	0.054	4	0.01	138	2.4	44

(1) : $\mu gC.\mu gChla^{-1}.h^{-1}.(\mu E.m^{-2}.s^{-1})^{-1}$
(2) : $\mu gC.\mu gChla^{-1}.h^{-1}$.
(3) : $\mu E.m^{-2}.s^{-1}$

The photosynthetic efficiency α reported on Table 7 does not significantly differ from one phytoplankton habitat to another. No clear tendance was to be found between α and the mean light environment of the cells evolving in the upper mixed layer, as illustrated by Fig.13. From this figure, a mean α value of 0.065 could be

considered as typical of end–summer phytoplankton in the studied area. This value is however one order of magnitude higher than those reported by Tilzer *et al.* (1986) for early spring phytoplankton populations, but very close to those reported for sea ice microalgae (Palmisano *et al.*, 1985).

Fig. 14, which illustrates the relationship between the so–called light adaptation parameter Ik and the mean light intensity in the upper mixed layer, shows Ik values very closed to their light environment indicating that phytoplankton cells are well adapted to their specific light environment. Im values on the other hand, i.e. the light intensity at which maximal photosynthesis is observed , is as a general trend a 3 factor higher than their mean light environment (Fig.14).

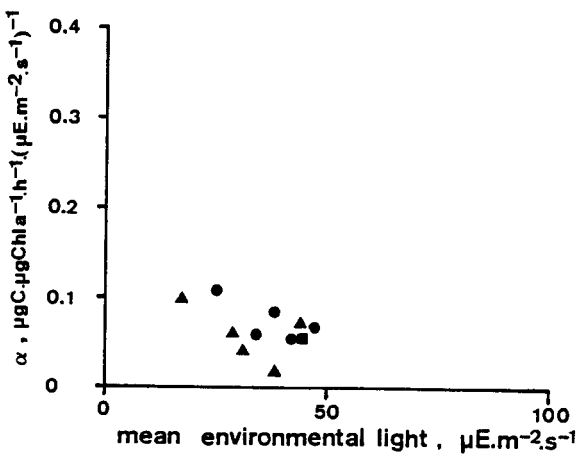


***Figure* 13** : *Empirical relationship between the photosynthetical efficiency α and the mean light environment.*

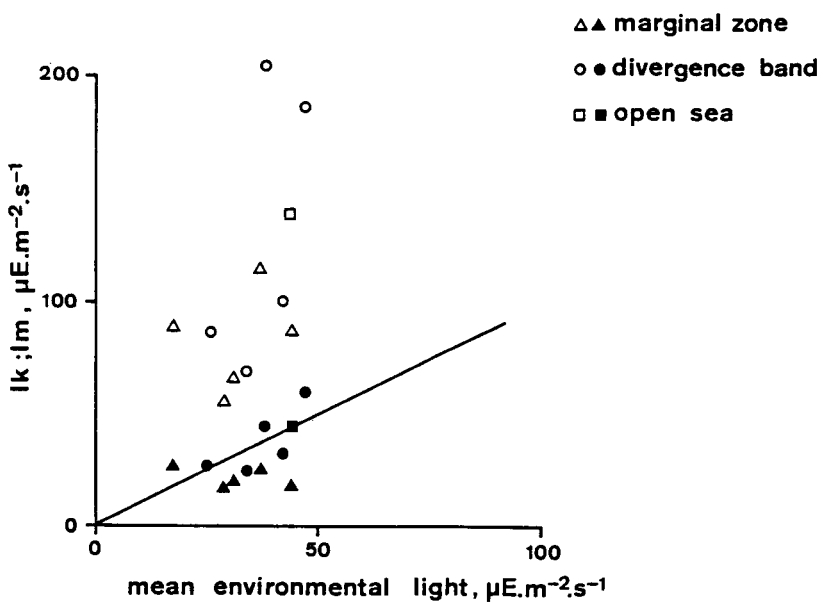


Figure 14 : *Empirical relationship between the light adaptation parameter Ik (closed symbols), Im (open symbols) and the mean light environment. The line indicates a* 1:1 *relationship.*

Maximal potential photosynthetic capacity kmax was shown to vary in a wide range according to the phytoplankton habitat and the environmental temperature (Table 7).

Extreme values of 0.42 and 3.52 were reported for the marginal ice zone in agreement with those reported for similar areas in the Arctic (Platt *et al.*, 1982) and with those reported for similar environmental temperature in the Southern Ocean (Tilzer *et al.*, 1986). Higher extreme values ranging between 2.78 and 6.82 were typical of the open sea/divergence area according to the higher *in situ* temperature. Figure 15, which shows the relationship between kmax and environmental temperature, suggests an exponential dependence, at least in the range –2, +2°C. However, some departure from the exponential curve is observed as temperatures close to the extremes are approached. The slope becomes indeed increasingly steeper

close to lowest temperatures although a plateau or a decrease is observed near upper extreme.

The comparizon with photosynthetic properties of temperate phytoplankton communities growing under similar luxurious nutrient conditions (Fig.15) indicates that although little change of Kmax is apparent when temperature increases from zero to 22°C , there exists for each phytoplankton community a similar exponential relationship between Kmax and temperature defined on a very narrow range of this latter. This calls for a distinction between resistance and capacity adaptations in attempting to relate the physiological charateristics of phytoplankton activities to temperature and to their environment in general, as recommended by Precht (1958). Resistance adaptation to temperature refers to mechanisms that determine the upper and lower temperature extremes limiting growth. Capacity adaptation occurs at temperature between the extremes and are described by kinetics as the exponential relationship reported on Fig.15.

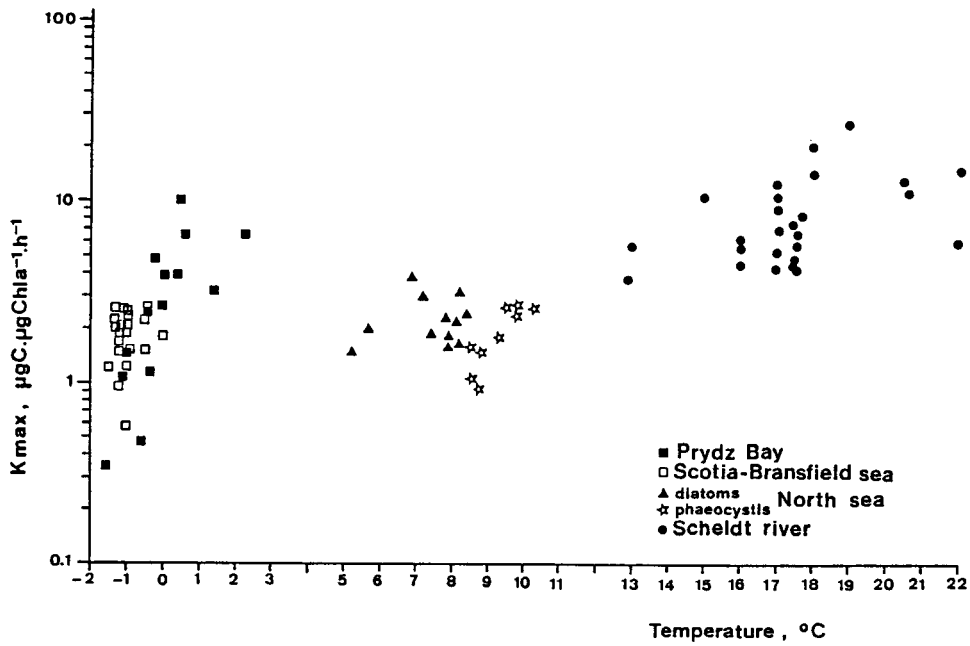


***Figure* 15** : *Empirical relationship between the potential maximal photosynthetic capacity kmax and environmental temperature observed for natural phytoplankton of temperate and cold seas.*

Resistance adaptation to temperature by end–summer antarctic phytoplankton was determined on basis of data relative to short–term effect of temperature on kmax values. Results expressed in % of maximum kmax value are reported on Fig.16. This figure shows clearly that antarctic phytoplankton photosynthesizes at its maximal rate when temperatures range from 2 to 11°C, in agreement with Tilzer and Dubinsky's (1987) data. Below and above these temperatures, Kmax values decrease very sharply, according to similar observations by Neori & Holm–Hansen (1982) in the Western Scotia sea and Bransfield Strait. The case of lower temperatures is particularly interesting. Indeed, such short–term changes in temperature can occur in stratified waters of the Antarctic ocean when storm is suddenly raging. Effect of short–term changes in low temperature (–1.8 to +1°C) would be studied more precisely in the next future.

The **photoinhibition index** β was on average one order of magnitude higher in the open sea/divergence area than in the marginal ice zone. In the latter, photoinhibition by phytoplankton does not appear to be a significant process and may be neglected. The positive correlation observed between β and kmax (Fig. 17) suggests a dependence of this parameter on temperature. The so–called photoinhibition observed at high light intensities possibly reflects increased catabolic processes.

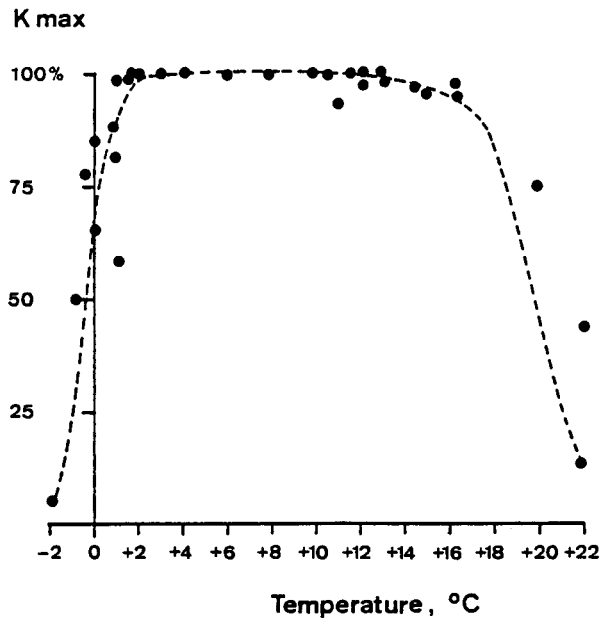


***Figure* 16 :** *Resistance adaptation to temperature by end-summer antarctic phytoplankton.*

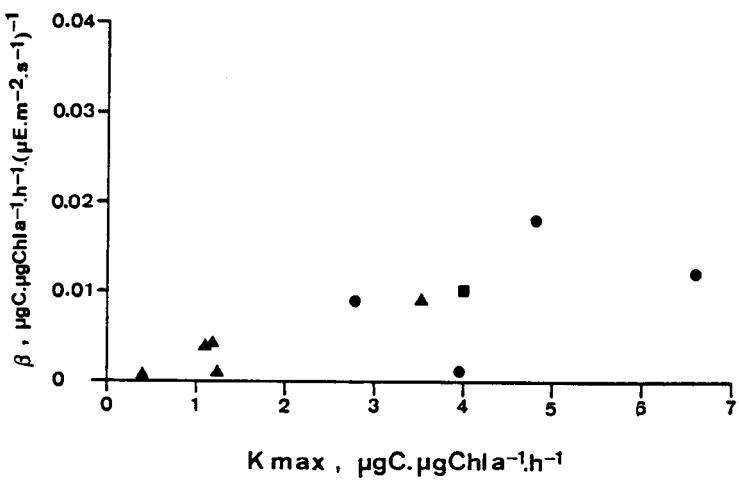


***Figure* 17 :** *Empirical relationship between the photoinhibition index β and the potential maximal photosynthetic capacity kmax.*

3.3.2.1. *Growth parameters*

Maximum specific growth rates, μmax, were shown to range between 0.0008 and 0.008, according to environmental temperature. Figure 18a, which shows the relationship between μmax and *in situ* temperature, suggests that capacity adaptation of growth to temperature obeys an exponential law.

On the other hand, resistance adaptation is characterized, as expected, by the same range of lower and upper temperatures as those observed for maximal photosynthetic capacity kmax, as seen by comparizon of Fig.16 and Fig. 18b.

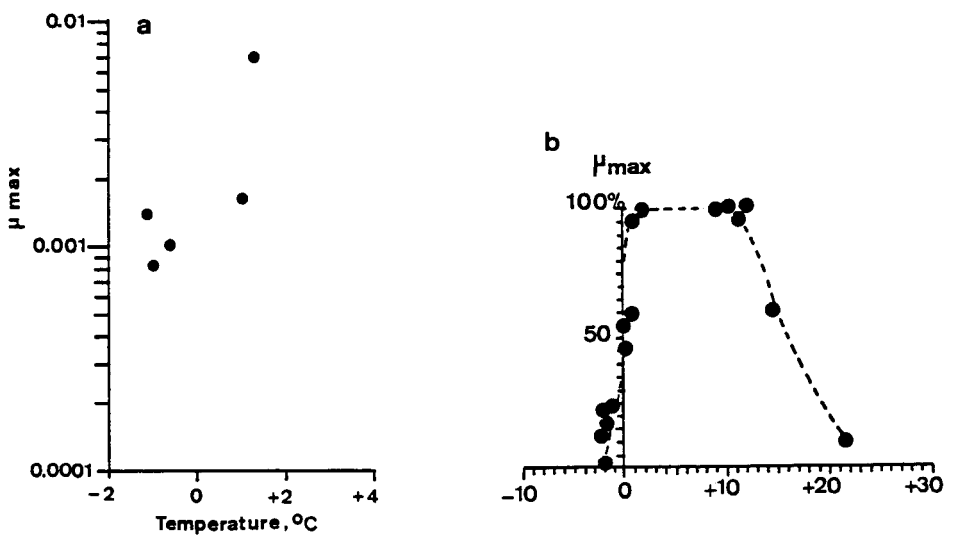


***Figure* 18:** *Capacity* (a) *and resistance* (b) *adaptation to temperature of phytoplankton growth in the Southern Ocean.*

The **half-saturation constant, K_N** which characterizes Michaelis–Menten. function governing assimilation of inorganic **N** into proteins was evaluated to 4 μmoles.l^{-1} by similarity to that experimentally determined by Lancelot *et al.* (1986) in eutrophicated temperate coastal waters. The winter level of inorganic nitrogen in these latters is 35 μmole l^{-1} i.e. very close to that of Southern Ocean.

The **half saturation constant,** K_S which characterizes the Michaelis–Menten function governing macromolecular synthesis of small intracellular metabolites, was assumed to be equal to the cellular quota S. The latter is assumed to represent about 5% of F macromolecules (Mayzaud & Martin, 1975). Ks was therefore estimated from the protein content of phytoplankton cells calculated from Chlorophyll a and assuming that proteins represent 85% of the structural and functional macromolecules F. A protein/chlorophyll a ratio of 130 was experimentally determined for these end–summer communities.

The value of the **maintenance metabolic rate, maint** was experimentally determined from 24 hours–kinetics of ^{14}C assimilation into proteins and polysaccharides of phytoplankton communities incubated at very low temperature. Under these conditions, dark protein synthesis does not proceed (Fig. 19). The negative slope of dark ^{14}C assimilation into reserve polysaccharides can therefore be considered as a measure of the relative rate of maintenance. Absolute rate of maintenance is then calculated on the basis of the pool size of reserves products. This latter is calculated from corresponding chlorophyll a using a 3.2 ratio between reserves polysaccharides and chlorophyll a, as experimentally determined. Specific rate is finally deduced from the size of structural and functional macromolecules determined as above.
According to this, **maint** was estimated to 0.0006 h^{-1} and 0.0019 h^{-1} for the marginal and divergence areas respectively, in good agreement with the range of 0.0007 and 0.002 h^{-1} reported by Geider *et al.* (1986).

The **cost of synthesis** ξ should be calculated from a consideration of the biological pathways leading to the synthesis of the major classes of macromolecules including the costs for assimilation of nutrients. However, according to Penning de Vries *et al.* (1974), the model assumes ξ to have a fixed value dependant on the inorganic source of nitrogen, namely 0.32 and 0.67 for ammonium and nitrate sources respectively.

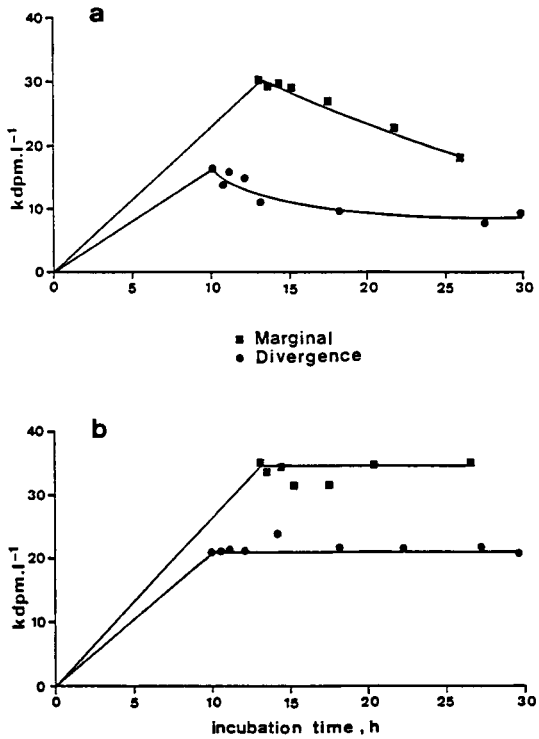


***Figure* 19 :** *Kinetics of* ^{14}C *dark assimilation into storage products* (a) *and proteins* (b) *by phytoplankton incubated at* $-1^{0}8$ *C.*

3.3.3. Modelling phytoplankton growth in the Prydz Bay area.

Temperature and light regime mediated by the hydrodynamics of the antarctic sector under study were shown to be the dominant factors determining growth of phytoplankton cells evolving in the upper mixed layer. Indeed, according to the relative depth of euphotic and mixed layer, 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., depending on the previous light history of the cells.

The conjugated control of phytoplankton growth by variations in environmental temperature and in the stability of the upper mixed layer was established for an end summer phytoplanktonic community of Prydz Bay by means of the mathematical model described in § 3.1. Daily specific rates of growth and autocatabolism by phytoplankton were calculated by integration of equations 1–6 on the variations of PAR and on the depth down to the bottom of the mixed layer. The values of the parameters are those discussed in § 3.3.2.

Several runs of the physiological model were performed, illustrating typical environmental conditions experienced by phytoplankton cells in the Prydz Bay area during end–summer.

Figure 20 plots the predicted daily specific growth and autocatabolism rates in function of the depth of the mixed layer. Examination of Fig. 20a shows that specific daily growth decreases exponentially when mixed layer becomes deeper, while specific daily autocatabolism increases slowly with depth and stabilizes as a consequence of the simultaneous decrease in phytoplankton biomass. The critical depth, i.e. the depth at which growth exactly compensate autocatabolism on a daily average, is situated at –30m under these particular growing conditions. Results from several runs of the model under different growing conditions (changes in optical properties of the water column (Fig. 20b), changes in daily PAR (Fig. 20c), decrease in temperature resulting in a decrease in Kmax, μmax and maint (Fig.20d) show that the critical depth is determined together by the depth of the mixed layer, the optical properties of the water column, the temperature and the physiology of phytoplankton. This contrasts with Sverdrup's (1953) theory of the compensation depth, which assumes a single control by vertical stability.

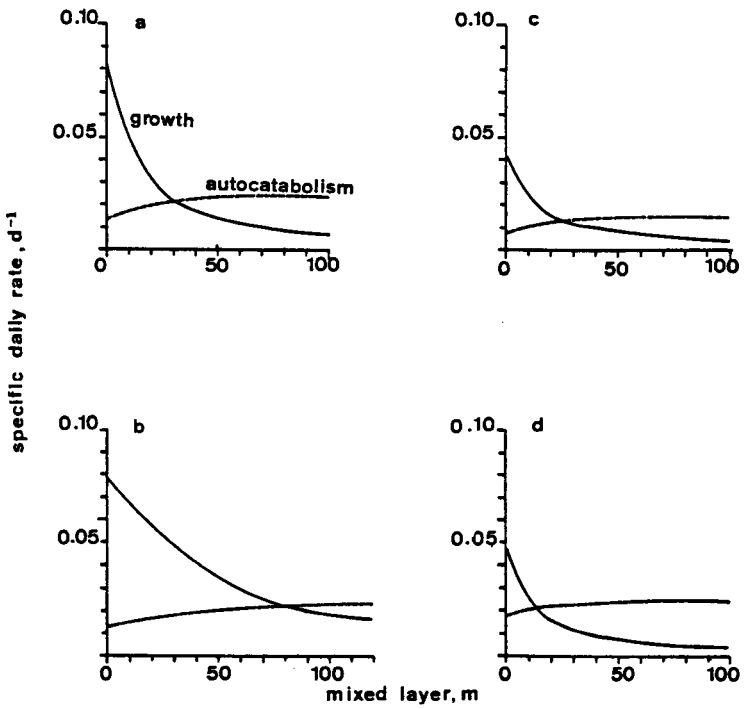


***Figure* 20:** *Daily specific growth and autocatabolism rates calculated for different depths of the mixed layer under different in situ growing conditions*
a: $\eta = 0.29\ m^{-1}$ $\phi = 17h$ $T = 1^0C$
b: $\eta = 0.10\ m^{-1}$ $\phi = 17h$ $T = 1^0C$
c: $\eta = 0.29\ m^{-1}$ $\phi = 13h$ $T = 1^0C$
d: $\eta = 0.29\ m^{-1}$ $\phi = 17h$ $T = 1.8^0C$

From these predictions and assuming that optical properties of the water column are mostly dependant on phytoplanktonic biomass according to Fig. 11, it is possible to calculate the steady state biomass of phytoplankton for the extreme conditions of temperature and light prevailing in Prydz Bay during end–summer 1987. Upper and lower predicted curves are shown in Fig. 21, together with field data. Comparizon between prediction and observation indicates that from a physiological point of view, growth and autocatabolism of phytoplankton are most of the time well–balanced in the Prydz Bay during this end–summer period. No net increase of phytoplankton biomass should therefore be observed at this period.

Assuming that krill grazing was not significant at this period, any discrepancy with respect to the predicted equilibrium field should be interpreted in terms of the growth state of phytoplanktonic populations. Chlorophyll levels situated higher than the predicted equilibrium field should indicate a declining phytoplankton community, while lower chlorophyll levels should indicate growing populations. Accordingly, growing communities are mostly located in the marginal area, whereas declining phytoplankton belongs to the open sea zones (Fig.21).

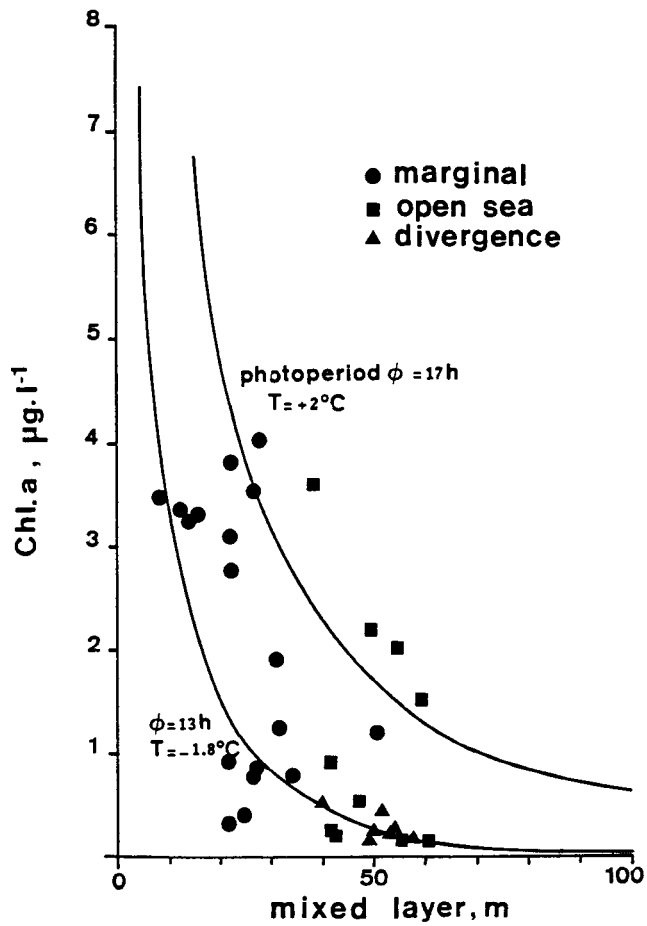


Figure 21 : *Relationship between phytoplankton biomass and the depth of the mixed layer. Calculated steady-state phytoplankton biomasses for different extreme growing conditions compared with corresponding observations.*

Using the same model and hypothesis, the steady state biomass of phytoplankton was calculated for a large range of mixed layer depths reproducing ice edge system on the one hand and oceanic areas on the other hand. Temperature was kept constant and the physiological characteristics of the phytoplankton community were assumed to be identical. Results of these calculations are illustrated by Fig. 22 They show an assymptotical dependence of steady state phytoplankton biomass on the depth of the mixed layer. At shallow mixed layer as in the marginal zone, steady state biomass tends to fabulous chlorophyll a concentrations, in perfect agreement with values recorded by El–Sayed (1971) in surface waters of the Weddell Sea. Conversely, for very deep mixed layer, steady state biomass tends to undetectable concentrations, as usually recorded in the oceanic area (cf. El–Sayed, 1987).

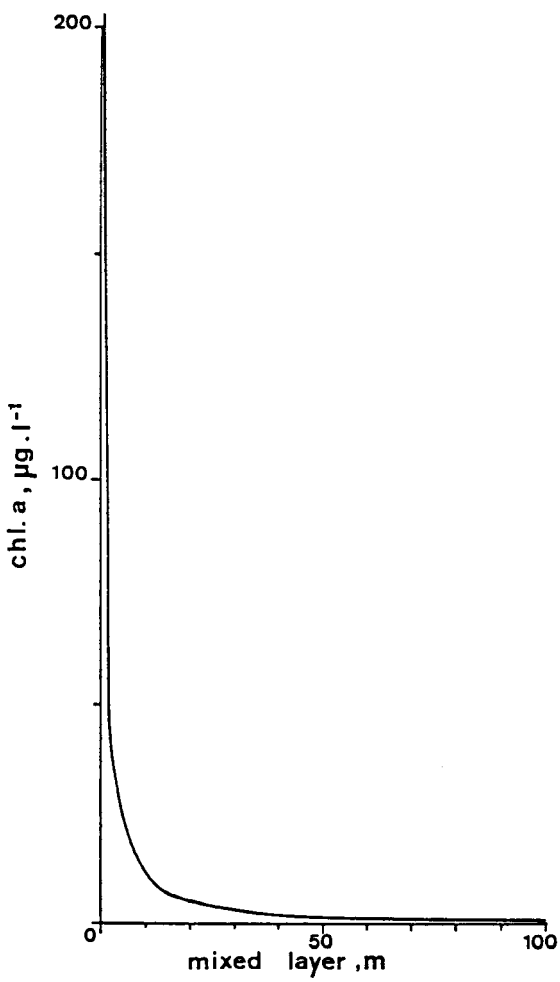


***Figure 22**: Calculated relationship between steady–state phytoplankton biomass and the depth of the mixed layer.*

3.3.4. Estimation of net primary production in the Prydz Bay area

The preliminary simulation experiments of phytoplankton growth described above indicate that the conceptual mathematical model of phytoplankton growth developed here is able to predict the major trends of the variations in antarctic phytoplankton on the basis of the knowledge of ecophysiology of phytoplankton and the vertical mixing of surface waters. This model was therefore used for calculating the mean daily gross (photosynthesis) and net (growth) primary production in Prydz Bay area during end–summer 1987. The results of these calculations are shown on table 8 which gathers mean daily activities (photosynthesis, growth, excretion and respiration) within the three phytoplanktonic habitats considered.

The value of the parameters of the equations of the model were estimated on the basis of the empirical relationships presented in § 3.3.2. assuming a mean environmental temperature of -1^0C and $+0.5^0$C respectively for the marginal and divergence/open sea areas. The mean phytoplanktonic biomasses and vertical light attenuation coefficients were those reported in table 3 and 4 respectively. A mean mixed layer of 20, 40 and 55 m was considered as characteristic of the marginal, divergence and open sea areas respectively. As far as the marginal area is concerned, additional runs of the model were performed for simulating the particular conditions of either highly stabilized or more deeply mixed conditions occurring at the ice edge areas. The extreme values of mean daily photosynthesis and growth calculated for these conditions are also indicated in table 8.

Table 8. Mean daily rates of primary production in the Prydz Bay area during end-summer 1987 ($mgC.m^{-2}.d^{-1}$).

Habitat	photosynth.	growth	excretion	respir.	growth yield
marginal area (*)	460 (110–695)	127 (29–235)	23	310	0.3
divergence	240	24	12	204	0.1
open sea	170	20	8	142	0.1

(*) Values in bracket are calculated for a 35 m and a 7.5 m deep upper mixed layer.

Examination of table 8 indicates that gross primary production is about twice as high in the marginal as in the divergenc/open sea area. The values calculated for the latter environment are in good agreement with those reported as characteristic of the Southern Ocean (El Sayed, 1987). Also, extreme values for marginal phytoplankton photosynthesis lie within the range of those cited by Wilson et al. (1986) in a stabilized ice edge of Ross Sea.

Calculated net primary production rates reported in Table 8 are the first available for the Southern Ocean, as only photosynthesis measurements were previously reported in the literature. Such estimations can indeed only result from the application of a physiological model. As can be seen, the values found are particularly low in the open sea/divergence area, owing to the importance of catabolic processes in deep mixed layer.

From the photosynthesis and growth rates reported in Table 8 , a mean growth yield of 0.3 and 0.1 was calculated for the marginal and open sea/divergence area respectively. The former value is close to that found for well growing phytoplankton communities of temperate seas (Lancelot, in Reid et al, 1989).

The ecophysiological model developed in this section therefore represents an important tool for the overall estimation of net primary production of the antarctic ecosystem. Better knowledge of phytoplankton physiology in the different antarctic habitats (water, melting ice, ice), together with the development of hydrodynamical models for the prediction of verticval mixing of surface waters and sea ice dynamics 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 finctionning of the antarctic ecosystem.

4. BACTERIOPLANKTON

4.1. CONCEPTUAL MODEL OF ORGANIC MATTER UTILIZATION BY BACTERIOPLANKTON

4.1.1. Principle

As a guideline for our analysis of heterotrophic bacterial activity, Figure 23 shows a diagrammatic representation of our general view of the basic processes involved in bacterial organic matter utilization in aquatic environments (Servais, 1986; Billen & Fontigny, 1987).

Biodegradable organic matter in the sea is mostly supplied by phytoplankton, either through excretion or through cell lysis. While in the former process small monomeric substrates are directly produced, in the latter process, most of the organic matter is released under the form of macromolecular biopolymers (Billen, 1984).

On the other hand, it is recognized for a long time that bacteria can only take up low molecular weight substrates like amino–acids, carboxylic acids, monosaccharides or their oligomers, that we will call ***direct substrates*** **S** , which are recognized by specific permeases. High molecular weight polymers **H** , like proteins or polysaccharides, cannot be metabolized without being first hydrolized through the action of extracellular enzymes (Rogers, 1961).
Extracellular hydrolysis therefore appears as a key process controlling the overall rate of organic matter degradation in aquatic environment. Accordingly, the most important fraction of biodegradable organic matter present in natural waters consists in high molecular weight compounds, while direct substrates are maintained at steady low concentrations (Billen *et al.* 1980; Billen, 1984; Fuhrman & Ferguson, 1986; Fuhrman, 1987).

Once taken up by bacteria, direct substrates are either catabolized or anabolized. In the former case, at least under oxic conditions they are mainly oxidized into CO_2, while in the latter they are used for producing bacterial biomass B. The ratio between biosynthesis and total organic matter utilization defines the growth yield Y.

The bacterial biomass formed is destroyed by mortality. This process consists either in grazing by protozoans Z or in spontaneous or phage–induced cell lysis (Servais *et al.* 1985; Becquevort *et al.*, 1989). The former process transfers part of bacterial biomass to higher trophic levels, while the latter results in recycling it into the pool of organic matter.

This view of the interactions between bacteria and organic matter is admittedly idealized. Its usefulness, however, lies in the fact that powerful methods have been developed for directly measuring the rate of most of the basic processes listed above (exoenzymatic activity, uptake of direct substrates, bacterial biomass production and bacterial mortality) and to study their kinetics and control mechanisms.

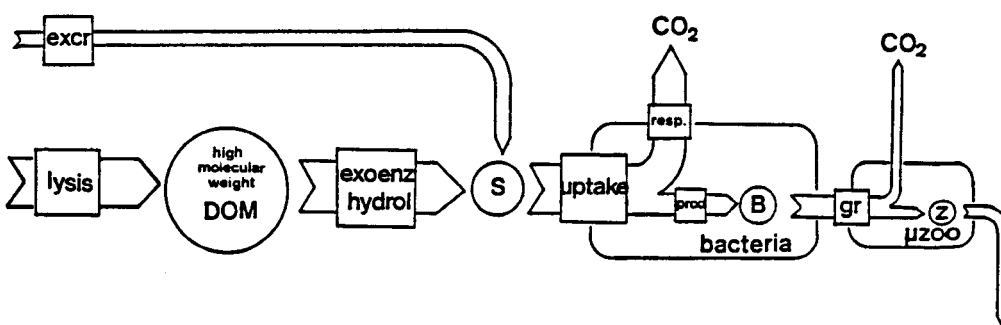


Figure 23 : *Diagrammatic representation of the basic processes involved in bacterial utilization of organic matter in the planktonic phase. S stands for directly usable small low molecular weight organic substrates (direct substrates); B, for bacterial biomass; Z, for heterotrophic nanozooplankton.*

4.1.2. Mathematical formulation

Extracellular hydrolysis of biopolymers was shown to obey a Michaelis–Menten kinetics (Somville & Billen, 1983; Somville, 1984). Bacterial exoenzymes are mostly attached to bacterial envelopes and present in constant amount with respect to biomass (Fontigny *et al.*, 1987). Servais (1986) has shown that it is possible to describe the bacterial utilization of phytoplanktonic derived organic matter by assuming that it is made of two fractions (H_1, H_2) with different susceptibilities to extracellular hydrolysis, hence different parameters of their Michaelis–Menten degradation kinetics.

The uptake of direct substrates was also shown to obey an overall Michaelis–Menten kinetics (Parsons & Strickland, 1962; Wright & Hobbie, 1966). A constant fraction Y of the amount of substrates taken up is used for biomass production, the remaining part being respired (Servais, 1986).

The process of bacterial mortality can be represented, as a first approximation, by a first order kinetics.

The following equations can therefore be written for describing the dynamics of bacterial growth in the sea :

$$\frac{dH_1}{dt} = -e_1max \frac{H_1}{H_1 + KH_1} B + pH_1 \qquad (8)$$

$$\frac{dH_2}{dt} = -e_2max \frac{H_2}{H_2 + KH_2} B + pH_2 \qquad (9)$$

$$\frac{dS}{dt} = e_1max \frac{H_1}{H_1 + KH_1} B + e_2max \frac{H_2}{H_2 + KH_2} B - bmax \frac{S}{S + Ks} B + pex$$

$$\frac{dB}{dt} = Y\, bmax \frac{S}{S+Ks} B - kd\, B \qquad (11)$$

where

e_1max, e_2max	are the maximum rates of polymers hydrolysis per unit bacterial biomass
K_{H_1}, K_{H^2}	are the half saturation constants of polymers hydrolysis
p_{H_1}, p_{H_2}	are the rate of production of polymers through phytoplankton lysis
bmax	is the maximum rate of substrate uptake by bacteria
K_s	is the half saturation constant of substrate uptake
Y	is the growth yield
kd	is the mortality constant
pex	is the rate of production of substrate through phytoplankton exudation

4.2. METHODS

4.2.1. Bacterial biomass determination

4.2.1.1. *Direct counts (AODC)*

Bacterial biomass was determined by epifluorescence microscopy after acridine orange staining (AODC) according to the procedure of Hobbie *et al.* (1977). Microscope slides were prepared immediately after collection of samples and checked with a Zeiss epifluorescence microscope available on board. They were then stored in the dark at 4°C until return to the laboratory where cell numbers were counted with a Leitz Dialux microscope, and biovolumes visually estimated by comparison with a calibrated grid. Except in few instances of very high bacterial densities, where larger cells were observed, the bacterial volume was generally between 0.020 and 0.07 μm^3. Biomass was calculated from biovolume, using a conversion factor of 1.2 10^{-7} $\mu gC.\mu m^{-3}$ (Watson *et al.*, 1977).

4.2.1.2. *Potential exoproteolytic activity (PEPA)*

A fluorimetric method for measuring potential exoproteolytic activity of marine waters was developed by Somville and Billen (1983). It is based on following the rate of hydrolysis of the peptide–analog L–leucyl–β–Napthylamide. The enzyme unit (e.u.) was defined as the amount of enzyme catalysing the cleavage of 1 nmol β–Naphtylamine.min^{-1} at 20°C at saturating concentration of the substrate. The bacterial nature of this activity was demonstrated by Vives–Rego *et al.* (1985) as well as the fact that these exoenzymes are attached to the external envelope of bacteria. More recently (Fontigny *et al.*, 1987), we showed that in the North Sea no important regulation processes occurred under natural condition for adjusting the level of exoproteolytic enzymes per cell, so that PEPA could be used as an indirect but very convenient index of bacterial biomass. A conversion factor of 0.44 e.u.μgC^{-1} was found between PEPA and bacterial carbon.

Parallel determinations of PEPA and AODC performed in antarctic waters demonstrated that the same holds for this environment. Incubating the samples at 13°C (ambient temperature of the laboratory), a correlation (r = 0.92) was found between PEPA and bacterial biomass with a slope of 0.28 e.u.(13°C)μgC^{-1} (Fig. 23). An experiment was carried out for determining the direct effect of temperature on PEPA . This effect was found exponential throughout a large range of temperature, and could be characterized by a Q_{10} of 2.28. Using this correcting factor, it is easily shown that the same relationship between PEPA and bacterial biomass holds in Antarctic waters.

Based on this, bacterial biomass was estimated either from AODC or from PEPA measurements when the former could not be carried out.

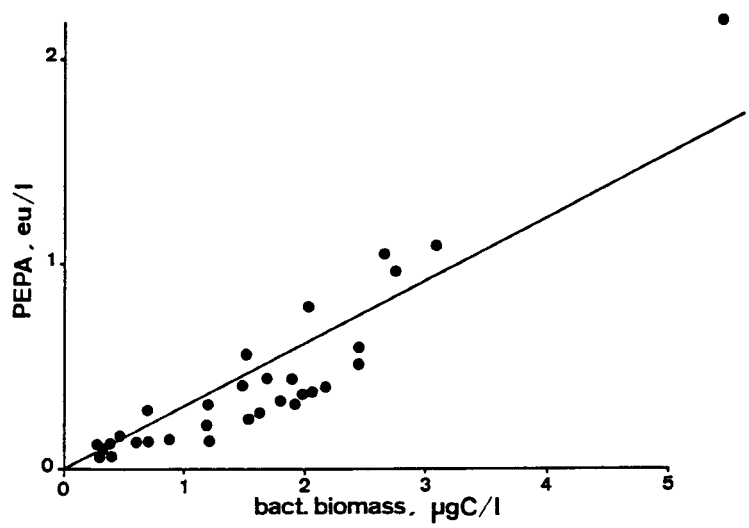


Figure 24 : *Relationship between potential exoproteolytic activity (measured at an incubation temperature of* 13°C) *and bacterial biomass in antarctic waters.*

4.2.2. Bacterial production and growth rate measurements

Thymidine incorporation into cold TCA insoluble material was measured following the procedure of Fuhrman & Azam (1982). 20 ml samples were inoculated with 20 μCi methyl-^{3}H-thymidine, making a final concentration of about 25 nmoles/l. After incubation, 10 ml cold 15 % TCA was added to the sample for precipitating macromolecules. After 3 minutes, the samples were filtered and rinced with 5 % TCA. Control samples incubated with $HgCl_2$ gave incorporation similar to those blocked with TCA at time zero (about 1000 cpm). This control was deduced for calculation.

Conversion of thymidine incorporation into cell production is still a matter of uncertaincy, as the conversion coefficient, either theoretically calculated (Fuhrman & Azam, 1982; Fallon *et al.*, 1983; Riemann *et al.*, 1984; Bell & Kuparinen, 1984; Lovell & Konopka, 1985) or empirically determined (Bell *et al.*, 1983; Billen & Fontigny, 1987; Scavia *et al.*, 1986; Riemann *et al.*, 1986; Servais, 1986) ranges from 0.5 to 12 10^9 cells produced per nmole thymidine incorporated into cold TCA insoluble material. By following both cell number increase and thymidine incorporation in 0.2 μ filtered sterilized surface water reinoculated with 2 μ filtered water and incubated at 2–4 and 10°C respectively, the conversion factor could be determined for our own site (Fig. 25). A value of 5 10^9 cells nmole^{-1} thymidine was found.
Note that this factor is only applicable to the upper mixed layer. Below the pycnocline, it is quite possible, and a few measurements suggest that a greater part of thymidine incorporates into other macromolecules than DNA, as already shown for starved populations of bacteria by Servais *et al.* (1987) and Azam *et al.* (pers.comm.). Due to a failure of our sonicator, this could not be quantified and we are unable to establish a conversion factor for the lower layers.

Carbon production rates were calculated from cell production rates, taking into account the mean cell volume determined microscopically and a specific biomass/biovolume ratio of 1.2 10^{-7} μgC μm^{-3}, as discussed above.

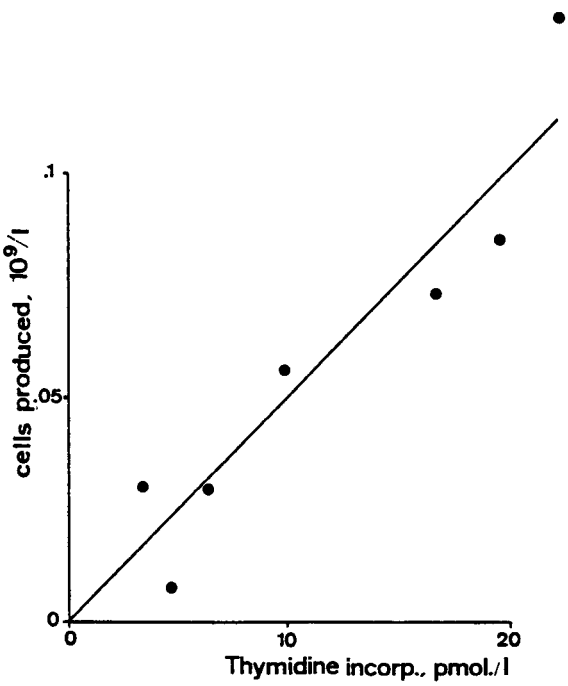


Figure 25 : *Empirical calibration of thymidine incorporation into cold TCA insoluble fraction in terms of bacterial cells produced.*

4.2.3. Bacterial mortality

The rate of bacterial mortality was estimated according to a procedure modified from that developed by Servais *et al.* (1985). A sample was incubated for about 24 h. at *in situ* temperature with 25 nmole.l^{-1} (methyl-^{3}H)-thymidine. It was then put for 10–20 h. in a dialysis bag in a flow of seawater, in order to eliminate the unincorporated thymidine. The disappearance of radioactivity from the DNA of the bacteria was then followed for about 50 h. A linear decrease was observed in semilog

plot, the slope of which give the first order specific mortality coefficient (kd). Filtration of the sample after the dialysis step through 2 µm Nuclepore membrane allowed to distinguish bacterial grazing by > 2 µm microzooplankton from a *residual* mortality due to other causes. An example of result is given in Fig. 26.

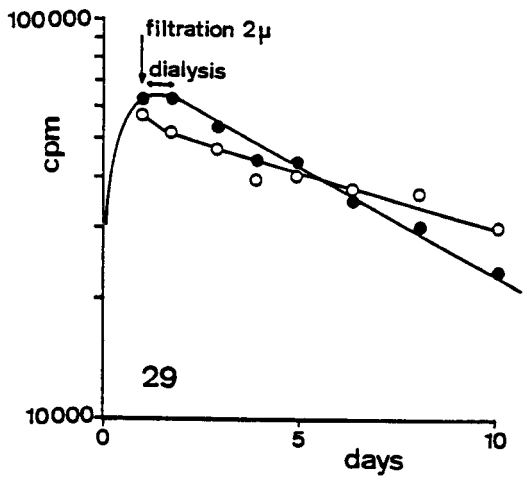


Figure 26 : *Example of result obtained by our method of mortality rate determination : exponential decrease of the radioactivity in the DNA of a bacterial community, labeled with ^3H-Thymidine, dialysed and incubated at* in situ *temperature.*

Solid symbols : unfiltered sample
Open symbols : sample filtered through 2 µ membrane in order to remove the microzooplankton.

4.3. DESCRIPTION OF BACTERIOPLANKTON DYNAMICS IN THE PRYDZ BAY AREA

4.3.1. Absence of dissolved organic matter accumulation in Antarctic waters during late summer

DOC concentrations, as measured by UV assisted persulfate oxidation followed by CO_2 determination by infrared spectrometry (using a Dohrmann DC–80 analyser), vary little in surface water. The total range is between 0.6 and 1.3 mgC.l^{-1}. Values higher than 1 mgC.l^{-1} are only found in the most coastal areas of Prydz Bay. This is the range cited for open ocean situations (Williams, 1975). We never observed values as high as those reported by Bolter & Dawson (1982). The situation observed by the latter authors certainly results from the presence of a *Phaeocystis* bloom and is by no means a general characteristics of the Antarctic Ocean. Similar observations of temporary high DOC concentrations associated with *Phaeocystis* blooms have been reported in temperate marine systems (Eberlein *et al.*, 1985; Billen & Fontigny, 1987).

Vertical profiles of DOC (Fig. 27) show a clear decrease with depth. Below the pycnocline, DOC concentrations are typically 0.6 mgC.l^{-1}, whatever the value in the upper layer. This value is quite similar to that found in the deep ocean at lower latitudes.

A few determinations of biodegradable dissolved organic carbon have been carried out, according to the procedure described by Servais *et al.* (1985). The results are in the range 0.02 to 0.15 mgC.l^{-1} (i.e. 2 to 22 % of DOC) in the upper layer, while lower values are found below the pycnocline, in the range 0 to 0.01 mgC.l^{-1} (i.e. 0–2 % of DOC). These percentages of biodegradable organic matter are rather low when compared to those found in the Belgian coastal waters (typically 30 %).

All these results clearly refute the statements made by some authors that organic matter is preserved in antarctic waters and exported to lower latitudes by deep water circulation.

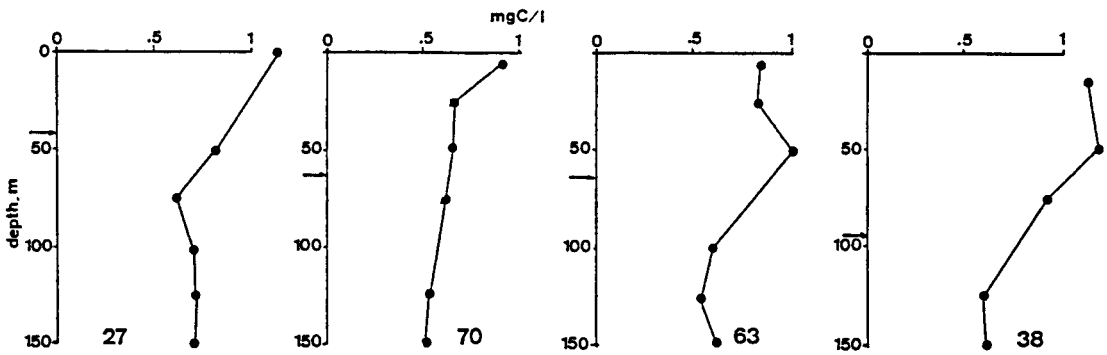


Figure 27 : Vertical profiles of the concentration of dissolved organic carbon in February-March 1987.

4.3.2. Bacterial biomass and its relationship with phytoplankton

4.3.2.1. *Geographical and seasonal variations of bacterial biomass*

Vertical profiles of bacterial biomass observed in February–March 1987 show rather uniform values within the upper mixed layer, then a sharp decrease below the pycnocline (Fig. 28).

Figure 29 shows the geographical distribution of bacterial biomass in the upper layer in Prydz Bay area, as observed in February–March 1987. The highest values are observed south of the 66th parallel, and particularly on the continental plate. Within Prydz Bay, the highest values are located in the eastern part. In the offshore area, all north–south transects reveal a secondary maximum (Fig. 30), which is exactly associated with the position of the divergence (see Fig. 8).

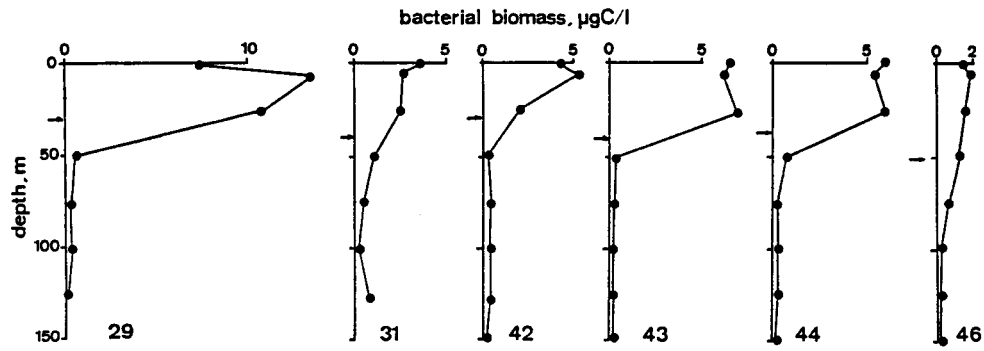


Figure 28 : *Vertical profiles of bacterial biomass in the Prydz Bay area in February-March* 1987.

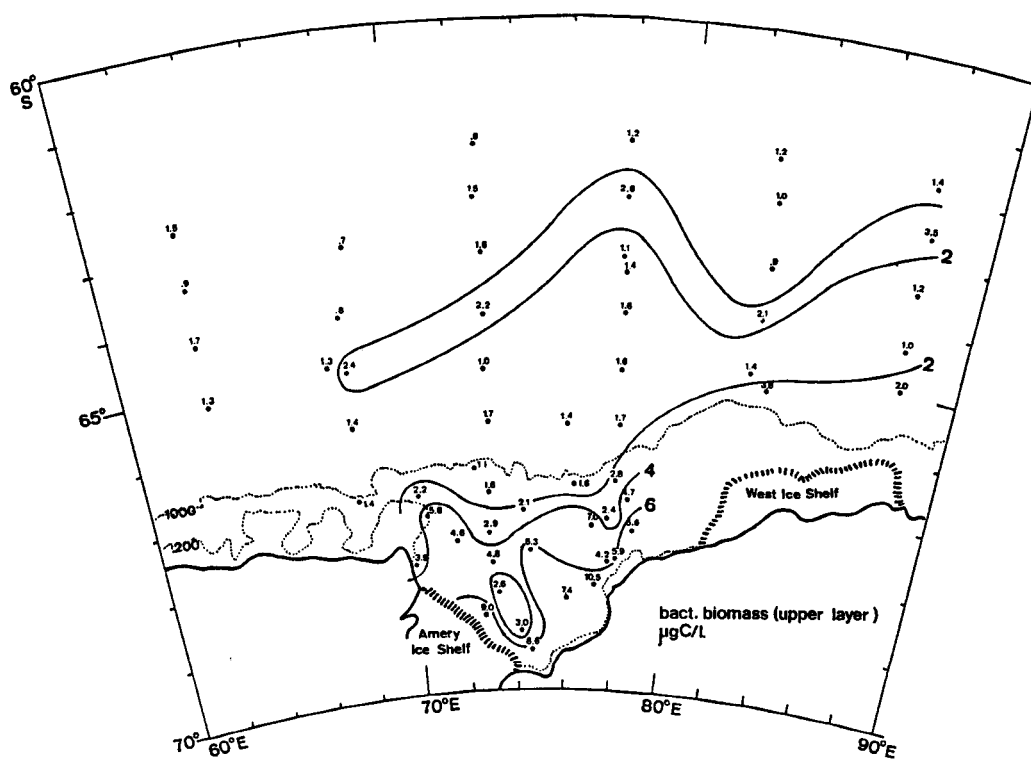


Figure 29 : *Distribution of bacterial biomass in the upper layer in February–March* 1987.

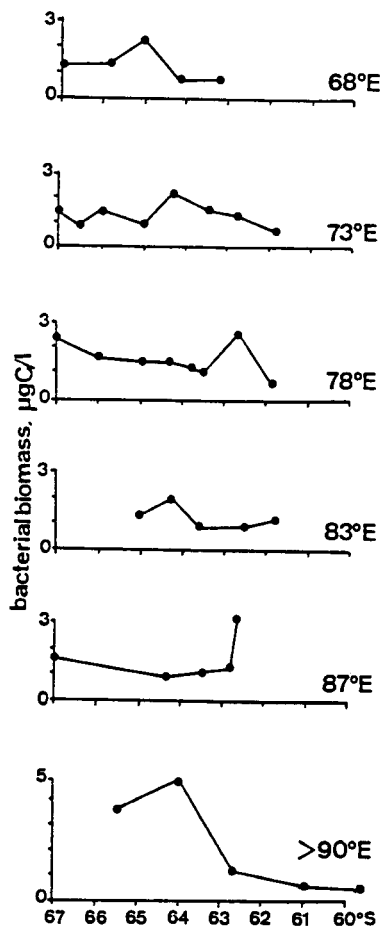


Figure 30. *North–South transects of the bacterial biomass in the upper layer off Prydz Bay, in March* 1987.

As these observations were not synchroneous, the geographical distribution shown by Fig. 29 might be biased somehow by seasonal variations. These seasonal variations are clearly shown in Fig. 31, where the data from a limited area off Prydz Bay (between 62 and 66°S) have been gathered. This area is entirely located in the marginal zone in mid–January. We have included the observations carried out by W. Overloop, Y. Dezan and Cl. Joiris during the *Indigo* cruise on board of the R.V. *Marion Dufresne* from 18th to 21st January 1987. The data show low bacterial biomasses at the end of January, much higher values one month later, and then a regular decrease from the beginning to the end of March.

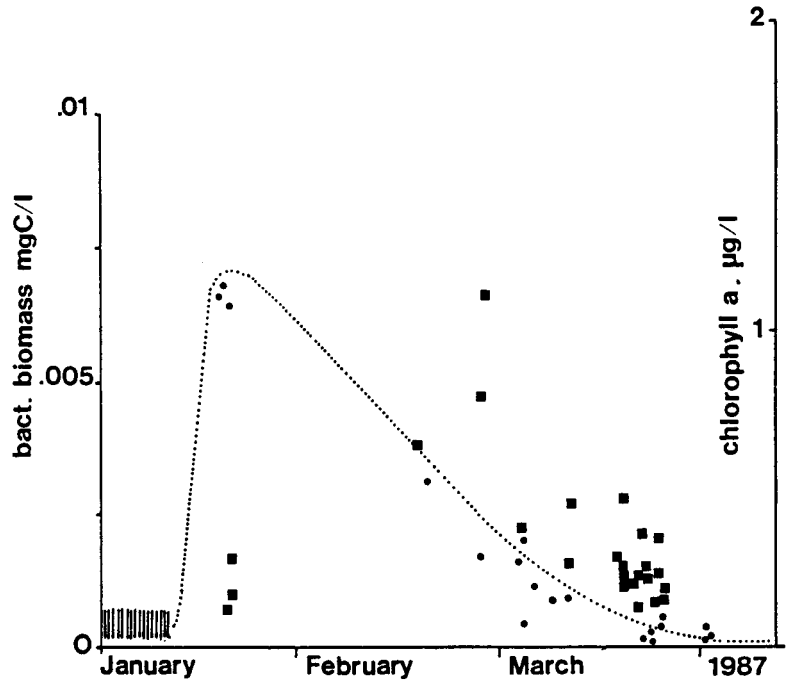


Figure 31: *Observed variations of phytoplanktonic* (•) *and bacterial* (■) *biomass in the Prydz Bay area (between* 62 *and* 66^0 *S) after melting of the ice in summer* 1987.

4.3.2.2. *Bacterial biomass–chlorophyll a relationship*

Vertical and geographical distributions of bacterial biomass observed in Prydz Bay in February–March 1987 suggest a close control by phytoplankton. Much higher biomasses exist above the pycnocline than below and the highest values in the upper layer are found in the areas characterized by a shallow mixed layer, which were shown above to be able of sustaining higher phytoplankton biomasses.

A correlation between bacterial and phytoplankton biomasses is classical in most temperate aquatic environments (Linley *et al.*, 1983; Bird & Kalf, 1984). Several authors, however, did not found it back in the Southern Ocean. Thus, Mullins & Priddle (1987) observed only low bacterial biomasses, without any

relationship with phytoplankton in the Bransfield Strait in end–January. So did Davidson (1984) in mid–December off Prydz Bay. Similarly, the data collected in Prydz Bay by our Belgian colleagues on board of the *Marion Dufresne* in mid–January (Joiris *et al.*, 1987) do not show any significant relationship between the low bacterial biomass and the comparatively high chlorophyll a concentration (Fig. 32). Our data in February, for their part, show a clear relationship with chlorophyll a, with much higher bacterial biomass (Fig. 32). In March, phytoplankton biomasses are much lower, but bacteria remain at relatively high concentrations, in good agreement with the data collected in beginning April by Painting *et al.* (1985) in the same area (Fig. 32).

Put together, all these apparently contradictory data are easily reconciled : they indicate the existence of a *delayed* relationship between phytoplankton and bacteria. Such a delay was already described in the North Sea (Billen & Fontigny, 1987; Billen *et al.*, 1988), where the peak of bacterioplankton follows the phytoplankton spring bloom by about 10 days. Comparison of the data of bacterial biomass with those of phytoplankton shown in Fig. 31 suggests that the delay between phytoplanktonic and bacterial peaks is of about 1 month in Antarctica, the former occurring in early February, the latter in early March.

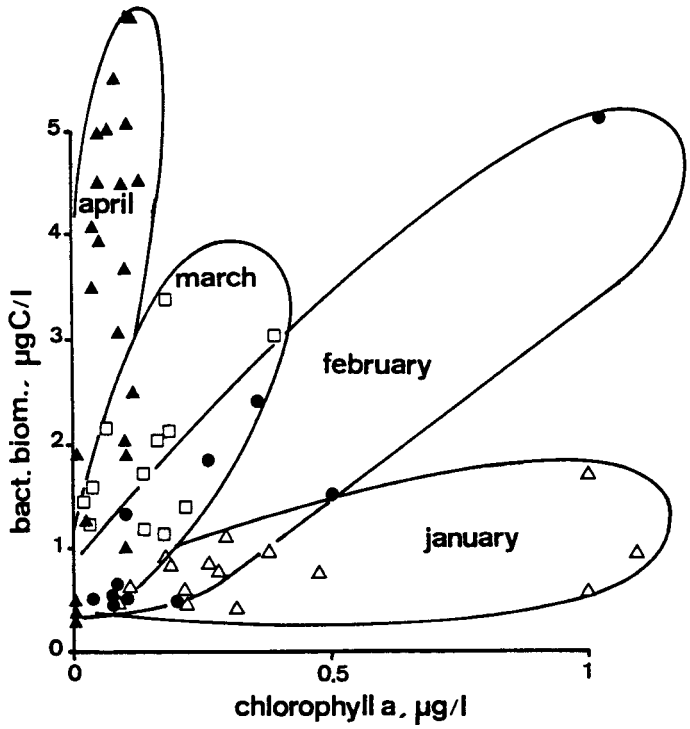


Figure **32** : *Relationship observed between bacterial biomass and chlorophyll* a *concentration in Prydz Bay at different times of the ice-free period.* (△) *January, Joiris* et al., *this volume*; (●) *February and* (□) *March, own observations*; (▲) *early April, Painting* et al., 1985.

4.3.3. Bacterial growth and mortality rates.

In order to further characterize the dynamics of bacterioplankton populations in Prydz Bay, measurements of the fluxes of production and mortality, which together govern the variations of bacterial biomass, have been carried out.

Bacterial production rates in the upper mixed layer are the highest in the Eastern inshore area (0.1–0.3 µgC.l^{-1}.h^{-1}). In the offshore zone, they range between 0.02–0.04 µgC.l^{-1}.h^{-1}. A regular decrease is observed in all areas until the end of March, when production rates have dropped by nearly two orders of magnitude.

The ratio of production rate to bacterial biomass gives the specific growth rate (μ) (Fig. 33). The highest values observed in Antarctica are quite similar to those observed in temperate marine systems (see eg. Billen *et al.*, 1988), in spite of the low temperatures. They decrease regularly from mid–February to end–March.

Mortality rates, on the other hand, seem much more constant during this period, as also shown in Fig. 33. These values are significantly lower than the specific mortality rate constants found in temperate marine systems (Billen *et al.*, 1988), indicating a slower turnover rate of bacterial biomass in the Southern Ocean. Grazing by > 2 μ protozoans contributes for 22 to 100 % to total mortality rates.

Growth rates are clearly higher than mortality in February, corroborating our conclusion that the bacterial population is actively growing at that time. By end–March, specific growth rates are very close to, or lower than mortality rates, indicating a declining bacterial population.

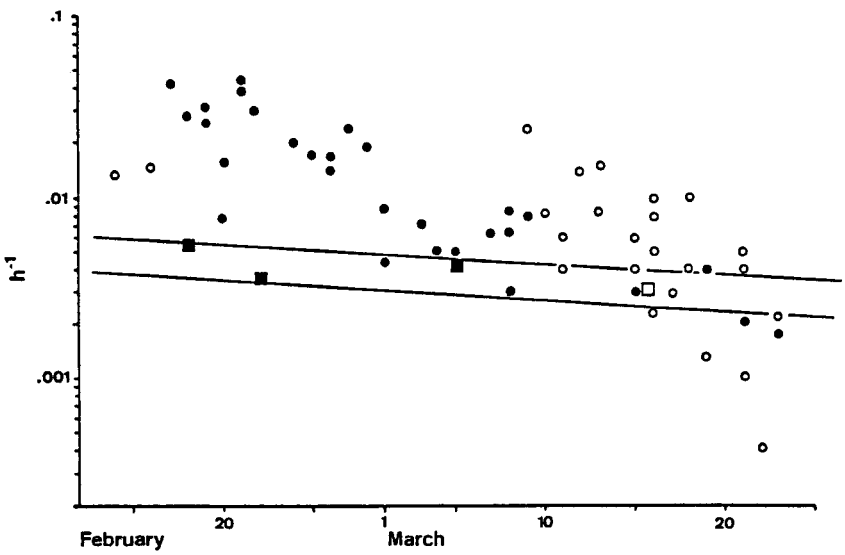


***Figure* 33** *Specific bacterial growth (circles) and mortality (squares) rates observed in the inshore (closed symbols) and offshore (open symbols) zone of Prydz Bay in February–March* 1987.

4.3.4. *Tentative budget of the role of the bacterial loop in organic matter cycling.*

Our biomass and production measurements in Prydz Bay, along with those reported in the literature for the same area, allow a first estimate of the budget of organic matter at the first trophic levels during the ice–free period (i.e. from January to end–March for the inshore area and from December to mid–April for the offshore zone). The figures and assumptions leading to these estimations are presented in Table 9. Except for values in brackets, which are best guess estimates, the figures of bacterial biomass and specific growth rates mentionned in this table are the rounded averages of the observations made by ourselves or by other authors and discussed in this paper. Bacterial production figures were then calculated from these data.

Table 9. Tentative budget of bacterial production rates in Prydz Bay during the ice–free period.

	Inshore area				**Offshore area**			
	biom. $\mu gC.l^{-1}$	**μ** h^{-1}	**dpth** m	**prod.** $mgC.m^{-2}d^{-1}$	**biom.** $\mu gC.l^{-1}$	**μ** h^{-1}	**dpth** m	**prod.** $mgC.m^{-2}d^{-1}$
Dec	–	–	–	–	.5	(.01)	30	4
Jan	(.5)	0.035	30	13	.8	(.02)	30	12
Fev	4	0.030	30	85	2.5	.014	50	42
Mar	2	0.008	50	19	1.5	.006	50	10
Apr	–	–	–	–	1.5	.006	50	10
bact.prod. ($gC.m^{-2}.period^{-1}$)				3.3				2.1

In the absence of nutrient limitation, a growth yield of .25–.3 is a reasonable estimate for heterotrophic bacteria (Lancelot & Billen, 1986; Servais et al, 1987). On the basis of this figure, the total flux of primary produced organic matter flowing through the bacterial compartment can be estimated to 11 and 7 $gC.m^{-2}.period^{-1}$ for the inshore and the offshore zones respectively. This must be compared to the value

of net primary production, including excretion, for the same area and the same period. Only a very crude estimation of these can be given at the present time on the basis of the data provided in Table 8. The range is about 5–15 $gC.m^{-2}.period^{-1}$ for both areas.

This indicates that the overall importance of microheterotrophs in utilizing primary produced organic matter is as large in Antarctica as it is in temperate marine systems, in good agreement with the conclusions of Hodson et al.(1981) and Hanson et al.(1983). However, a much longer delay in the response of bacteria to phytoplankton development has been evidenced by our observations and could explain the conclusion reached by other authors that bacteria do not play a significant role in the utilization of primary produced organic matter in antarctic waters, on the basis of observations mostly carried out at the early stage of the vegetation season.

4.4. MODELISATION OF BACTERIOPLANKTON DYNAMICS

The purpose of this section is to show that the conceptual model described in section 4.1. is able to explain the major trends of the dynamics of bacterioplankton observed in Prydz Bay during the austral summer 1987, in terms of the physiology of antarctic bacteria and the input of available organic matter from phytoplankton. This requires determination of some key parameters characterizing the kinetics of the metabolic processes involved.

4.4.1. Growth rate of antarctic bacteria and the effect of temperature

Specific bacterial growth rates measured at –2 – +2°C in the Prydz Bay area (Fig. 33 above) lie roughly in the same range (0.001–0.1 h^{-1}) as those recorded in temperate systems at much higher temperatures. (see Billen *et al.*, 1988 for a review). This indicates the **resistance adaptation** of antarctic bacterial communities to the low range of temperature characterizing their environment.

Short term exposition to temperatures higher than 15°C results in a decrease of the growth rate (see Fig. 34). Moreover, Hodson *et al.* (1981) reported that 1h preexposition to a temperature of 21°C resulted in the suppression of growth at 2°C. On the other hand, Li & Dickie (1984) showed that 8 h incubation at 30°C induced a rapid opportunistic growth of non psychrophilic members of the bacterioplankton. These results lead to the view that antarctic microheterotrophic communities are dominated by psychrophilic thermosensitive bacteria with an optimum temperature around 10–15°C, while low densities of non psychrophilic bacteria are present, but probably not active in the normal temperature range.

Capacity adaptation to temperature of the dominant bacterial populations within the range $-2^0 - +15^0C$ was studied by measuring the maximum specific growth rate (thymidine incorporation rate, converted into cell number production and divided by cell abundance) during 4 hours incubation period following filtration through a 2 µm Nuclepore membrane to remove the grazers and addition of a mixture of direct substrates at saturating concentration. Also, the increase of thymidine incorporation rate over a period of 24 h allowed to get an independant estimate of the growth rate in the same experiments.

The results are gathered in Fig. 34a. For comparison, similar data obtained in the North Sea (Belgian coastal zone) are shown in Fig. 34b. A very similar value of the optimum growth rate is observed in both environments, at about 15^0C in Antarctica and at about 30^0C in the North Sea.

The following relationships describe the best the effect of temperature on the maximum growth rate in the range -2^0C to $+15^0C$ for antarctic bacterioplankton :

$$\mu max\ (h^{-1}) = 0.18 \exp -\left(\frac{T - Topt}{T_i - Topt}\right)^2$$

with $Topt = 15^0C$

$T_i = 5^0C$

according to the formalism proposed by Lehman *et al.*(1975).

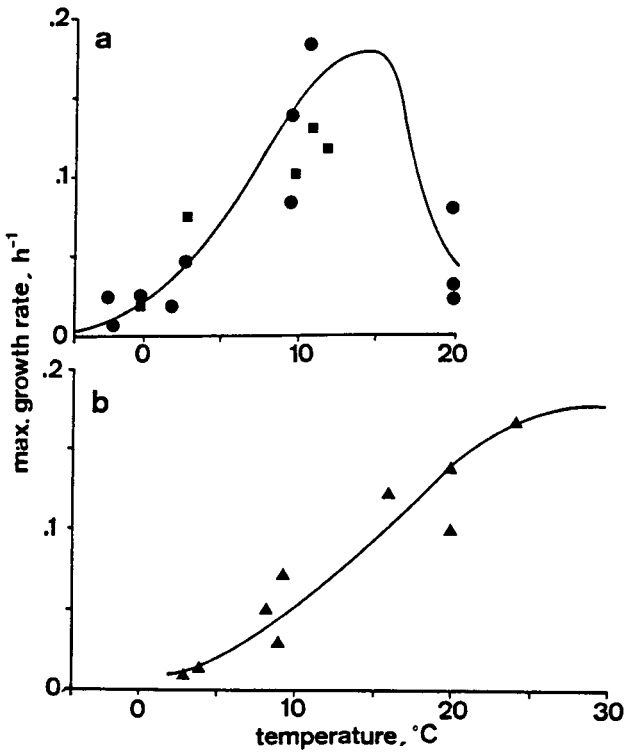


Figure 34 *:Short term effect of temperature on the maximum growth rate of natural assemblages of bacteria from Prydz Bay* (a) *and the Belgian coastal zone of the North Sea* (b).
(●) *Short term thymidine incorporation.* (■) *Initial rate of increase of thymidine incorporation;* (▲) *Initial rate of increase of bacterial numbers during incubation in enriched medium.*

4.4.2. Supply and bacterial utilization of organic matter from phytoplankton.

4.4.2.1. *Processes involved in organic matter supply to bacterioplankton.*

Two extreme paradigms have been proposed for describing the trophic relationship between phyto– and bacterioplankton. In the first paradigm (Larsson & Hagström, 1979; Wolter, 1982; Moller–Jensen, 1985), bacteria depend mainly on the exudation by phytoplankton of low molecular weight organic substrates with very short turnover times. In the second paradigm (Jassby & Goldman, 1974; Billen, 1984; Lancelot & Billen, 1985), lysis of aging phytoplankton cells or spillage of algae by zooplankton grazing, cause leakage of predominantly macromolecular organic material which constitutes the bulk of dissolved organic matter used by bacterioplankton after extracellular hydrolysis. In fact, both processes probably coexist, with varying relative importance according to the season or the environment. Because of the predominantly different forms (either monomeric or macromolecular) under which organic matter is supplied by these two processes, they must however be taken separately into account in bacterial dynamics.

Bjornsen (1988) has recently argued that phytoplankton exudation should in fact be considered as a *property tax* instead of an *income tax* to the phytoplankton, being proportional to phytoplanktonic biomass rather than to production. As an average, exudation of small substrates should represent about 2–5% of phytoplankton biomass per day (about 0.001 – 0.002 h^{-1}). Exudation rates of phytoplankton in Prydz Bay were, however, under the limit of detection of the procedure used.

Very few data are available, on the other hand, on the kinetics of phytoplankton lysis. A first order kinetics will be assumed as a first approximation. A value of about 0.0045 h^{-1} for this first order constant of phytoplankton lysis has been used for describing the development of bacteria in response to the spring phytoplankton bloom in the Belgian coastal zone (Billen, 1988). In Prydz Bay, the specific growth rate of phytoplankton in the upper mixed layer is in the range 0.0008 – 0.008 h^{-1} (see above, Fig. 18). This put an obvious upper limit to the first order constant of phytoplankton lysis.

4.4.2.2. *Kinetics of bacterial utilization of phytoplankton lysis products.*

Because at least 90% of the cellular content of phytoplankton is made of high molecular weight compounds (Billen, 1984; Cuhel & Waterbury, 1984), lysis products of phytoplankton markedly differ from exudates in the mechanism of their utilization by bacteria. Indeed, macromolecules have first to be hydrolysed through the action of extracellular enzymes before being taken up by bacteria.

In order to characterize the kinetics of growth of bacteria on products of phytoplankton lysis, the following experiment was carried out : an enriched culture of phytoplankton was sonicated (Branson Sonic S–75 adjusted at 4.2 A for 5 minutes) and filtered through a 0.2 µm membrane. The dissolved organic material in the filtrate was considered as representative of phytoplankton lysis products. The culture was inoculated with a natural assemblage of bacteria filtered through 2 µm membrane in order to remove protozoa. The development of bacteria and the reduction in dissolved organic carbon was followed for about 15 days (Fig. 35).

The growth pattern of bacteria could be simulated according to the model presented above (equations (8) to (11)). The value of the parameters e_1max and KH_1 at 20°C were taken identical to those determined for the kinetics of protein hydrolysis by marine bacterial exoproteolytic enzymes (Fontigny *et al.*, 1987). The parameters e_2max and KH_2, and the relative part (α:1–α) of H_1 and H_2 fractions in H were determined by adjustment of the solution of the model to the experimental results (Fig. 35).

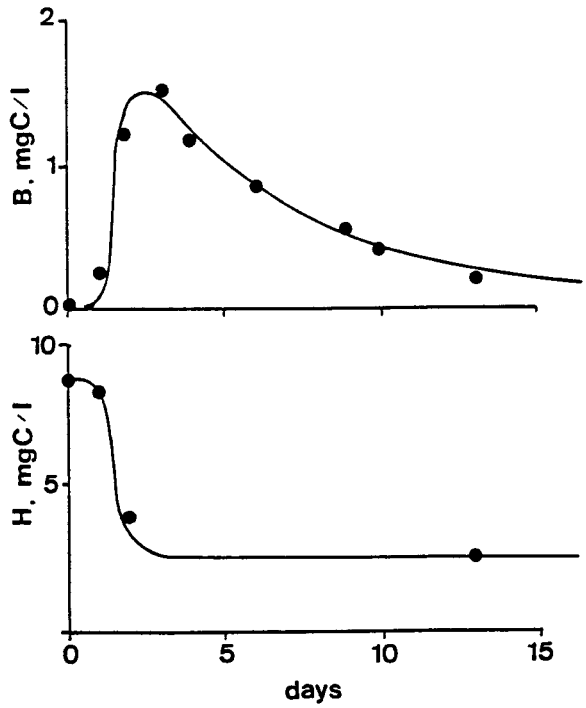


Figure 35 : *Time course of bacterial biomass and dissolved organic carbon in a batch experiment in which a sonicated and filtered phytoplankton culture was inoculated with a natural assemblage of bacteria; The curve represents the solution of the model described in the text for the following values of the parameters:*

$e_1max = 0.75\ h^{-1}$ $KH_1 = 0.1\ mgC.l^{-1}$
$e_2max = 0.25\ h^{-1}$ $KH_2 = 2.5\ mgC.l^{-1}$
$\alpha = 0.5$

4.4.3. Simulation of bacterial development in Prydz Bay

The development of bacterioplankton in a sub-area off Prydz Bay (between 62 and 66°S) has been simulated by the HSB model described in section 4.1 (equations (8) to (11)).

As justified in the preceeding sections, it has been assumed that organic matter is produced by phytoplankton through two distinct processes : (i) **exudation,** producing low molecular weight substrates (S) at a rate proportional to its biomass (k_{exud}); (ii) **lysis**, producing high molecular weight biopolymers of two classes of utilizability (H_1, H_2) in a ratio 1:1. The observed variation of phytoplanktonic biomass is used as an input data for the calculation.

The kinetics of bacterial dynamics is characterized by the following values of the parameters :

(i) exoenzymatic hydrolysis of macromolecules :

$e_1max(Topt) = 0.75\ h^{-1}$, $KH_1 = 0.1\ mgC.l^{-1}$

$e_2max(Topt) = 0.25\ h^{-1}$, $KH_2 = 2.5\ mgC.l^{-1}$

The same dependence to temperature as for μmax (see below) has been taken into account.

(ii) growth of bacteria :

$$\mu max(Topt) = Y\ bmax(Topt) = 0.18\ h^{-1}$$

$$\mu max(T) = \mu max(Topt)\ \exp\left(-\left(\frac{T-Topt}{T_i-Topt}\right)^2\right)$$

with Topt = 15°C

T_i = 5°C

The value of Y, in the absence of nutrient limitation, is generally close to 0.3 (Billen & Servais, 1988). In the North Sea, values as low as 0.1 have been measured, owing to nitrogen limitation.

bmax is calculated as $\mu max(T)/_Y$

Ks is taken arbitrarily as 0.01 mgC.l^{-1}

(iii) mortality

Experimental determinations of the total mortality rate constant kd at *in situ* temperature vary little around a value of 0.004 h^{-1}.

The basic simulations will be run at the mean observed temperature in the concerned area (+ 0.5°C).

Figure 36 shows the simulation of bacterioplanktonic development for different values of the first order constant of phytoplankton lysis (k_{lys}) within a plausible range.

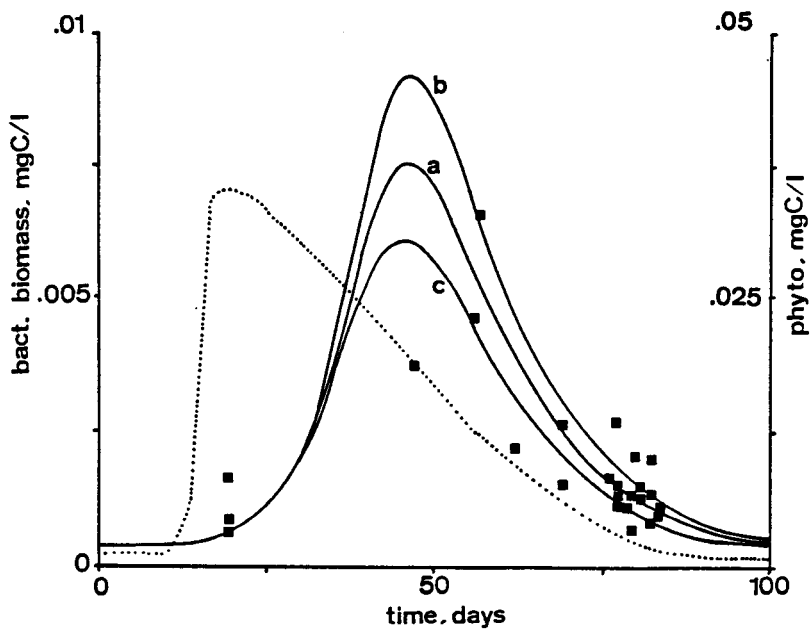


Figure **36** : *Simulation of bacterial growth in response to observed phytoplankton development (dotted curve) according to the* HSB *model, for different values of the rate of phytoplankton lysis* k_{lys} (0.002 h^{-1} (a); 0.003 h^{-1} (b); 0.001 h^{-1} (c)).
The black squares represents the observed values of bacterial biomass.

Figure 37 shows the results of varying the bacterial growth yield (Y) within the likely range 0.2 – 0.3.

All these simulations provide results in reasonable general agreement with the observed data. They all show a delay in bacterioplankton development with respect to phytoplankton of about one month.

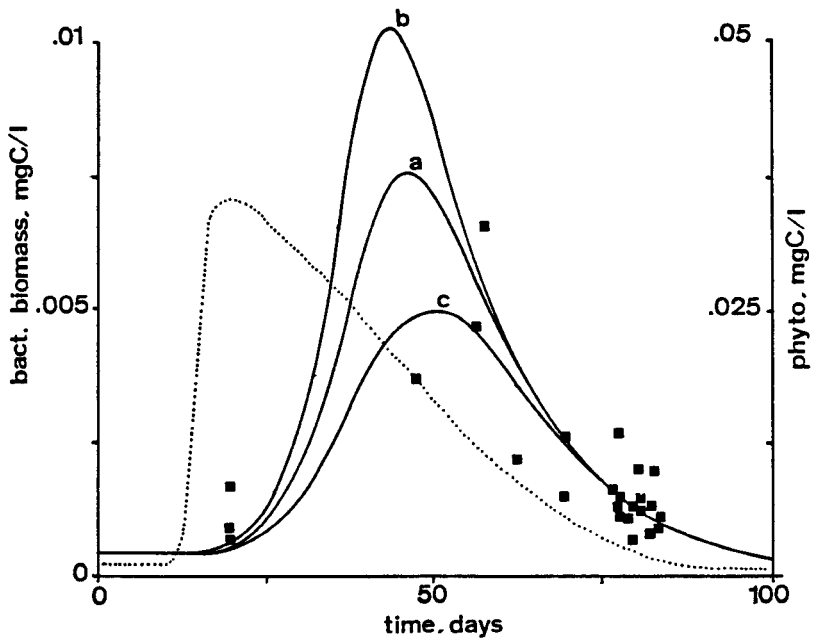


Figure **37** : *Simulation of bacterial growth in response to observed phytoplankton development (dotted curve) according to the* HSB *model, for different values of* Y (k_{lys}=0.002 h^{-1}; Y = 0.25 (a); 0.3 (b); 0.2 (c)).
The black squares represents the observed values of bacterial biomass.

As seen in Fig. 38, this delay should be much shorter if phytoplankton exudation was a major process in the production of dissolved organic matter.

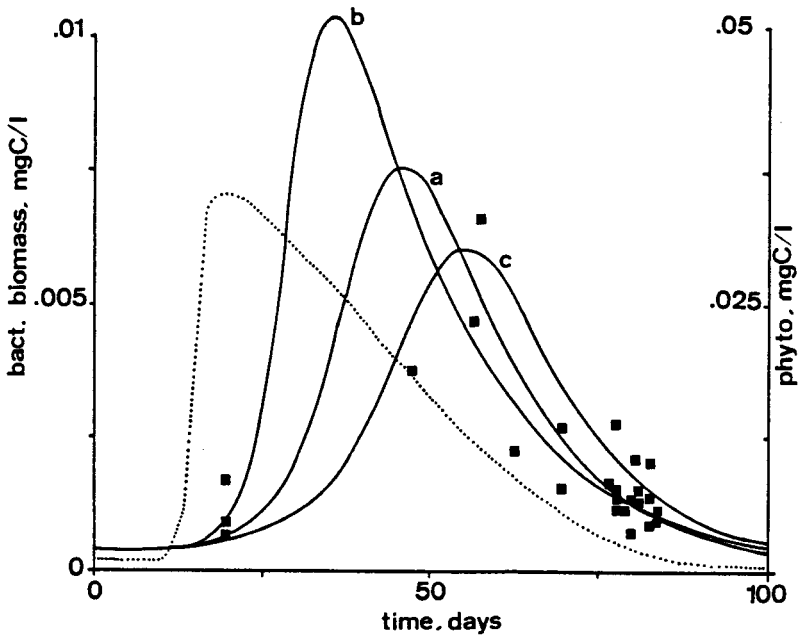


Figure 38 : *Simulation of bacterial growth in response to observed phytoplankton development (dotted curve) according to the* HSB *model, for different values of the rate of lysis* k_{lys} *and the rate of exudation* k_{ex}
(k_{lys}= 0.002 h^{-1} k_{ex}= 0.0005 h^{-1} (a)
k_{lys}= 0.0005 h^{-1} k_{ex}= 0.002 h^{-1} (b)
k_{lys}= 0.002 h^{-1} k_{ex}= 0.0001 h^{-1} (c)).

Also, Fig. 39 shows the extreme sensibility of this delay toward temperature.

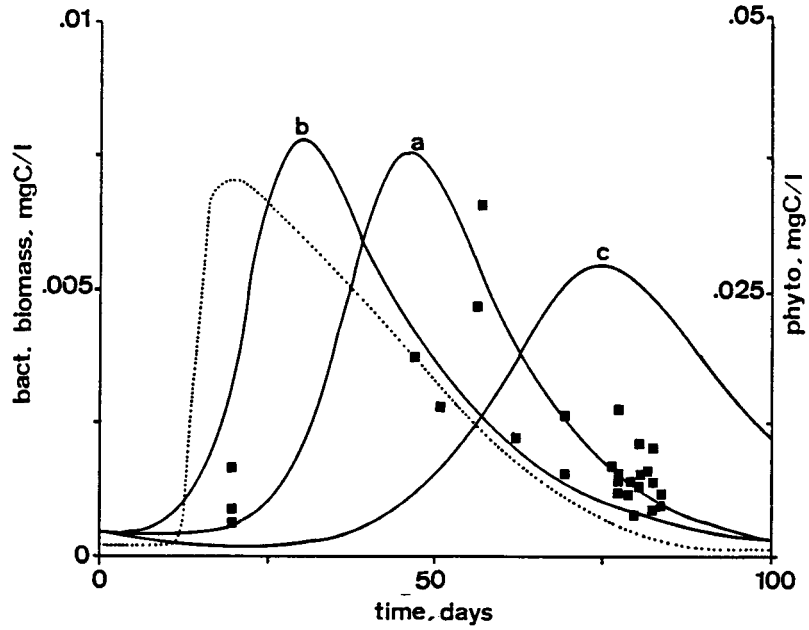


Figure 39 : *Simulation of bacterial growth in response to observed phytoplankton development (dotted curve) according to the* HSB *model, for different temperatures*: +0.5°C (a); +2°C (b); −1°C (c)
k_{lys}= 0.002 h^{-1} ; k_{ex}= 0.0005 h^{-1} ; Y = .25

5. CONCLUSIONS.

The approach used in our ecophysiological study of phyto– and bacterioplankton in Prydz Bay has enabled us to identify the major control mechanisms governing the functioning of the antarctic marine ecosystem at its first trophic levels.

Summarizing, the data we presented support the following view of the dynamics of phytoplankton in the Southern Ocean.

In open sea areas, phytoplankton development is kept at a minimum throughout the year due to the unfavourable light regime resulting from the rapid turbulent vertical mixing of the water column down to deeper depths than the photic layer. Under or within sea ice, on the contrary, a stable environment exists, where favourable conditions for phytoplanktonic development may occur from the early spring. Due to the enhanced vertical stability of the water column resulting from sea ice melting, phytoplankton can rapidly develop in the marginal ice zone, more especially as it is inoculated from the sea ice communities themselves. Progressive mixing of the upper less saline water with deeper water results in a deeper upper mixed layer and in a decrease of phytoplankton concentration.

High levels of phytoplankton biomass and production are therefore limited to the edge of the retreating sea ice or other local areas with stable water column. The distribution of primary resources in the Antarctic ecosystem is thus extremely limited, both in time and space.

The krill, and most other higher organisms belonging to the krill–vertebrates food web, are adapted to thrive on these localized **pulses** of resources, owing to their high mobility, their large capacity to store reserves and to survive to long starvation periods. Their reproduction rate is generally very low.

The surprizingly large stocks of higher organisms, including krill, in the Southern Ocean thus probably reflects the typical K–strategy adopted by most animals in the Southern Ocean and the resulting very slow turnover of their biomass, instead of being the consequence of a particularly high availability of vegetal organic matter. Our observations confirm that primary production is most of the time very low. Also, the apparent **richness** of the Southern Ocean is not to be explained, as suggested by some authors (Pomeroy & Deibel, 1986), by a generally low activity of heterotrophic micro–organisms, leaving most of the primary production available to grazers. The microbial loop quantitatively plays the same role in the Antarctic marine ecosystem as in temperate environments. A longer delay between phytoplankton and bacterioplankton development in Antarctica than in temperate seas probably explains the apparently contradictory results published in the literature regarding the importance of the bacterial loop in the Southern Ocean.

The apparent abundance of the krill–vertebrates food chain organisms is therefore misleading, as it reflects the slow turnover of these organisms rather than their ability to sustain intensive exploitation. An evaluation of the potential primary resources available for krill grazing at the scale of the Southern Ocean as a whole should therefore be very important for assessing the potential for krill exploitation.

Such an evaluation is rendered difficult at the present time because of the spatial and temporal variability of phytoplankton distribution, which, as we just saw, is a basic characteristics of the antarctic ecosystem. Multiplication of descriptive observations and measurements will not result in a significant improvement of this estimation. This can only be achieved through a modelling approach coupling a good knowledge of the physiological processes involved in the dynamics of the first trophic levels of the food chain and their control mechanisms on the one hand, with a comprehensive description of the hydrodynamics, the vertical mixing of the water column, the rate of sea ice progression and retreat, on the other hand.

The results presented in this report show that considerable progress have been achieved in this direction.

The control of phytoplankton photosynthesis and growth by light and temperature have been studied in details for the open sea and marginal ice communities. A conceptual model has been developped which is able to predict the major trends of variations of phytoplankton biomass and activity in Antarctic waters from the knowledge of the physical characteristics of the environment.

Similarly, the dynamics of the microbial loop has been studied in details and a model of bacterioplankton development in response to phytoplankton has been elaborated.

It remains to better understand the conditions of development of sea ice microbial communities which appear to play an important role both as a direct source of food for krill and as an inoculum of the shallow upper layer in melting ice areas.

It remains also to couple the available models of the ecophysiology of phyto– and bacterioplankton together, and with hydrodynamical and climatological models developped for predicting the environmental characteristics of water column vertical mixing and sea ice dynamics. This will be the purpose of our future work on the Antarctic marine system.

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ZOOPLANKTON BIOCHEMISTRY AND ECODYNAMICS

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PROGRAMME ON ANTARCTICA
SCIENTIFIC RESULTS OF PHASE ONE
(OCT 85 - JAN 89)
VOLUME I: PLANKTON ECOLOGY

ABSTRACT

The ecohydrodynamical approach of the Southern Ocean during INDIGO III cruise demonstrates that the diversity of the areas and time scale is so rich that all possibilities of ecobiochemical mechanisms may occur.

Phytoplanktonic pigments distribution, studied by HPLC, shows that the spatial structure of maximum chlorophyll a concentrations is bound up with the main frontal systems which have the characteristics of a convergence and, in the Antarctic Surface Water, with the areas of increased stability. However, biomasses are fairly low (< 1.2 mg chl a/m^3).

Biochemical contents of the subsurface plankton allow us to understand the mesoscale structure and functioning of the Antarctic subsurface ecosystem. It seems that in summer, the stabilization of the upper layers of the water column due to the retreat of the constantly melting ice-edge induces a series of phytoplanktonic and zooplanktonic blooms, from the north to the south. Patchy distributions of the different trophic levels and their biochemical characteristics are observed, with, to the north, old zooplanktonic populations and to the south, young phytoplankton. The spatial scale depends on the speed of the pack-ice retreat.

An new and original study of the planktonic ecosystem, using fatty acids distribution and their physiological meaning, shows that maximum values of planktonic food chain efficiency are not found close to the Antarctic continent (where phytoplanktonic biomasses are important but turnover is low) but between the Antarctic Polar Front and the Subtropical Convergence (where each trophic level is quickly consumed by the following one with a high turnover rate).

CONTENTS

A. THEME OF RESEARCH AND OBJECTIVES

In the Southern Ocean, hydrodynamical constraints control the ecosystem and structure the euphotic zone in a multicompartments system, each one characterized by different parameters.

In the Austral Ocean, the water column has to be considered as a varying system of convergences and divergences, resulting in the advection of nutrient-rich water. In these areas, very limited in time and space, phytoplanktonic productivity increases may occur.
Moreover, strong meridian currents carry watermasses and associated planktonic communities. During the transport, the different trophic levels are growing with different significative times.
In these circumstances, in North Sea, in Mediterranean Sea and in Bering Sea, our team has shown that herbivorous Copepods store large amounts of lipids. This accumulation of lipidic components helps herbivorous Copepods to endure the alternance of nutrition and diet periods and provides many pelagic consumers with an energetic food.

During the phase 1 of **THE BELGIAN SCIENTIFIC RESEARCH PROGRAMME ON ANTARCTICA**, our aim was to study, in the Antarctic, the distribution and the biochemical speciation of the lipidic content of zooplankton as a function of environmental parameters.
Development of this **ECOHYDRODYNAMICAL** approach of the Antarctic planktonic ecosystem requires a good knowledge of:
1. The hydrodynamics of the Southern Ocean, and especially of the associated frontal systems, responsible of biological enhancement.
2. The quantitatively important planktonic communities.
3. The biochemical and physiological adaptations of the organisms to the Antarctic conditions.

B. STATE OF THE ART

1. GENERAL HYDRODYNAMICS OF THE ANTARCTIC BASIN

1.1 Characteristics of the Polar Oceans

Polar oceans belong to the "Cold Water Sphere" where no vertical density discontinuity appears in the upper layers, contrary to tropical and subtropical waters ("Warm Water Sphere") where a strong pycnocline occurs in subsurfaces layers. For this reason, in polar oceans, processes of density increasing (cooling, evaporation, ice formation) generate instabilities responsible of convections between surface and bottom.
Isopycnal slopes created by convergences and divergences (from wind origin) in quite homogeneous surface layers induce slope currents which extend in depth. Slopes due to pressure gradient run to the depth for the same reason.
Lastly, in polar oceans, the Eckman system is particularly accentuated.

2.2 Antarctic Ocean Circulation

The Southern Ocean, surrounding the Antarctic Continent, is the sole circular Ocean in the world. It covers 16% of the surface of the globe (about 80 10^6 km^2) and the mean depth is 4000 meters. The northern boundary is the 40°S parallel.

In relation to the general wind circulation, waters flow eastward in the ANTARCTIC CIRCUMPOLAR CURRENT (= WEST WIND DRIFT), except along the continent where the waters flow towards the west (EAST WIND DRIFT). These circumpolar currents reach the bottom of the Ocean and are greatly affected by its topography (Sverdrup et al., 1942; Marr, 1962). Fig.1.
At the boundary of these currents, eddies occur on vertical and horizontal planes (Koopmann, 1953). In that area, high vertical velocities occur and lead to convergences and divergences, resulting in the advection of nutrient-rich water.

Strong HORIZONTAL MERIDIAN CURRENTS carry watermasses and associated planktonic communities perpendicular to the divergences.
This system is acting like A CHEMOSTAT, quasi-stationary in time and regulated by continuous exportation of produced organic material.
Global Meridian Currents (800 10^6 m^3/s) are superposed on the Antarctic

Circumpolar Current (150-190 10^6 m^3/s; Neumann et Pierson, 1966) and are four to five times as big.

Finally, all these currents are affected by periodic and aperiodic fluctuations of the same order of magnitude than those observed for the Gulf Stream (Iselin, 1940; Hela, 1952).

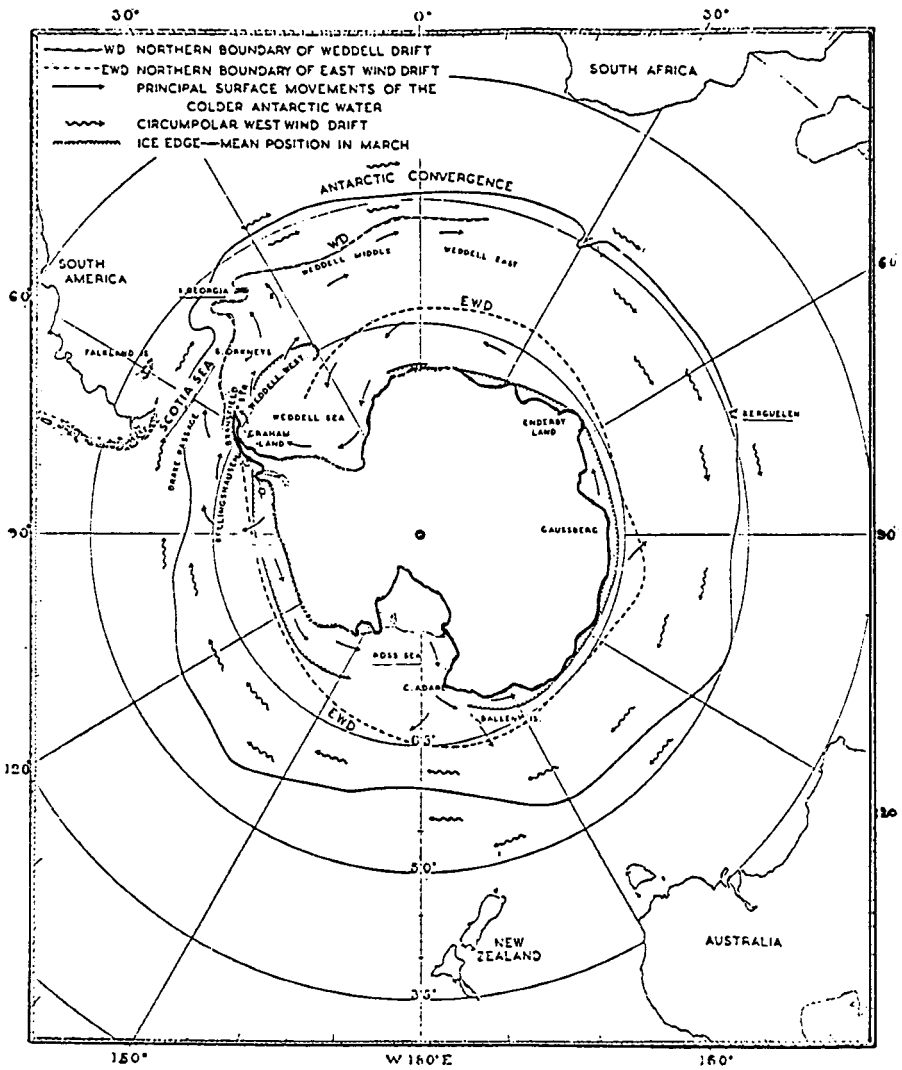


Fig. 1: Map of the Antarctic Ocean describing watermasses limits and currents in surface layers (Marr, 1962)

1.3 Divergences, Convergences, Frontal Systems and Watermasses

In the Southern Ocean, in relation with the general circulation, typical

physical boundaries, associated to frontal systems, are recognized. They are characterized by a succession of convergences and divergences (Koopman, 1953; Lutjeharms et al., 1985). Fig.2.

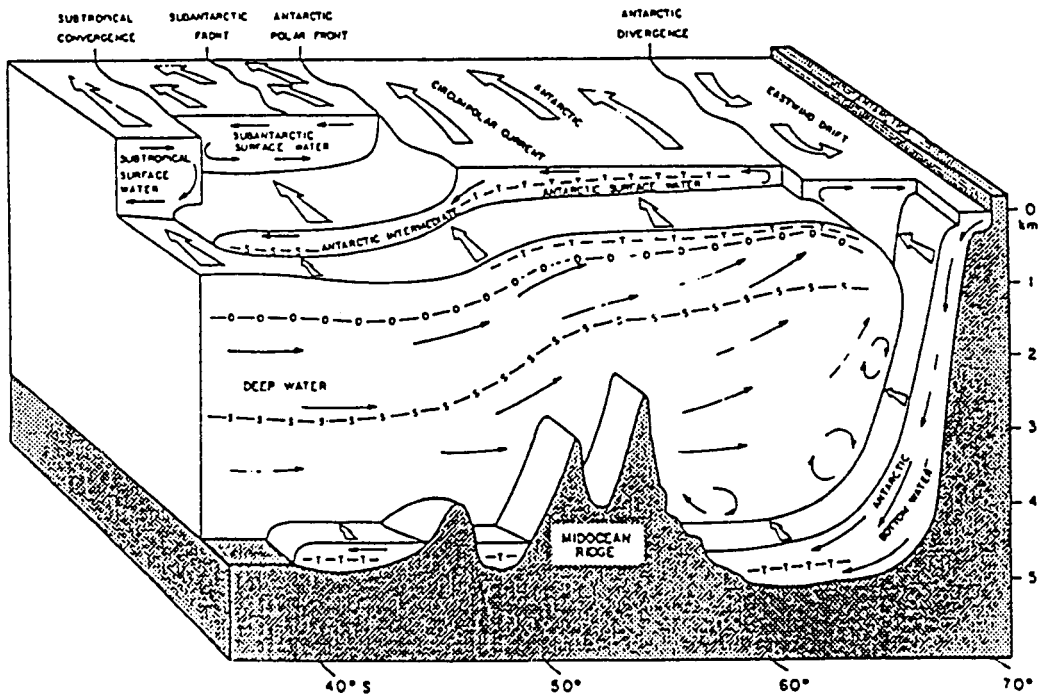


Fig. 2: Schematic view of the different watermasses and their movements in the Southern Ocean south of Africa. Open arrows indicate lateral movements. Full-line arrows indicate vertical and meridian movements. In depth, temperature, salinity and oxygen maxima are noted by T, S, O letters (from Lutjeharms & al., 1985).

One can recognize from the South to the North:

THE CONTINENTAL CONVERGENCE occuring near the continent, between the uniform shelf's waters and the oceanic waters (Deacon, 1982).

THE ANTARCTIC DIVERGENCE, which is the presumed boundary between the Antarctic Circumpolar Current (West Wind Drift) and the East Wind Drift (Lutjeharms et al., 1985). The mean position fluctuates from 63 to 65°S. In places, the Antarctic Divergence and THE WEDDELL GYRE flow together (Gordon et al., 1982).

THE ANTARCTIC CONVERGENCE , (or ANTARCTIC POLAR FRONT). This front must be considered as a zone more than a line. It separates cold and dense Antarctic Water from warmer and lighter Subantarctic Water. The position of the Antarctic Polar Front is strongly affected by wind stress and varies during the year from 50 to 60 °S (Everson, 1976).

THE SUBANTARCTIC FRONT, located in the Subantarctic Surface Water, may be recognized at the sea-surface by an average decrease in temperature of 3.9°C at a mean latitude of 46°S 23' (Lutjeharms, 1985). No physical hypothesis has yet been advanced to explain its existence (Lutjeharms et Valentine, 1984).

THE SUBTROPICAL CONVERGENCE separating the Subtropical Surface Water and the Subantarctic Surface Water. On the average, it lies between 40 and 45°S and exhibits a strong horizontal thermal gradient (7°C) (Lutjeharms et Valentine, 1984).

In the SUPERFICIAL LAYER, these frontal systems isolate five watermasses, clearly distinguished by temperature, salinity and nutrients (especially N/P and N/Si ratios, Le Corre et Minas, 1983).
In the Indian, Atlantic and Pacific sectors of the Southern Ocean, it is possible to identify:

The Water of the CONTINENTAL AREA and the water of the EAST WIND DRIFT, south of the Antarctic Divergence and not well documented because of quite permanent ice covering.

The ANTARCTIC Water, to the north of the Antarctic Divergence. At the surface, the Antarctic Water is cold (T° between 1.5° and 6.6°C) and not very salty ($S°/_{oo} < 34°/_{oo}$). In the summer, a subsuperficial temperature minimum layer is typical, whose depth varies from 75 meters in the south (-1.5°C) to 250 meters in the north (2.1°C) (Gamberoni et al., 1982).
In the whole Antarctic area, very high nutrients levels are found, just showing some loss in the surface during summer. Concentrations ranges are respectively 22 - 28 µgat/l for nitrate, 5 - 30 µgat/l for silicate and 1.4 - 1.8 µgat/l for phosphate. At the maximum of surface enrichment, concentrations of 30 µgat/l in NO_3, 2 µgat/l in PO_4 and 60 - 70 µgat/l in $Si(OH)_4$ have been measured (Le Corre et Minas, 1983).

The SUBANTARCTIC Water, to the north of the Antarctic Polar Front. The

surface temperature is higher than in the Antarctic Surface Water but the salinity is quite constant. A quasi isohaline layer of a few hundred meters overcomes a minimum of temperature.
The latitudinal extension of the subantarctic region varies from 7 to 13°, depending on the oceanic area (Gamberoni et al., 1982).
The Superficial Subantarctic Waters are characterized by a important disproportion between nitrate and phosphate concentrations (respectively 17.7 and 1.22 µgat/l) and silicate concentration (2 µgat/l) (Le Corre & Minas, 1983).

The SUBTROPICAL Water, north of the Subtropical Convergence, warm ($T° > 17°C$) and very salty ($S°/_{oo} > 35\ °/_{oo}$) (Lutjeharms et al., 1985; Deacon, 1982).
During summer, superficial layer is quite exhausted in nitrate (less than 3.0 µgat/l) and in phosphate (less than 0.3 µgat/l) (Gamberoni et al., 1982).

2. PHYTOPLANKTONIC DISTRIBUTION IN THE SOUTHERN OCEAN

The Southern Ocean is not ecologically uniform as is implied by the general term "Antarctic and Subantarctic Ecosystem" (Hempel, 1985).

At the surface, phytoplankton communities distribution in the antarctic and subantarctic areas, related to watermasses pattern, is characterized by a **HIGH SPATIAL AND TEMPORAL HETEROGENEITY**:

Highest phytoplanktonic biomasses occur in the pack area, **within** the ice (Ice Algae).

In the water column, greatest concentrations in phytoplankton are detected below the permanent pack-ice and at the ice edge.

High levels of chlorophyll a are associated with sea-surface fronts wherever such frontal systems have the characteristics of a convergence (Lutjeharms et al., 1985). They are observed at the Continental Convergence (Continental Water Boundary) (Hempel, 1985; Lutjeharms et al., 1985), at the Antarctic Convergence (Jacques et Minas, 1981; Lutjeharms et al., 1985) and at the Subtropical Convergence (Jacques & Minas, 1981; Lutjeharms et al., 1985; Furuya et al., 1986).

Smaller increases of the chlorophyll a concentration may be observed at the Subantarctic Polar Front (Lutjeharms et al., 1985) and around 60°S, in the Antarctic Surface Water, where surface warming increases significantly the stability in the upper 80 meters of the water column (Jacques et Minas, 1981; Lutjeharms et al., 1985).

In these particular areas, chlorophyll a concentrations have been determined by in vivo fluorescence (Weber and El-Sayed, 1985), by fluorometric method (Fukuchi et al., 1985; Furuya et al., 1986) or by spectrophotometric method (Weber and El-Sayed, 1985). The different results are not directly comparable but it is possible to determine the RANGE OF CHLOROPHYLL A VALUES for each important area:

Within the ICE, geographical distribution of Ice Algae is very heterogeneous (EPOS, personal observation) but chlorophyll a concentrations may reach huge values (2829.7 mg chl a/m^3 in November; Hoshiai, 1985).

Below the PERMANENT PACK-ICE, in the vicinity of the continent (Lützow-Holm Bay), maximum phytoplanktonic biomasses are observed in late January (from 7.01 to 11.30 mg chl a/m^3). High concentrations are restricted to the upper 100 meters. By late March, chlorophyll-a concentrations are less than 0.5 mg/m^3. From April to November, they are below 0.10 mg/m^3 (Fukuchi et al., 1985).

At the ICE EDGE, large biomass levels (4 - 5 mg chl a/m^3) have been reported in January. In the Ross Sea, concentrations average 4.08 $\pm$ 1.46 mg chl a/m^3 at 12 meters deep (depth of the chlorophyll maximum, Smith and Nelson, 1985).

At the CONTINENTAL CONVERGENCE, chlorophyll a concentrations higher than 2 mg chl a/m^3 are observed during summer (Lutjeharms et al., 1985).

At the ANTARCTIC POLAR FRONT, chlorophyll a concentrations reach 1.5 mg chl a/m^3 during January (Lutjeharms et al., 1985).

At the SUBTROPICAL CONVERGENCE, highest chorophyll a concentrations (from 0.6 to 1.5 mg /m^3) occur between December and late January (Furuya et al., 1986; Lutjeharms et al., 1985).
At the end of the summer, the biomass is less than 0.5 mg chl a/m^3 (Jacques et Minas, 1981).

In the OTHER AREAS, (with some exceptions for the Subantarctic Front and for a latitudinal zone around 60°S), phytoplankton biomass is close to the one observed in oligotrophic waters (0.1 - 0.3 mg chl a/m^3) (Jacques et Minas, 1981).

During summer, vertical profiles of chlorophyll a generally show a maximum around 40 meters deep (Jacques et Minas, 1981; Furuya et al., 1986).

In winter, apart from the coastal areas, no information about phytoplankton distribution is available, principaly due to ice-cover (60 % of the ocean south of the Antarctic Convergence at the end of winter (Deacon, 1982).

Floristic composition and phytoplankton zonation are discussed by Hart (1934) who discovered species typical of each of the Antarctic, Subantarctic and Subtropical zones.
At the southern edge of the Subtropical Convergence area, phytoplankton community is Diatom-dominated (> 90 %) (Furuya et al., 1986).
At the northern edge of the Subtropical Convergence area, phytoplankton community comprises Diatoms (29.8 - 53.4 %), Dinoflagellates (23.3 - 51.4 %) and other taxa (Coccolithophorids, Cyanophyceans, Flagellates - 15.5 %).

3. ANTARCTIC ZOOPLANKTONIC COMMUNITIES

3.1 Distribution of Zooplankton

Most researches on zooplankton in the Southern Ocean have focused on the Antarctic Krill, *Euphausia superba*, ignoring the fact that the larger part of the Antarctic ecosystem is occupied by food webs without much Euphausiids (Hempel, 1985).

In fact, like discussed previously for phytoplanktonic communities, the heterogeneity of the Antarctic Ocean is obvious.
BIOGEOGRAPHICAL DIVISIONS, based on main watermasses, fronts and seasonal ice cover allow to distinguish among food webs typical of (Hempel, 1985):

The PERMANENT PACK-ICE ZONE, which extends from the continent to the Continental Convergence. Phytoplanktonic productivity is intense but very brief. Zooplankton biomass is low and the Krill is replaced by the small *Euphausia cristalloraphias*.

The SEASONAL PACK-ICE ZONE, concerning the East Wind Drift and the northern branch of the Weddell Gyre. This area is covered by ice in winter and spring but is mainly ice-free in summer and autumn. This is the most productive zone. With the retreat of the pack-ice and the resulting stabilization of the upper layers of the water column, a series of phytoplankton blooms occurs from north to south. The food web is dominated by *Euphausia superba* but the zooplanktonic community comprises also Salps, Copepods, fish larvae, Euphausiids and Chaetognaths.

The ICE-FREE ZONE, the largest antarctic region, is situated to the north of the Antarctic Divergence (West Wind Drift). This area is rich in nutrients but relatively poor in primary production and phytoplankton biomass ("paradox of the Antarctic productivity"). The zooplankton is quite similar to that of the northern North Atlantic with herbivorous Copepods, Salps and small Euphausiids. Except for South Georgia, Krill is mostly absent.

3.2 Some aspects of the Zooplanktonic Ecophysiology

The most important feature of the Antarctic zooplankton is the particular adaptation of animals to intense but brief primary production periods. The unimodal zooplankton bloom occurs in response to phytoplankton peak but generation time extends over several seasons (Nemoto et Harrison, 1981). Life cycles of secondary producers are relatively long, inducing development of survival mechanisms during diet periods.

Some species, like *Euphausia superba*, are able to "browse" the Ice Algae aggregated at the surface of the ice (Whithaker, 1981; EPOS observations).

Others exhibit a seasonal change in nutrition. Using fatty acids pattern, Lee (1974) has shown that *Calanus hyperboreus* (Arctic), herbivorous during summer, becomes carnivorous during the phytoplankton-deficient winter.

However, the general tendency for most of the **HERBIVOROUS ORGANISMS** is to develop the storage of **LIPIDS**, used as a food reserve during winter. Polyunsaturated fatty acids, **PUFA**, are specifically synthetized by marine phytoplankton and accumulated by herbivorous copepods proportionnaly to the grazing on phytoplankton. The level of accumulated PUFA depends on the turnover rate of the pelagic food chain.

Given the dietary origin of part of lipids of an organism, lipids analyses can be used to probe predator - prey relationships. The specificity of the approach depends on the extent to which individual lipid components are specific to individual species. Given species-specific "markers", the transfer efficiency from one trophic level to another one can be determined (Sargent and Whittle, 1981).

In the future, such approach will permit to distinguish areas of low and high productivity in the Southern Ocean, basing on fatty acids patterns.

C. WORK AT SEA

Traditional ideas on the productivity of the Southern Ocean have greatly changed.
The primary production of the oceanic part of the Southern Ocean is much lower than previously estimated (Jacques & Minas, 1981; Hempel, 1985).
On the other hand, the "Krill System", dominated by *Euphausia superba*, seems to be dominant only in the seasonal pack-ice zone (Hempel, 1985; Clarke, 1985).

In order to obtain the necessary knowledge for an understanding of the functioning of the Antarctic marine ecosystem and before studying the ecophysiology of the planktonic compartmentation, a quantitative evaluation of phytoplankton and zooplankton stocks is needed not only in the pack-ice area but in all sectors of the Southern Ocean.

Our first investigation of the Southern Ocean during INDIGO III cruise was concerned with the Indian sector of the Antarcic Ocean.
Anne Goffart and J.H.Hecq, invited by Prof. A. Poisson, chief scientist, took part in INDIGO III from January 3^{d} to February 27th, 1987, on board of the R.V. MARION DUFRESNE. The cruise track covered the area between the Subtropical Convergence and the northern limit of the pack-ice (latitudes 38 to 67°S, longitudes 18 to 84°E). Fig. 3.
Phytopigments, analysed by HPLC directly on board of the Marion Dufresne, and biochemical contents of zooplankton have been evaluated during the oceanographic stations. Between Antarctica and South Africa, phytoplankton has been measured continuously in relation with watermasses distribution.

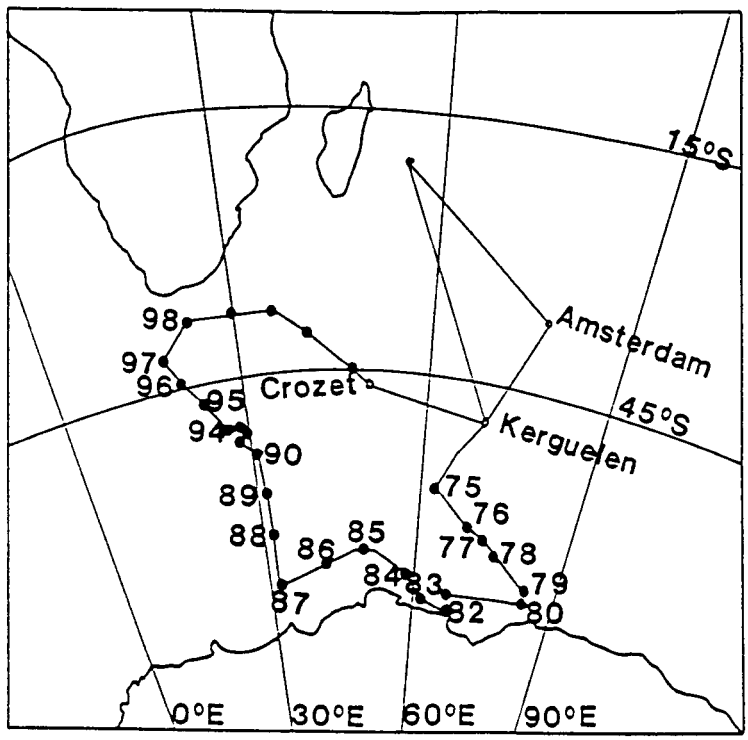


Figure 3: INDIGO III cruise track.

During austral summer 1988, the EPOS European campaign has provided the opportunity to study the ice edge of the Western Weddell Sea - Fig. 4 -. From October 10th to November 20th, 1988, Anne Goffart was on board of the R.V. POLAR STERN for the leg 1 of EPOS.

Polar Stern followed 4 tracks between open water and consolidated pack ice, with a particular attention paid to the ice edge. A total number of 450 samples of phytoplankton and 23 vertical hauls of zooplankton have been performed. Pigments composition and fatty acids patterns will be analysed in relation to ice situation and watermasses distribution. Biochemical contents of some ice algae samples, collected by divers, will improve the knowledge of this particular phytoplankton. At the same time, lipidic contents of the main zooplanktonic taxa (including Krill) will be studied.

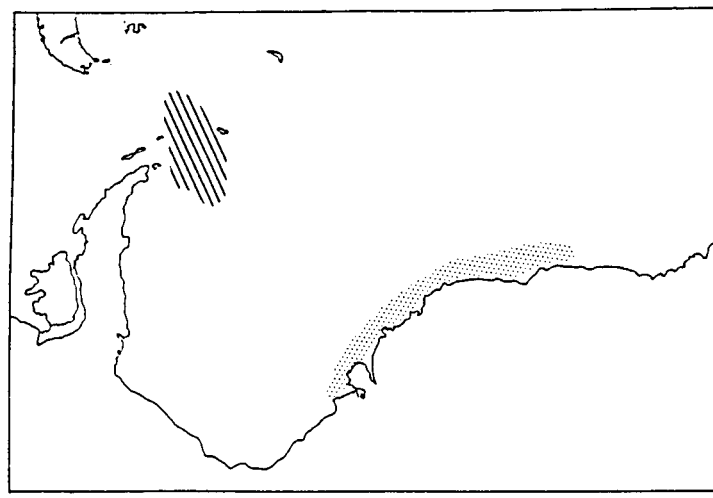


Figure 4: Map of the Weddell Sea, showing the area where research by EPOS has been conducted (hatched).

D. SCIENTIFIC RESULTS OF INDIGO III CRUISE

1. MATERIALS AND METHODS

At the stations (Fig. 3) and along cruise tracks, salinity and temperature were determined on board by Dr. A. Poisson's INDIGO III research team.

Nitrate, silicate and phosphate concentrations were analysed with Technicon II Autoanalyser Systems, respectively by Dr. F. Dehairs and L. Goeyens (NO_3) and by Dr. A. Poisson's INDIGO III research team (SiO_2 and PO_4).

Phytoplankton samples were collected using Niskin bottles (10 depths between 0 and 200 meters).
Between Antarctica and South Africa (Stations 87 to 98), surface seawater sampling was carried out at 2 hours intervals to picture the spatial variability of chlorophyll a distribution on a finer scale.
After filtration of 2 or 3 liters of seawater through Whatman GF/C glass fiber filters, chlorophyll a was determined directly on board using a High-Performance Liquid Chromatograph (HPLC).

At the stations, zooplankton was sampled with 180 µ WP2 nets. Subsurface and vertical hauls (0 - 200 meters) have been performed. Based on main taxa, including Krill, samples were roughly sorted and immediately freeze-dryed.
Biochemical contents of each sample were analysed using:
- Schacterle and Pollack's method for proteins (Schacterle et Pollack, 1973)
- Dubois's method for sugars (Dubois et al., 1956)
- Sulfophosphovanillin method for lipids (Barnes & Blackstock, 1973).

Main lipids classes (phospholipids, triacylglycerols and wax ester) were separated by Thin Layer Chromatography and planktonic fatty acids analysed by Gas Liquid Chromatography (Hecq & Goffart, 1984).

2. PLANKTONIC COMMUNITIES AND WATERMASSES

2.1 Hydrology and Phytoplanktonic Distribution

From the complete data set, we consider three separate tracks (Fig.3), identified as the western track (Stations 98 to 87)
the eastern track (Stations 75 to 80)

the southern track (Stations 87 to 80)

2.1.1 Western Track

2.1.1.1 Horizontal distribution of watermasses

During INDIGO III, surface continuous measurements of temperature and salinity between Antarctica and South Africa allow us to recognize the Antarctic Polar Front (Antarctic Convergence), the Subantarctic Front and the Subtropical Convergence (Figure 5).
According to the literature, the average characteristics at the sea-surface for each of these fronts are summarized below for the Indian sector of the Southern Ocean and compared with the results of INDIGO III horizontal sea-surface track (*"italic"* typewriting).
Temperature and salinity decrease and nutrients increase from northern to southern limits of the fronts.

THE ANTARCTIC POLAR FRONT (ANTARCTIC CONVERGENCE) (APF) consists in the confluence of the Antarctic Surface Water and Subantarctic Surface Water.

Geographical location: 50° 18', mean latitude (Lutjeharms et al., 1985)
48° 54' - 50° 44', northern and southern limits of the gradient.

Decrease in temperature: 1.8° C (Lutjeharms, 1985).
3.2° C (from 6.80°C at 48° 54' to 3.60°C at 50° 44')

Salinity: No detected gradient. Lutjeharms, 1985
No detected gradient

In the Antarctic Polar Front area, sharp increases of surface nitrate and silicate concentrations have been observed from north to south (Figure 6). However, the great interval between the stations does not allow us to give a characteristic value for the gradient.

THE SUBANTARCTIC FRONT (SAF) is located in the Subantarctic Surface Water

Geographical location: 46° 23', mean latitude (Lutjeharms et al., 1985)
46° 24' - 47° 34', northern and southern limits of the gradient.

Decrease in temperature: 3.9° C (Lutjeharms et al., 1985).
3.85° C (from 9.25°C at 46° 24' to 5.40°C at 47° 34')

Decrease in salinity: *0.19 °/₀₀* (from 33.52 °/₀₀ at 46° 24' to 33.33 °/₀₀ at 47°34')

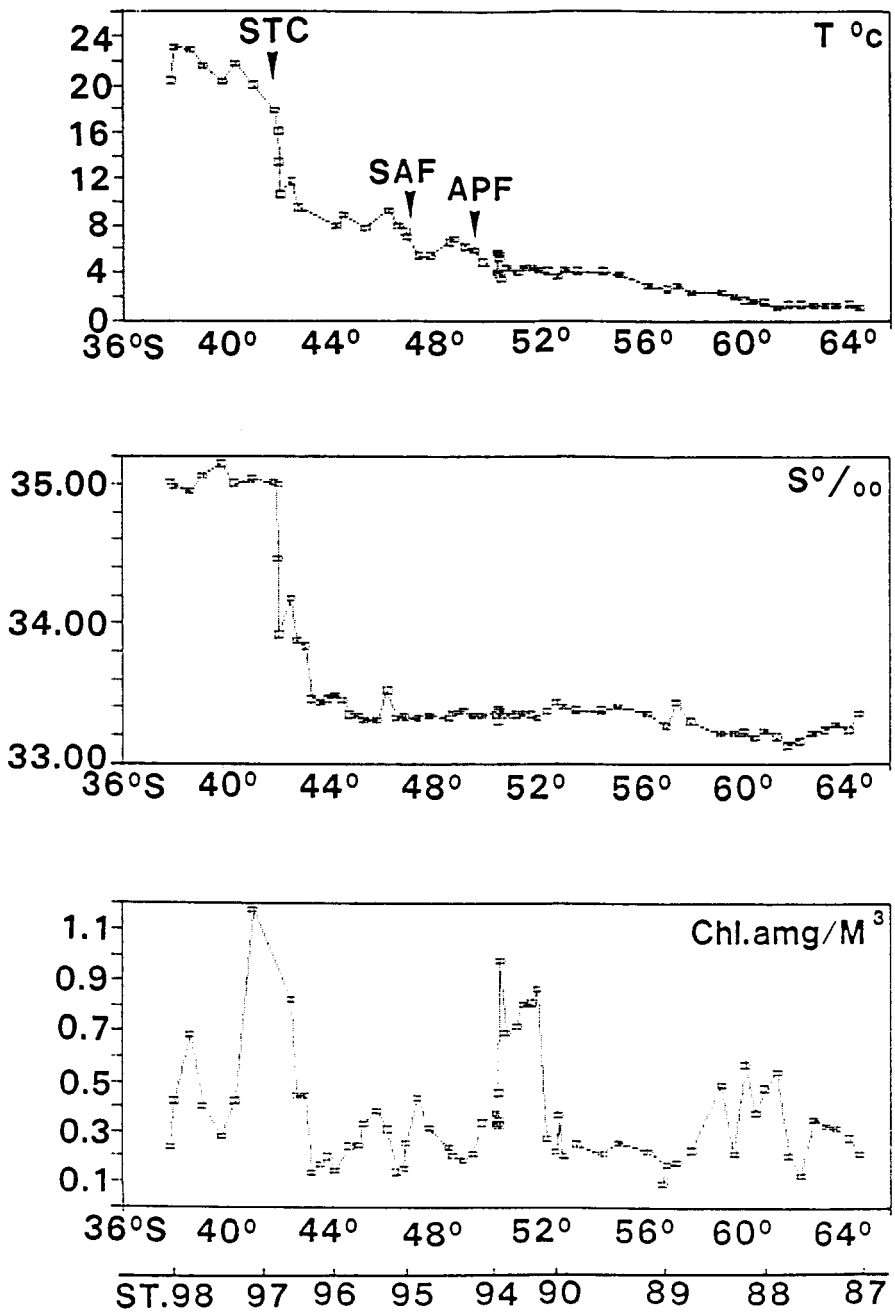


Figure 5: Distribution of temperature * (°C), salinity* (°/oo) and chlorophyll a concentration (mg chl a/m^3) at the sea-surface along the western track between Antarctica and South Africa. STC: Subtropical Convergence, SAF: Subantarctic Front, APF: Antarctic Polar Front.

**: A. Poisson's INDIGO III research team data.*

THE SUBTROPICAL CONVERGENCE (STC) shows a sharp transition between the Subantarctic Surface Water and the Subtropical Surface Water.

Geographical location: 41° 40', mean latitude (Lutjeharms et al., 1985)
46° 45', mean latitude (Furuya et al., 1986).
39° 54' - 42° 08', northern and southern limits of the gradient.

Decrease in temperature: 7.3° C (from 17.9° C north of the Convergence to 10.6° C south) (Lutjeharms et al., 1985)
6.85° C (from 20.35° C at 39° 54' to 13.50° C at 42° 08')

Decrease in salinity: 0.5 °/oo (from 35.1 °/oo north of the Convergence to 34.6 °/oo south) (Deacon, 1982)
> 0.7 °/oo (from 35.1 °/oo north to less than 34.4 °/oo south) (Furuya et al., 1986)
0.69 °/oo (from 35.15 °/oo at 39° 54'to 34.46 °/oo at 42° 08'

Increase in nitrate: 8.7 µgatN/l (Allanson et al., 1981)
16.7 µgatN/l, between stations 98 and 96, situated on each side of the Convergence.

Increase in phosphate: 0.60 µgatP/l (Allanson et al., 1981)
1.0 µgatP/l, between stations 98 and 96, situated on each side of the Convergence.

2.1.1.2 Vertical structure of watermasses

Isopycnals and chlorophyll a distribution, obtained from the data collected at the stations between 0 and 200 meters deep, are presented in the next figures. Because of stations interval, these diagrams are to be interpretated carefully.

Between 38° and 50°S, the subsurface expression of the three frontal systems discussed above is easily recognizable (Figure 6).

On the contrary of the other watermasses, the Antarctic Surface Water (Stations 90 to 87) is stratified, especially in the southern part of the track (Station 87), where a sharp pycnocline is found between 30 and 40 meters deep.

Between 62° and 66° S, strongly sloping isopycnals are proceeding towards

the surface, probably due to the vicinity of the Antarctic Divergence. Highest values in silicate are observed at station 87: 48.7 µgatSi/l at surface, 73.4 µgatSi/l at 100 meters deep (Figure 7).

2.1.1.3 Chlorophyll a distribution

Along the horizontal track through the watermasses between Antarctica (64° 46'S) and South Africa (37° 53'S), the two major peaks in chlorophyll a concentrations observed at the sea-surface occur respectively at the Subtropical Convergence and at the Antarctic Polar Front (Figure 5).

At the SUBTROPICAL CONVERGENCE, surface chlorophyll a concentration reaches *1.18* mg chl a/m^3. At station 97, situated on the Subtropical Convergence, concentrations greater than 1.0 mg chl a/m^3 are found down to 70 meters deep (Figure 6).
Further to the north, a smaller increase in chlorophyll a occurs (0.69 mg chl a/m^3).

South of the ANTARCTIC POLAR FRONT, surface chlorophyll a concentration reaches *0.98* mg chl a/m^3.

In the area of the SUBANTARCTIC POLAR FRONT, two significant peaks are observed on each side of the gradient (*0.44 et 0.38* mg chl a/m^3).
Within the Subantarctic Frontal Zone and the Antarctic Convergence area, the vertical structure of phytoplankton distribution is not well documented because of stations interval. However, below the surface chlorophyll a maximum, a subsurface phytoplankton peak (0.4 - 0.5 mg chl a/m^3) is found between 50 and 75 meters deep.

In the ANTARCTIC SURFACE WATER, over a wide latitudinal zone from 58° to 64°S, mean phytoplanktonic biomasses are relatively high (from *0.13 to 0.57* mg chl a/m^3).
At the southern limit of this track, a subsurface maximum (0.4 - 0.7 mg chl a/m^3) occurs between 40 and 95 meters.

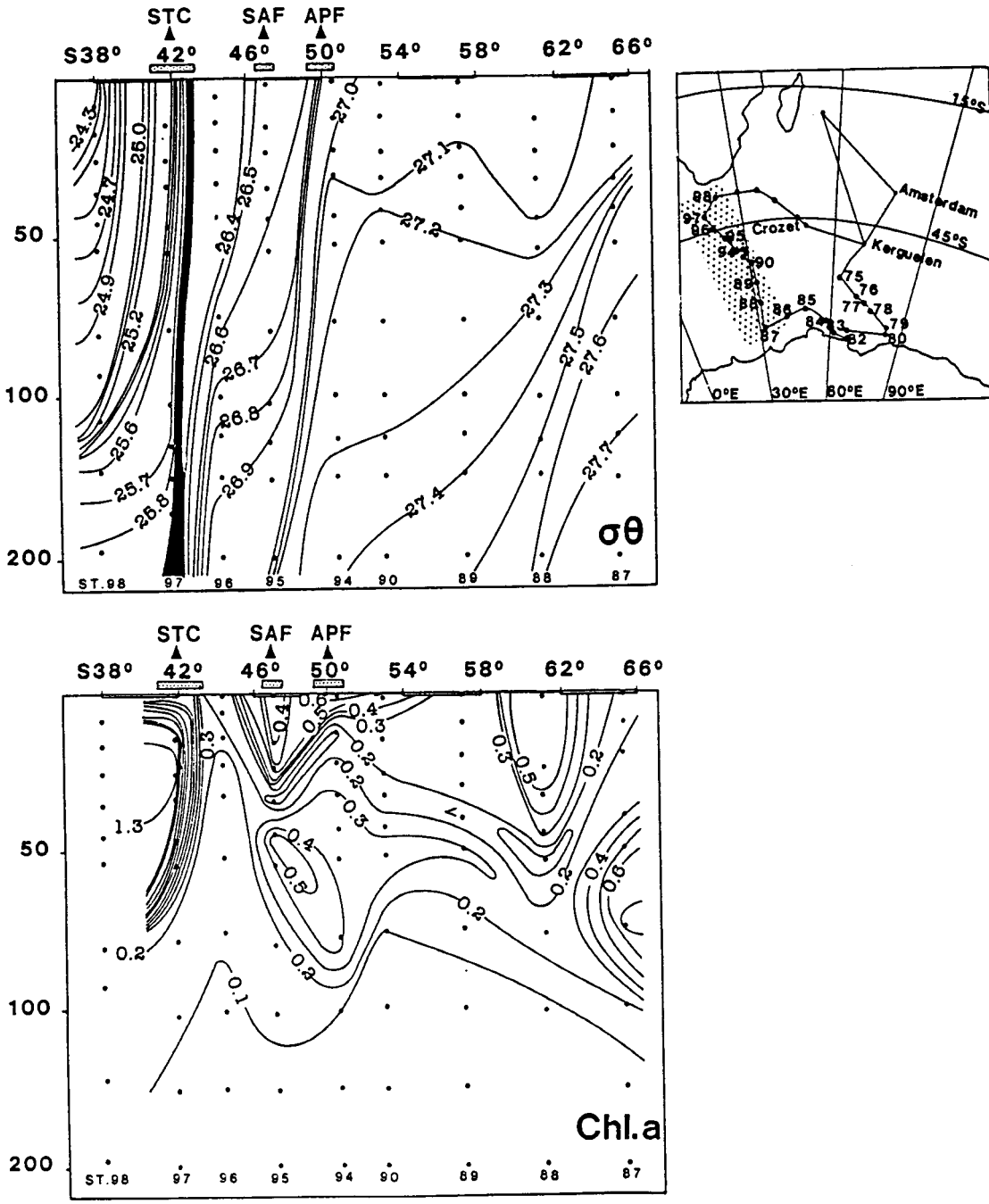


Figure 6: Vertical distribution of density (σ_θ) and chlorophyll a concentration (mg chl a/m^3) from surface to 200 meters deep along the western track (Stations 98 to 87). *Density has been calculated from temperature and salinity data of A.Poisson's INDIGO III research team.*

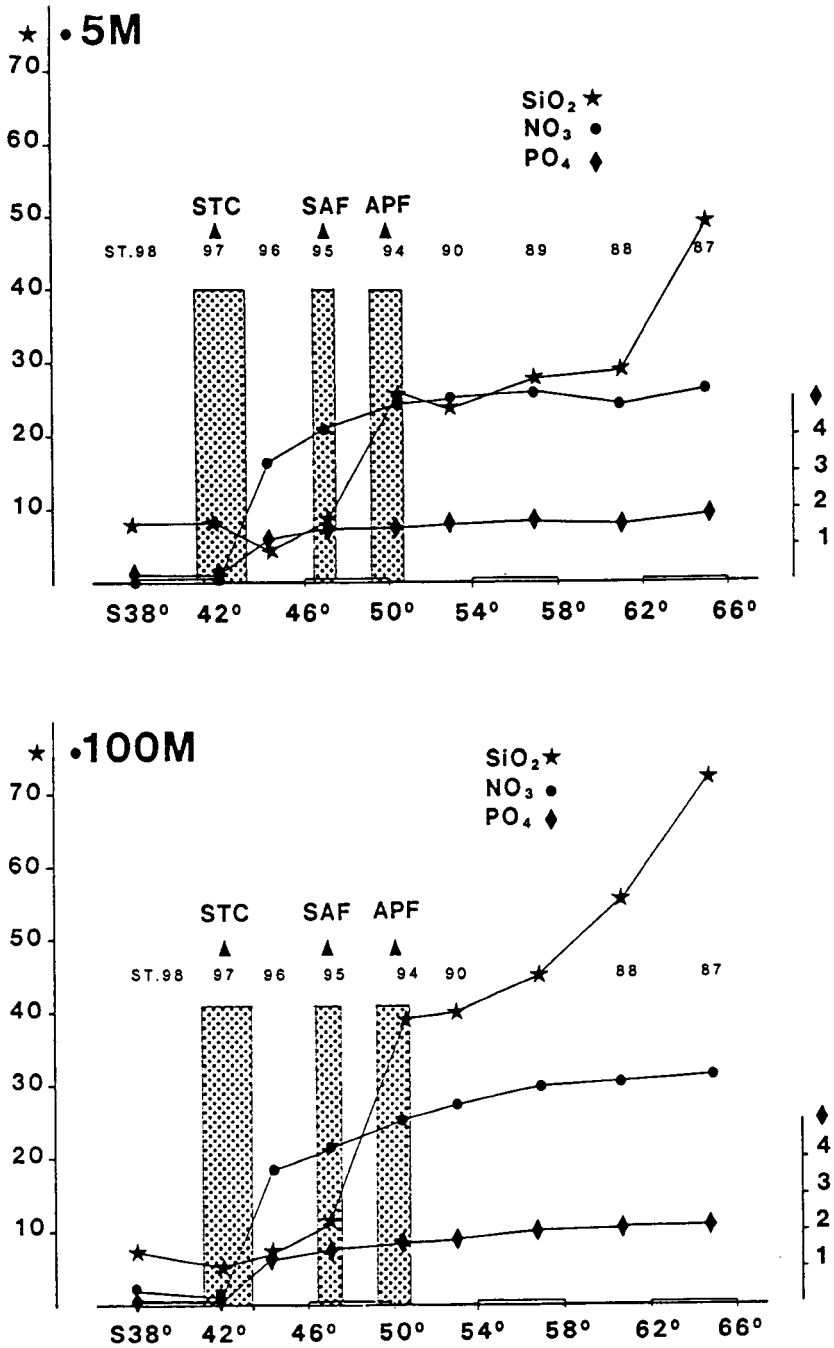


Figure 7: Horizontal distribution of reactive phosphate, silicate and nitrate at the sea-surface and at 100 meters deep (µgat/l) along the western track (Stations 98 to 87). *Data obtained from A.Poisson's INDIGO III research team (PO_4 and SiO_2) and F.Dehairs and L.Goeyens (NO_3).*

2.1.2 Eastern Track

2.1.2.1 Hydrology

The hydrological structure of this section, situated in the Antarctic Surface Water, is shown at Figure 8. It is obviously very similar to the one described above for the western track between 54° and 66°S (Stations 90 to 87).
South of the track, at station 80, a sharp pycnocline, resulting from isopycnals constriction, occurs about 20 meters deep. At this station, very high values of silicate are observed, simultaneously at the sea-surface and at 100 meters deep (respectively 42.8 and 73.4 µgat/l - Figure 9 -).

2.1.2.2 Chlorophyll a distribution

Investigations performed at the stations from surface to a depth of 200 meters show a strong heterogeneity in chlorophyll a distribution related to the hydrological structure (Figure 8).

In the southern part of the track, phytoplanktonic biomasses are high and chlorophyll a distribution follows the general slope of the isopycnals. Concentrations higher than 1 mg chl a/m^3 are measured from the surface down to 10 meters deep at station 80 and from the surface to as deep as 65 meters at the station 78. At this station, living chlorophyll a seems to be accumulated around 55 meters deep where the highest phytoplankton biomass (more than 1.5 mg chl a/m^3) is observed.

In the northern part of this section, chlorophyll a concentration is close to those observed in oligotrophic waters (less than 0.2 mg chl a/m^3).

2.1.3 Southern Track

2.1.3.1 Hydrology

Density distribution between longitudes 32° to 84°E and latitudes 62° to 67°S is presented in Figure 11.
As observed previously in the Antarctic Surface Water, isopycnals are proceeding towards the surface, from the most northern station (Station 85) to the southern stations (Stations 87, 83, 82 and 80) (Figure 10).

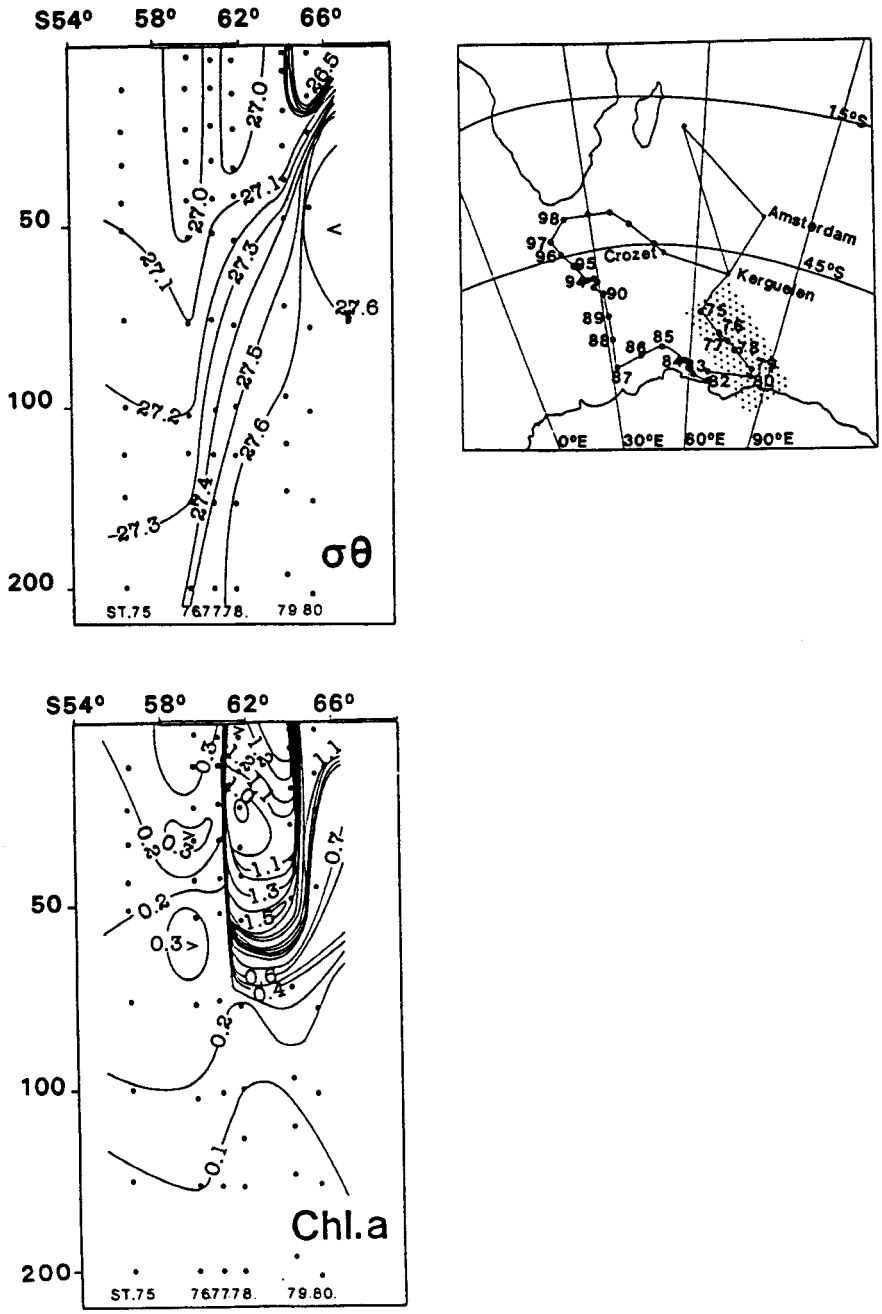


Figure 8: Vertical distribution of density (σ_θ) and chlorophyll a concentration (mg chl a/m^3) from the surface to 200 meters deep along the eastern track (Stations 75 to 80). *Density has been calculated from temperature and salinity data of A.Poisson's INDIGO III research team.*

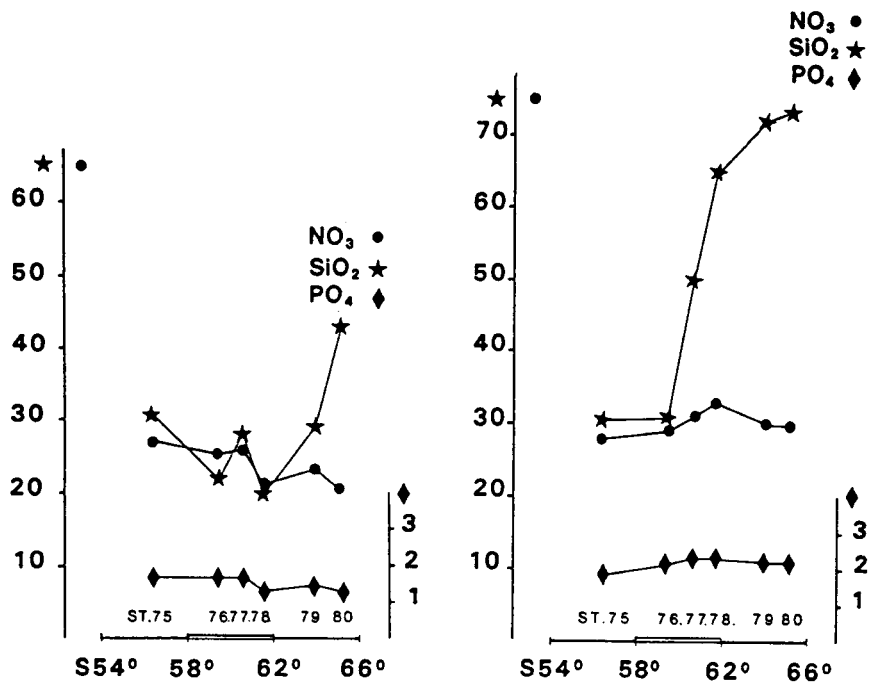


Figure 9: Horizontal distribution of reactive phosphate, silicate and nitrate at the sea-surface and at 100 meters deep (µgat/l) along the eastern track (Stations 75 to 80). *Data obtained from A.Poisson's INDIGO III reseach team (PO_4 and SiO_2) and F.Dehairs and L.Goeyens (NO_3).*

Highest silicate concentrations are associated to the most southern stations, except for the station 80, where surface concentration decrease is probably correlated to the high phytoplankton biomass (Figure 11).

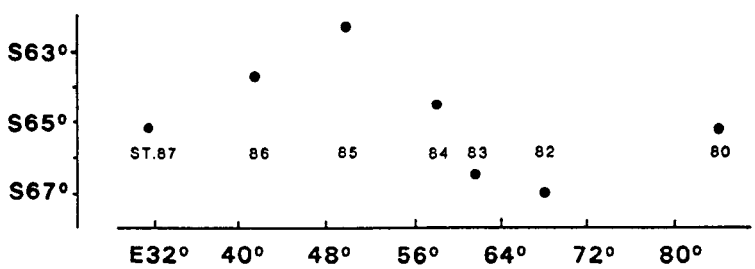


Figure 12: Latitudinal position of the stations along the southern track.

2.1.3.2 Chlorophyll a distribution

Two maxima in phytoplankton biomasses are recorded along this section: one westwards, below the pycnocline (0.4 - 0.7 mg chl a/m^3) and the other over a wide latitudinal zone, between 60° and 84°E - Figure 11 -. In this area, high levels in chlorophyll-a concentration (0.5 - 1.1 mg chl a/m^3) occur above the pycnocline. Between Stations 83 and 84, living chlorophyll-a seems to be carried along the isopycnals as deep as 100 meters deep.

Between these two areas of phytoplankton accumulation, chlorophyll a concentration is very low (0.1 mg chl a/m^3).

2.2 Surface Cartography

Surface distributions of physical, chemical and biological parameters allow to have a "synoptic" and macroscale view of the structure of the INDIGO III sampling area.

Density, salinity and temperature are presented at figures 13B, 14A and 14B. When examining the gradients for these three parameters, it is obvious that the most conspicuous changes are at the Subtropical Convergence, identified along the western track at station 95 (see § 2.1.1.1 p. 14).
Temperature decreases and density increases regularly from the north to the south. Southeastern, a lens of very cold water (less than 0° C) of low salinity results in a local density decrease.

Concerning nitrate distribution (Figure 15A), the Subtropical Convergence area corresponds to a sharp increase of the concentrations, from the north, where nitrate is quite exhausted, to the south. In the Antarctic and Subantarctic areas, nitrate concentrations show little variations.

Silicate concentrations (Figure 15B) clearly increase from the north of the Subantarctic area to the south of the Antarctic area, showing a behaviour different from nitrate.

Along the western track, chlorophyll a distribution, widely described above, exhibits maxima of biomasses in relation with the main frontal structures (§ 2.1.1.3 p. 17). Southeastern, in the Antarctic Water, high levels

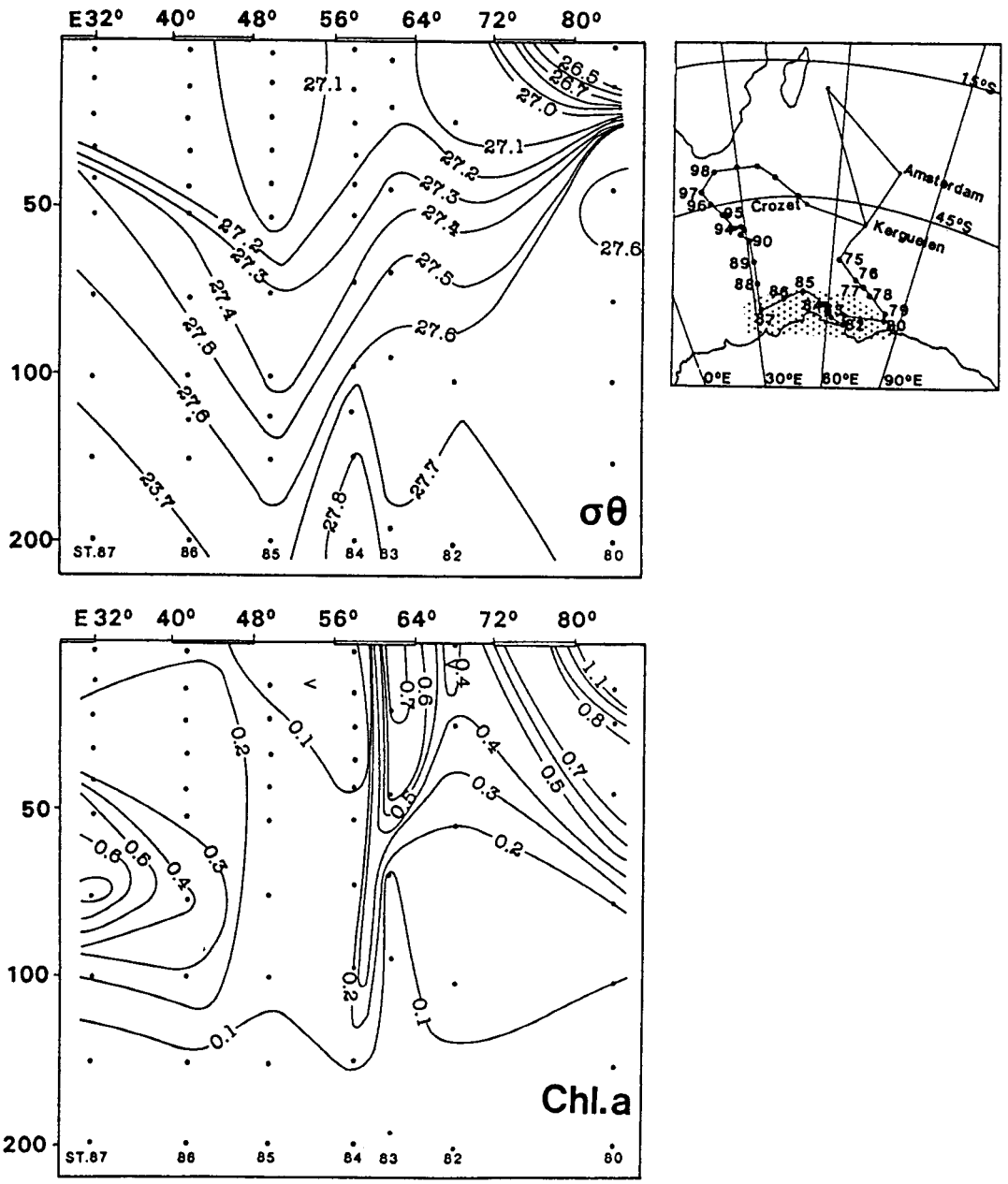


Figure 11: Vertical distribution of density (σ_o) and chlorophyll a concentration (mg chl a/m^3) from the surface to 200 meters deep along the southern track (Stations 87 to 80). *Density has been calculated from temperature and salinity data of A.Poisson's INDIGO III research team.*

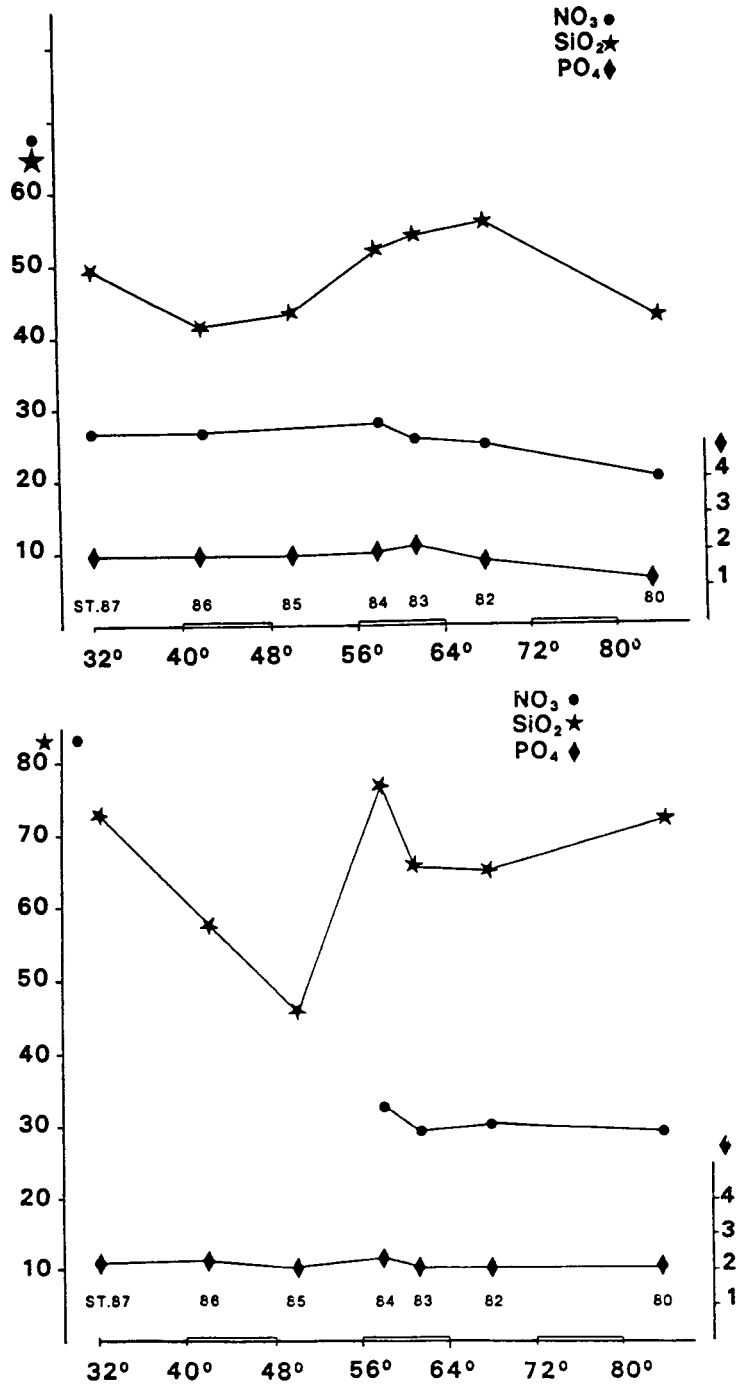


Figure 12: Horizontal distribution of reactive phosphate, silicate and nitrate at the sea-surface and at 100 meters deep (µgat/l) along the southern track (Stations 87 to 80). *Data obtained from A.Poisson's INDIGO III research team (PO_4 and SiO_2) and F.Dehairs and L.Goeyens (NO_3).*

of biomasses are detected (Figure 16).

2.3 Zooplankton: Distribution and Biochemical Characteristics

Subsurface plankton biomasses (-5 m), sampled with a 180µ WP2 net, are presented at Figure 17B. Values range extends from less than 0.1 g of fresh weight per cubic meter to 130 g F.W./m^3 (station 79).

In the Antarctic Surface Water, biomasses higher than 1.1 g F.W./m^3 are dominated by phytoplankton (Table 1) and located south of the INDIGO III sampling area. Zooplankton dominating samples occur at stations 90, 89 and 75.

South of the Antarctic Convergence, proteins and lipids contents (in % of dry weight) are extremely low in the southern part of the Antarctic Surface Water, in the phytoplankton dominated area (Figure 18).
Further to the north, in the zooplankton dominated area, proteins percentage increases, with maximum values at stations 89 and 75 (> 20% of D.W.). Lipids contents show the highest value at station 90 (41.88 % of D.W.), north of the maximum of proteins.

North of the Antarctic Convergence, variations of biochemical contents have to be studied in relation with the faunistic composition.

2.4 Discussion

Data obtained during Indigo III cruise show again that wide geographical variation of planktonic parameters in the Southern Ocean is common.

Hydrological structure has been established with a great degree of confidence, referring to many authors. Results from the horizontal sea-surface track between Antarctica and South Africa have allowed to describe the geographical location of the main frontal systems (Antarctic Convergence, Subantarctic Front and Subtropical Convergence) and associated watermasses.
When considering temperature, salinity, density, nitrate and phosphate gradients from the Antarctic Continent to the Subtropical Water, the most conspicuous change occurs at the Subtropical Convergence. This suggests that one should include all waters south of the Subtropical Convergence, instead of the Antarctic Convergence, in the study of the Southern Ocean (Holm-Hansen, 1985).

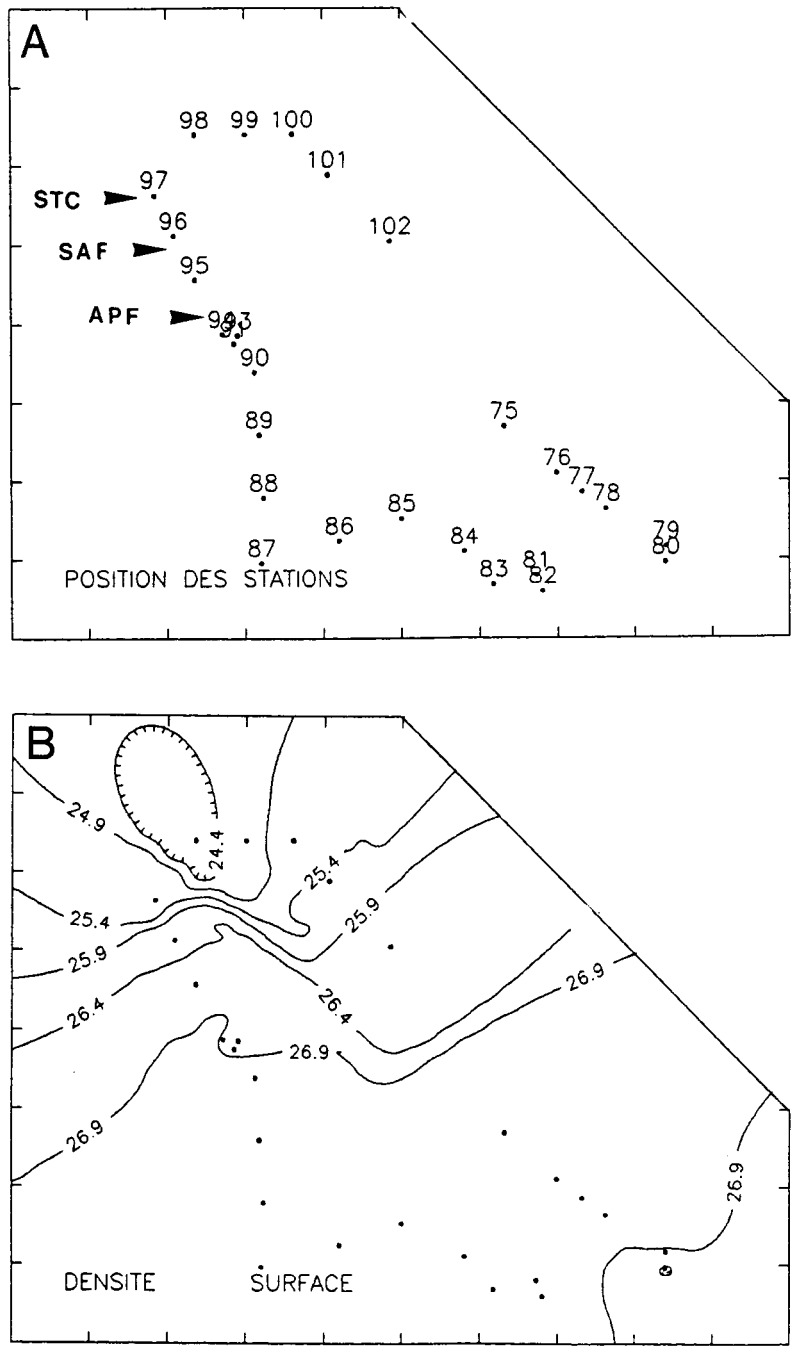


Figure 13: A. INDIGO III sampling area and position of the stations.
B. Subsurface map of the Density distribution (σ_o).
Arrows show the position of the main frontal structures, identified along the western track (see § 2.1.1.1).
Density has been calculated from temperature and salinity data of A.Poisson's INDIGO III research team.

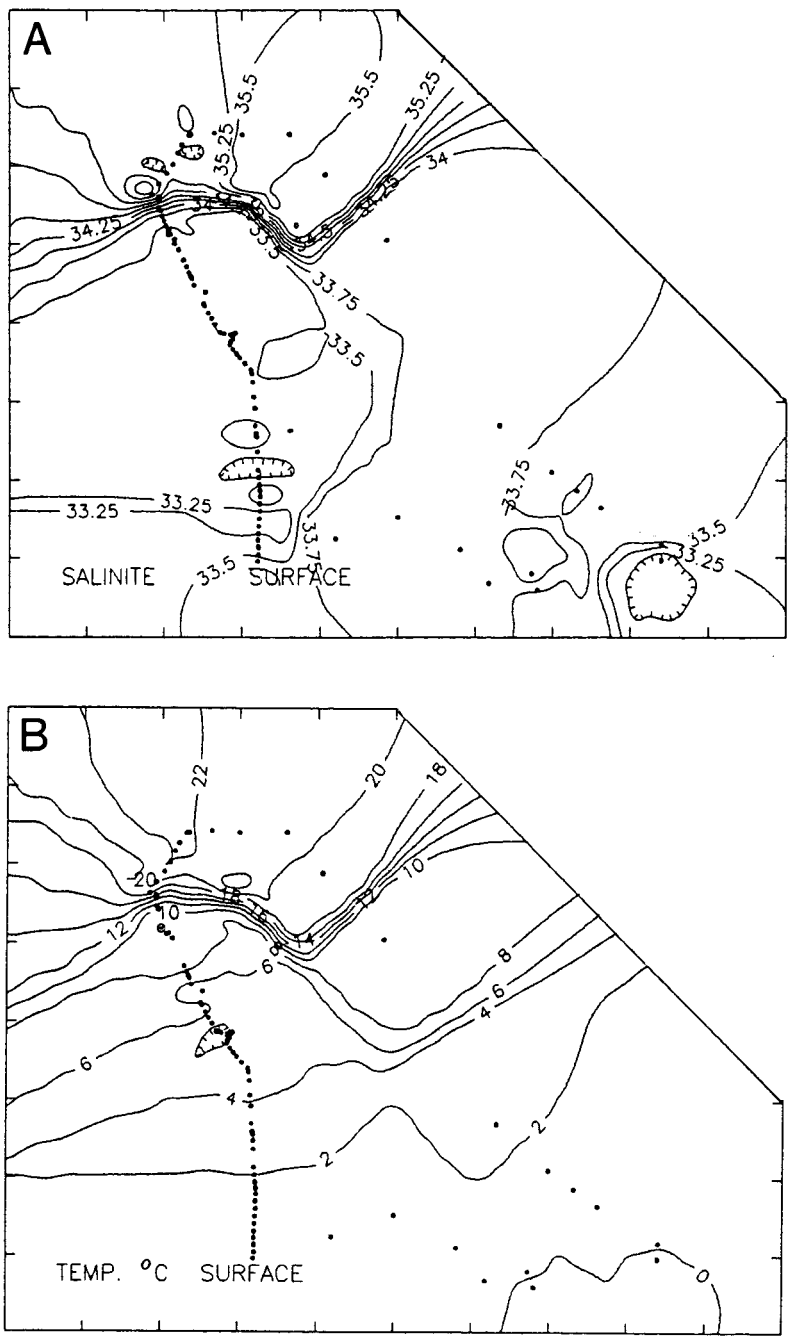


Figure 14: Subsurface distribution of the Salinity (°/oo) (A) and of the Temperature (°C) (B).

Data obtained from A.Poisson's INDIGO III research team.

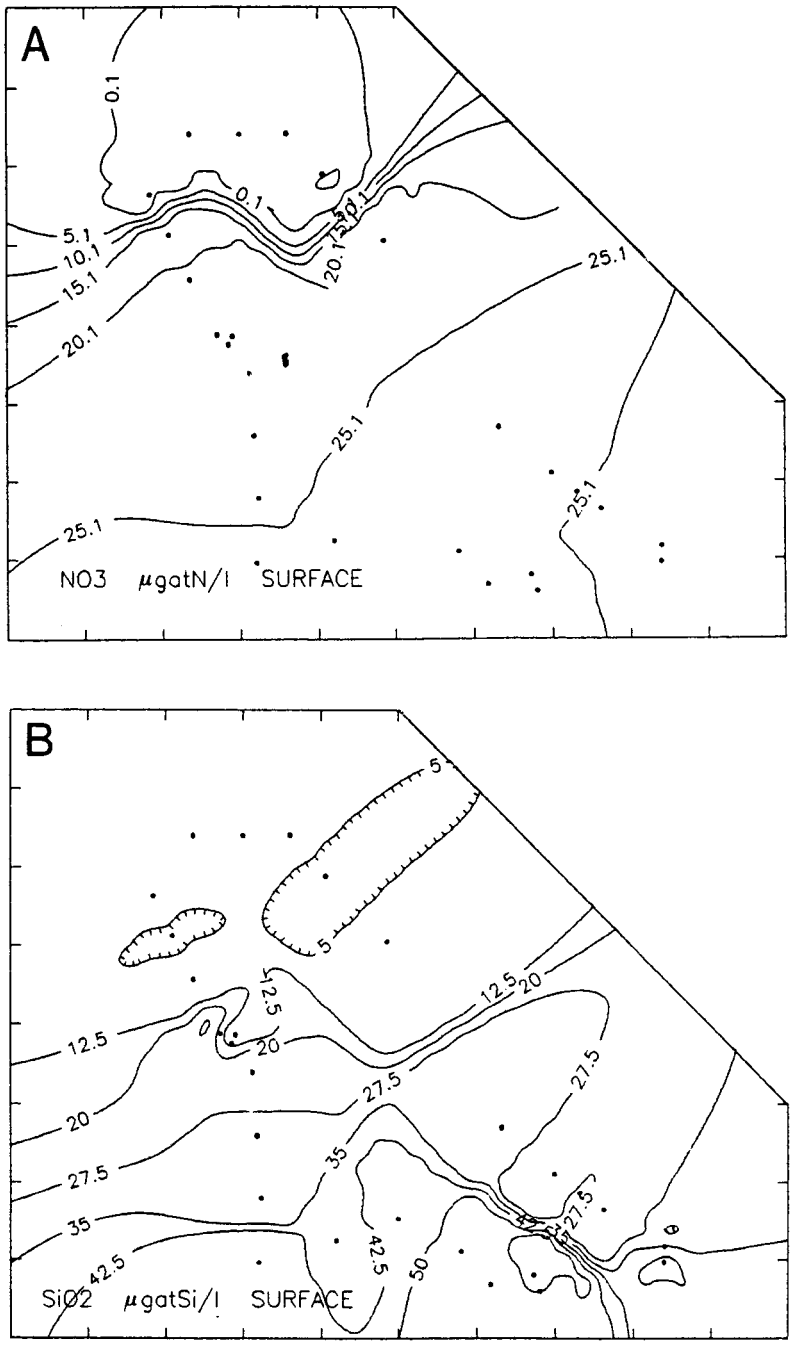


Figure 15: Subsurface distribution of Nitrate (µgatN/l) (A) and of Silicate concentrations (µgatSi/l) (B).

Data obtained from A.Poisson's INDIGO III research team (SiO_2) and F.Dehairs and L.Goeyens (NO_3).

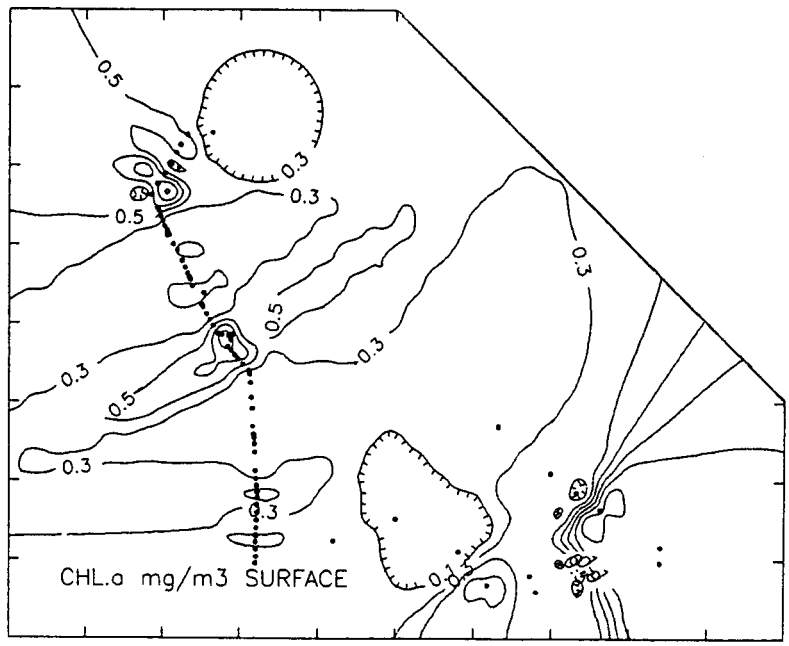


Figure 16: Subsurface distribution of Chlorophyll a (mg chl a/m3)

Station: 75 Zooplankton
76 Gelatinous colonies of Phytoplankton
78 Gelatinous colonies of Phytoplankton
79 Gelatinous colonies of Phytoplankton
81 Phytoplankton + Zooplankton
84 Gelatinous colonies of Phytoplankton
85 Phytoplankton + Zooplankton
86 Gelatinous colonies of Phytoplankton
87 Gelatinous colonies of Phytoplankton
88 Gelatinous colonies of Phytoplankton
89 Zooplankton
90 Zooplankton
94 Gelatinous colonies of Phytoplankton
95 Phytoplankton + Zooplankton
96 Zooplankton
97 Zooplankton
98 Zooplankton
99 Gelatinous Zooplankton
100 Zooplankton + Gelatinous
101 Zooplankton + Gelatinous
102 Eggs

Table 1: Dominance of phyto- or zooplankton in the subsurface plankton.

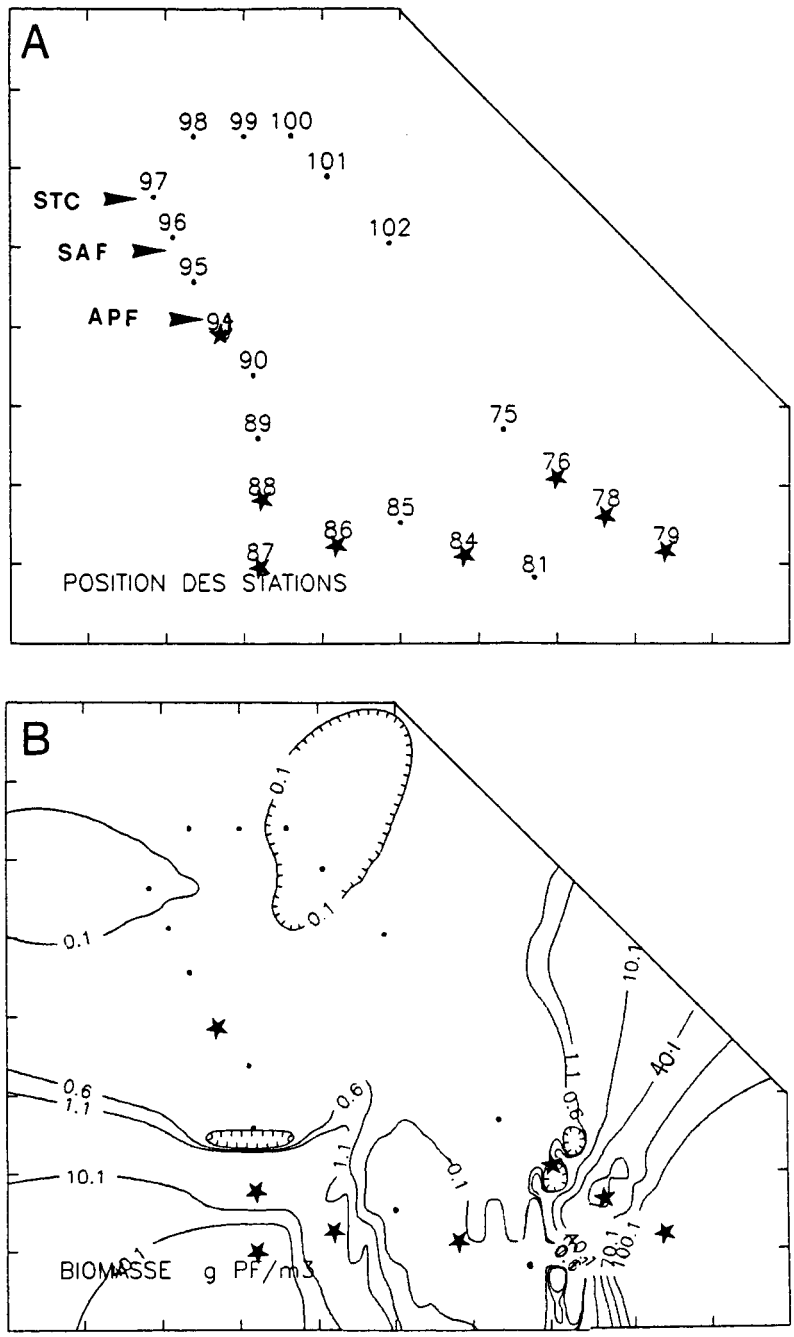


Figure 17: A. INDIGO III sampling area and position of the stations.
B. Subsurface map of the plankton biomasses (g F.W./m3).
★ indicate phytoplankton dominated samples.
Arrows show the position of the main frontal structures, identified along the western track (see § 2.1.1.1).

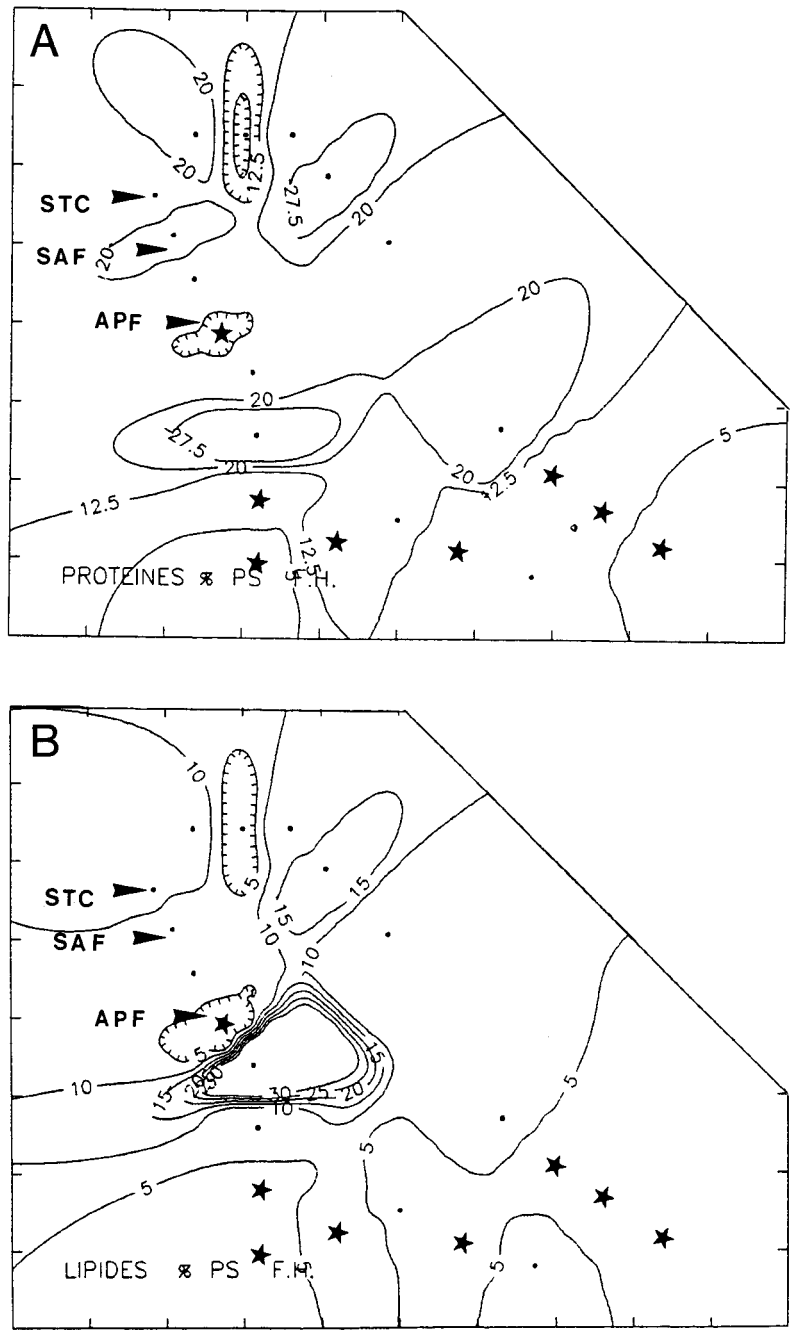


Figure 18: Distribution of proteins (A) and lipids contents (B) (% of D.W.) in the subsurface plankton.

★ indicate phytoplankton dominated samples.

Arrows show the position of the main frontal structures, identified along the western track (see § 2.1.1.1).

In the southern part of the INDIGO III sampling area, and especially at stations 87 and 80, strongly sloping isopycnals, proceeding towards the surface, suggest the vicinity of the Antarctic Divergence. Very dense water (σ_θ>27.7) below 100 meters deep and maximum values of silicate confirm this hypothesis.

Phytoplankton distribution study demonstrates that the spatial patchiness of high chlorophyll a concentrations is bound up with the frontal systems and with the areas of increased stability.

INDIGO III results confirm that **FRONTAL SYSTEMS** do not act only as physical boundaries but that they themselves may be areas of enhanced biological activity.
At the sea-surface, along the western track, the two major peaks in chlorophyll a concentration (0.8 - 1.1 mg chl a/m^3) are associated with the frontal systems which have the characteristics of a convergence: the Subtropical Convergence and the Antarctic Polar Front.
According to Planke (1977) and Lutjeharms et al. (1985), the Subtropical Convergence south of Africa is characterized by a "dramatic dynamic variability". So, the peak observed north of the gradient could be associated with cross-frontal eddies moving northwards.
Chlorophyll a results of INDIGO III confirm general patterns of phytoplankton distribution reported by Planke (1977), Jacques & Minas (1981) and Lutjeharms et al. (1985).

The vertical phytoplankton distribution, shown between surface and 200 meters deep, must be carefully interpreted, because of stations interval, especially in the frontal areas.
However, despite this, phytoplankton accumulations seem to be strongly correlated with the surface and subsurface expressions of the main frontal systems. At the surface, high phytoplankton biomasses (0.5 - 1.5 mg chl a/m^3) are observed close to the density gradients and more than 0.5 mg chl.a/m^3 are found till a depth of 70 meters (stations 97 and 78 - 79) or 85 meters (station 87). On the other side, in interfrontal areas, phytoplankton is always situated in the upper layers of the water column. There, in spite of high nutrients disponibility, chlorophyll concentration is very low (0.1 - 0.3 mg chl a/m^3), except for the two particular areas discussed hereafter.

In the frontal areas of the Southern Ocean, the high living chlorophyll a standing crops observed between surface and 70 - 80 meters deep suggest a

downwards transport of phytoplankton along the strongly sloping isopycnals in relation with vertical currents associated with the frontal hydrodynamics.
At an other spatial scale, at the Liguro-Provençal Front (Mediterranean Sea), Hecq et al.(1986) have shown that phytoplankton biomass increases accross the density gradient and that living chlorophyll a, produced at the sea-surface, is carried along the isopycnals, in relation with the frontal convergence.
A similar mechanism should exist in the Southern Ocean but a more intensive and detailled study of the antarctic frontal systems (continuous measurements, frequent vertical sampling, meteorological data acquisition) is essential to have a better understanding of the phytoplankton distribution and productivity.

Moreover, south of the Antarctic Surface Water, phytoplankton blooms are observed in areas where the **STABILITY** of the water column increases significantly.
Along the western track, an increase in chlorophyll a is observed over a wide latitudinal zone between 58 and 64°S. During summer, Jacques et Minas (1981) and Lutjeharms et al. (1985) have observed similar phytoplankton increases around 60°S, in areas where surface warming involves a stabilization of the water column. During INDIGO III, stations removal does not allow to observe a possible superficial stratification.
At stations 79 and 80, increased stability is obviously connected to a superficial density decrease due to a lens of very cold water of low salinity. In this particular area, surface chlorophyll a concentration reachs 1.30 mg chl a/m^3 (station 78) and fresh weight of the phytoplanktonic gelatinous colonies is very high.

Although we now have a fair knowledge of horizontal and vertical phytoplankton distribution in the Southern Ocean, we still have a poor understanding of the factors which limit the primary productivity in these waters. According to Holm-Hansen & Huntley (1984), the nutrients levels in the Antarctic Surface Water should be able to support a phytoplankton biomass of at least 25 mg chl a/m^3. However, the contradiction between potential and observed productivity is still uncompletelely resolved.

Biochemical contents of the subsurface plankton and dominance of phyto- or zooplankton in the nets allow to understand the mesoscale structure of the Antarctic subsurface ecosystem.
With the seasonal retreat of the pack-ice, situated just south of station 82, a provisional stabilization of the superficial layer occurs, as observed mainly at

stations 79 and 80 (Fig. 14B). In this stratified area, phytoplankton biomasses may enhance (stations 87, 76, 78 and 79) and give support from the base of the food web. A few days later, OR some miles northern, typical zooplanktonic communities are observed, in a *destratified* area. Just north of the phytoplankton rich area, high proteins values and fairly low lipidic contents characterize YOUNG zooplankton (stations 89 and 75, figure 18). Further to the north (station 90), maximum lipidic contents (41.88 % D.W.) and lower proteins values are typical of ADULT zooplankton.

So, it seems that during summer, the stabilization of the upper layers of the water column due the retreat of the constantly melting ice-edge may enhance a series of phytoplanktonic and zooplanktonic blooms, from the north to the south. A patchiness of the different trophic levels is observed, with, northern, old zooplanktonic population and southern, young phytoplankton.
The spatial scale depends on the speed of the pack-ice retreat.
More frequent samples will improve a better understanding of this fundamental mechanisms.

During all the INDIGO III cruise, Krill and whales were mostly absent.

3. LIPIDS AND FATTY ACIDS DISTRIBUTION AND PROBLEMATIC

Biochemical composition and especially lipids an fatty acids composition of Antarctic krill has become intensive in recent years, as a result of its potential importance as food. The chemical composition of *Euphausia superba* and *E. christallarophias* is relatively well known (Bottino, 1974).
On the other hand, in the areas where the krill is mostly absent, very little is known about lipids and fatty acids of the planktonic ecosystem (phytoplankton and "non krill" zooplankton).
The fatty acids composition of organisms is to a great extend conditioned by both nutritional (type and amount) and physiological factors. The values can be used to compute the metabolic activity of planktonic communities (Sargent and Whittle, 1981).

During INDIGO III, fatty acids analysis in subsurface plankton nets have been carried by a method developed in our laboratory (Hecq and Goffart, 1984) and discussed in relation to watermasses. Low quantities of methyl esters of fatty acids are injected "on column" in a gaz chromatographer SILAR 10C. The advantage of the method is the good identification of polyunsaturated fatty acids

without hydrogenation) (Fig 19).

Fatty acids data of subsurface horizontal nets are presented as a percentage of total fatty acids in table 2(1) 2(2) and 2(3) and in figures 20 to 29. In tables 3(1), 3(2) and 3(3) and figures 30 to 43, the results of fatty acids are presented in mg per g. of dry weight.
In tables, RT represents the retention time of fatty acid in chromatography. The "name", for example 22:6w3 (or docosahexaenoic acid) means a fatty acid with 22 carbon atoms, 6 double bonds and 3 carbon atoms between terminal methyl and dubble bond.

The percentage of fatty acids in the subsurface plankton shows the predominance of the 20:5w3 and 22:6w3 polyunsaturated fatty acids (PUFA) , with sometimes 50% of total fatty acids, especially in the northern stations (stations 95 to 102), with old zooplankton communities (fig. 20 & 21). Comparatively, typical Antarctic water is poorer in PUFA.
Other important fatty acids are the saturated 14:0 (fig 22) which is dominant in the Antarctic Surface Water and the 16:0 (fig 23), more equally distributed.
Monounsaturated fatty acids appear in lower percentage, excepted 18:1w9 (fig 26) and 16:1w7, dominant in the Antarctic Surface Water (fig 25).

The results of fatty acids presented in mg per g. of dry weight are more independent of individual fatty acid fluctuations.
The pictures 30 to 43 show that saturated and monounsaturated C14 and C16 fatty acids concentrations are relatively constant in all samples (excepted at station 90, very rich in lipids).
On the other hand, concentrations in longer fatty acids (C18:0, 20:5W3 and 22:6W3) are higher in the Subantarctic area.
Finally, C18:2w3 is typically represented in the Antarctic Water.

The polyunsaturated fatty acids of w3 series, specific of the pelagic food chain (Bottino, 1974; Moreno et al., 1979) are de novo synthetized by phytoplankton, especially Dinoflagellates and *Phaeocystis* (Sargent et al., 1981). The balance between polyunsaturated fatty acids (PUFA) on position-2 of the glycerol backbone and a saturated or monounsaturated fatty acid on position-1 determines the fluidity of the cellular membranes. This important factor, controled by lowest temperature in polar and deep oceanic waters explains the high PUFA concentrations (especially 22:6w3) in our phytoplankton rich samples.

The PUFA biomasses of INDIGO III cruise are higher than generally found in literature, perhaps due to the used method, unaffecting the double bonds of PUFA.
These compounds are transmitted by food chain via triacylglycerols on position-2 of glycerol and are generally stable. Animals being unable to elaborate PUFA, the fatty acid level and composition of PUFA in zooplankton, especially carnivorous and fishes of the antarctic pelagic food chain, will be dependant on diet actual but also in the passed. That explains the higher PUFA concentrations in zooplankton rich samples. The highest PUFA concentrations correspond to the maximum feeding activity and/or to the oldest or "most cumulatively feeding" communities.

Given the dietary origin of the lipidic contents of an organism, lipids analyses can be used to probe predator - prey relationships. The specificity of the approach depends on the extent to which individual lipid components are specific to individual species.

The major marine saturated fatty acids are Myristic acid (C14:0) and Palmitic acid (C16:0). Stearic acid (C18:0) is generally present in trace amounts in marine lipids except in phospholipids of marine animals (Ackman & Hooper, 1974; Bottino, 1977).
Myristic acid (C14:0) is known as prominent constituent of phytoplanktonic lipids, especially in Diatoms (Bottino, 1974). Its accounts for up to 20% of the total fatty acids in the mixed Antarctic phytoplankton. On the other hand, phospholipids of marine animals contain very small amounts of 14:0 acid. (Lee et al., 1971; Morris & Sargent, 1973) but that acid appears in large quantities in waxes of calanoid Copepods. Since that acid is abundant in neutral lipid but absent from phospholipid, it is used only for production of metabolic energy. Therefore, it may be a useful marker for lipid metabolic energy transmitted through the trophic levels phytoplankton - zooplankton - fishes (Sargent & Whittle, 1981).

Thus, if abundance of PUFA reflects old and reserves rich zooplankton, the abundance of 14:0 in some INDIGO III samples reflects the young planktonic communities with immediately usable high energetic contents.

On the basis of similarity between samples in point of view of fatty acids pattern (especially PUFA and C14:0), it is possible to distinguish 4 groups of stations characterized by ecobiochemical properties (cfr table 4, fig. 44 & 45).

The A-Group (stations 76, 78, 84, 85, 87, 94) presents very young planktonic communities with low lipidic contents, high level of energetic reserves (high C14:0 concentration) and relatively high biomass. These stations are related to divergence area rich in nutrients and heavily influenced by vertical circulation. The PUFA are quite absent, reflecting communities without storage. The stations are generally close to the Antarctic continent.

The B-Group (stations 79, 81, 86, 88) has the characteristics of growing planktonic communities with highest biomasses and an increase of polyunsaturated fatty acids. The C14:0 energetic fatty acid is quite high .

The C-Group (stations 75, 89, 90) corresponds to the phytoplanktonic bloom associated to the Antarctic Polar Front. Lipidic contents is high and fatty acid pattern corresponds to older planktonic communities (high PUFA concentration and low C14:0).

The D-Group includes the northern stations with the highest polyunsaturated fatty acid values but a decrease of the lipidic contents. Those stations represent a more stable and dynamic food chain.

In conclusion, fatty acid data confirm the hypothesis that maximum values of planktonic food chain efficiency are not found close to the Antarctic continent (where phytoplanktonic biomasses are important but turnover low) but between the Antarctic Polar Front and the Subtropical Convergence (where each trophic level is quickly consumed by the next with a high turnover rate). More detailed analysis on specific levels of the Antarctic food chain (integrated on the watercolumn) and the knowledge of total fatty acids pool will allow to calculate the metabolic fluxes and turnover rates of the Antarctic ecosystem.

E. APPLICATIONS

Data obtained during ANTAR PROGRAMME first phase have permitted to distinguish, in the Southern Ocean, different areas of planktonic productivity associated to hydrodynamical active phenomenons. Each area corresponds to a specific pattern in terms of biochemical quality of pelagic marine food chain. The diversity of the areas and time scales in the Southern Ocean is so rich that it is possible to found all possibilities of ecobiochemical mechanisms.
In other words, our researchs will allow us to predict the nutritional quality of marine products on the base of ecohydrodynamical terms. Well known polyunsaturated fatty acids in plankton and fish oils are a good application.

F. GENERAL CONCLUSION

Scientific knowledge of the mechanisms controlling phyto- and zooplankton and their availability for the upper levels of the trophic chain are fundamental to ensure the protection of the Antarctic environment.

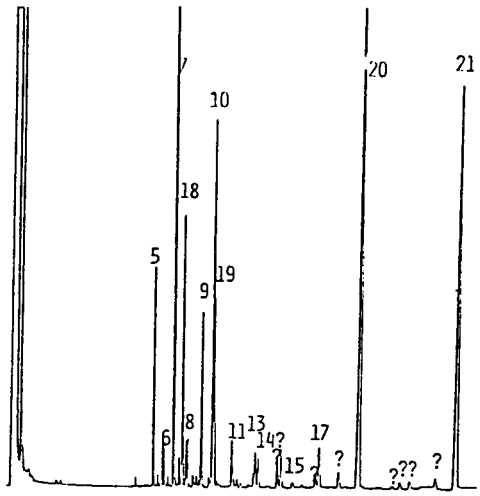
During Phase One of the Belgian Scientific Research Programme on Antarctica, the Ecohydrodynamics Unit of the University of Liège has developed studies on the mechanisms of distribution and biochemical speciation, especially lipids contents, of the planktonic ecosystem, as a function of environmental parameters.

INDIGO III results confirm the ecological heterogeneity of the Southern Ocean and provide confirmation of the fairly low biomasses of phyto- and zooplankton in the open water.

Phytoplankton distribution study demonstrates that the spatial structure of high chlorophyll a concentrations is bound up with the main frontal systems which have the characteristics of a convergence and, in the Antarctic Surface Water, with the areas of increased stability.

Biochemical contents of the subsurface plankton allow us to understand the mesoscale structure and functioning of the Antarctic subsurface ecosystem. It seems that in summer, the stabilization of the upper layers of the water column due to the retreat of the constantly melting ice-edge may induce successive phytoplanktonic and zooplanktonic blooms, from the north to the south. A patchy distribution of the different trophic levels is observed, with, to the north, old zooplanktonic population and to the south, young phytoplankton. The spatial scale depends on the speed of the pack-ice retreat.

Fatty acids data confirm the hypothesis that maximum values of planktonic food chain efficiency are not found close to the Antarctic continent (where phytoplanktonic biomasses are important but turnover is low) but between the Antarctic Polar Front and the Subtropical Convergence (where each trophic level is quickly consumed by the following one whit a high turnover rate). More detailed analysis on specific levels of Antarctic food chain (integrated on the watercolumn) and the knowledge of total fatty acid pool will allowed to calculate metabolic fluxes and turnover rates of the Antarctic ecosystem.



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3	10:0	10	18:1 ω9 -	17	20:4 ω6
4	12:0	11	18:2 ω6	18	16:1 ω7
5	14:0	12	20:0	19	16:3 ω3
6	15:0	13	20:1 ω9	20	20:5 ω3 -
7	16:0 -	14	18:3 ω3	21	22:6 ω3 -

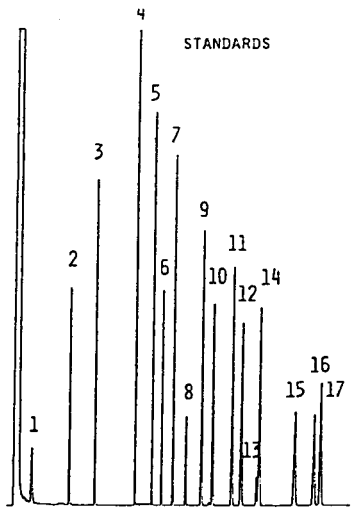

Fig. 19.- Exemple of chromatogramm of fatty acids methyl ester in antarctic Krill and standards.

TABLE 2(1) : INDIGO III RESULTS
FATTY ACIDS PERCENTAGES IN HORIZONTAL NETS

RT	NAME							
STATIONS		75H	76H	78H	79H	81H	84H	85H
9.1	10:0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11.0	12:0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
12.4		0.0	0 0	0.0	0.0	0.0	0.0	0.0
12.7	14:0	8.6	19.1	22.8	16.0	13.4	16.8	10.8
13.1		0.2	0.0	0.0	0.0	0.1	0.0	0.0
13.4		0.3	0.7	0.0	0.0	0.3	0.0	0.7
14.0		2.6	2.0	1.3	0.0	0.1	0.0	0.0
14.3	16:0	24.6	39.6	21.6	13.8	20.2	39.4	35.7
14.8	16:1w?	5.9	15.0	16.6	18.9	7.3	6.1	10.1
15.0		0.3	0.5	0.0	0.0	0.3	0.3	1.0
15.6	16:2	8.2	2.8	2.2	0.0	0.3	1.0	0.0
15.9	18:0	1.8	2.0	1.6	0.0	1.2	9.4	2.8
16.3	18:1w9	14.0	12.1	21.6	5.2	10.1	15.2	18.3
16.4	16:3w3	0.2	0.0	0.0	0.0	0:0	0.0	0.0
16.7	18:2w3	0.2	0.0	1.0	4.3	0.4	0.2	0.0
16.9		0.0	0.0	0.0	0.0	0.0	0.0	0.0
17.1	18:3w3	1.1	0.9	2.3	3.1	1.4	1.8	1.9
17.3		0.1	0.0	0.0	0.0	0.0	0.0	0.0
18.0	20:0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
18.3	18:4w3	3.4	0.0	0.4	0.0	5.5	5.6	1.5
18.5		0.0	0.0	0.0	0.0	1.1	0.0	0.0
19.0		0.9	0.0	0.3	0.0	0.8	0.0	0.0
19.5		0.0	0.0	0.0	0.0	0.0	0.0	0.0
20.1		0.0	0.0	0.0	0.0	0.0	0.0	0.0
21.0	22:0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21.1	20:4w6	10.2	0.0	0.9	0.9	1.8	0.3	0.0
22.0	20:4w3	0.1	0.0	0.0	0.0	0.3	0.0	0.0
22.4		0.0	0.0	0.0	1.7	0.0	0.0	0.0
23.0	20:5w3	7.9	2.5	3.5	25.8	22.9	0.4	6.8
24.8		0.0	0.0	0.0	0.0	0.0	0.0	0.0
25.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0
25.4	22:5w6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
25.6		0.6	0.0	0.0	0.0	0.0	0.0	0.3
26.1	22:5w3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
27.7		0.0	0.0	0.0	0.0	0.0	0.0	0.0
28.8	22:6w3	8.1	1.4	2.2	3.3	12.2	0.2	5.3
36.5		0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOTALPUFA		15.9	3.8	5.7	29.1	35.2	0.6	12.1
LIP%PS		5.7	3.4	2.0	2.4	6.8	3.1	4.4
PS(MG/M3)		21	10	5667	10270	4	8	4
LIP(MG/M3)		1.2	0.3	112.2	246.5	0.3	0.2	0.2
		75H	76H	78H	79H	81H	84H	85H

TABLE 2(2) : INDIGO III RESULTS
FATTY ACIDS PERCENTAGES IN HORIZONTAL NETS

RT	NAME							
STATIONS		86H	87H	88H	89H	90H	94H	95H
9.1	10:0	0.0	0.0	0.0	0.1	0.1	0.0	0.1
11.0	12:0	0.1	0.0	0.5	0.2	0.3	0.6	0.0
12.4		0.0	0.0	0.0	0.0	0.1	0.0	0.0
12.7	14:0	9.2	28.0	13.9	7.1	8.9	12.6	5.5
13.1		0.1	0.0	0.0	0.2	0.2	0.3	0.0
13.4		0.4	0.0	0.2	0.4	0.3	0.7	0.6
14.0		0.2	0.0	0.8	0.9	0.4	4.9	0.4
14.3	16:0	20.4	14.0	15.7	22.5	15.1	30.6	19.3
14.8	16:1w?	7.4	35.5	13.3	3.8	4.6	8.1	4.9
15.0		0.6	0.0	0.4	0.4	0.4	0.7	0.3
15.6	16:2	0.5	0.0	1.4	1.4	0.3	4.5	0.7
15.9	18:0	1.5	1.8	2.1	5.1	1.3	6.2	2.7
16.3	18:1w9	11.2	6.8	11.1	25.1	10.0	24.3	9.8
16.4	16:3w3	2.1	0.0	0.0	0.0	0.0	0.0	0.0
16.7	18:2w3	0.3	0.0	0.8	0.0	0.1	0.3	0.0
16.9		0.0	0.0	0.0	0.0	0.0	0.0	0.4
17.1	18:3w3	2.1	1.3	1.0	7.8	2.0	1.7	1.7
17.3		0.1	1.1	2.9	0.0	0.1	0.3	0.2
18.0	20:0	0.3	0.0	0.6	0.0	0.1	0.4	0.2
18.3	18:4w3	1.0	0.0	0.0	0.8	9.3	0.0	0.0
18.5		1.1	0.0	0.0	0.2	0.0	0.5	0.7
19.0		1.0	0.0	1.1	2.3	0.6	0.0	1.3
19.5		0.0	0.0	0.0	0.3	0.2	0.6	0.0
20.1		0.0	0.0	0.2	2.4	0.2	0.0	0.1
21.0	22:0	0.1	0.0	0.2	0.0	0.0	0.0	0.0
21.1	20:4w6	3.0	0.5	2.3	0.0	23.3	0.3	2.5
22.0	20:4w3	0.7	0.0	0.3	0.7	0.5	0.0	0.6
22.4		0.5	0.0	0.2	0.2	0.1	0.0	0.2
23.0	20:5w3	19.8	10.2	18.0	7.1	11.3	1.7	19.4
24.8		0.0	0.0	0.0	0.0	0.1	0.0	0.0
25.0		0.0	0.0	0.0	0.0	0.1	0.0	0.0
25.4	22:5w6	0.0	0.0	0.0	0.1	0.1	0.0	0.8
25.6		0.4	0.0	0.2	0.0	0.1	0.0	0.0
26.1	22:5w3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
27.7		0.0	0.0	0.0	0.0	0.3	0.0	0.6
28.8	22:6w3	14.4	0.8	11.4	9.0	7.6	1.0	25.0
36.5		0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOTALPUFA		34.2	10.9	29.4	16.1	18.8	2.6	44.4
LIP%PS		8.8	1.3	3.2	8.8	41.9	4.0	7.4
PS(MG/M3)		118	3450	584	14	55	21	25
LIP(MG/M3)		10.4	45.9	18.9	1.2	23.1	0.9	1.8
		86H	87H	88H	89H	90H	94H	95H

TABLE 2(3) : INDIGO III RESULTS
FATTY ACIDS PERCENTAGES IN HORIZONTAL NETS

RT	NAME						
STATIONS		96H	97H	98H	99H	100H	101H	102H
9.1	10:0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11.0	12:0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
12.4		0.0	0.0	0.0	0.0	0.0	0.0	0.0
12.7	14:0	3.8	8.7	8.7	18.2	5.3	2.4	5.8
13.1		0.2	0.2	0.1	0.0	0.2	0.2	0.0
13.4		0.2	0.1	0.7	0.9	0.9	0.1	0.3
14.0		0.5	0.8	0.5	0.0	0.5	0.5	0.8
14.3	16:0	18.7	21.9	24.0	25.3	26.7	17.1	14.7
14.8	16:1w?	3.2	7.7	8.4	6.1	3.6	1.5	2.3
15.0		0.6	1.4	1.4	1.9	2.4	0.8	0.7
15.6	16:2	1.7	3.0	1.2	0.0	1.2	5.8	0.8
15.9	18:0	2.5	4.5	4.2	2.3	4.7	2.5	2.6
16.3	18:1w9	9.9	10.6	9.9	6.4	9.3	11.9	15.4
16.4	16:3w3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16.7	18:2w3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16.9		0.0	0.7	0.3	0.0	0.0	0.0	0.0
17.1	18:3w3	1.2	1.5	1.3	2.1	1.4	1.7	3.1
17.3		0.0	0.0	0.0	0.0	0.0	0.0	0.0
18.0	20:0	0.0	0.0	0.3	0.0	0.0	0.1	0.2
18.3	18:4w3	0.5	0.8	1.2	0.0	0.6	0.4	1.1
18.5		1.0	0.0	0.0	0.0	0.0	0.2	1.1
19.0		1.1	1.1	0.9	2.8	1.0	1.1	0.4
19.5		0.2	0.0	0.0	0.0	0.0	0.0	1.5
20.1		0.0	0.0	0.0	0.0	0.0	0.0	0.0
21.0	22:0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21.1	20:4w6	1.5	1.1	2.3	0.0	1.0	0.7	2.3
)	20:4w3	0.4	0.0	0.2	0.0	0.0	0.3	0.5
22.4		0.0	0.0	0.0	0.0	0.0	0.0	0.0
23.0	20:5w3	17.7	13.4	12.6	4.8	8.1	12.2	14.3
24.8		0.0	0.0	0.0	0.0	0.0	0.0	0.0
25.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0
25.4	22:5w6	0.5	0.0	0.3	0.0	0.0	1.5	0.0
25.6		0.0	0.0	0.0	0.0	0.4	0.0	0.0
26.1	22:5w3	0.0	0.0	0.4	0.0	0.5	0.3	0.0
27.7		0.0	0.0	0.0	0.0	0.0	0.0	0.1
28.8	22:6w3	33.5	19.2	19.9	29.2	32.0	38.3	31.0
36.5		0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOTALPUFA		51.2	32.6	32.5	34.0	40.1	50.5	45.3
LIP%PS		7.1	11.3	10.7	2.0	13.9	16.0	5.3
PS(MG/M3)		16	4	37	33	8	13	50
LIP(MG/M3)		1.1	0.4	3.9	0.6	1.1	2.1	2.7
		96H	97H	98H	99H	100H	101H	102H

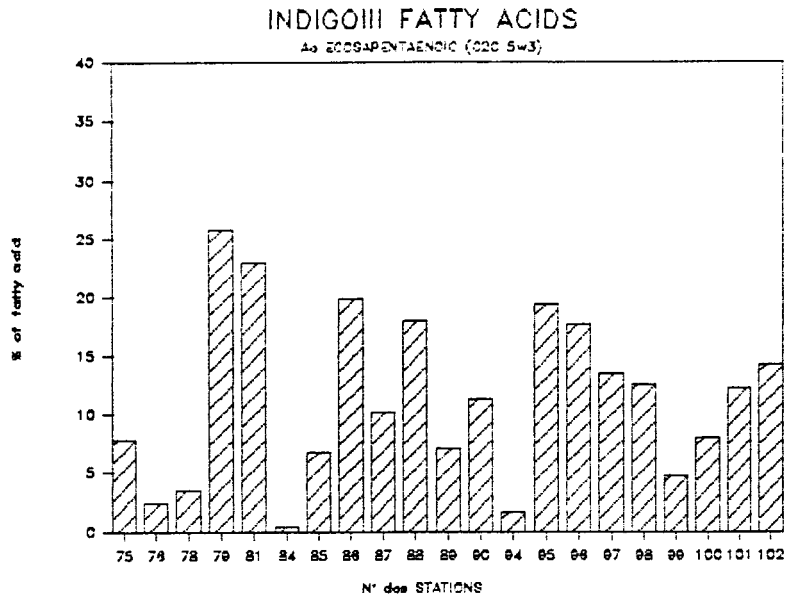

Fig. 20.- Percentage of C20:5w3 in fatty acids of horizontal nets at INDIGO III stations.

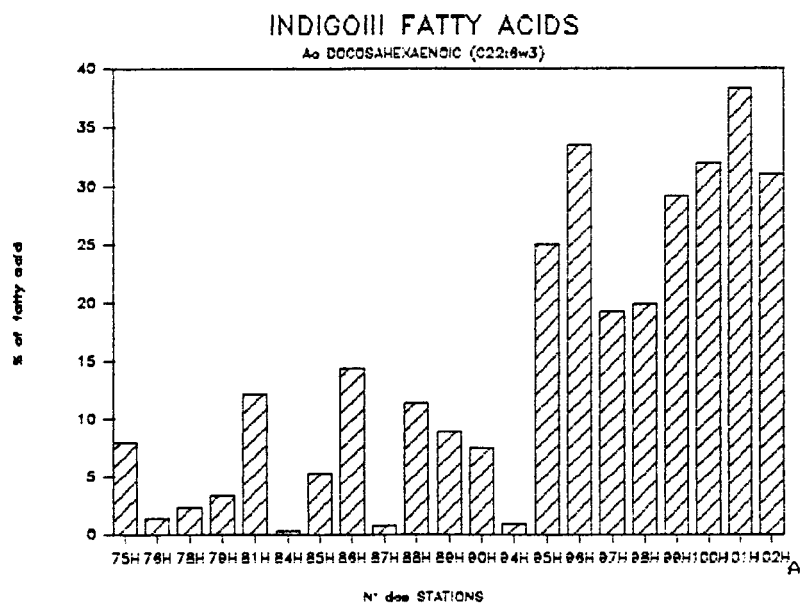

Fig. 21.- Percentage of C22:6w3 in fatty acids of horizontal nets at INDIGO III stations.

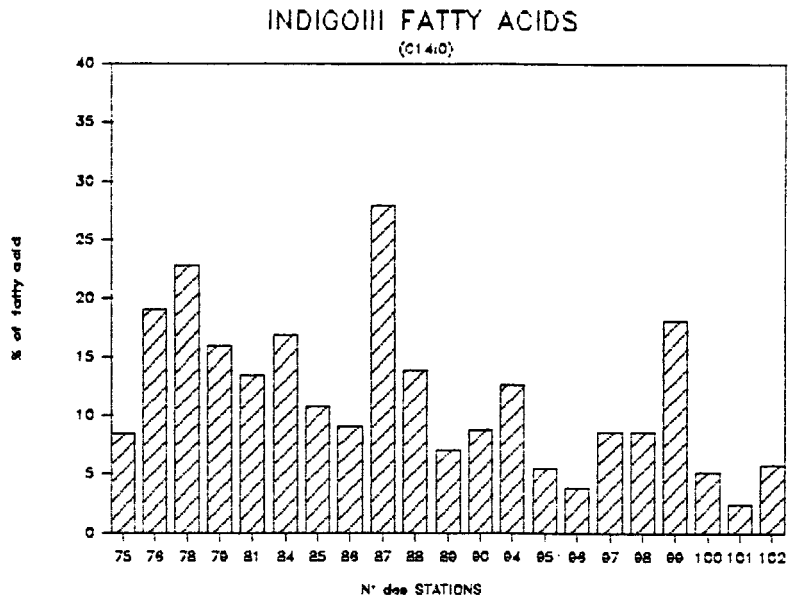

Fig. 22.- Percentage of C14:0 in fatty acids of horizontal nets at INDIGO III stations.

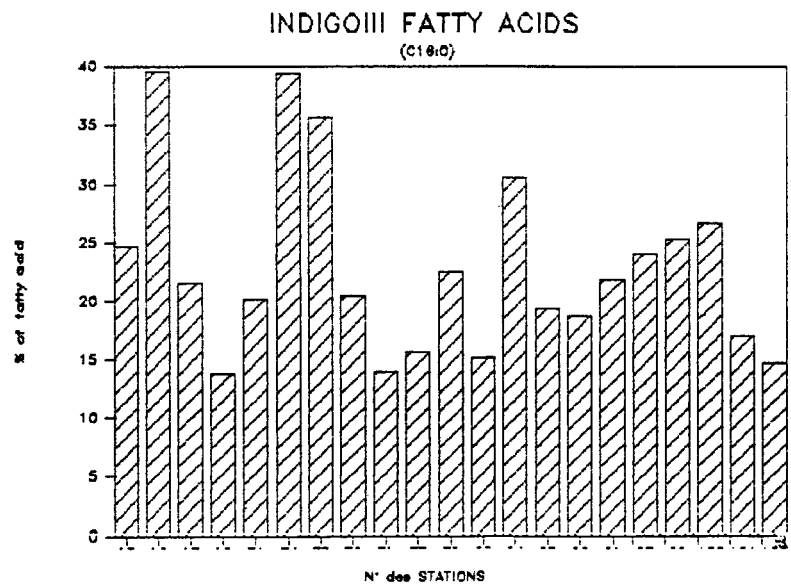

Fig. 23.- Percentage of C16:0 in fatty acids of horizontal nets at INDIGO III stations.

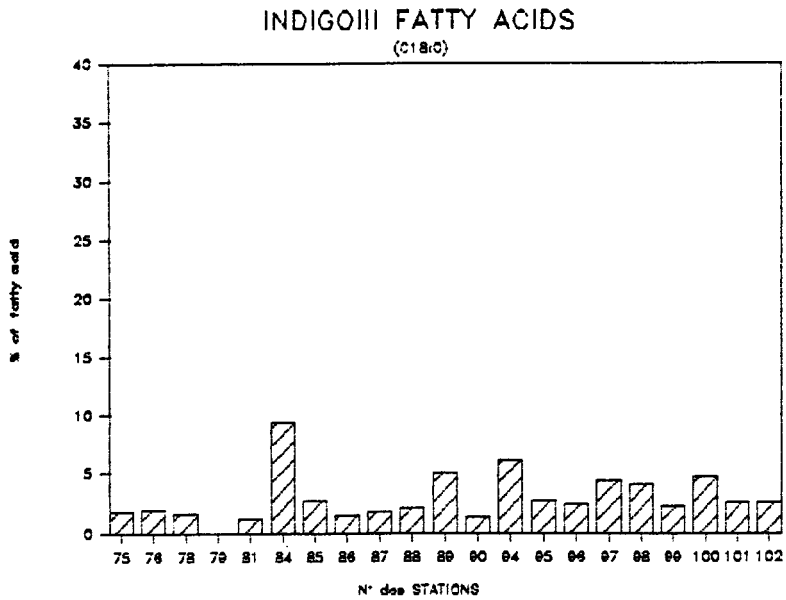

Fig. 24.- Percentage of C18:0 in fatty acids of horizontal nets at INDIGO III stations.

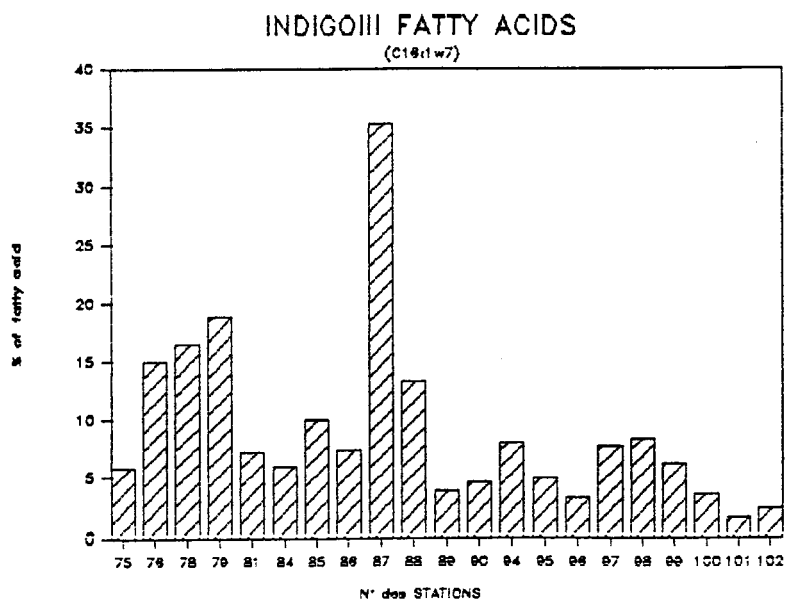

Fig. 25.- Percentage of C16:1w7 in fatty acids of horizontal nets at INDIGO III stations.

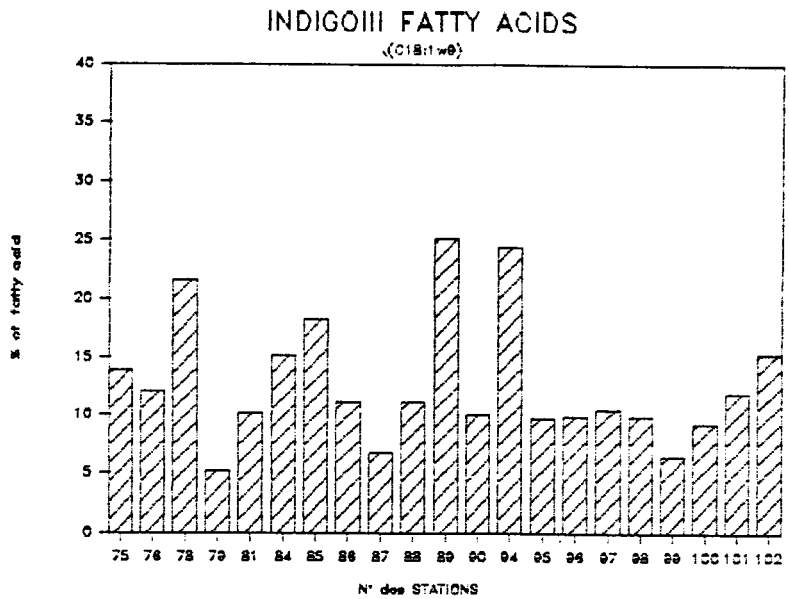

Fig. 26.- Percentage of C18:1w9 in fatty acids of horizontal nets at INDIGO III stations.

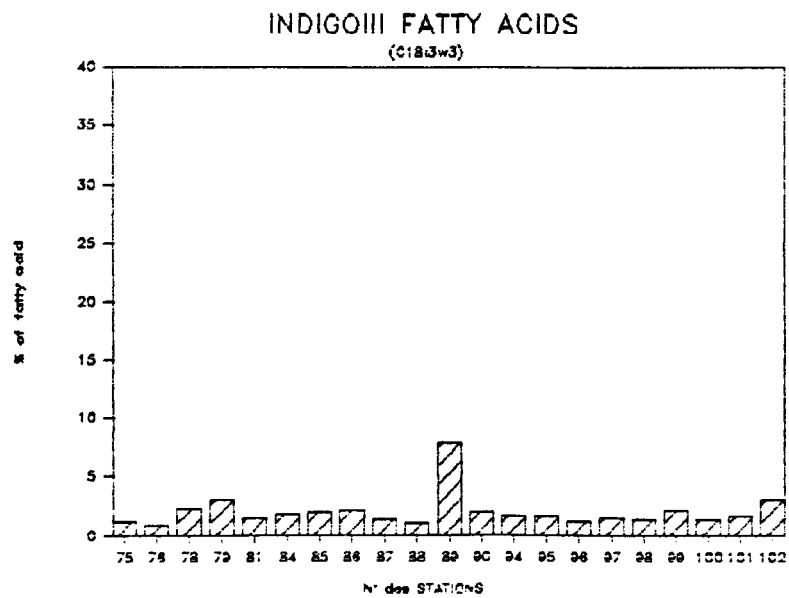

Fig. 27.- Percentage of C18:3w3 in fatty acids of horizontal nets at INDIGO III stations.

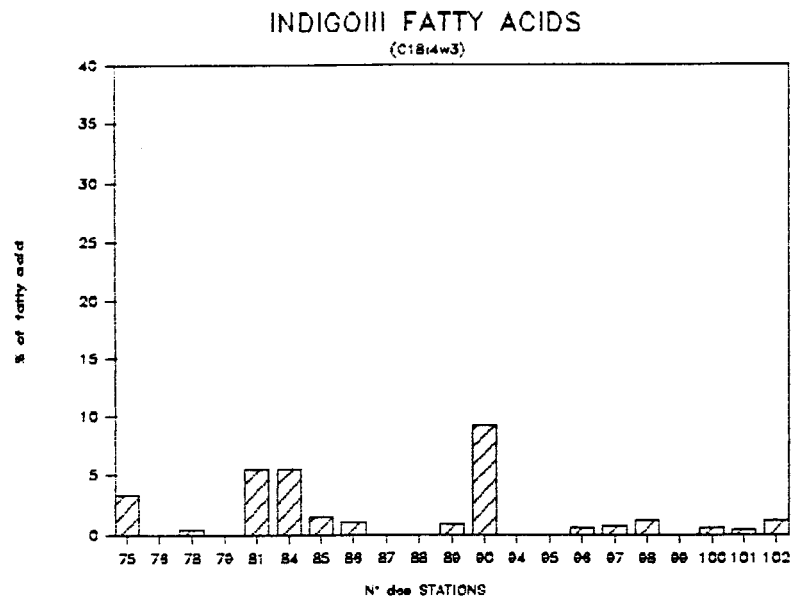

Fig. 28.- Percentage of C18:4w3 in fatty acids of horizontal nets at INDIGO III stations.

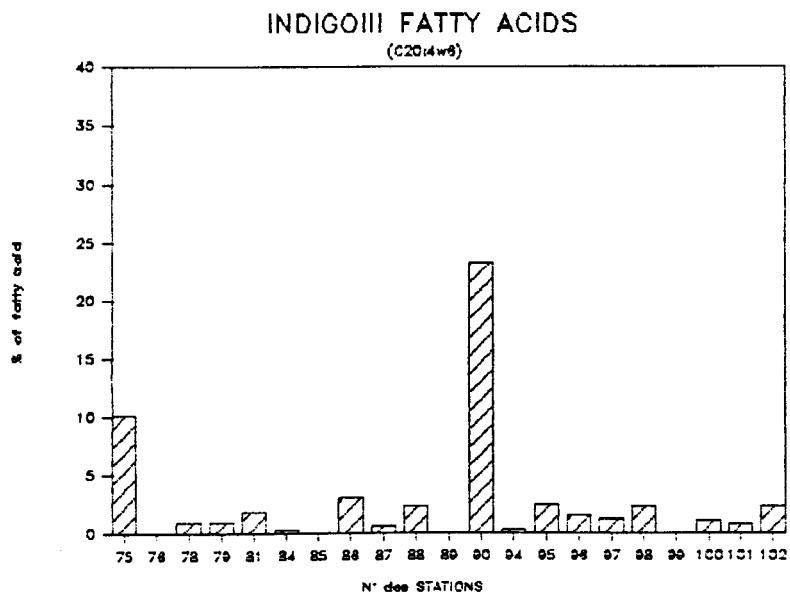

Fig. 29.- Percentage of C20:4w6 in fatty acids of horizontal nets at INDIGO III stations.

TABLE 3.(1) : INDIGO III RESULTS
FATTY ACIDS CONCENTRATION (PER UNIT OF DRY WEIGHT).
(MGFA/GDW)

RT	NAME							
STATIONS		75H	76H	78H	79H	81H	84H	85H
11.0	12:0	0.03	0.00	0.00	0.00	0.00	0.00	0.00
12.4		0.00	0.00	0.00	0.00	0.00	0.00	0.00
12.7	14:0	2.44	3.25	2.28	1.92	4.57	2.61	2.38
13.1		0.05	0.00	0.00	0.00	0.02	0.00	0.00
13.4		0.10	0.12	0.00	0.00	0.11	0.00	0.15
14.0		0.73	0.34	0.13	0.00	0.03	0.00	0.00
14.3	16:0	7.01	6.73	2.16	1.66	6.87	6.11	7.85
14.8	16:1W?	1.68	2.56	1.66	2.26	2.47	0.94	2.22
15.0		0.10	0.09	0.00	0.00	0.10	0.04	0.23
15.6	16:2	2.33	0.47	0.22	0.00	0.10	0.15	0.00
15.9	18:0	0.51	0.34	0.16	0.00	0.42	1.46	0.61
16.3	18:1w9	3.99	2.06	2.16	0.62	3.45	2.35	4.03
16.4	16:3w3	0.06	0.00	0.00	0.00	0.00	0.00	0.00
16.7	18:2w3	0.06	0.00	0.10	0.52	0.14	0.03	0.00
16.9		0.00	0.00	0.00	0.00	0.00	0.00	0.00
17.1	18:3w3	0.32	0.15	0.23	0.38	0.49	0.28	0.43
17.3		0.02	0.00	0.00	0.00	0.00	0.00	0.00
18.0	20:0	0.00	0.00	0.00	0.00	0.00	0.00	0.04
18.3	18:4w3	0.98	0.00	0.04	0.00	1.87	0.87	0.33
18.5		0.00	0.00	0.00	0.00	0.37	0.00	0.00
19.0		0.26	0.00	0.03	0.00	0.26	0.00	0.00
19.5		0.00	0.00	0.00	0.00	0.00	0.00	0.00
20.1		0.00	0.00	0.00	0.00	0.00	0.00	0.00
21.0	22:0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
21.1	20:4w6	2.89	0.00	0.09	0.11	0.62	0.05	0.00
22.0	20:4w3	0.04	0.00	0.00	0.00	0.09	0.00	0.00
22.4		0.00	0.00	0.00	0.20	0.00	0.00	0.00
23.0	20:5w3	2.24	0.42	0.35	3.10	7.80	0.06	1.50
24.8		0.00	0.00	0.00	0.00	0.00	0.00	0.00
25.0		0.00	0.00	0.00	0.00	0.00	0.00	0.00
25.4	22:5w6	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25.6		0.16	0.00	0.00	0.00	0.00	0.00	0.07
26.1	22:5w3	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27.7		0.00	0.00	0.00	0.00	0.00	0.00	0.00
28.8	22:6w3	2.30	0.23	0.22	0.40	4.16	0.03	1.17
36.5		0.00	0.00	0.00	0.00	0.00	0.00	0.00
TOTALPUFA		8.45	0.65	0.70	3.61	14.54	1.01	3.00
LIP%PS		5.7	3.4	2.0	2.4	6.8	3.1	4.4
PS(MG/M3)		21	10	5667	10270	4	8	4
LIP(MG/M3)		1.2	0.3	112.2	246.5	0.3	0.2	0.2
		75	76	78	79	81	84	85

TABLE 3 (2) : INDIGO III RESULTS
FATTY ACIDS CONCENTRATION (PER UNIT OF DRY WEIGHT).
(MGFA/GDW)

RT	NAME	STATIONS	86H	87H	88H	89H	90H	94H	95H
11.0	12:0		0.05	0.00	0.08	0.10	0.54	0.11	0.00
12.4			0.00	0.00	0.00	0.00	0.11	0.00	0.00
12.7	14:0		4.03	1.82	2.23	3.13	18.55	2.53	2.03
13.1			0.06	0.00	0.00	0.09	0.47	0.06	0.00
13.4			0.18	0.00	0.03	0.19	0.69	0.14	0.22
14.0			0.07	0.00	0.13	0.41	0.94	0.97	0.15
14.3	16:0		8.98	0.91	2.51	9.89	31.69	6.12	7.15
14.8	16:1w?		3.26	2.31	2.13	1.69	9.62	1.62	1.81
15.0			0.25	0.00	0.06	0.16	0.94	0.14	0.11
15.6	16:2		0.20	0.00	0.22	0.59	0.57	0.89	0.27
15.9	18:0		0.64	0.12	0.34	2.26	2.70	1.23	1.00
16.3	18:1w9		4.91	0.44	1.78	11.05	20.90	4.86	3.62
16.4	16:3w3		0.94	0.00	0.00	0.00	0.00	0.00	0.00
16.7	18:2w3		0.15	0.00	0.13	0.00	0.19	0.07	0.00
16.9			0.00	0.00	0.00	0.00	0.00	0.00	0.14
17.1	18:3w3		0.90	0.08	0.15	3.44	4.11	0.33	0.63
17.3			0.06	0.07	0.46	0.00	0.20	0.06	0.06
18.0	20:0		0.13	0.00	0.10	0.00	0.16	0.07	0.07
18.3	18:4w3		0.45	0.00	0.00	0.36	19.47	0.00	0.00
18.5			0.47	0.00	0.00	0.10	0.00	0.10	0.25
19.0			0.44	0.00	0.17	1.03	1.28	0.00	0.47
19.5			0.00	0.00	0.00	0.15	0.42	0.12	0.00
20.1			0.00	0.00	0.03	1.06	0.49	0.00	0.05
21.0	22:0		0.04	0.00	0.03	0.00	0.00	0.00	0.00
21.1	20:4w6		1.31	0.03	0.37	0.00	48.81	0.06	0.92
22.0	20:4w3		0.31	0.00	0.05	0.31	0.94	0.00	0.23
22.4			0.23	0.00	0.04	0.07	0.17	0.00	0.09
23.0	20:5w3		8.70	0.66	2.88	3.12	23.60	0.34	7.19
24.8			0.00	0.00	0.00	0.00	0.17	0.00	0.00
25.0			0.00	0.00	0.00	0.00	0.20	0.00	0.00
25.4	22:5w6		0.00	0.00	0.00	0.06	0.10	0.00	0.28
25.6			0.17	0.00	0.04	0.00	0.14	0.00	0.00
26.1	22:5w3		0.00	0.00	0.00	0.00	0.00	0.00	0.00
27.7			0.00	0.00	0.00	0.00	0.72	0.00	0.20
28.8	22:6w3		6.34	0.05	1.83	3.95	15.85	0.19	9.25
36.5			0.00	0.00	0.00	0.00	0.00	0.00	0.00
TOTALPUFA			17.10	0.75	5.13	7.81	108.79	0.59	17.86
LIP%PS			8.8	1.3	3.2	8.8	41.9	4.0	7.4
PS(MG/M3)			118	3450	584	14	55	21	25
LIP(MG/M3)			10.4	45.9	18.9	1.2	23.1	0.9	1.8
			86	87	88	89	90	94	95

TABLE 3(3) : INDIGO III RESULTS
FATTY ACIDS CONCENTRATION (PER UNIT OF DRY WEIGHT).
(mgFA/GDW)

RT	NAME	96H	97H	98H	99H	100H	101H	102H
STATIONS								
11.0	12:0	0.04	0.00	0.00	0.00	0.00	0.00	0.00
12.4		0.00	0.00	0.00	0.00	0.00	0.00	0.00
12.7	14:0	1.34	4.92	4.63	1.82	3.67	1.92	1.55
13.1		0.06	0.11	0.07	0.00	0.12	0.12	0.01
13.4		0.07	0.07	0.39	0.09	0.63	0.08	0.07
14.0		0.16	0.45	0.27	0.00	0.35	0.38	0.21
14.3	16:0	6.64	12.37	12.86	2.53	18.58	13.68	3.89
14.8	16:1w?	1.13	4.35	4.50	0.61	2.50	1.19	0.61
15.0		0.22	0.79	0.73	0.19	1.66	0.64	0.18
15.6	16:2	0.59	1.70	0.63	0.00	0.81	4.64	0.22
15.9	18:0	0.88	2.52	2.22	0.23	3.29	2.01	0.68
16.3	18:1w9	3.53	5.96	5.30	0.64	6.47	9.51	4.08
16.4	16:3w3	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16.7	18:2w3	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16.9		0.00	0.37	0.15	0.00	0.00	0.00	0.00
17.1	18:3w3	0.43	0.85	0.70	0.21	0.98	1.36	0.82
17.3		0.00	0.00	0.00	0.00	0.00	0.00	0.00
18.0	20:0	0.00	0.00	0.15	0.00	0.00	0.08	0.06
18.3	18:4w3	0.17	0.42	0.62	0.00	0.42	0.28	0.30
18.5		0.34	0.00	0.00	0.00	0.00	0.18	0.28
19.0		0.40	0.62	0.48	0.28	0.70	0.86	0.11
19.5		0.09	0.00	0.00	0.00	0.00	0.00	0.39
20.1		0.00	0.00	0.00	0.00	0.00	0.00	0.00
21.0	22:0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
21.1	20:4w6	0.52	0.64	1.21	0.00	0.67	0.54	0.60
)	20:4w3	0.15	0.00	0.12	0.00	0.00	0.24	0.12
22.4		0.00	0.00	0.00	0.00	0.00	0.00	0.00
23.0	20:5w3	6.29	7.57	6.74	0.48	5.63	9.74	3.79
24.8		0.00	0.00	0.00	0.00	0.00	0.00	0.00
25.0		0.00	0.00	0.00	0.00	0.00	0.00	0.00
25.4	22:5w6	0.19	0.00	0.17	0.00	0.00	1.21	0.00
25.6		0.00	0.00	0.00	0.00	0.26	0.00	0.00
26.1	22:5w3	0.00	0.00	0.21	0.00	0.33	0.23	0.00
27.7		0.00	0.00	0.00	0.00	0.00	0.00	0.02
28.8	22:6w3	11.89	10.87	10.65	2.92	22.23	30.64	8.22
36.5		0.00	0.00	0.00	0.00	0.00	0.00	0.00
TOTALPUFA		19.21	19.50	19.71	3.40	29.27	42.88	13.03
LIP%PS		7.1	11.3	10.7	2.0	13.9	16.0	5.3
PS(MG/M3)		16	4	37	33	8	13	50
LIP(MG/M3)		1.1	0.4	3.9	0.6	1.1	2.1	2.7
		96	97	98	99	100	101	102

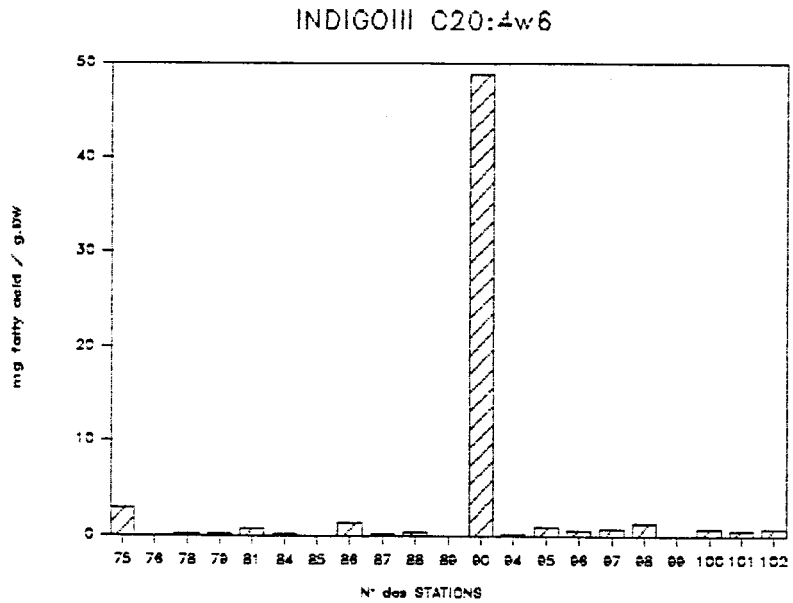

Fig. 30.- Distribution of C20:4w6 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

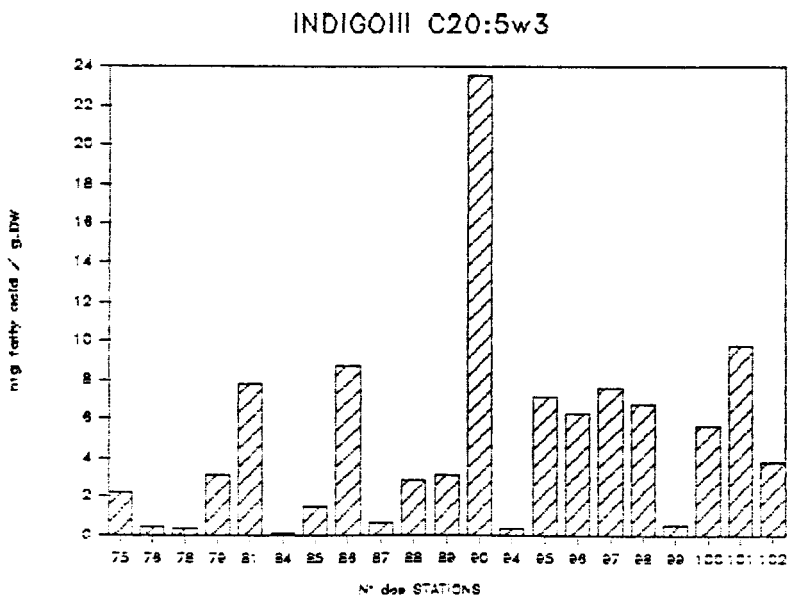

Fig. 31.- Distribution of C20:5w3 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

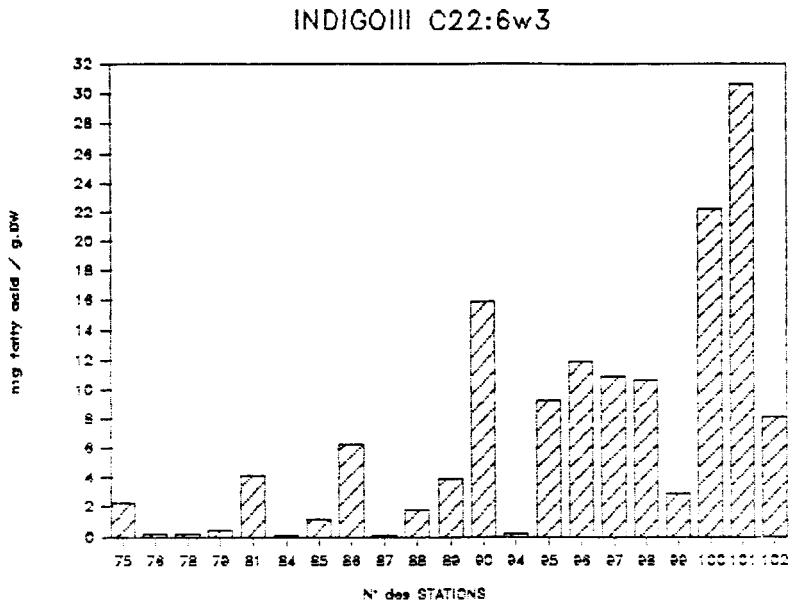

Fig. 32.- Distribution of C22:6w3 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

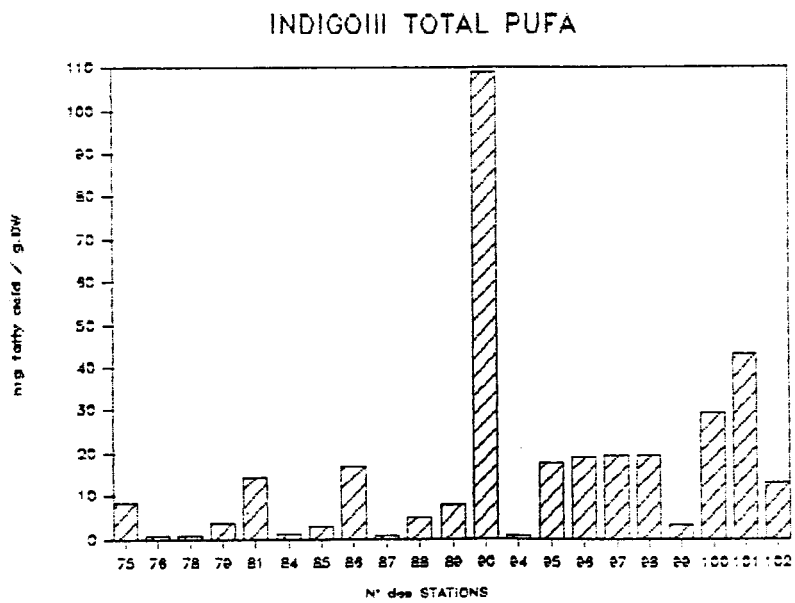

Fig. 33.- Distribution of total Polyunsaturated Fatty acids contents (mg. of FA/ g. of dry weight) in horizontal nets at INDIGO III stations.

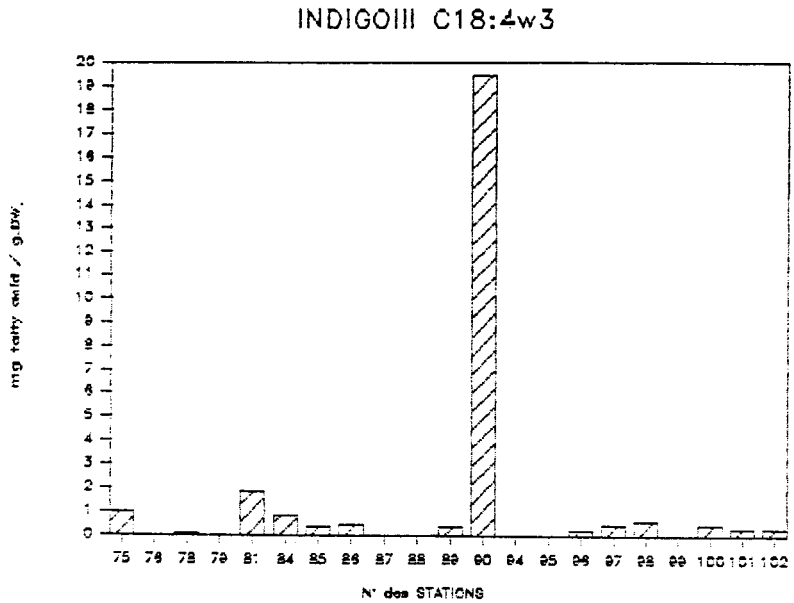

Fig. 34.- Distribution of C18:4w3 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

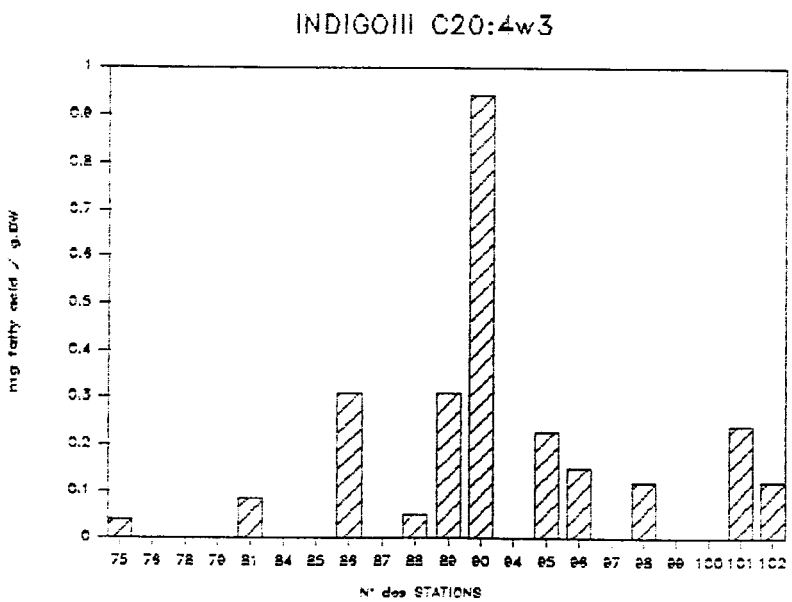

Fig. 35.- Distribution of C20:4w3 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

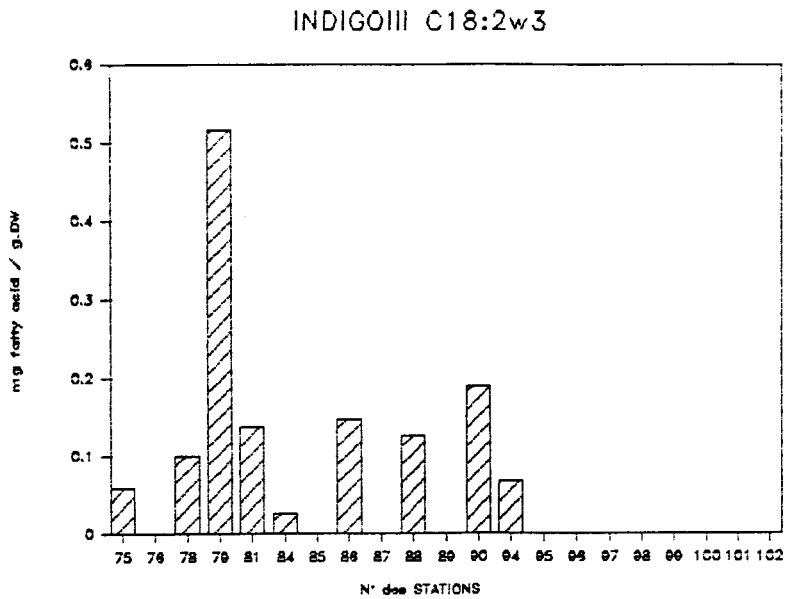

Fig. 36.- Distribution of C18:2w3 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

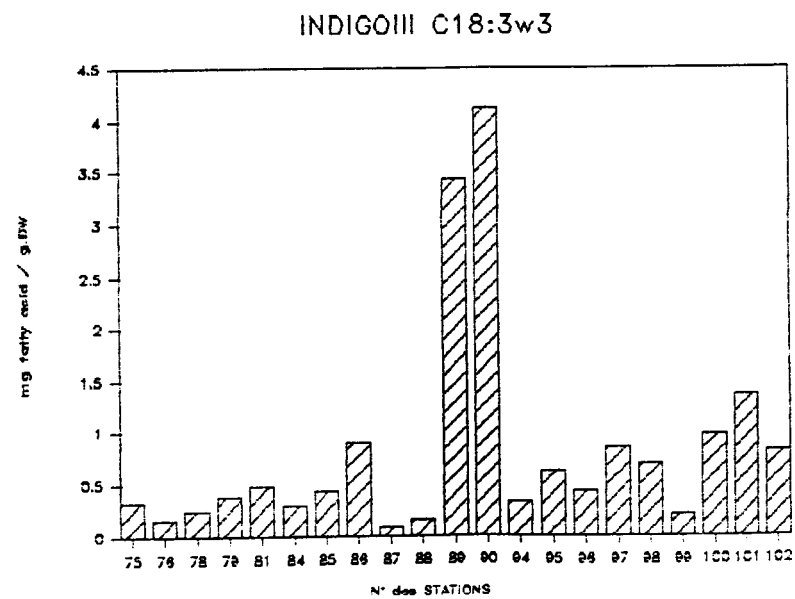

Fig. 37.- Distribution of C18:3w3 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

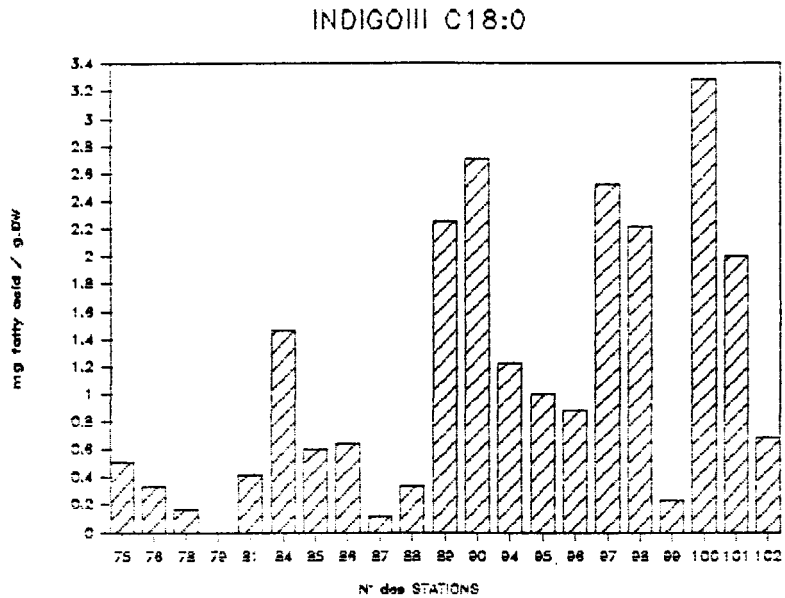

Fig. 38.- Distribution of C18:0 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

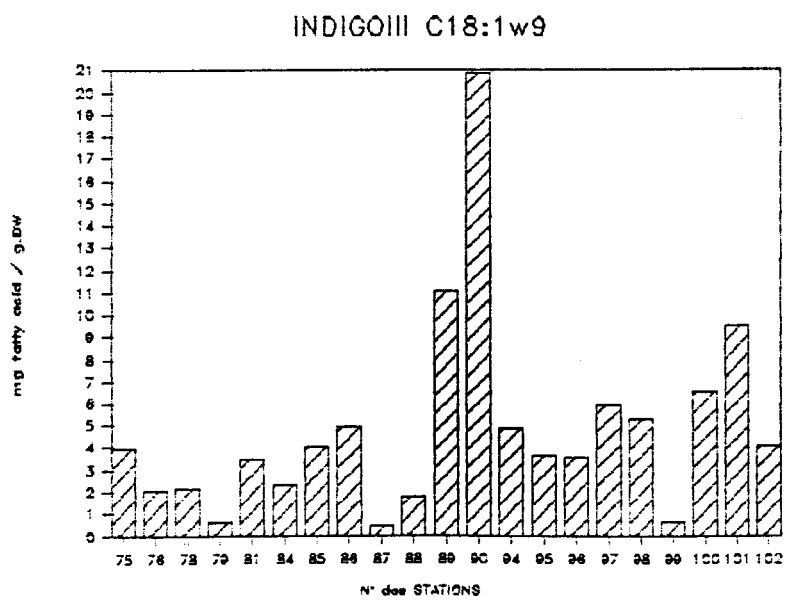

Fig. 39.- Distribution of C18:1w9 contents (mg. of FA/ g. of dry weight) in horizontal nets at INDIGO III stations.

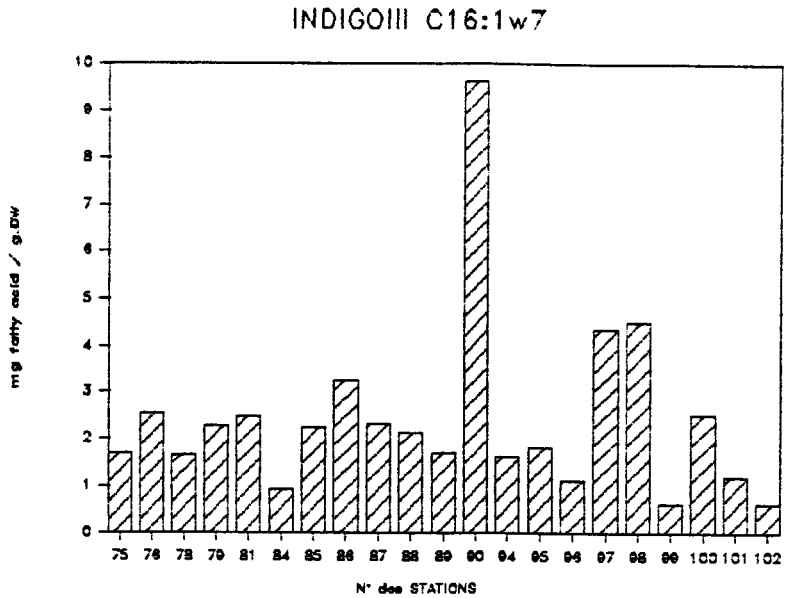

Fig. 40.- Distribution of C16:1w7 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

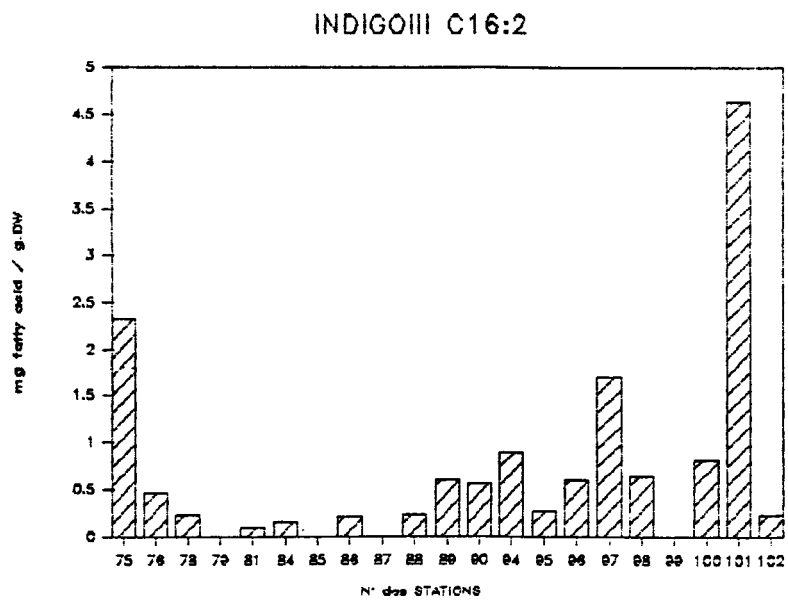

Fig. 41.- Distribution of C16:2 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

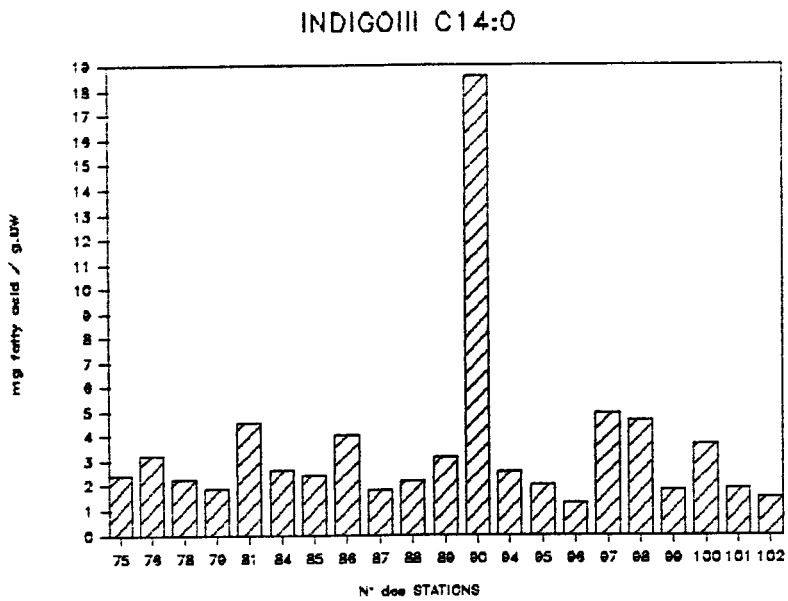

Fig. 42.- Distribution of C14:0 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

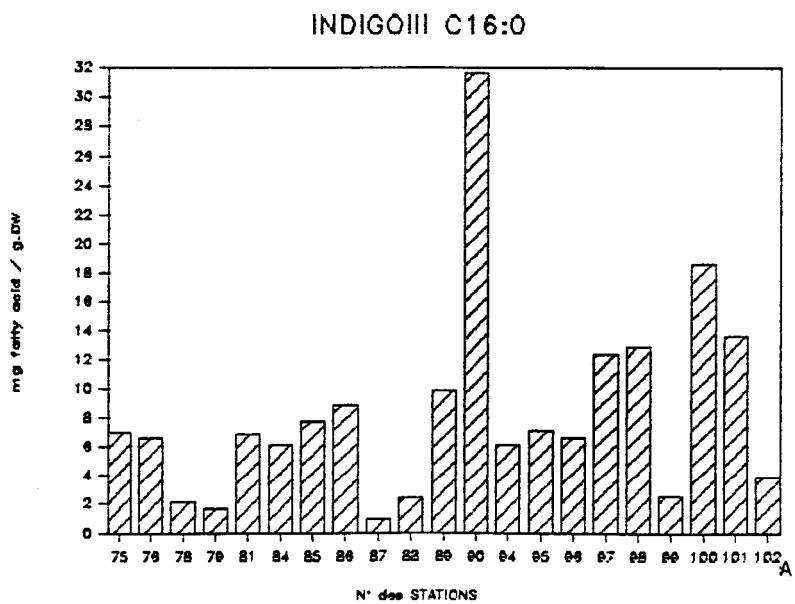

Fig. 43.- Distribution of C16:0 contents (mg. of FA / g. of dry weight) in horizontal nets at INDIGO III stations.

TABLE 4 : INDIGO III RESULTS
FATTY ACIDS PERCENTAGES IN HORIZONTAL NETS
MEAN VALUE FOR DIFFERENTS TYPES OF STATIONS

RT	NAME	A	B	C	D
9.1	10:0	0.0	0.0	0.1	0.0
11.0	12:0	0.1	0.2	0.2	0.0
12.4		0.0	0.0	0.0	0.0
12.7	14:0	18.4	13.1	8.2	7.3
13.1		0.1	0.1	0.2	0.1
13.4		0.4	0.2	0.4	0.5
14.0		1.4	0.3	1.3	0.5
14.3	16:0	30.1	17.5	20.7	21.0
14.8	16:1w?	15.2	11.7	4.8	4.7
15.0		0.4	0.3	0.4	1.2
15.6	16:2	1.7	0.5	3.3	1.8
15.9	18:0	4.0	1.2	2.7	3.2
16.3	18:1w9	16.4	9.4	16.4	10.4
16.4	16:3w3	0.0	0.5	0.1	0.0
16.7	18:2w3	0.2	1.5	0.1	0.0
16.9		0.0	0.0	0.0	0.2
17.1	18:3w3	1.7	1.9	3.6	1.7
17.3		0.2	0.8	0.1	0.0
18.0	20:0	0.1	0.2	0.0	0.1
18.3	18:4w3	1.2	1.6	4.5	0.6
18.5		0.1	0.5	0.1	0.4
19.0		0.0	0.7	1.3	1.2
19.5		0.1	0.0	0.2	0.2
20.1		0.0	0.1	0.9	0.0
21.0	22:0	0.0	0.1	0.0	0.0
21.1	20:4w6	0.3	2.0	11.2	1.4
22.0	20:4w3	0.0	0.3	0.4	0.3
22.4		0.0	0.6	0.1	0.0
23.0	20:5w3	4.2	21.6	8.7	12.8
24.8		0.0	0.0	0.0	0.0
25.0		0.0	0.0	0.0	0.0
25.4	22:5w6	0.0	0.0	0.1	0.4
25.6		0.1	0.2	0.2	0.0
26.1	22:5w3	0.0	0.0	0.0	0.1
27.7		0.0	0.0	0.1	0.1
28.8	22:6w3	1.8	10.4	8.2	28.5
36.5		0.0	0.0	0.0	0.0
TOTALPUFA		6.0	32.0	17.0	41.3
LIP%PS		3.0	5.3	18.8	9.2
PS(MG/M3)		1526.5	2744.0	29.9	23.1
LIP(MG/M3)		26.6	69.0	8.5	1.7

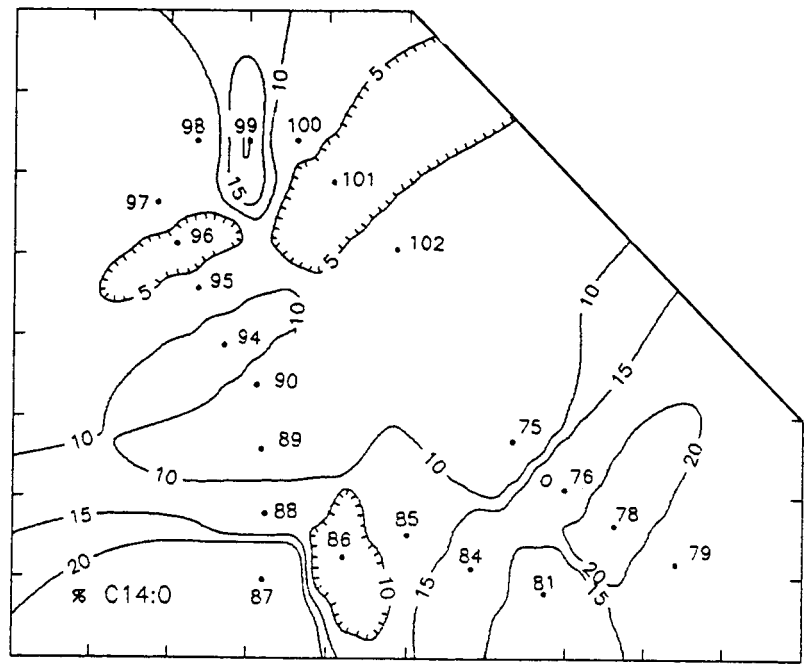

Figure 44: Distribution of the percentage of C14:0 in the subsurface plankton.

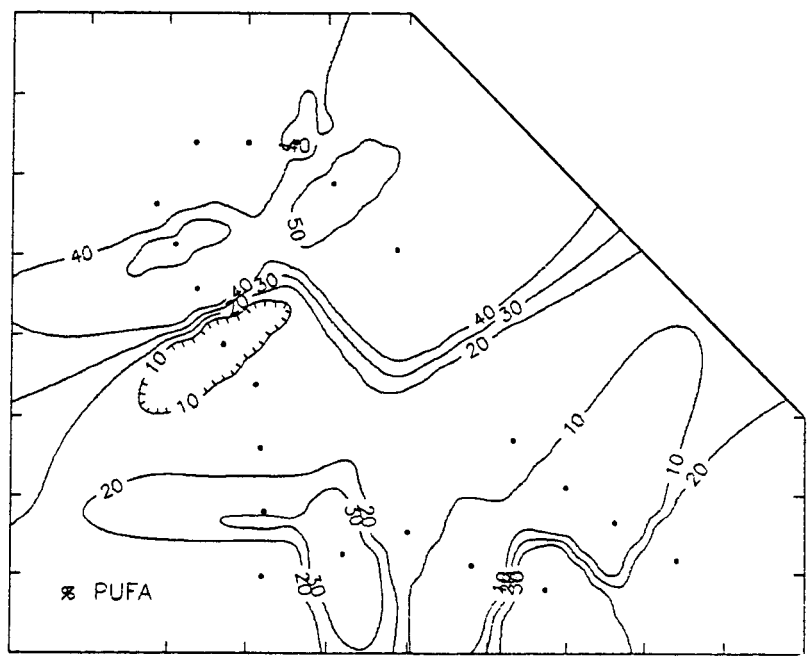

Figure 45: Distribution of the percentage of C22:6w3 in the subsurface plankton.

ANNEX 1: METHODOLOGY FOR PHYTOPIGMENTS ANALYSIS

Advantages of the High-Performance Liquid Chromatography

Chlorophyll-a concentrations are routinely used to estimate phytoplankton biomass and productivity. However, the commonest methods, based on spectrophotometric or spectrofluorometric measurements, are subject to a number of drawbacks.

These methods are often inaccurate because of the low sensivity and the poor precision. They do not distinguish adequately between the three chlorophylls a, b and c. The absorption and emission bands of chlorophyll-b and -c overlap with those of chlorophyll-a, giving rise to poor precision and even to "negative" values.
The error in prediction of algal biomass by the spectrophotometric procedure may be too high by 75% in water and 400 % in sediments (Mantoura et Llewellyn, 1983).

With High-Performance Liquid Chromatography techniques, nearly all pigments and their degradation products are separated and quantified accurately.
The various chlorophyll-a degradation products may provide useful information about the state of the phytoplankton crop. *Chlorophyllide-a* (phytol-free derivative from chlorophyll-a, formed by the action of the enzyme chlorophyllase) can be found in high concentrations in senescent cells. *Pheophorbide-a* and *pheophytin-a*, formed by loss of magnesium from chlorophyllide-a and chlorophyll-a respectively, are the results of zooplankton grazing.
Moreover, the pigment composition can be used for chemotaxonomic purposes.

Method used on board of the R.V. "Marion Dufresne" during INDIGO III cruise

2,5 to 3 liters of seawater were filtered under slight negative pressure on to Whatman GF/C filters. Pigments were extracted immediately in 70% acetone, using a Potter grinder with a teflon pestle. 200 µl were injected into a LKB HPLC chromatograph, using a C_{18} Chromospher column (21 cm). Chromatographic separation of pigments was obtained by linear gradient elution from 75% acetonitrile to 90% acetone in 30 minutes. Total flow rate was 1 ml/min.

The absorbance was mesured at 430 nm and peaks area calculated by Intersmat integrator. Measurement precision was 20 ng chl.a/m^3. Figure A1.

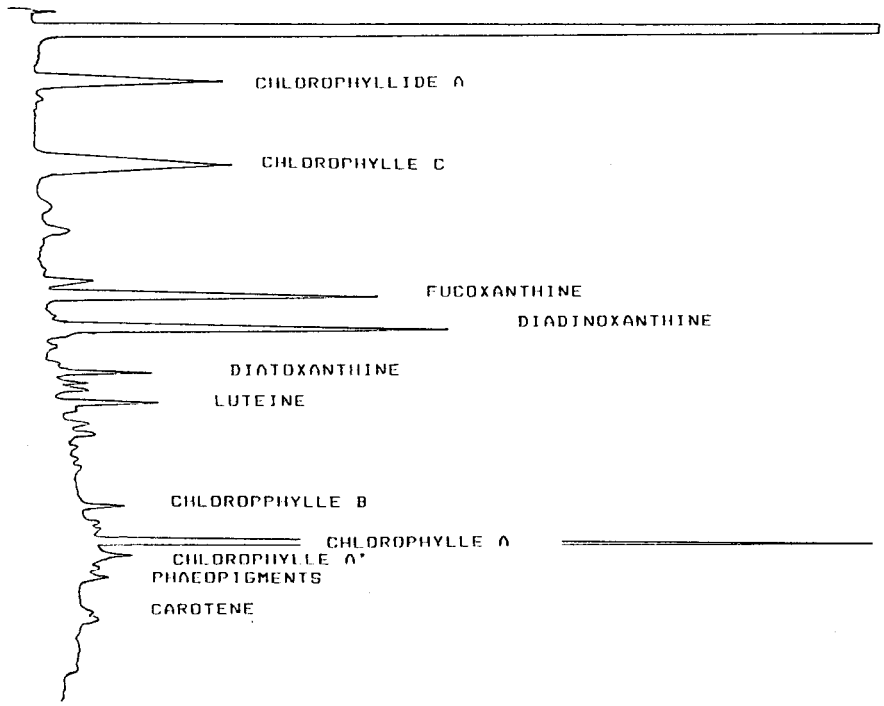

Figure A1: Chromatogram of antarctic phytoplankton obtained on board of the R.V. "Marion Dufresne".

After the Indigo III cruise, an iron-pairing reagent has been included to achieve good resolution with the most polar pigments.

Chlorophyll-a calibration was done using commercial chlorophyll-a from Sigma Chemical Company.

Chlorophyll degradation products and carotenoids, prepared from algal cultures, were separated on thin layers of cellulose powder (Macherey - Nagel MN 300). Identification of chlorophylls and carotenoids was carried out by eluting the pigments after chromatography in an appropriate solvent, measuring the absorption spectrum in a recording spectrophotometer (Jeffrey, 1968) and injecting the fractions in the HPLC chromatograph.

Extinction coefficients were used for the calculation of pigments concentrations. Figures A2 et A3.

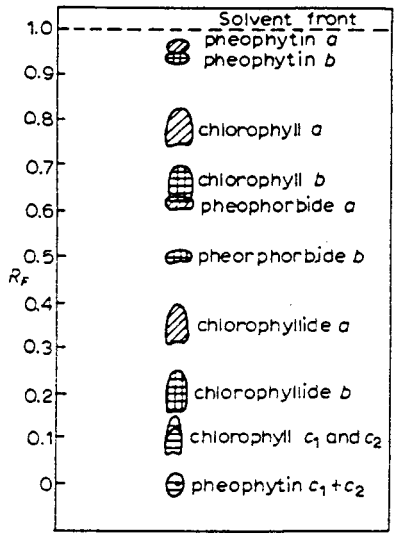

Figure A2: Separation of chlorophyll derivatives on thin layers of cellulose. Solvent system: 20 % acetone in light petroleum (60-80°). After Jeffrey, 1968.

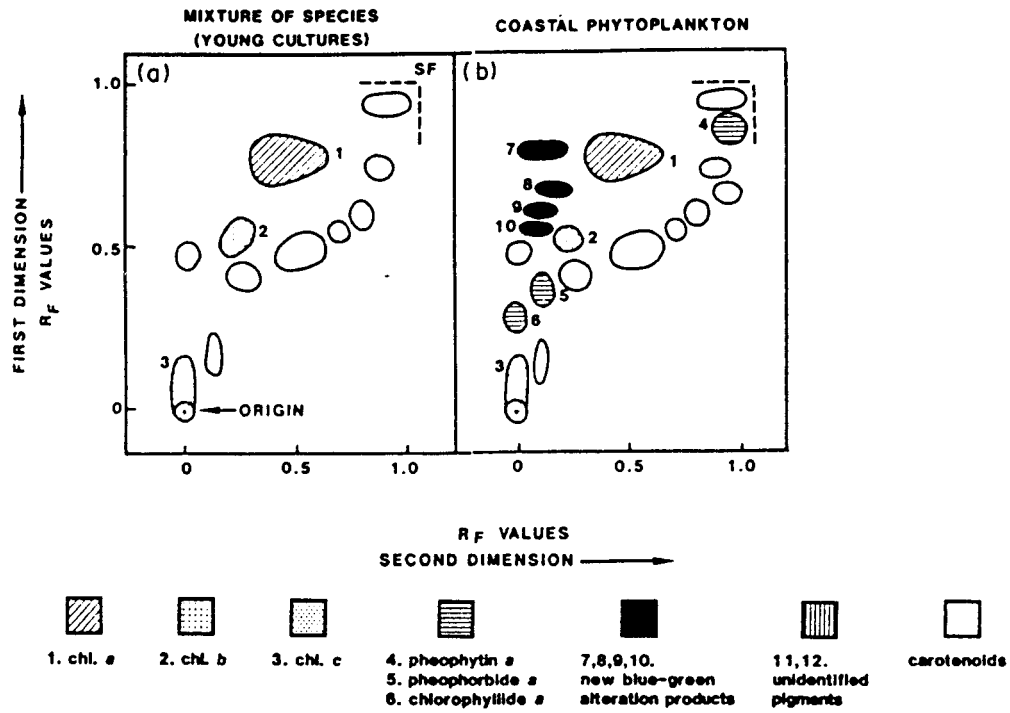

Figure A3: Thin layer Chromatograms of chlorophyll and chlorophyll degradation products. A. Mixture of young cultures of a diatom, dinoflagellate and green flagellate. B. Natural phytoplankton. Solvent system: first dimension: n-propanol in light petroleum (2:98, V/V); second dimension: chloroform:light petroleum:acetone (25:75:0.5, V/V/V). After Hallegraef & Jeffrey, 1985.

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PCB's, ORGANOCHLORINE PESTICIDES AND MERCURY IN THE LOWER TROPHIC LEVELS OF THE INDIAN SECTOR OF THE ANTARCTIC MARINE ECOSYSTEM

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Abstract

Making use of the expertise acquired during more than one decade in the North Sea in the field of ecotoxicology (transfer- and accumulation mechanisms of stable pollutants), we started a comparable study of the Antarctic ecosystems. The aim of this study is to test the generality of the concepts developped for the North Sea systems, and to obtain more information on Antarctica, where fragmentary data only are available, in order to increase the knowledge on the global distribution of stable pollutants and of their transfer and accumulation mechanisms, and to provide the essential basic information needed for controlling pollution on a large scale.

From January 3^{d} to February 27th, 1987, we participated to the INDIGO 3 cruise on board the French R.V. Marion Dufresne. The cruise track covered the Indian sector of the Southern Ocean between latitudes 38°S to 67°S and longitudes 18°E to 84°E.

PCBs concentration in particulate matter (mainly phytoplankton) appears to be high: 0.75 µg/g dry weight, a level similar to the one of temperate zones. No significant geographical difference was detected. In order to interpretate such results correctly, it is however necessary to express them in other units like per volume of seawater and per lipid weight. Per water volume, the contamination seems more constant, but lower than in northern temperate zones. The explanation is that the Antarctic ecosystems are less contaminated than temperate regions -- as expected - but that the very low biomasses present cause high levels per unit of biomass. These results confirm the necessity of using different systems of units.

Due to the heterogeneity of the netplankton samples (variable phytoplankton/zooplankton composition), the contamination is compared both with particulate matter and zooplankton of temperate zones. The relative contribution of the zooplankton to the contamination level of the samples can however not be determined with precision.

The levels of organochlorine pesticides such as lindane, dieldrin, heptachlor-epoxide and aldrin are either low, found as traces or not detected at all. DDT and DDE were the lowest of all detected organochlorines. High DDT/DDE ratios reflect the recent use of these pesticides in southern developping countries.

The total mercury contamination was also determined and provided results leading to similar conclusions as for PCBs.

Content

State of the Art

PCB's and DDT's in the Antarctic environment.

The discovery of DDT residues in the Antarctic (Slade et al., 1966) was a first indication of a worldwide distribution of this stable pollutant and made the scientific community well aware of their persistence and long distance transport. Risebrough et al., (1976) concluded that atmospheric transport of DDT's as well as PCB's is the most important route. Since than, a lot of studies dealed with the geochemical and biochemical behaviour of PCB's and organochlorine pesticides in the open ocean: their concentrations are generally very low in the air and the water (range of ppt) but they are widely distributed in the world oceans.

Little information is however available on the distribution of these pollutants in the southern hemisphere. The industrialized countries have restricted or banned their use, but in the developing countries, especially in the tropical regions of the southern hemisphere, they are still used at a large scale in the agriculture and for human health (malaria). This suggests an urgent need for measuring these pollutants in the southern marine environment.

Recent studies showed indeed clearly the aerial transport pathway by measuring a decline of chlorinated hydrocarbons concentration in the air from other continents till Antarctica, which indicates that low latitudes serve as a major source of these pollutants for their transport to Antarctica.

Concentrations in the Antarctic are low, due not only to the distance from the heavily contaminated industrial latitudes, but also to specific natural conditions, namely the important ice-cover blocking the fall-out from the atmosphere, possible during a short summer period only.

These determinations of PCB's and DDT's in Antarctic air and water not only contribute to the description of their global distribution, but also provide basic information for the evaluation of their bioaccumulation in Antarctic ecosystems, and to improve our knowledge of the different transfer mechanisms though the trophic chain.

Reports on contamination of Antarctic marine organisms are not so abundant as atmospheric data, and concern mainly higher organisms such as krill (Risebrough, 1976; Lukowski 1978a), fish (Subramania et al., 1983), dolphins (Abarnou et al, 1985), seals (Hidaka et al., 1983) and birds (Risebrough, 1976; Lukowski, 1978b,

1983a, 1983b); no data seem to be available on phytoplankton (particulate organic matter).

The major problem that resorts when comparing these different studies is the lack of uniformity in the expression of the data, in respect of the units used (fresh, dry or lipid weight), and the qualitative description of the PCB's (complete mixture as 1254 or 1260; or some congeners only: which ones, results expressed as total PCBs or the sum of the measured congeners, etc...). This makes comparison extremely difficult and suggests an urgent need for normalisation.

Introduction.

Our approach in the study of stable pollutants such as PCBs, DDTs and heavy metals in the Antarctic environment is based upon our expertise acquired in the North Sea ecosystem. In order to describe and to understand pollution in marine ecosystems and so to be able to predict the evolution of the contamination, it is necessary to make a detailed study of transfer mechanisms of stable pollutants between the biological compartments. A lot of results have been gathered in the North Sea ecosystem on PCBs, DDTs and mercury transfer and accumulation mechanisms (Delbeke and Joiris,1985). The problem was studied in different steps:
- the contamination of the main compartments was determined: particulate matter (phytoplankton), zooplankton, fish, seabirds and sediments;
- the results were expressed in different systems of units: fresh weight, dry weight, lipid weight and water volume;
- the contamination of different periods and zones of the North Sea was compared.

The main conclusions and concepts from this study were that:
- the most important mechanism for particulate matter contamination seems to be adsorption/partition since its PCB levels remain constant per volume of seawater: PCBs are mainly bound to particles and especially their lipids; very little remains in solution;
- the PCB level in zooplankton is comparable with the one of phytoplankton. Together with the absence of a clear lipid-PCB relationship: these indications are in favour of PCB intake through the food as main mechanism (indirect contamination);
- no important bioaccumulation is taking place at the level of fish. A strong lipid-PCB relationship points out to the importance of partition as regulation, although much controversy exists in the literature on fish contamination: argumentation is found as well for direct (from the water) as for indirect contamination through their food. Additional laboratory experiments should clear this out;
- the most important bioaccumulation is taking place at the level of the seabirds, up to 40 times higher contamination than in fish;
- similar studies on mercury contamination show striking analogies with the organochlorines ,indicating the existence of similar accumulation mechanisms.

The aim of our study in Antarctica concerning bioaccumulation and transfer mechanisms of stable pollutants is to test the generality of the concepts described

above in other environments, consisting on the one hand of a coastal system characterized by physicochemical and hydrological conditions comparable to the well studied North Sea systems (Bouquegneau and Joiris, 1987), on the other hand of a more pelagic system, where much less is known about bioaccumulation. This will allow us to compare coastal and pelagic ecosystems and to compare the existing data with results gathered in the Southern Seas, isolated from direct local influence of human activities.

Besides this added scientific value to the ecotoxicology of the North Sea, the determination of concentrations in the Antarctic, where only fragmentary data exist, is of utmost importance in order to increase the knowledge of the global distribution of these pollutants and to provide the essential basic information needed in order to master the pollution at a global scale.

The contamination will first be determined in the lower trophic levels: particulate matter (phytoplankton) and zooplankton.

Hydrography of the area of investigation

From January 3^{d} to February 27th, 1987, we participated to the INDIGO 3 cruise on board R.V. Marion Dufresne. The cruise track covered the Indian Ocean sector of the Antarctic between latitudes 38°S to 67°S and longitudes 18°E to 84°E.(Fig. 1).

The main watermasses in the area could be identified from their physico-chemical and biological parameters (temperature, salinity, dissolved oxygen, chlorophyll) measured on board. Considering the salinity (Fig. 2) and the temperature (Fig. 3) of two separate tracks (the eastern track composed of the stations 100, 101, 102, 75, 76, 77, 78, 79, 80, 81 and 82; the western track of the stations 98, 97, 96, 95, 94, 91, 90, 89, 88 and 87.), the main frontal systems are positioned as follows, from North to South: Subtropical Convergence between 41°S and 43°S; less pronounced the Subantarctic Front at 47°S and the Antarctic Convergence or Polar Front at 50°S and very clear again the Antarctic Divergence at 66°S. The Antarctic Divergence could only be determined with data from the eastern track, the most southern station of the western track is still located north of the Antarctic Divergence.

On the basis of bacterial counts of the upper mixed layer, three major zones are recognised: (from South to North) between the continent and the Antarctic Divergence ($17 \cdot 10^{4}$ bacteria /ml); between the Divergence and the Sub-tropical front ($9 \cdot 10^{4}$ bacteria /ml), described as Antarctic water: no differences were detected at the

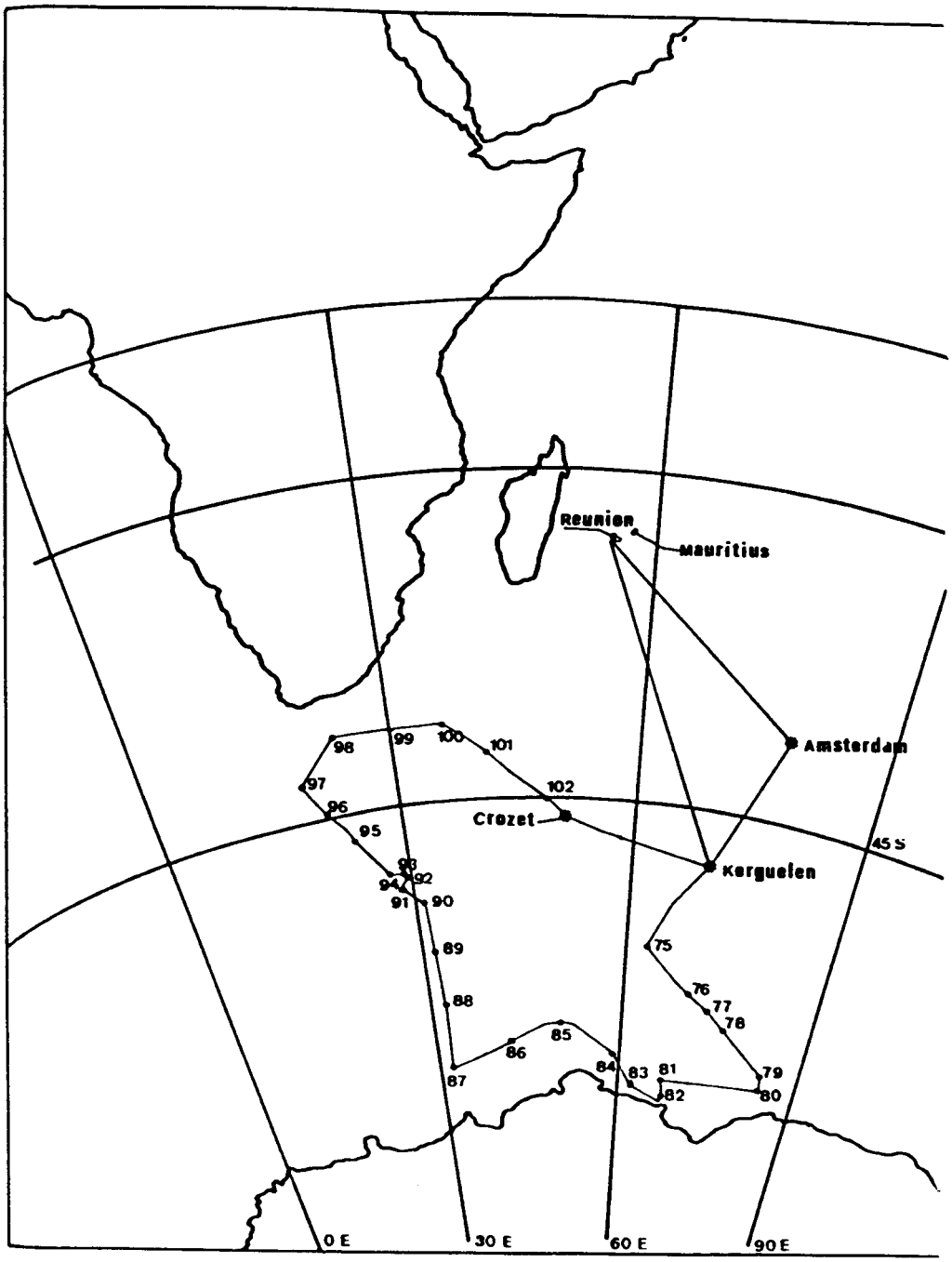

Figure 1 : INDIGO 3 cruise track.

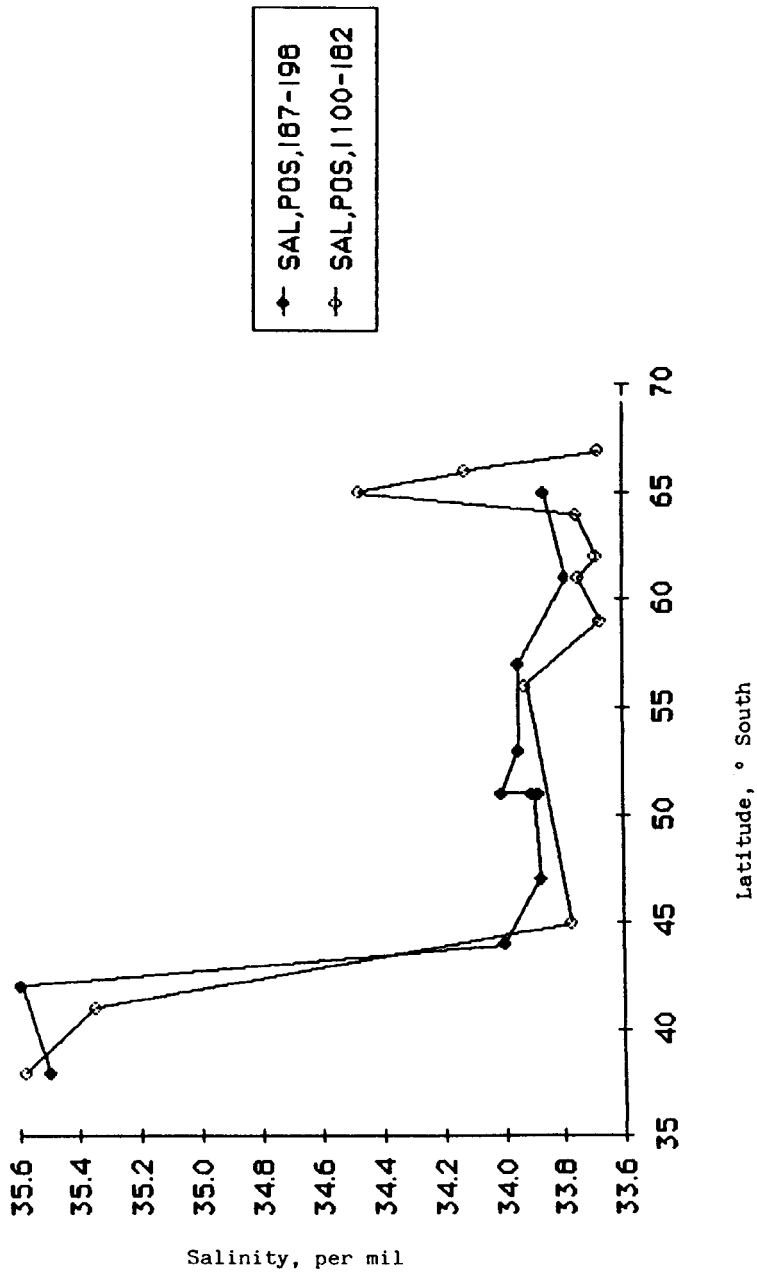

Figure 2 : Comparison between eastern and western tracks.

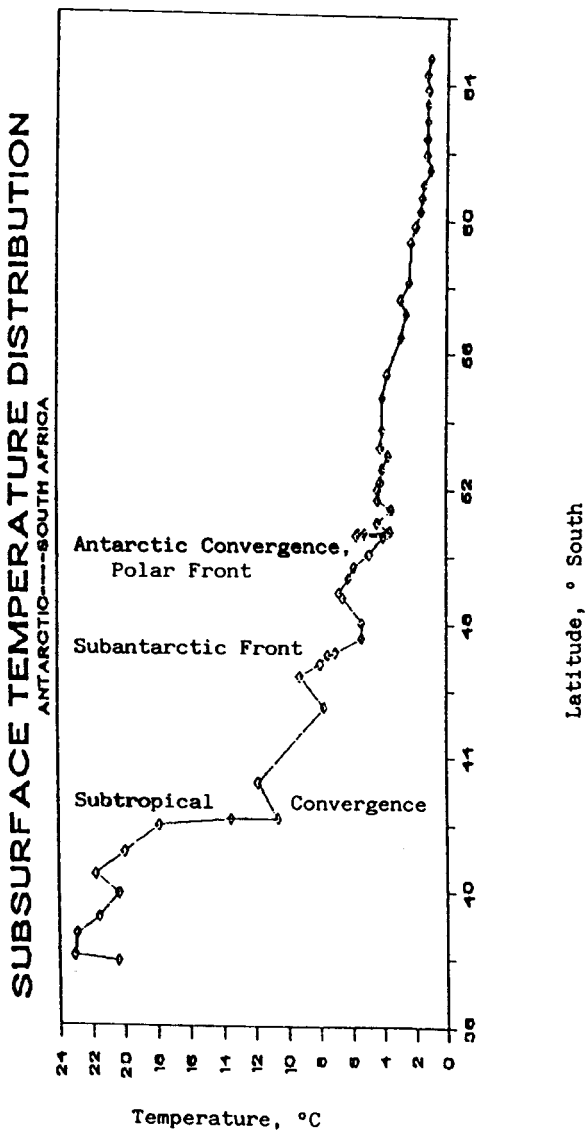

Figure 3 : Subsurface temperature distribution in the western track - Data obtained from continous profiling.

Subantarctic front nor the Antarctic convergence as described above; and sub-tropical water north of the Subtropical convergence (Fig 4). The existence of heterogeneities within the zones could be due to spatial variations, but temporal variations are not excluded, in connection for instance with the evolution of the phytoplankton bloom because of the delay between the eastern and western legs.

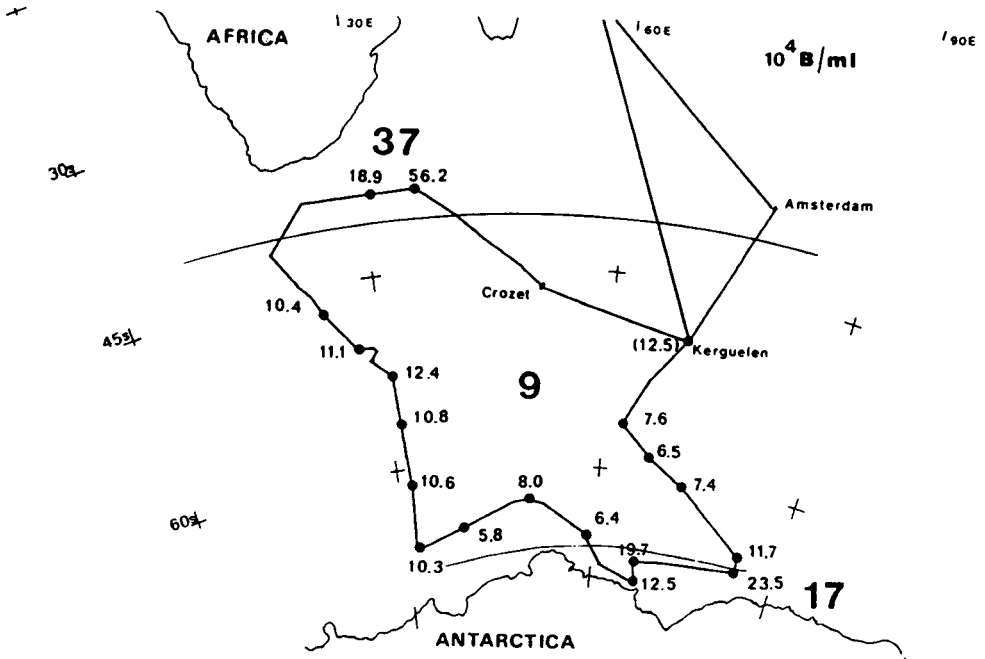

Figure 4: Bacterial (direct) counts in the mixed upper layer of the water column (10^4 bacteria/ml, mean value); mean value per zone represented by big figures.

Material and methods.

Sampling.

Particulate matter (mainly phytoplankton) was sampled during the INDIGO III cruise by continuous centrifugation, and samples recolted about every 24 hours in order to obtain sufficient material to determine PCBs, DDTs and heavy metals. This resulted in 37 samples (Fig 5).

Netsamples were taken every station with a 200 µm net towed horizontally during 20 min. at 2 nautical miles.(Fig 1.)

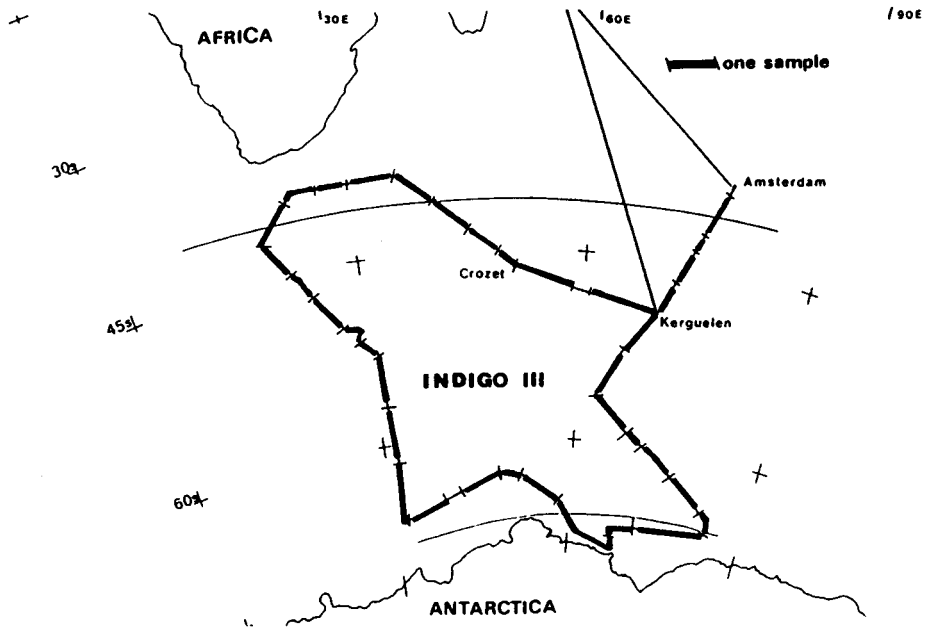

Figure 5: Localization of the sampling stations for particulate matter (continuous centrifugation).

Analysis.

Extraction and clean-up.

- 1 à 20 g. sample (wet weight) are homogenized after addition of water free Na_2SO_4: the material becomes completely pulverized and waterfree.
- Lipophilic compounds are extracted by Soxhlet extraction with 100 ml hexane during 10 hours. The extract is concentrated to 5 ml volume and the extracted lipids are weighted.

A clean-up with florisil column is performed (exact quantity of florisil is determined after standardization). Separation of the organochlore compounds is effectuated by two successive elutions: 1) hexane 100 ml and 2) hexane-ether 1/1 100ml.

In the first elution PCBs and DDE will be determined; in the second elution the organochlorine residus.

Determination.

The organochlorine residues are determined with gaz-liquid chromatography (Packard Instruments model 437), capilar column, electron capture detection, Shimadzu CR 1A integrator, automatic injection LS607, temperature programme.

The following technical procedure is used:
injection: splitless with injectorflush after 0.5 min (50 mlN2/min); injection volume: 1 µl; injector temperature 250°C; carrier gaz 0.6 bar N2; bypass 20 ml/min N2; column: fused-silica CPSil 8CB (25 m length; 0.22 mm diameter; 0.12 µm film/thickness); oven temperature programme:

First elution:	Second elution:
- 90°C: 2 min	-90°C :2min
- 90° - 180°C: 20°C/min	- 90 - 180°C :20°C/min
- 180 - 190°C: 2°C/min	-180 - 190°C :2°C/min
- 190 - 220°C: 2°C/min	-190°C :10 min
- 220 - 270°C: 4°C/min	-190 - 220°C : 4°C/ min
- 270°C: 10 min.	-220 - 270°C : 5°C/ min
	-270°C :15 min

On the obtained chromatograms, PCBs are recognized: 13 peaks of a standard mixture Arochlor 1254 and 9 individual congeners (see further).

Mercury analysis.

Mercury was determined with atomic adsorption spectrometry (MAS- 50 Mercury analyser , Perkin-Elmer) after mineralization of the sample with sulphuric acid (H_2SO_4, 97%) and oxidating the mercury to Hg^{2+}. After reducing the Hg^{2+} to Hg^0 with stanous chloride the volatile Hg^0 is bubbled into the closed system of the MAS-50 analyser. The mercury content is calculated with use of an external standard curve after deducting blanco values.

Results and discussion.

I PCBs

Identification.

The identification of PCB residues is based on the utilization of two kinds of standardization: firstly by comparing with the standard mixture "Arochor 1254" (this mixture is close to the PCB pattern found in marine samples), and secondly by comparing with nine of the most "classical" PCB congeners, namely 28, 52, 101, 118, 138, 153, 170, 180 and 194, in order of increasing chlorine content (Fig.6). The chromatograms of the first elution show peaks comparable to the standard mixtures,

although more highly chlorinated PCBs are present in the sample than in the 1254 mixture. Such a difference could be explained by the long distance from the sources of PCBs, higher chlorinated congeners being slightly more stable.

Quantification.

Quantitative evaluation of PCBs constitutes a complex problem, even if most publications do not mention it and avoid the discussion. The first approach makes use of external standardization with an Arochlor 1254 mixture: this "total PCB" concentration is calculated on the basis of the main 13 peaks. Separete congeners can be used as well: the sum of the 9 selected congeners gives an underestimated PCB level; they account for about 33 percent (mean value; min 16 to max 54, n=35) of the "total PCB" for particulate matter samples. Fig.7 shows a strong correlation

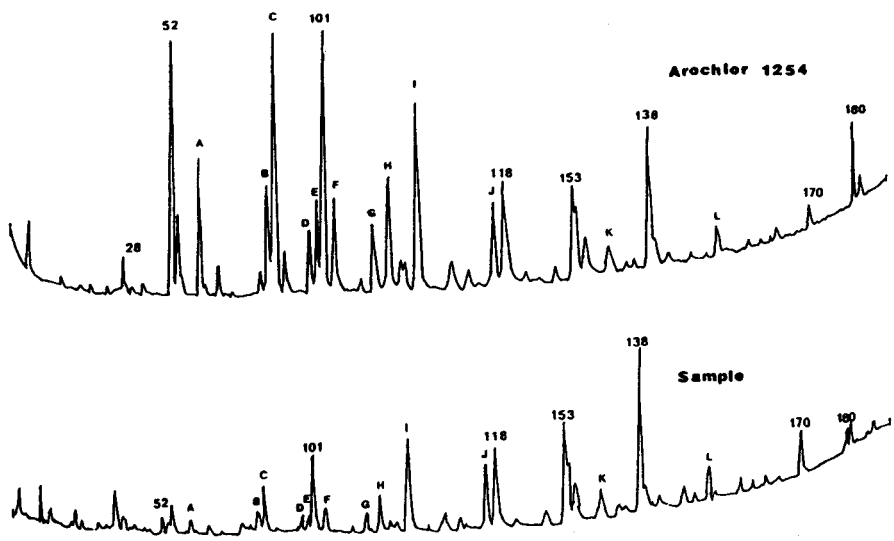

Figure 6: Chromatograms of PCBs in particulate matter and of standard mixtures: Arochlor 1254 (A to L) and individual congeners (28 to 194).

between the sum of 9 congeners and "total PCB". This correlation also exists for the individual congeners 24 to 180 *versus* "total PCB" (see annex). In netplancton samples, they account for 31 percent (mean value;min16 to max 54) (see annex)..
Further in this discussion, we will consider the concentration of "total PCB" expressed as Arochlor 1254 as being closer to the real contamination level.

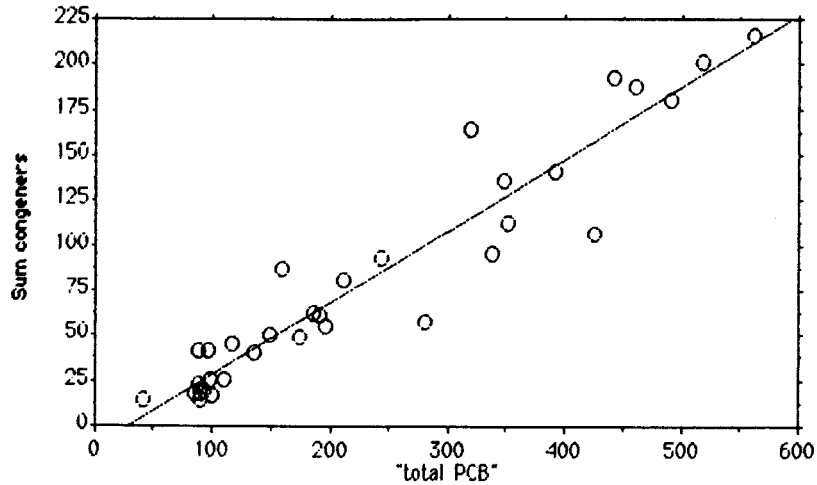

Figure7: Correlation between "total PCB" (as 1254) and the sum of 9 individual congeners (see text), in particulate matter (arbitrary units).

Geographical interpretation .

1 Particulate matter .

The PCB concentrations have to be expressed in different systems of units , in order to elucidate the main transfer mechanism (see introduction).

Three major zones are compared, as described above: Subtropical, Antarctic and South of the Divergence. On the basis of dry weight (DW), a slightly higher contamination level is detected in the subtropical zone: 1.43 µg PCB/g DW mean value instead of 0.68 in the two other zones (Fig 8). Expressed per seawater volume (m^3) (Fig.9), no significant difference exists between the three zones: PCB concentration is 1.18 µg/m^3 mean value for the whole region.

Compared with the North Sea ecosystem (Table I), the results indicate a rather high PCB level expressed per dry weight and per fat weight, but per water volume the contamination is lower and more constant. These findings are again in favour of the theory elaborated in the North Sea, namely that the most important mechanism for particulate matter contamination is adsorption/partition.

Antarctica is indeed less contaminated than temperate regions - as expected -but the low biomass causes a high level of PCB per unit of biomass.

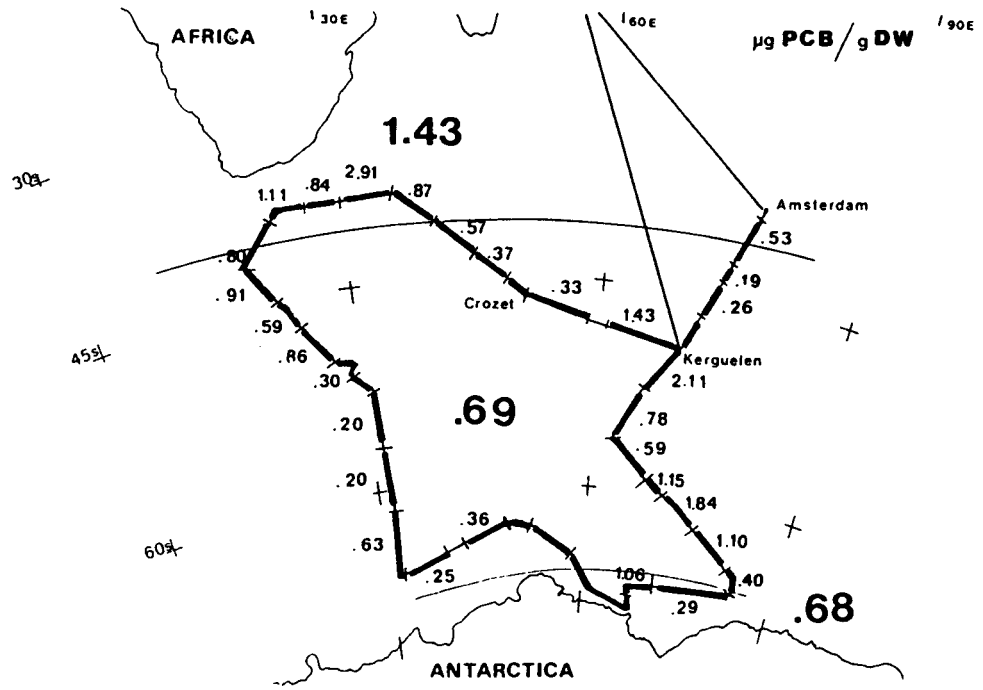

Figure 8: Geographical distribution of PCBs in particulate matter (µg PCB/g dry weight)

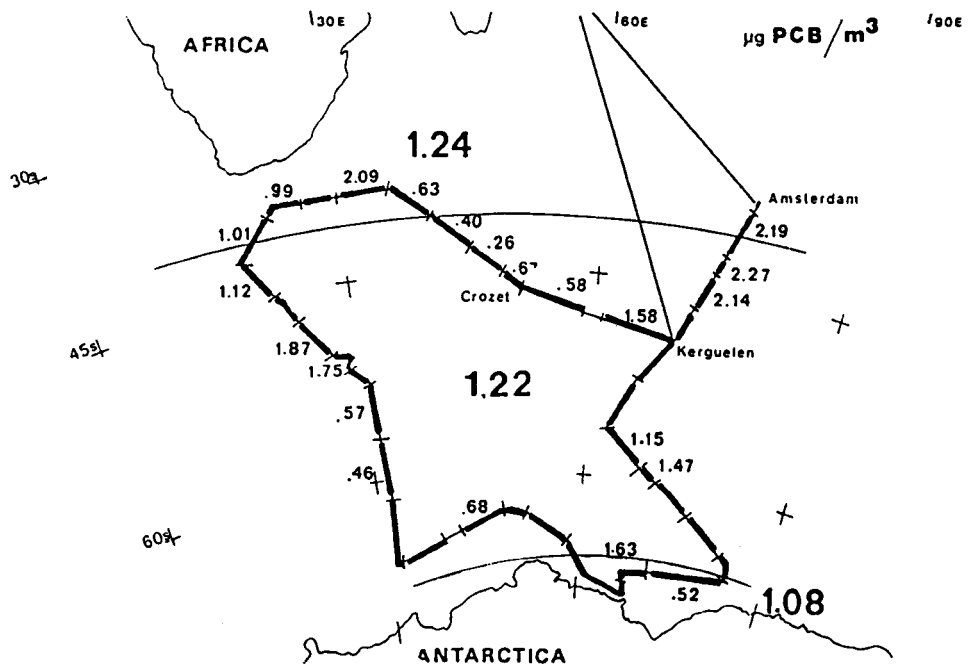

Figure 9: Geographical distribution of PCBs in particulate matter (µg PCB/ m^3 seawater).

Table I: PCB contamination of POM expressed in different units for the different zones (plus a coastal sample near Kerguelen) (see text).

Zone	µg PCB/ DW	µg PCB/ FW	µg PCB/ m^3
Sub-tropical	1.43 *(4)*	24.6 *(4)*	1.24 *(3)*
Antarctic water	0.69 *(22)*	15.4 *(25)*	1.22 *(16)*
S-Divergence	0.68 *(2)*	10.0 *(2)*	1.07 *(2)*
Kerguelen	0.36 *(3)*	20.6 *(3)*	
Total	0.76 *(31)*	16.6 *(34)*	1.18 *(22)*
North Sea	0.40 *(17)*	125.0 *(17)*	6.00 *(17)*

2. Netplankton

Netplankton samples (sampled with a 200 µm net) represent a broad range of composition, from zooplankton to phytoplankton with in between all types of mixtures; only one sample was pure krill (*Euphausia superba*: station 86). The heterogeneity in the samples should be considered when interpreting the results, therefore the small differences in contaminaton observed from one station to another cannot be explained in terms of different sample composition translated in different lipid weights and different accumulation mechanisms (phytoplankton versus zooplankton) as in the North Sea system.

No significant difference is found when comparing the three zones on the basis of dry weight (Fig. 10 and table II): PCB concentration is 0.37 µg /g DW mean value for the whole region, 0.37 for the Subtropical zone; 0.38 for the Antarctic zone; and 0.30 South of the Divergence. Expressed per seawater volume, differences appear however between the three major zones: Subtropical 0.01 µg /m^3; Antarctic 0.04 µg/m^3 and South of the Divergence 0.001 µg/m^3, with a mean value for the whole region of 0.03 µg/m^3.

The PCB levels are comparable in the Antarctic and the North Sea on dry weight and fat weight basis (Table III). The value per water volume (µg PCB/m^3) should however carefully be interpreted, due to the heterogeneity of the net samples: if most of the samples consist in phytoplankton, the value should be compared with the particulate matter contamination per m^3 in the North Sea. A lower contamination is

than found, an indication for a low biomass being responsible for a higher level of PCB per unit of biomass. From these results it is however not possible to deduce a mechanism for zooplankton contamination: the relative contribution of zooplankton to the contamination level of the sample could not be determined with enough precision.

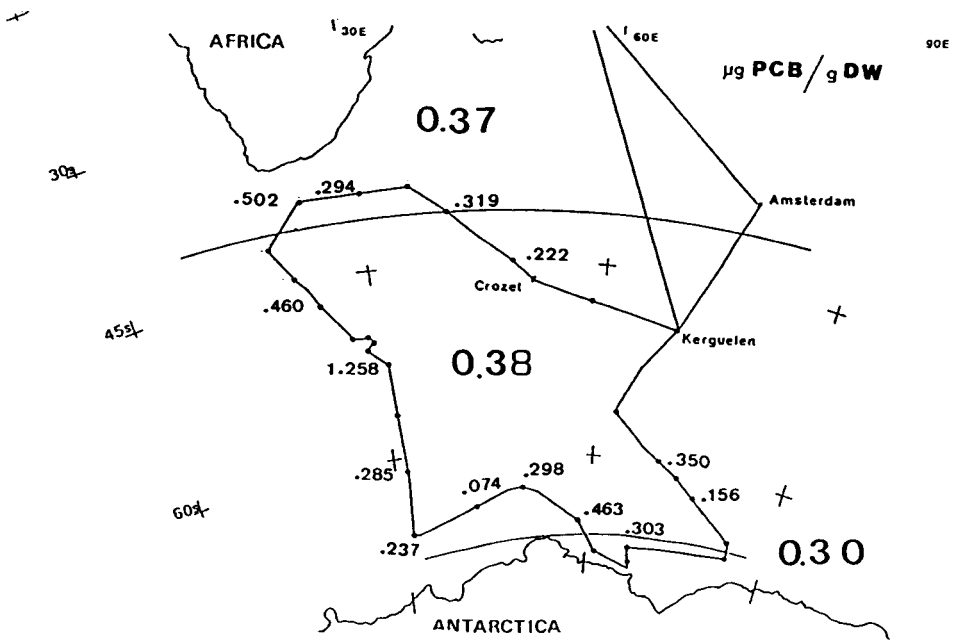

Fig.10: Geografical distribution of PCBs in netplankton: µg PCB/g DW.

Table II: PCB contamination of Antarctic netplankton expressed in different units, individual stations.

Station	µg PCB/g DW	µg PCB/g FW	µg PCB/m^3
98	.502	6.284	.0184
99	.294	7.313	.0096
101	.319	4.915	.0042
102	.222	4.700	
76	.350	8.981	.0033
78	.156	7.525	
81	.303	2.946	.0013
84	.463	2.963	.0035
85	.298	3.446	.0012
86	.074	3.408	.0095
87	.237	8.805	
88	.285	7.655	.1665
90	1.258	8.321	.0693
95	.460	4.568	.0114

Table III: PCB contamination of netplankton expressed in different units for the three zones (DW: dry weight; FW: fat weight).

Zone		µgPCB/g DW	/g FW	/m^3
Subtropical		0.37 *(3)*	6.17 *(3)*	0.01 *(3)*
Antarctic		0.38 *(10)*	6.04 *(10)*	0.04 *(7)*
South Divergence		0.30 *(1)*	2.95 *(1)*	0.001 *(1)*
Whole region		0.37 *(14)*	5.84 *(14)*	0.03 *(11)*
North Sea	zooplankton	0.70 *(20)*	7.0 *(20)*	0.02 *(20)*
	particulate matter	0.40 *(17)*	125 *(17)*	6.0 *(7)*

Comparison between the two compartments

Before comparing particulate matter with netplankton, a few important qualitative aspects must be considered. In order to allow the comparison of the contamination levels expressed as "total PCB" (Arochlor 1254) it must be questioned whether the PCB patterns are the same in both samples; if not, the comparison between different compartments should be made on the basis of values obtained by somation of individual congeners. As discussed higher, the sum (Σ) of the congeners represent 33% (min 16 to 54 max) of the "total PCB" value in particulate matter and 31% (min 15 to 54 max 54).in net samples. Considering this, no major qualitative change seems to occur between particulate matter and zooplankton

The relative contribution of the individual congeners to the sum of all congeners (percentage) was compared between the particulate matter and net samples (Fig. 11). For the measured congeners (101 to 170), the differences are relatively small (max 10%). These small qualitative differences are not reflected in different contamination levels when comparing them as sum congeners: considering the whole region in particulate matter 0.24 µg PCB/g DW; 5.39 µg/g FW and in netplankton 0.10 µg/g DW; 1.68 µg/g FW. These values are respectively approximatively 33 and 31% of the values obtained by expressing the contamination as "total PCB" (Arochlor 1254). These results, indicating a very small difference in PCB pattern between the two compartments, allow to compare them on basis of "total PCB" expressed as Arochlor 1254 (Table IV).

Table IV: PCB contamination of Antarctic netplankton and particulate matter expressed in different units.

	Particulate matter	Netplankton
µgPCB/g DW	0.76	0.37
µgPCB/g FW	16.60	5.84
µgPCB/m^3	1.18	0.03

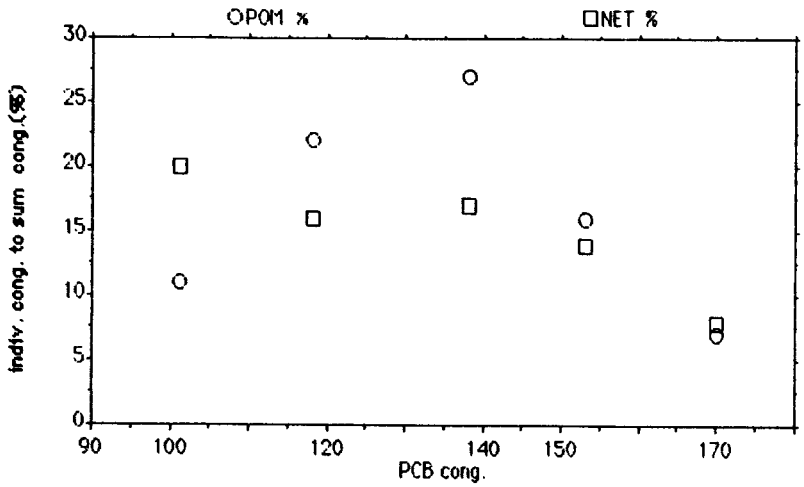

Fig 11 : Relative contribution of five individual congeners to Σ congeners in particulate matter and net samples..

The PCB levels in netplankton and particulate matter are comparable on a dry weight basis; they are clearly higher in particulate matter on a fresh weight base, indicating a lower lipid content than in netplankton. Per volume of seawater, finally, the difference between particulate matter and netplankton contaminations is still more marked, reflecting the higher abundance of particulate matter than netplankton in Antarctic waters.

II. Organochlorine pesticides: DDT, DDE, lindane, dieldrin, aldrin, heptachlor-epoxide, heptachlore.

Together with PCBs, samples were analysed fof organochlorine pesticides. The levels of contamination are low and in many samples just above the detection limit (traces) or not detected at all. Heptachlor and aldrin were not detected; following pesticides were present in most samples: lindane with average values of 0.019 µg/g DW (0.343 µg/g FW), heptachlorepoxide 0.027 µg/g DW (0.342µg/g FW), and dieldrin 0.009 µg/g DW (0.153µg/g FW). No significant difference between the zones was detected.

In the North Sea ecosystem, these organochlorine residues were not found at all in particulate matter, nor in zooplankton, only in higher trophic levels like seabirds

(Delbeke and Joiris, 1985). Their presence in Antarctic ecosystems could indicate a more recent and abundant use in the southern developing countries. It should be noted however that the detection limit in this study was improved by the use of capillary technique (a value of 0.009 µg/g DW dieldrin was not detectable with glass column).

DDT and DDE were present as traces only or not detected at all in particulate matter. 50% of the net samples contained DDT and DDE but in very low concentrations, with an average of 0.004 µgDDT/g DW and 0.007 µgDDE/g DW. The DDT to DDE ratio provides usefull information on the age of the residues, since DDT is slowly metabolised in more stable DDE. This ratio varies between 0 (DDE present, DDT not detected) and 8, within a small series of 6 positive samples. In North Sea plankton samples, DDTwas never detected: this clear difference reflects the recent use of DDT in southern countries, while in Europe it stopped around 1970. Such findings are confirmed by the results found by Abarnou (1986) in dolfins from the Kerguelen islands, with two times higher DDT than DDE concentrations.

III. Mercury

Mercury contamination was determined in netplankton, with average values of 0.32 µg Hg/g DW (0.03 min. - 0.83 max., n=13); 4.99 µg Hg/g FW and 0.009 µg Hg/m^3 and in a few particulate matter samples: 0.06 and 0.07 µg Hg/g DW. The contamination levels are comparable in the Antarctic (netplankton) and in the North Sea zooplankton (Table V) both on a dry weight, a fat weight basis and per volume seawater. Due to the uncertainity in the composition of the netplankton samples (see higher), it is however difficult to decide if they are more to be compared with zooplankton or particulate matter.

The difference in contamination between dry weight and fat weight is of the same order of magnitude as the difference between PCB contamination expressed per DW and FW, which reflects the liposolubility of mercury (mainly organic mercury) in the ecosystem. This analogy is found back when comparing PCB and Hg accumulation through the trophic chain in the North Sea and in Antarctic ecosystems (see introduction).

Table V: Mercury contamination expressed in different units in North Sea and Antarctic ecosystem.

	µg Hg/g DW	µg Hg/g FW	µg Hg/m^3
Antarctic: particulate matter	0.06 *(2)*		
netplankton	0.32 *(13)*	4.99 *(12)*	0.009 *(11)*
North Sea: particulate matter	0.16 *(2)*	15.20 *(2)*	2.20 *(2)*
zooplankton	0.24 *(2)*	2.70 *(2)*	0.007 *(2)*

Conclusions

The PCB contamination of particulate matter (sampled by continous centrifugation and consisting mainly of phytoplankton) is of the same order of magnitude -- or even higher - in the Antarctic as in the northern temperate zone (North Sea) when expressed as a concentration per dry weight. One expects however Antarctic ecosystems to be much less contaminated than temperate ones, especially the heavily polluted North Sea, since the direct, local contamination is extremely limited and the stable pollutants have to be imported from adjacent inhabitated zones.

In order to understand these high levels, one has to express the results in different unit systems -- and this confirms the importance of such an approach : per volume of seawater, the PCB level is six times lower than in the North Sea. This is the figure to be used in order to compare the contamination of different zones. Due to the basic contamination mechanism of particulate matter -- adsorption, absorption and partition - and due to the much lower biomass present in the Antarctic, similar levels are however reached per unit of biomass. The fact that the contamination expressed per fat weight is lower in Antarctic particulate matter, reflects its higher lipid content. This leads to the paradoxal consequence that, even if the Antarctic ecosystem is six times less contaminated by PCBs than the North Sea, its biological components might be as contaminated -- or even more contaminated - than in the North Sea.

At the zooplankton level, indeed, the PCB contamination of the Antarctic and the North Sea ecosystems might be comparable, but this conclusion still has to be confirmed because the Antarctic netplankton samples were not consisting of pure zooplankton, but often contained large amounts of phytoplankton as well.

The presence of other organochlorines was noticed at levels varying between low, traces and not detected: lindane, heptachlorepoxide, dieldrin, DDE and DDT. This constitutes a striking difference with the North Sea ecosystems, where DDE only is found in the lower trophic levels. From the qualitative point of view, the recent origin of Antarctic organochlorines is reflected in the high DDT/DDE ratio.

Since, on the other hand, the organochlorines are still in use, in increasing amounts, in the southern hemisphere while it is strongly limited or forbidden in western countries, one must expect still increasing levels in the Antarctic. Together with the possible high contamination of products consumed by man, like fish and krill, indicates an urgent need for improving our knowledge of the levels and the fate of stable pollutants in the southern hemisphere and more especially in the Antarctic.

Preliminary results on the mercury levels seem to reflect a situation very similar to the one of PCBs. This is not an unexpected observation, regarding the high liposolubility and ecological stability of both the organochlorines and (organic) mercury. Future research should include the determination of organic mercury and improve our knowledge of the relationship between the transfer and accumulation of both types of stable residues.

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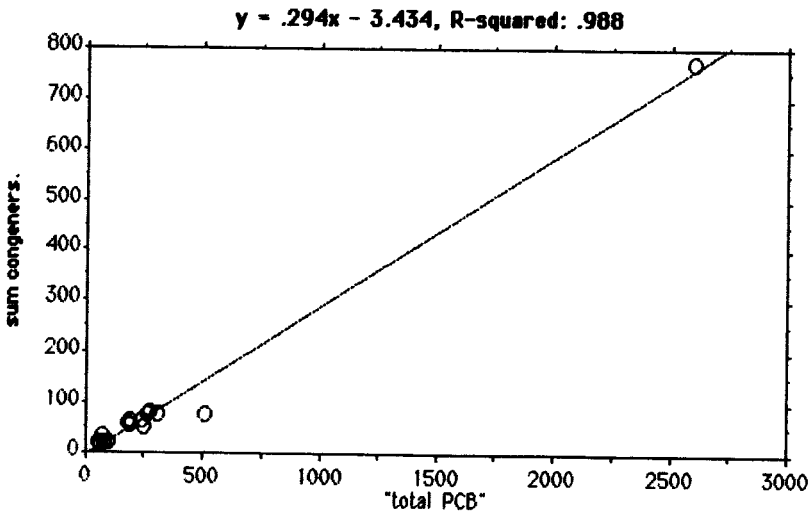
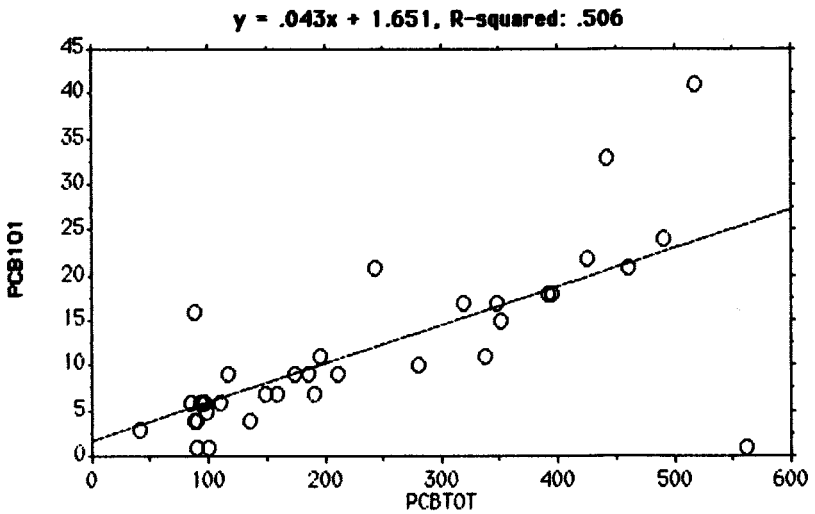
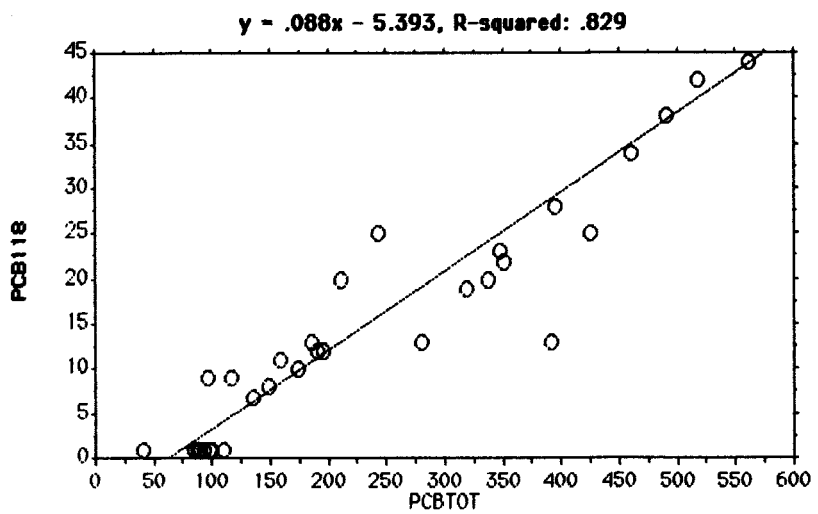
Annex

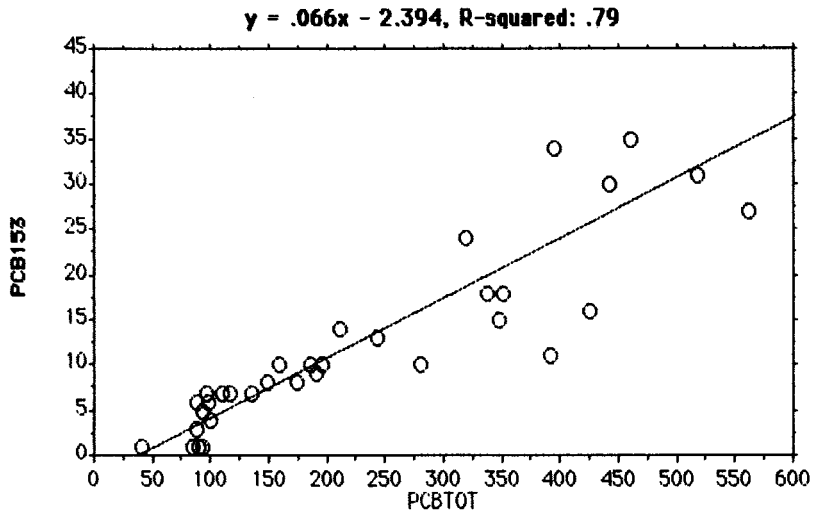


Corelation between "total PCB" (as 1254) and the sum of individual congeners in netplankton (see text) (arbitrary units).

Correlation between "total PCB" (as 1254) and the individual congeners 101 to 170 in particulate matter (arbitrary units).



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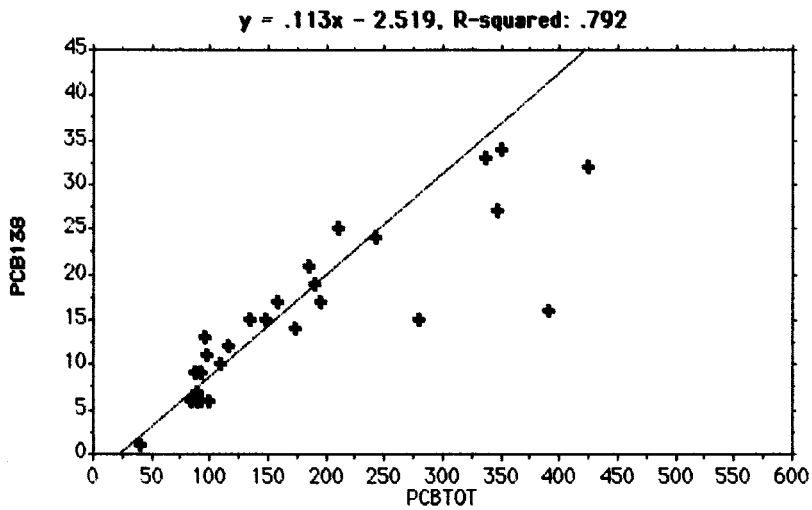
PCB153
PCBTOT
0
5
10
15
20
25
30
35
40
45
0
50
100
150
200
250
300
350
400
450
500
550
600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PCB138
PCBTOT
0
5
10
15
20
25
30
35
40
45
0
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100
150
200
250
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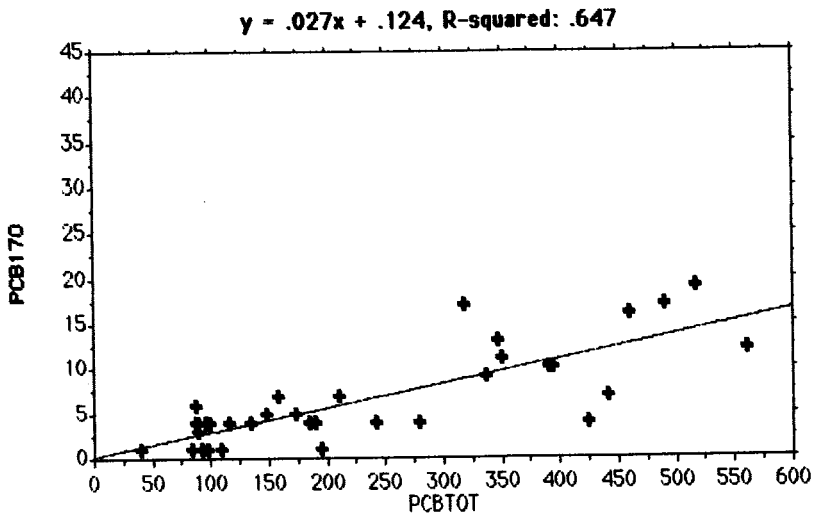
500
550
600


y = .027x + .124, R-squared: .647
PCB170
PCBTOT
0
5
10
15
20
25
30
35
40
45
0
50
100
150
200
250
300
350
400
450
500
550
600