PRIMARY PRODUCTION IN THE OPEN ANTARCTIC OCEAN DURING THE AUSTRAL SUMMER. A REVIEW

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Laboratoire Arago, Université Pierre & Marie-Curie, U. A. CNRS 117, F 66650 Banyuls-sur-Mer

ANTARCTIC OCEAN
PRIMARY PRODUCTION
REVIEW

ABSTRACT — The increasing number of cruises confirm the scarcity of the phytoplankton in the oceanic zone of the Antarctic Ocean, but patches of higher production appear in the marginal ice zone and in the frontal zones. We have to consider a multiparametric regulation of the primary production, especially with regard to factors that control the growth rate : mainly the temperature, because there is no justification for attributing a limiting role to the light. Not enough attention has been devoted to the factors regulating the biomass accumulation in the euphotic layer : grazing and sedimentation. The rapid lowering of silicates and of the Si/N and Si/P ratios in the northern part of the Antarctic control the level of production. Future programmes should focus on phytoplankton size distribution, because recent papers have emphasized the role of a rich and diverse pico- and nano- based microbial food web.

OCEAN ANTARCTIQUE
PRODUCTION PRIMAIRE
SYNTHESE

RÉSUMÉ — La pauvreté du phytoplancton dans la zone océanique de l'Océan Antarctique est confirmée mais des floraisons ont été décrites dans la zone marginale de la glace et les zones frontales. Nous devons considérer que plusieurs facteurs concourent à réguler la production primaire, particulièrement ceux qui contrôlent le taux de croisssance : principalement la température, car il n'y a pas à attribuer un rôle majeur à la lumière. Une attention insuffisante a été portée aux facteurs dont dépend l'accumulation de biomasse végétale dans la couche euphotique : le broutage et la sédimentation. La décroissance des teneurs en silicates et des rapports Si/N et Si/P dans la partie nord de l'Antarctique contrôle le niveau de production. Les futurs programmes devront se focaliser sur la distribution en taille du phytoplancton, car des articles récents attirent l'attention sur un réseau trophique «microbien», riche et diversifié.

INTRODUCTION

The history of phytoplankton studies in the Antarctic Ocean is a long one : more than a century has passed since the botanist Hooke reported the ubiquity of diatoms in the Antarctic Ocean, after the expeditions of the *Erebus* and the *Terror* (1839-1843). However, in the 1960s there were practically no valid quantitative measurements for the open-ocean system, neither for biomass nor for phytoplankton production. Although Hart disputed as early as 1942 the validity of the idea that this was a rich ecosystem, most authors perceived it as a eutrophic region, even well into the 1970s. Moreover, the world distribution maps of primary production in most modern treatises reproduce this anomaly.

The idea of great richness rests on the observation of blooms in the areas frequently visited by the ships relieving the Antarctic bases, such as the approaches to the Antarctic Peninsula, the coastal regions, and the ice-edge. At the beginning of the austral summer, the usual season of these missions, these areas are often the site of remarkable blooms, either in ice (epontic algae) or in open water.

But the idea of richness of the open sea grew mainly out of the intuitive association of a high primary production with high concentrations of nutrients. This nevertheless should not have led some authors to attribute to the Antarctic an annual production exceeding 200 gC. m^{-2}, a value close to the tropical coastal upwellings. At the Antarctic Divergence the annual irradiance is less than 300 kJ. cm^{-2}, whereas it greatly exceeds 600 kJ in the upwelling regions. And, above all, the solar radiation, which is very constant in the tropics, varies by a factor of 4 at middle latitudes and exhibits prolonged periods of light or of total darkness south 65°S. To reach a high level of primary production, often all that is needed is the simultaneous or successive appearance of nutrients and favorable light (as is the case with the spring bloom of temperate seas). Everyone thus expected the Antarctic open sea to be very productive, at least during the spring/summer period when the ice is receding and the light is strong, even exceeding the tropical values. Such assumptions of a high primary production in summer have two effects on ideas about the pelagic system in the Antarctic :

— due to the immense area of open ocean (38 million km^2), the marginal systems (convergences, continental sheet, marginal ice zone, the epontic environment) contribute little to the total production.

— given the low temperature of the water, its turbulence, and its richness in nutrients (especially silicates) it was only natural to believe pioneer observations of a simple food web : diatoms fully adapted to this environment (Margalef, 1978) and krill, a pivot towards the higher trophic levels of the Antarctic Ocean.

The seventies were marked by the beginning of intensive research of the Southern Ocean related to the increasing interest in the exploitation of krill. Multidisciplinary oceanographic cruises replaced the scattered measurements along the routes of relief ships.

REVIEW OF DATA AND DISCUSSION

1. The low production of the oceanic system

Recent reviews on Antarctic aquatic ecosystems (Fogg, 1977; El-Sayed, 1984; Jacques and Tréguer, 1986; Priddle *et al.*, 1986a; Tréguer and Jacques, 1986) clearly state that primary production in the Antarctic is low, as is shown strikingly by the graphs of optical characteristics of the oceanic waters (Fig. 1). Thus, such high values as 5.3 $gC.m^{-2}.d^{-1}$ in the Bransfield Strait (El-Sayed, 1970), 3.6 $gC.m^{-2}.d^{-1}$ near Deception Island (Mandelli and Burkholder, 1966), 3.2 $gC.m^{-2}.d^{-1}$ in the Gerlache Strait (El-Sayed, 1970), 2.8 $gC.m^{-2}.d^{-1}$ in the waters off Signy Islands (Horne *et al.*, 1969), 1.7 $gC.m^{-2}.d^{-1}$ (Bröckel, 1985) and 1.4 $gC.m^{-2}.d^{-1}$ (El-Sayed and Mandelli, 1965) in the coastal region of the Weddell Sea should be regarded as exceptional.

The mean values (Table I) reflect the real picture much more accurately. These data (also the mean estival production of 0.13 $gC.m^{-2}.d^{-1}$ calculated on the basis of three campaigns on the *Eltanin*; El-Sayed and Turner, 1977), are consistent with the estimation of an annual production of the order of 20 $gC.m^{-2}$ (Nemoto and Harrison, 1981). This is much less than the 100 gC proposed by Ryther (1963) and even than the range 25-80 gC indicated by Fogg (1977). If the data and future models confirm this order of magnitude, as is likely, the Southern Ocean might turn out to be the least productive plant ecosystem on the planet ! Its annual production is sometimes matched during a single day in the rich Peruvian upwelling system.

On the other hand, some investigators, using seasonal chemical and geochemical changes (O_2 accumulation, sedimentation rates, nutrient depletion rates), suggest that the primary production is two to four times greater than the value calculated from the ^{14}C uptake (Jennings *et al.*, 1984 ; Nelson and Smith, 1986). According to Rivkin and Putt (1987), the midday incubations can explain this strong discrepancy. If similar diel periodicity as observed in McMurdo Sound occurs in other polar areas, primary production would be significantly higher than previously estimated from ^{14}C measurements.

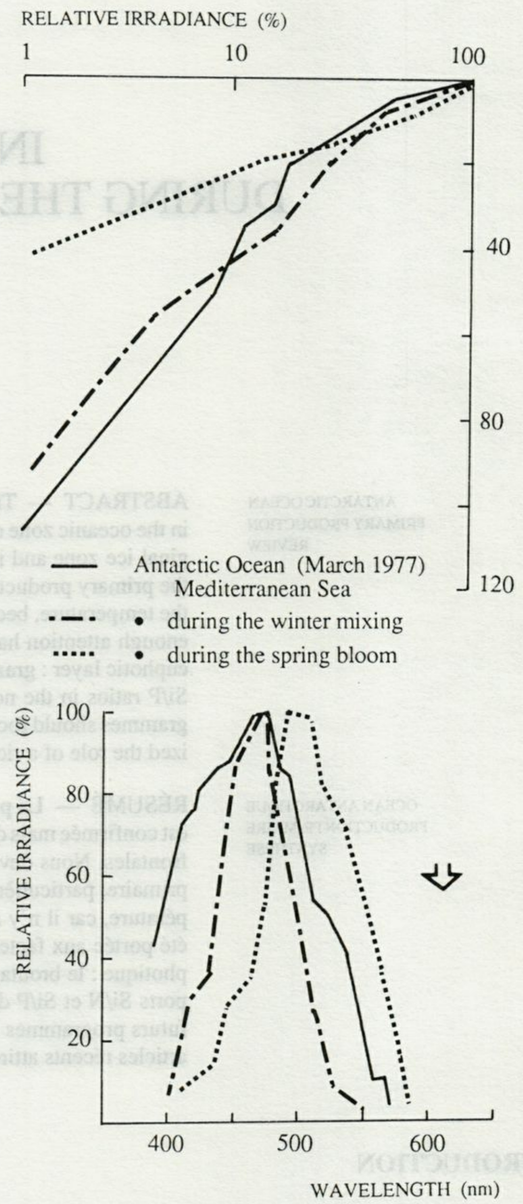

Fig. 1. – Optical properties of Antartic oceanic area compared with Mediterranean waters. Above : Relative irradiance (quanta-meter). Below : Downwelling spectral irradiance (spectro-irradiance-meter). From Boutler, 1970 ; Morel and Prieur, 1978; Prieur *et al.*, 1978.

As would be expected in a turbulent sea, the vertical distribution of phytoplankton is rather homogeneous. However, the vertical profiles of chlorophyll often show a slight maximum towards the base of the mixed layer.

Table I. – Primary production ($gC. m^{-2}.j^{-1}$) in various areas of the Antarctic Ocean.

Geographic area	Carbon fixation Minimum	Mean	Maximum	Source of data
Weddell Sea				
oceanic zone	-	0.3*	-	Jennings *et al.*, 1984
		0.1	-	El-Sayed and Taguchi, 1981
coastal areas	0.08	0.7	1.7	Bröckel, 1985
		0.4		El-Sayed and Taguchi, 1981
		0.35		Marra and Boardman, 1984
Indian Sector	0.05	0.1	0.2	Jacques and Minas, 1981
	0.08	0.2	0.4	Miller *et al.*, 1985
Bellingshausen Sea	0.1	0.3	0.7	El-Sayed, 1970
Gerlache Strait	0.4	1.7	3.2	"
Bransfield Strait	0.4	2.8	5.3	"

* estimated from depletion of nutrients

Occasionally, when this layer is not very deep, the maximum biomass increases : in the open sea off the Antarctic continent, Hayes *et al.*, (1984) found a concentration of 1 mg. m^{-3} at 20 m, while the surface water was very poor. The maximum production is generally located at depths corresponding to 10 % of surface light intensity. Moreover, the Antarctic phytoplankton show an aptitude for photosynthesis at low light intensity. The fraction represented by the production below the depth defined by the 1 % surface light layer relative to the total production possibly rises to 15 % in the neritic regions of the Weddell Sea, and reaches more than 30 % in the open-sea stations of this same region (El-Sayed and Taguchi, 1981). Deep productivity maxima can be explained by lowlight adaptation of deep-living phytoplankton (Sakshaug and Holm-Hansen, 1986).

2. *Antarctic Ocean : a series of ecosystems*

Open sea

Low production is related to the open sea off the continental shelf, which constitutes the largest and the most homogeneous (and the poorest ?) ecological entity on the planet. This is true for the region between South America and the Antarctic coast of the Weddell Sea. The horizontal profiles of temperature, nutrients and chlorophyll fluorescence sometimes contrast very abruptly in this area, and biomass and production vary rather widely. This is not surprising in a region where many factors act together to create foci of high production, and thus gradients : the bottom topography, the mixing of water masses, the presence of numerous island/land masses and the narrowing of the ocean between South America and the Antarctic Peninsula. But a similar situation, though less marked, also exists in the more oceanic areas such as the southern Indian Ocean (Simon and Sarano, 1987). Low production thus remains the rule for the oceanic region, including the western part of the Antarctic Peninsula (the Bellingshausen Sea and the Drake Passage); the high values sometimes cited for the latter zone are due to the fact that authors usually include the more productive part of the Scotia Sea. It seems therefore that biomasses of 0.05-0.3 mg Chl *a*. m^{-3} and productions of 0.1-0.3 gC. m^{-2}. d^{-1} actually are the rule in the open oceanic region.

Are there factors likely to lead to local or temporary growth of phytoplankton ? The formation of eddies has been described in the Scotia Sea near the Antarctic Divergence (Makarov *et al.*, 1970). But it is the contribution of spatial techniques, with the monitoring of drifting buoys and the utilization of radar altimetry, that has been decisive in this field. Eddy activity is strong, as the Southern Ocean is the only ocean that has regions of great variability far from the coasts, being mainly dependant of the bottom topography. Meanders and eddies, such as those described south of the Crozet Islands Plateau and the Antarctic Divergence, have amplitudes of the order of 80 km, wavelengths of 500 km, and periods of around 20 days (Daniault, 1984). Thus, their lifespans and dimensions are compatible with the scale of the patches of phytoplankton in this ocean (Okubo, 1978), where the rates of division are close to 0.3 doublings. d^{-1} (Holm-Hansen *et al.*, 1977). The positive effect of eddies on production can be due to decreased turbulence in the euphotic layer, increased temperature, high biomass import and partial retention (Heywood and Priddle, 1987) and slowing of the sedimentation, depending on the case. Indeed, in anticyclonic eddies, the rate of upwelling, of the order of 1 m d^{-1} (Priddle *et al.*, 1986 a), may partially counterbalance this sinking. This may explain how the greater biomasses reported in this type of structure in the Indian Ocean are maintained (Jacques and Minas, 1981).

Frontal zones

Frontal systems have been the focus of attention of oceanographers for the past several years. They represent shifts in certain physical and chemical variables, which again result in profound changes in production and biological structure of ecosystems. A newer concept is that these fronts not only represent physical boundaries for the communities, but in themselves constitute specific areas of enhanced biological activity.

The oceanic fronts have been the least studied. This applies particularly to the Southern Ocean : Subtropical Convergence, Subantarctic Front, Antarctic Polar Front, Antarctic Divergence. The multidisciplinary approach to studies of the functioning of this type of system requires suitable means and strategy, which the remoteness of these frontal zones makes it difficult to put into practice : repetition of observations, utilization of multiparametric profiles for a small-scale study, support of the remote sensing, which at present is almost limited to the study of temperatures and surface currents, etc...

What emerges most clearly from multiparametric continuous surface monitoring is that the underwater topography in the main affects the localization of the fronts and thus of the gradients nutrients (Hayes *et al.*, 1984). Thus, for the southern Indian Ocean, Simon and Sarano (1987) write «We should mention the close relationship between the southward inflexion of the Antarctic Convergence and the U shaped bathymetric profile : the slope of the Crozet and Kerguelen-Heard shelves coincide with abrupt drops in the concentrations of nutrients ».

The scarcity of phytoplankton is often associated with the Polar Front, as it is the confluence of Antarctic and Subantarctic surface waters. Recently, on a transect between South Africa and the Antarctic, Lutjeharms *et al.* (1985) demonstrated a peak of chlorophyll at the Polar Front which is probably a combination of convergences and divergences (Ostapoff, 1963). Another example is provided by the Antarctic Divergence,of which the location is far from clear. Few authors have suggested any biological effect of this front, until Hayes *et al.* (1984) found, in the eastern part of the Weddell Sea near 65°S, an elevated abundance of phytoplankton. The reason for this may be the increase of both the surface temperature and the lag time of development of the zooplankton, as has often been observed in the upwelling areas.

The neritic regions

The remarkable blooms encountered in inshore waters have contributed to the myth of Antarctic richness. One can mention extensive blooms of the colonial flagellate *Phaeocystis pouchetii* : one extending over nearly 600 km and up to 180 km off the continent south of the Ross Sea, and another observed in the Bransfield Strait with a concentration between 5 and 10 mg Chl *a*. m^{-3} (Bodungen *et al.*, 1981).

Hayes *et al.* (1984) suggested a relation between richness in phytoplankton and depths of less than 1000 m based on continuous monitoring of the surface profiles in the southern Atlantic Ocean between 10 and 70°W. They mention peaks of chlorophyll on the continental shelf south of the Drake Passage (1 mg. m^{-3} for *T. tumida*), on the Patagonian plateau (1.2 mg. m^{-3}), in the southwestern sector of South Georgia (1 mg for *Corethron criophilum v. inerme*), near the icy Antarctic Brunt Plateau (4 mg for *Phaeocystis antarctica*), and near the Southern Sandwich Isles in an open-pack zone. This relative richness of neritic areas is natural, since a good number of the factors likely to limit production in the open sea (vertical turbulence, «conditioning» of the water, etc...) disappear. The areas near the Antarctic continent are, on the other hand, those where the pack-ice is permanent, which constitutes *a priori* a favorable element, a question that will be now developed.

Marginal Ice Zone

In the Antarctic, unlike the Arctic, multi-annual sea-ice is not widespread. Every summer, therefore, the major part of the pack-ice, which covers 25 million km^2 at its maximum extent in September (7 % of the world's oceans), disappears. The climatic consequences of these exchanges between polar ice, ocean, and atmosphere have not been overlooked by physicists, who have launched two large international programs : in the 1970s the AIDJEX (Arctic Ice Dynamic Joint Experiment) project, devoted to the sectors with a heavy ice concentration, and in the 1980s, the MIZEX (Marginal Ice Zone Experi-

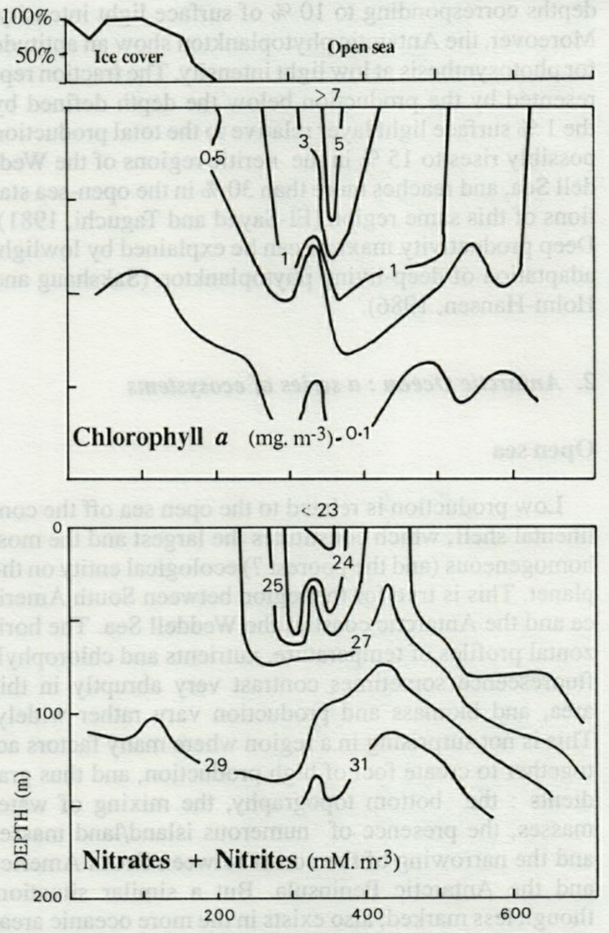

Fig. 2. – Distribution of chlorophyll and oxidized forms of nitrogen on a north-south transect through the ice-edge zone in the Weddell Sea at the end of November 1983. From Nelson *et al.*, 1984.

ment) program, also in the Arctic just devoted to the ice-edge zone.

This major oceanic frontal zone between sea-ice and open water profoundly affects the marine ecosystem. The marginal ice zone (MIZ) is considered to be a reservoir of biological resources : phytoplankton blooms (Fig. 2), abundance of young krill, concentrations of sea birds (particularly of the snowy petrel, *Pagodroma nivea*), penguins and whales. Note, however, that this hypothesis still needs support, since it has been documented only in rare cases in the Antarctic (El-Sayed, 1971; Alexander, 1980; Marra and Boardman, 1984; Smith and Nelson, 1985).

Several hypotheses have been advanced to explain why the MIZ is a locus of high primary production in the open sea :

— physical cause ⇒ stratification of the water column. The decrease of wind near the ice-pack and, mainly, the lowering of surface salinity through melting of the ice stabilizes the first 5 to 10 meters, bringing about a bloom. The triggering of upwellings at the boundary between the ice-pack and free water has also been pointed out.

— chemical cause ⇒ «conditioning» of the water by trace elements. These trace elements and chelators are produced by the bacterial and heterotrophic communities of the ice and are released into the water as the ice-pack is melting.

— biological cause ⇒ supply of algae from the pack-ice. As the ice melts, the phytoplankton communities growing in it are released. Either they constitute an inoculum which grows later, or they are an essential part of the growing phytoplankton stock.

Of all these hypothesized causes, which could have combined effects, it is the increased stability of the surface layer that most authors put forward, as the strong turbulence is considered the main limiting factor of Antarctic production. Such an effect is clearly advanced in the case of the Ross Sea, with a bloom extending 200 km out from the edge of the ice-pack (Smith and Nelson, 1985). Only a few studies, aside from Dunbar's (1981) on Arctic plankton, lend support to the concept of biological conditioning. Likewise, the role of epontic algae in the development of blooms is not very clear; however, estimates based on chlorophyll concentrations in the ice show that for some time after melting, epontic algae can represent a significant part of the biomass (El-Sayed and Taguchi, 1981; Smith and Nelson, 1985).

The second key question is to determine the impact of phenomena related to the MIZ on the biogeochemical cycles and biological production of Antarctica as a whole. The matter is of some importance, for though the extent of the MIZ at any given moment is tiny compared to the whole of the Antarctic Ocean, every year the ice-pack impacts an area of nearly 20 million km^2 in size.

A hypothesis would be to consider that, if turbulence is the sole factor limiting production in the open ocean, the retreat of the pack is accompanied, everywhere and all summer long, by an intense phytoplankton bloom in the 50 to 100 km wide band stabilized by the melting of the ice. The data from recent studies dedicated to the MIZ, either in the Weddell Sea (the USSR-USA Polynya cruise of the *Mikhail Somov* in October-November 1981; the *Polarstern* cruise from January to March 1983; the Ameriez 1983 cruise of the R/V *Melville* and the USCGC *Westwind* in November-December 1983) or in the Ross Sea (the *Glacier* cruise in January-February 1983) provide a more realistic view :

— blooms associated with the MIZ do not always reach the exceptional values that have been cited. The average chlorophyll concentrations range from 1 to 5 mg.m^{-3}.

— the increase of phytoplankton activity in the MIZ is probably limited in time and space. Several authors (El-Sayed and Taguchi,1981; Glibert *et al.*, 1982) have no noted any increase of chlorophyll at the pack-ice limit at the height of summer. Therefore the enhancement of primary production is probably limited to the period when the pack is breaking up. The closer to the Antarctic continent, then, the later this bloom would be. Likewise, aside from the deep embayments of the Ross and Weddell seas, there is no evidence that stabilization by melting necessarily leds to a bloom. This seasonal aspect of the functioning of the MIZ is surely valid for all open seas : comparative data obtained in the Indian Ocean during the SIBEX (Second International BIOMASS Experiment) cruises show that the bloom happens in late November to early December; two months later the biochemical characteristics of the seston still show traces of their activity (Bedo, 1987).

Microbial communities of sea-ice

I shall be brief on the subject of communities of sea-ice, as that system is outside the scope of this report, which focuses on the open sea (see Bunt and Lee, 1970; Bunt and Wood, 1963; Palmisano and Sullivan, 1983 a, 1983 b; Palmisano *et al.*, 1987; Kottmeier *et al.*, 1984; Kottmeier and Sullivan, 1987). Such communities are of interest, however, because of their close association with the ice-melt zone just described, both in the physiology of the microalgae that live in this unusual environment (temperature -1.8°C ; salinity 5 times that of seawater; irradiation equivalent to 1/100 of that reaching the surface) and because they constitute one part of the whole production in high latitudes ecosystems. The contribution of Sea Ice microbial communities to the overall production of the Southern Ocean has not actually been estimated.

3. Regulation of primary production

Nutrients

The very high concentrations of nutrients south of the Polar Front reduce the probability that they may regulate

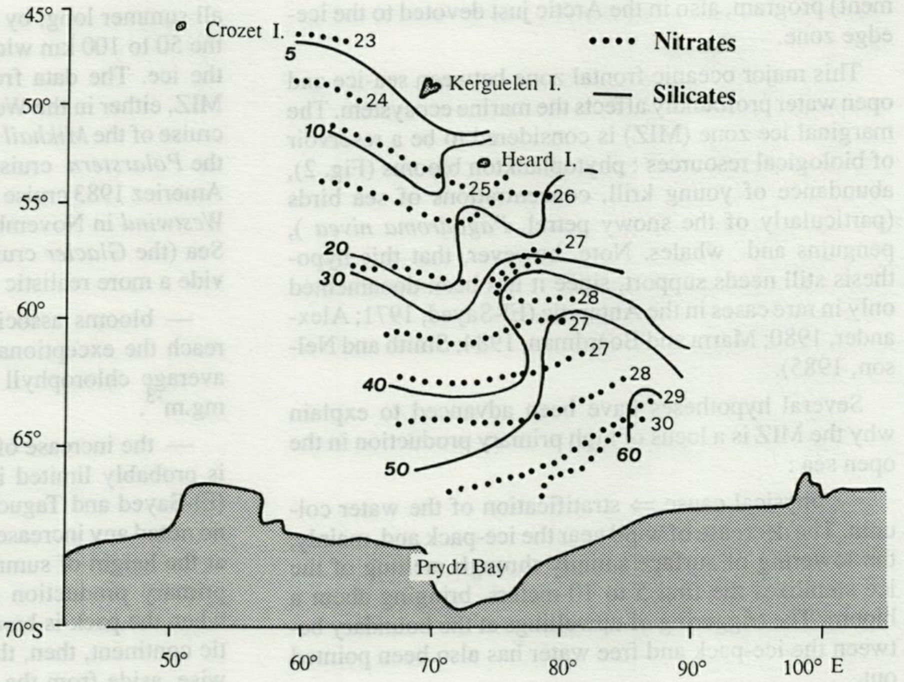

Fig. 3. – Distribution of silicates and nitrates (μM) in the surface water in the Indian sector of the Antarctic Ocean. From Tréguer *et al.*, 1987.

the growth of Antarctic phytoplankton. Even the lower values recorded (0.5 μM for phosphates in the Weddell Sea; 6.7 and 7.5 μM for nitrates in, respectively, the Ross Sea and the Bransfield Strait) would still sustain a large bloom. Furthermore, no test has shown any enhancement of phytoplankton growth after enrichment (Hayes *et al.*, 1984; Jacques *et al.*, 1984).

Silicates and Si/N and Si/P ratios

This last statement requires some qualification in the case of silicates :

— because they show a sharply decreasing south-to-north gradient (Fig. 3). Their concentration in Antarctic surface water remains above 10 μM, but the gradients are ecologically much more important than the absolute concentrations.

— because Antarctic diatoms have high cellular ratios Si_{part}/C_{part} and Si_{part}/N_{part}. The latter is more than 2.4 in Subantarctic surface water compared to less than 0.5 in subtropical water (Copin-Montegut and Copin-Montegut, 1978). These microalgae require high silicate concentrations to achieve their optimal growth. The half-saturation constants, established at 0°C by Sommer (1986), are 60 μM for *Corethron criophilum* and 90 μM for *Nitzschia kerguelensis*, very close to those reported by Jacques (1983) at 5°C. For diatoms with a thinner siliceous frustule (*Thalassiosira subtilis* and *Nitzschia cylindrus*), the values were lower : 22 μM for *Chaetoceros neglectum* , 8 μM for *N. cylindrus,* and 6 μM for *T. subtilis.*

There is anecdotal evidence of «siliceous cysts» as consumers of silicates in the Antarctic. These are probably nanoplanktonic algae (Marchant and McEldowney, 1986). Concentrations of the order of 100 000 cells per liter have been reported in the Weddell Sea. No evidence has ever been adduced that the ecosystem's overall production is limited by silica. However, the high silica requirement of Antarctic diatoms is indisputable. During one bloom in the Ross Sea extending up to 200 km from the marginal ice zone, Smith and Nelson (1985) found mean ratios of biogenic silica to organic carbon of 0.62 in phytoplankton in which *Nitzschia curta* was dominant. The very high ratios of silica to carbon compared with the oceanic mean of about 0.13 may represent an evolutionary change resulting from an environment regularly resupplied with silicates. It would be premature however to assume that this six-times-normal ratio applies to all Antarctic diatoms; but this observation makes increasingly more likely a biological hypothesis for explanation of the rapid decrease of silicates from the Antarctic Divergence. At the very least, these changes of the Si/N and Si/P ratios define interspecific competition between diatoms, since the growth of some of them can be limited by a lack of silicates. These ratios between nutrients also define the place of diatoms within the community. In the preceding example, *Corethron criophilum* and *Nitzschia kerguelensis* have an advantage in areas with a high Si/N ratio. But experimental proof of this idea is still needed, because the range of Si/N ratios used by Sommer (1986), from 3/1 to 400/1, is outside the classic variation in the Antarctic.

Nitrates and ammonium

The nitrate pool is greatly in excess of the needs of phytoplankton. Rönner *et al.* (1983) thought that it is recycled eight times before leaving the euphotic layer, in contrast to silica, which rapidly leaves the surface layer as particles (Le Jehan and Tréguer, 1985). The largest fraction (90 to 98 %) of inorganic nitrogen is found as nitrates, which is a very adequate nitrogen source in the euphotic zone even if ammonium ion is generally preferentially assimilated (Slawyk, 1979; Biggs, 1982). In the Scotia Sea (Olson, 1980; Glibert *et al.*, 1982), 50 to 95 % of the nitrogen requirement is probably met by the reserves in ammonium. The same has been verified for the Antarctic littoral near Mawson (Probyn and Painting, 1985). This experimental evidence, suggesting a nutrition largely based on the ammonium in a vast nitrate reservoir, is all the more puzzling, because the regenerated production is certainly underestimated, and urea must also be taken into account.

Nevertheless, none of the above authors has hypothesized that primary production is limited by nitrate once the ammonium-area pool is exhausted. However a reduction in the nitrate pool is however often observed after a bloom, but a simple case of limiting values in the euphotic layer has been reported. In the Drake Passage in December 1984, Sommer and Stabel (1986) found nitrate concentrations of 2.2 to 4.3 μM, or one order of magnitude lower than usual, while phosphates and silicates were within the usual range. There was no concomitant phytoplankton bloom. Competition experiments with semicontinuous cultures on the same samples (Sommer, 1986) showed that the growth of the principal species was greatly slowed in the medium : to 35 % of maximum for *Nitzschia cylindrus*, 56 % for *Chaetoceros neglectus*, 73 % for *Thalassiosira subtilis*, 75 % for *Nitzschia kerguelensis*, and 88 % for *Corethron criophilum*. In their conclusion, the authors wondered whether this was an exceptional event or recurred in every annual cycle. If the values reported for nitrate are correct, this is a discovery that overturns the usual conception of the Antarctic system. It seems to me difficult to imagine such an «anomaly», even at a limited site where there is a bloom, such as the MIZ or a neritic area. In certain conditions, when the hydrological and chemical factors are well understood, the production can even be calculated from the reduction in the concentrations of nutrients. The work of Jennings *et al.* (1984) in the Weddell Sea was trail-blazing : water at about 75 m during the austral summer actually carries a record of the characteristics of the previous winter. The lowering of nutrients between winter and summer, which can thus be calculated, reflects the springtime phytoplankton growth. Using C/N/P/Si ratios of 62/11/1/2.5, which are well suited to Antarctic phytoplankton, these authors calculated the consumption of nutrients and the derived primary production (Table II).

Trace elements and chelators

The low production in the open sea has sometimes been attributed to a lack of trace elements which are essential for the growth of phytoplanktonic algae (the Barber effect). A «land effect» and an «island effect» have been invoked to explain the greater richness of water near the Antarctic continent or the Antarctic and Subantarctic islands. Likewise, the high production of some oceanic areas is said to be due to the «complementarity» of water masses, as in the vicinity of South Georgia, where the waters from the Weddell Sea and the Drake Passage mix. The «conditioning» of free water by sea-ice is also suggested as one possible cause of the enhancement of primary production in the MIZ.

These hypotheses are strengthened by the very low concentrations, sometimes at the threshold of detection, of vitamins, especially B_{12}, which is known to be essential for the growth of some diatoms (Carlucci and Cuhel, 1977; Fiala and Oriol, 1984). On the other hand, the concentrations of metals in the Antarctic Surface Water are clearly higher than in the central waters of the large oceans : 0.5 to 1.5 nM. kg^{-1} for cadmium, 0.7 to 1.7 nM for copper, and 10 to 17 nM for zinc. Orren and Monteiro (1985), who provided indisputable preliminary results in the South Africa – Antarctica – Marion Island area, stated that these would in no case regulate the primary production.

There is thus little reason for suggesting that phytoplankton production is limited by trace elements, a hypothesis we advanced in 1981 (Jacques and Minas). The experiments testing the hypothesis gave negative results (Jacques *et al.*, 1984; Hayes *et al.*, 1984). On the other hand, there are many other possible causes for the high production cited.

Limitation by light ?

Light and turbulence

Phytoplankton development depends above all on the availability of light. What matters is the amount of energy available to the algae and the manner in which this flow varies over the whole range of time scales. Which mechanisms control this energy flow do not matter as far as photosynthesis is concerned, though in fact they are very diverse in nature :

— rotation of the earth : seasonal, geographical and nycthemeral fluctuations.

Table II. – Primary production estimated from depletion of nutrients between winter and summer in the Weddell Sea. From Jennings *et al.*, 1984.

Nutrients	Observed reduction (μM. m^{-2})	Depletion rate (μM. m^{-2}. j^{-1}) 90 days	60 days	Estimated primary production (mgC. m^{-2}. d^{-1})
Silicate	850	9.5	14.2	282-486
Phosphate	27	0.30	0.45	223-335
Nitrate	300	3.4	5.1	223-335

— changes in the atmosphere such as clouds.

— alterations of the air/sea interface : presence of ice, sparking, state of the sea.

— optical properties of the water, which affect both the quantity of photons and the spectral composition.

— movements of algae in the vertical light gradient as a function of turbulence.

At the height of summer, photoinhibition phenomena are frequent in all types of terrestrial bodies of water. Such phenomena also occur in inland seas : the mean solar radiation in February/March on the southeastern coast of the Weddell Sea is thus 1100 J. cm^{-2}. d^{-1} (Bröckel, 1985) ; this value is above the threshold of photoinhibition, which Holm-Hansen *et al.*, (1977) located, for Antarctic algae, at 800 J. cm^{-2}. d^{-1}. Additionally, these two studies show that the maximum production is found between 50 and 25 % of surface light. We will choose a context where the mean solar radiation penetrating into the sea is well above the lower limiting values, without any marked inhibition phenomenon. This corresponds well with the situation achieved in most of the open ocean and in the ice-edge zone (50 to 70°S) at the end of spring and in the summer, with an incident radiation ranging from 200 to 400 J.cm^{-2}. d^{-1}. This is exactly the situation in which it is important to look for evidence of any limitation due to light, but this reasoning has not been followed up with any rigor.

Mixed layer and euphotic zone

The weak vertical stability of surface water, preventing the organisms from staying in the optimum light zone long enough for extensive production, is the guiding idea of researchers confronted with the ecology of the Antarctic. Any bloom is then attributed to increased stability. Though the concepts of mixed layer, critical depth, and euphotic zone have been advanced, nothing definite has been demonstrated, with the following two exceptions :

— In the Indian sector, Jacques and Minas (1981) proved that the critical depth in the Sverdrup's acceptation, was markedly deeper than the mixed layer (Fig. 4). The vertical mixing thus maintains the phytoplankton within the euphotic layer. Priddle *et al.* (1986 b) came to the same conclusion regarding the waters off South Georgia.

— In a general study, Priddle *et al.* (1986 a) wrote : «It would seem therefore on these theoretical considerations that the importance of energetic vertical mixing and a deep mixed layer in diminishing Antarctic marine phytoplankton production during the summer grazing

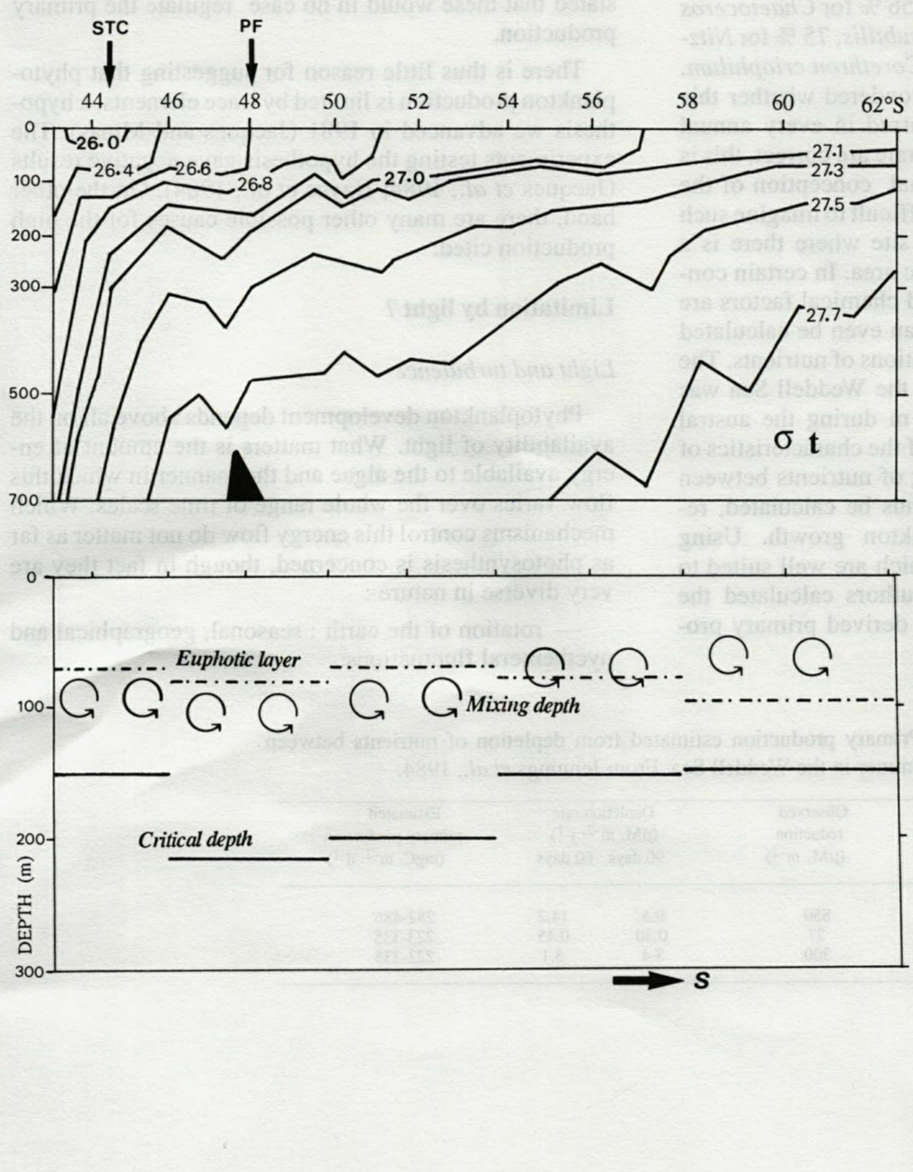

Fig. 4. – Euphotic layer, mixing layer and critical depth (below) in the southern Indian Ocean, compared with the density structure (above).

season has been overstated». That opinion was based on the application of Harris's (1978) model, which also permitted calculation of the critical depth:

$Z_{crit} = 21.7 / \mathbf{r}$, where **r** is the ratio between the respiration rate and P_{max}.

Using values of **r** established for springtime diatomaceous plankton in a temperate sea (but no indications exists that values for **r** from lower latitudes can be readily applied to the Southern Ocean), Priddle *et al* (1986 a) established a range of variation of the critical depth thus defined from 278 to 493 m ! The Sverdrup's theory nevertheless is a correct skeleton, these two previous examples rather reflecting that recent knowledge on physiology and growth had not been taking in account in most of the Antarctic litterature (Sakshaug, pers. comm.) :

- Losses by the way of sedimentation, grazing and extracellular production which have to be compensated by photosynthesis, as well as the dark respiration.
- The non-linearity of the P vs I curve when the irradiance is not low.
- The self-shading during the development of a bloom and the spectral distribution of irradiance.
- The rather large variation of the Chl/C ratio

Thereby, the «real» critical depth certainly is smaller than the one sensu Sverdrup. The paper of Sakshaug and Holm-Hansen (1984) demonstrating that planktonic bloom apparently do not term when the mixed layer exceeds about fifty meters, certainly show the right way. On the basis of a physiological model, Lancelot (pers. com.) as Bodungen *et al.* (1986) also voiced the same opinion : in the Prydz Bay area, the real critical depth reach about 30 m, deeper than previously calculated in neighbouring areas.

Rapid movements of phytoplankton in the euphotic layer

Rapid turbulent movements within the euphotic layer itself, with a time scale shorter than the division rate, represent the ultimate (?) way in which light can limit the growth of phytoplankton. This hypothesis (Jacques, 1983) has not been confirmed, quite the contrary. The list of publications showing that short-term fluctuations are not injurious to phytoplankton development has been growing for several years. Generally the photosynthetic efficiency is even enhanced. These studies include the following : Quéguiner and Legendre (1986) studying *Dunaliella tertiolecta* with a high-frequency light regime simulating waves; Abbott *et al.* (1982) investigating the effects of passing clouds on phytoplankton *in situ*; Marra (1978) comparing the effect of nycthemeral rhythm with a regime simulating Langmuir circulation. In three Antarctic diatoms (*Nitzschia turgiduloides*, *Corethron criophilum*, and *Stellarima microtrias*) Mortain-Bertrand (1988) showed that the amount of inorganic carbon incorporated in light, and also in darkness, was greater in a 2 h/2 h regime than in a 12 h/12 h, with a rather distinctly higher corresponding daily production.

Temperature

The permanent low water temperature impose another constraint to the phytoplanktonic growth. This factor was advanced long ago (Saijo and Kawashima, 1964) as the main regulator of primary production in Antarctica, since it determines the metabolic levels. Even at the height of summer the phytoplankton communities of the ice-edge zone are living at a temperature varying between -1.9 and -1.5°C, while those of the open ocean are between -1.5 and 3°C.

The primary productivity is principally affected by a decrease of photosynthesis at light saturation, as the dark reactions (P_{max} = the plateau of the curve of P *vs* I are regulated by enzymatic processes. But the low values of the parameters of the curves P *vs* I for the Antarctic concern both the P_{max} and a. In the Bransfield Strait, where the temperature is below 0°C, Tilzer *et al.* (1985) observed a photosynthetic capacity 4 to 7 times lower and a slope 2 or 3 times weaker than those found at lower latitudes (Platt and Jassby, 1976; Côté and Platt, 1983). Taking advantage of other measurements in the Scotia Sea and, again, in the Bransfield Strait, Tilzer *et al.* (1986) confirmed, and indeed clearly formulated for the first time, that temperature also acts on photosynthesis in limiting light.

The Antarctic algae thus have not developed specific mechanisms for overcoming the constraints due to low temperatures. Their enzymatic arsenal associated with the fixation of inorganic carbon is therefore similar to that of temperate species : RuBP carboxylase and PEP carboxykinase (Descolas-Gros and Fontugne, 1985). However, the affinity coefficient (K_m) for RuBP carboxylase is lowest at the temperature at which the Antarctic diatoms live, which allows them to fix carbon at these low temperatures (Descolas-Gros and De Billy, 1987); in this case, it is natural to speak of adaptation. It is thus possible to calculate the upper limit of photosynthesis if the absorption of available light by the pigments were complete : this would be, for water at 0°C, a little less than 200 mgC. m^{-2}. h^{-1} (Tilzer *et al.*, 1985), which corresponds to about 2 gC.m^{-2}.d^{-1}. The growth rate, which reflects the algal metabolism, clearly shows the limits of development of Antarctic phytoplankton (Neori and Holm-Hansen, 1982). Eppley (1972) suggested that the maximal growth rate in nonlimiting light and with continuous supply of nutrients is described by the equation :

$\mu max = 0.851 (1.066)^T$, T beiing the absolute temperature in ° Kelvin :

0.71 doubling per day at -1.9°C
0.85 doubling per day at 0.0°C
1.00 doubling per day at 2.5°C
1.17 doublings per day at 5.0°C

The real levels are generally a little below these theoretical maxima, as other regulating factors can intervene. It would be interesting to know if these levels can sometimes exceed the predicted values. Priddle *et al.* (1986 a) thought so, in view of the high biomasses sometimes encountered. The mean value of 1.23 in the southern Indian Ocean at a temperature around 1°C (Miller *et* *al.*, 1985) suggests that they were right, since this exceeds the theoretical μmax of 0.91 division per day (this is even more true for its maximal value of 2.10 doublings per day). I think it would be premature to count on such capacities, as the growth rates mentioned above were established indirectly, by the use in particular of a carbon/chlorophyll conversion factor of 30.

Exploitation of the phytoplankton biomass

So far we have discussed the main factors controlling primary production. However, even with a low level of growth, phytoplankton can at times reach high concentrations. This is the case for the community of microalgae of ice. For this to happen, all that is needed is that the biomass produced be not eaten much by herbivores or that it undergo few physical losses through dispersal, sedimentation, etc...

Concerning grazing, the only proven fact is the coexistence of low concentrations of Chl *a* (0.5 mg. m^{-3}) in the areas where krill is concentrated, mostly in the seasonal pack-ice zone : east wind drift and eddies along the Antarctic Divergence. For krill, the mean value of 3 % of the phytoplankton biomass consumed per day is without meaning, because krill forms localized swarms in which than can reach concentrations of 6 000 individuals per m^3 and can totally exploit the phytoplankton biomass present. Although estimates of primary production have been revised downwards for the past several years, so have those of the stocks and production of krill, which have dropped by an order of magnitude (Hempel, 1985).

In the region of permanent sea-ice, mainly the shallower parts of the Weddell and Ross seas, the period of phytoplankton production is brief but intense (sometimes near 2 gC. m^{-2}. d^{-1}). The phytoplankton stock seems not to be much utilized by the classical pelagic food web : diatoms ⇒ small euphausiaceae as *Euphausia crystallorophias* ⇒ pelagic fishes as *Pleuragramma antarcticum*. The largest fraction of the phytoplankton and epontic algae feeds the epibenthic fauna of echinoderms and suspension-feeding sponges. In this case, sedimentation is the main factor regulating the phytoplankton stock. There are two successive phenomena :

— blooming with an increase of the plant biomass in open water (melting of the ice), with no limiting factor except the physical regulating parameters.

— a heavy flow of organic material towards the sediment just after this phase of intense pelagic production.

Again it is in the oceanic ice free zone from the West Wind drift that our knowledge is most sparse, because biologists of the BIOMASS (Biological Investigations Of Marine Antarctic Systems and Stocks) program have devoted most of their efforts to the study of krill. Recent data have shown only that oceanic areas are occupied by a trophic web without krill (except around South Georgia) where the zooplankton community is quite similar to that of the north Atlantic : copepods, salps, small euphausiids. Although the krill-centered food web is unique and constitutes an important potential resource, it concerns mainly the seasonal ice-pack.

In regions with a deep mixed layer, only a negligible amount of sedimenting particles are resuspended. Also, particularly in the case of the diatoms which predominate in the areas of bloom, sedimentation takes place rapidly. For isolated cells, rates of 1 to 10 m per day have been suggested (Whitaker, 1982; Jacques and Hoepffner, 1984); these rates increase for the colonial forms and can reach 50 to 100 m per day when the algae are incorporated in the fecal pellets which predominate in the sediment traps (Dunbar, 1985). The rapid sinking of diatoms is also attested to by the observation of cells several hundred meters deep which are still fluorescent (Grall and Jacques, 1982), by the content of sediment traps (Bodungen *et al.*, 1986), and also by the accumulation of diatomaceous frustules in sediments. This is true both at shallow depths (Kellog and Kellog, 1984) and in the Antarctic abysses. Thus, in Quaternary sediments of the southern Indian Ocean, especially the more recent ones, the siliceous biogenic fraction, represented mainly by diatom frustules, predominates (Labracherie *et al.* 1987). The community composition with predominance of *Nitzschia kerguelensis* is quite similar to actual. This species having a very thick siliceous frustule sediments rapidly and dissolves slowly, one of the major characteristic of the Antarctic system.

The rapid removal of diatoms from the euphotic layer, which has major consequences for the biogeochemical silica cycle, certainly might help to account for the low biomasses in the production layer. However this remains to be shown, as the observations of El-Sayed and Taguchi (1981) are not convincing. The hypothesis advanced in their study in the Weddell Sea cannot be generalized to the whole oceanic zone where the presence of cold winter water at the bottom of the euphotic layer provides great stability.

4. *Microplankton and nanoplankton : towards a new trophic web ?*

We can now say that a significant fraction of the particulate primary production (auto- and heterotrophic) is due to organisms less than 2 μm in size (picoplankton) and that this production is at the base of «microbial loop», consisting of free-living auto- and heterotrophic bacteria, cyanobacteria, colorless nano- and picoflagellates or ones containing colored plasts, and microzooplankton. This food web is representative for oligotrophic conditions in which a sizeable fraction of the production is achieved through rapid recycling. The factor *f*, the ratio between nitrate-based production (so-called new production) and the total production, is often considered to be about 0.05. It is these small organisms (bacteria and, even more, microzooplankton) that provide up to 90 % of this recycling of nutrients; ammonium is reused by the phytoplankton as fast as it is released (regenerated production) (Glibert, 1982). These observations, originally made in tropical waters, raise questions of concepts and methods. The observations have grad-

Table III. – Relative contributions of various size fractions in the Antarctic phytoplankton.

Sector	Date	Parameter	Pico →← 1µm	3	5	Nano 10	→← 20	Micro 60	100	Ref.
N et S Australia 100-153 °E 35 °N-67 °S	Summer 83-84	Chl *a*	14%	→←		56%	→←	19%	→← 11%	(1)
S Australia 120-160 ° E 50-67 °S	Summer 80-81	Chl *a*		53%		→←	25%	→←	22%	(2)
Indian 40-120 °E		Chl *a*		30%		→←		70 %		(3)
Weddell Sea 28-54 °W 63-78 °S	Febr.-March 77	Chl *a*			74%		→←	26%		(4)
S Australie 110-150 °E 47-60 °S	Summer 83-84	Chl *a*	24%		→←	36%	→←	41%		(5)
		PC	11%		→←	33%	→←	56%		
Weddell Sea 10-41 °E 70-78 °S	Febr.-March 83	PC			70%		→←	23%	→← 7%	(6)
Mawson-Cape Ann 52-64 °E 62-65 °S	March-Apr. 84	PC	70% →←	23%		→←		7%		(7)
		N Upt.	40% →←	27%		→←		33%		
Weddell Sea 10-41 °E 70-78 °S	Febr.-March 83	Pr. Pr.		88%		→←		7%	→← 5%	(6)

PC = Particulate Carbon; N Upt. = Nitrogen Uptake; Pr. Pr. = Primary Production
(1) Kosaki *et al.*, 1985 (2) Yamaguchi and Shibata, 1982 (3) Sasaki, 1984 (4) El-Sayed and Taguchi, 1981
(5) Hosaka and Nemoto, 1986 (6) Bröckel, 1985 (7) Probyn and Painting, 1985

ually been extended to higher latitudes (Stockner and Antia, 1986), but only recently to the polar seas.

The idea that the Antarctic waters are rich in phytoplankton has for a very long time been linked with the image of spectacular blooms of large diatoms and with the simple food chain diatoms ⇒ krill ⇒ whales. Although similar observations were made earlier, it was Bröckel, in 1981, who first clearly drew attention to the importance of nanoplankton in the Antarctic Ocean. Note that most of the studies cited here concluded that diatoms, including the nanoplankton fraction, predominate (Table III). Of these studies, that of Kosaki *et al.* (1985) gives the clearest view of the problem because of the large number of size classes studied, the high density of stations and the coverage of a very broad range of geographic latitudes. It thus appears that while the picoplankton fraction (whether this is defined as < 3 µm or < 1 µm), which predominates in tropical waters, is negligible in the Antarctic, the nanoplankton (3 to 20µm) constitutes as much as 55 % of the chlorophyll biomass.

After having once thought of the Antarctic as an ocean inhabited by large diatoms, researchers now probably overestimate the importance of nanoplankton. The previous results rest only on size fractionation by filtration, a technique which is still open to question. In the Antarctic, as elsewhere, only the combined practice of differential filtration, observation of organisms *in vivo* in fluorescence microscopy, and flow cytometry will establish the precise place of nanoplankton. Finally, the research of Probyn and Painting (1985) (Table III) goes well beyond the simple distribution of phytoplankton into size classes, since it relates size structure and nitrogen assimilation pathways. In spite of very high NO_3 concentrations (20 to 30µM), NH_4 meets 50 to 95 % of the nitrogen demand, with the order of preference ammonium > urea > nitrates being observed because it results in the lowest energetic cost(an extra proof of the light limitation ?). This high flow of reduced nitrogen passes mainly through the nanoplankton, of which 62 % of the production is thus in a regenerated form, and through picoplankton, for which the percentage reaches 72 %. This high proportion of regenerated production, difficult to imagine heretofore, because of the nitrate reservoir (is this «repressed» in areas with high ammonium concentrations ?), leads to the idea of a trophic web representing an alternative to the classic food chain (Fig. 5). A fraction of the flow of matter follows the classical pathway : microplanktonic diatoms ⇒ krill. It is now well established that though krill adapts its efficiency of retention to the size of the particles, its level of filtration is nevertheless halved for nanoplankton particles (Weber and El-Sayed, 1985 ; Quetin and Ross, 1985). As for the organic matter synthesized by the autotrophic nanoplankton and picoplankton, this enters a different, more complex, and poorly understood web where microprotozoans with a preponderance of ciliates play a role (Table IV) (Garrison *et al.*, 1984; Heinbokel and Coats, 1984).

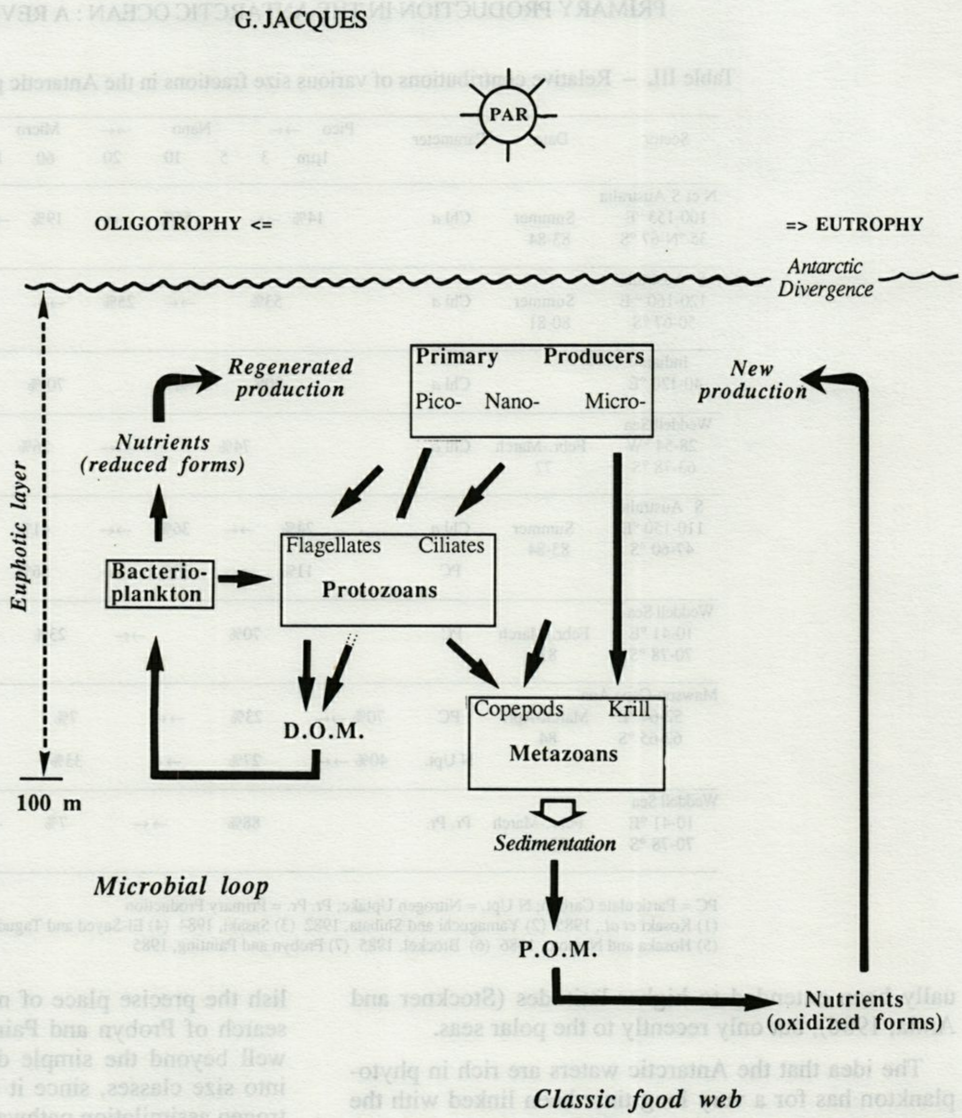

Fig. 5. – Coexistence in the Antarctic Ocean of the classic food web and the more recently discovered «microbial loop». Abbreviations : PAR = Photosynthetically Active Radiation; D.O.M. = Dissolved Organic Matter; P.O.M. = Particulate Organic Matter.

Table IV. – Biomass (mg C. m^{-3}) of heterotrophs in the ice-edge zone northeast of the Antarctic Peninsula. From Garrison *et al.*, 1984.

	Ice	Water
Heterotrophic flagellates	0.40 to 100	0.20 to 10
Heterotrophic dinoflagellates	.	0.04 to 5
Choanoflagellates	0.03 to 0.80	0.00 to 0.40
Naked ciliates	≠ 0	0.30 to 3
Tintinnids	.	0.30 to 1.5
Métazoans	4 to 22	.

Differing in the groups and the sizes concerned at each trophic level, these two pathways, between which there are many still-undefined interrelations, also differ profoundly in their significance in terms of biogeochemical flow.

— The «microbial» cycle proceeds principally in the euphotic layer with rapid recycling through the excretion of microheterotrophes and bacterial mineralization. The most reduced forms of nutrients (ammonium for nitrogen) are quickly used by the autotrophes; the factor *f* thus stays very low. This type of system is a weak exporter of organic matter to the deep layers, inasmuch as it is dominated by highly buoyant organisms.

— The «classical» cycle is based principally on new production (factor *f* reaching 0.8) from upwelling mineral reserves at the antarctic divergence (nitrates for nitrogen). A large fraction of the organic matter mainly produced by large diatoms is exported into deep water and sediment through the rapid sinking of large diatoms and fecal pellets.

These two pathways (Hewes *et al.*, 1985) coexist in all ecological situations, but the magnitude of the flow passing through each of them varies. Recent studies show that the «macro» pathway is preponderant whenever the total primary production is high (blooms), and the «micro» pathway is preponderant in situations where plankton is scarce. But continuous surface monitoring operations have shown that the Antarctic Ocean does not violate the rule, which is becoming more and more evident, of high variability of structures in space and time. Also, as Platt and Harrison (1985) predicted, we should expect that each province of the Southern Ocean can occupy, at a given time, in a given place, at a given depth (as defined on axes x, y, z, and t), any position at all in the range extending from extreme oligotrophy to eutrophy. This view is much more realistic than one which definitively classifies a given oceanic region as either eutrophic or oligotrophic.

CONCLUSION

Although the Southern Ocean has long fascinated scientists, it is only since the 1970s that it has been the object of intensive research with a view to exploiting its biological resources (BIOMASS Programme). In years to come, other matters of interest should intensify research on this ocean :

— Its impact on the climate, if only because of the freezing and melting of 20 billion tons of ice.

— Its influence on the general oceanic circulation, with the formation of Antarctic Intermediate Water and of Antarctic Deep Water.

— Its major role in the ocean fluxes of certain elements, especially silica, since it constitutes a silicon trap.

— The uniqueness of its trophic web, marked by the rarity of pelagic fish, the prominence of marine mammals, and the importance of birds.

— The physiological adaptations developed by the plants and animals that live there, because of the very low temperatures (-1.9 to 3°C).

Recent results have completely revised our notions about the Antarctic pelagic system. The overview presented here will be useful in defining future programs. These should take account of what ships can do (for example in penetrating pack-ice), of new technical methods (such as remote sensing, sediment traps, cytofluorometry), and of the existence of national and international programs relating to the effect of the ocean on climate (World Ocean Circulation Experiment) and the flow of matter in the ocean (Joint Global Ocean Flux Study).

A rather low primary production

Illusions about the fertility of the Antarctic Ocean are no longer suscribed to; but, in a classic swing of the pendulum, some researchers have probably gone too far in suggesting a value as low as 16 $gC.m^{-1}.year^{-1}$. Future research should show this level to be somewhat higher, for two reasons :

— Estimating production from standing stock and from short-term production experiments is inappropriate. The Antarctic is somewhat similar to a chemostat, and a correct estimate of production is achieved by measuring the biomass exported by the exiting flow. Indirect measurements (by collecting organic matter in sediment traps) or by monitoring the depletion of nutrients more accurately reflecting the biomass produced should be developed, as they integrate medium-scale production.

— The ice-edge zone is not adequately taken into account. An optimistic view would be to consider that the melting of the pack is accompanied by a bloom over the 20 million km^2 that it sweeps across. A more realistic examination of the data already shows that in the Weddell and Ross seas where the ice-pack is permanent, the bloom is limited to the period when the pack breaks up; this needs to be confirmed. It also remains to be seen if there is any systematic phytoplanktonic burst in the open sea at the end of spring , and this would require oceanographic cruises at that season. Taking into account this effect of the marginal ice zone will probably result in a moderate upward re-evaluation of overall production. The effect could be clearer in terms of flow of matter towards the deep layers and the sediment.

A heterogeneous ocean

Already composed of several well differentiated subsystems, such as ice-communities and marginal ice-zone, the Antarctic Ocean, as teledetection and continuous profiles have shown, presents a heterogeneity over space and time that was unsuspected several years ago. This is true for the most oceanic part, and not only for the triangle South America - Antarctic Peninsula - Weddell Sea. This heterogeneity is manifested first by the presence of frontal systems, which were described long ago but are much more complex on a medium scale than has been thought, with, frequently, a combination of convergent and divergent structures. It is also manifested by the creation of abnormal oceanographic conditions in the circumpolar flow, by example quasi-permanent events with a long lifetime, associated with the bottom topography. This influence on surface hydrological phenomena (the direction of the current in Ekman's layer, or the position of fronts, eddies, and meanders) has been underestimated, particularly in the Antarctic. In tropical seas these eddy structures have a beneficial effect on the production when their direction of rotation «pumps up» underlying waters rich in nutrients. The scarcity of available data on the Antarctic Ocean also indicate a direct influence of these phenomena on the distribution of the phytoplankton. These observations should be supplemented by the use of remote sensing to locate these eddies; in addition, their mode of action remains to be elucidated, since it necessarily differs from that advanced for tropical waters.

Factors controlling primary production. The end of a paradox ?

A little too much attention has been devoted to the factors controlling the levels of cell growth at the expense of the factors regulating the levels of cell accumulation in the euphotic layer, and hence the development of the community: grazing, water column stability and sedimentation. There is no justification for attributing in summer, a limiting role to the light factor, though this is still the predominant view. The first argument is the thickness of the mixed layer, which in summer is close to that of the euphotic layer and in any case is much less than the critical depth. The second argument lies in the fact that experimental studies all show that the rapid fluctuations of light that the algae undergo do not provoke a decrease in their photosynthetic activity compared with that in a stratified mass of water. Renewed consideration of this point of view would require the definition of new theories taking into consideration the combined effect of light and low temperature and modifying the critical depth concept.

Nutrients have been dismissed a little too soon as having no limiting effect. This assessment should be re-examined first with regard to nitrogen. That would obviously be the case if observations of very low concentrations of nitrates, such as those found by Sommer and Stabel (1986), were found elsewhere. But it is necessary to clarify whether an excess of ammonium blocks utilization of nitrates. It would also be necessary to verify whether the rapid lowering of silicates, and thus of the Si/N and Si/P ratios, goes beyond simple regulation of the composition of the flora to control the level of production in the northern part of the Antarctic Ocean. Recently, Martin *et al.* (1987) presented direct evidence in support of an iron-as-the-limiting-factor in the northeast Pacific Subarctic and suggested that Fe deficiency may also limit growth in the Southern Ocean : to prove its limiting effect, clean methods of sampling and experimentation will be required.

Temperature is therefore really still the main factor that sets the upper limit of cellular growth of Antarctic phytoplankton, which has a division rate of usually less than 0.5 per day.

The existence of high concentrations of phytoplankton would require that the pressure of grazing remain low for a long enough period, given the low growth rates. This is a little-known field in Antarctica. Grazing pressure is certainly strong on certain occasions, not only from swarms of krill but also from copepods, which sometimes consume the equivalent of 50 % of the primary production (Bodungen *et al.*, 1986). But the most constant factor in the decrease of the phytoplankton stock is certainly its elimination outside the euphotic layer by direct sedimentation (diatoms with heavy siliceous frustules have a high sinking rate) and by vertical mixing. Turbulence therefore remains an important factor, not so much for its direct action in the euphotic layer, as for that in the underlying water, where it provides rapid elimination of material coming from the surface water.

Size structure of the phytoplankton community, and its consequences for the food web

The study of size distributions within the phytoplankton community and of their consequences for the food web and the flow of matter need to be emphasized in future programs. It will be necessary to make sure that this study is based on differential filtrations by normalizing the types of filters and the porosities used, as that will constitute the only basis of comparison with other oceanic regions. But it will also be necessary to combine these observations with fluorescence microscopy of the live material and, above all, flow cytometry. The latter will be necessary because it combines the study of dimensional characteristics with that of fluorescent properties, which can account especially for the chlorophyll concentration and the cell- division cycle. Antarctic «oligotrophy» (if this term is used for primary production only) is quite different in nature from the oligotrophy of tropical oceans, which applies to nutrients as well as to phytoplankton. Whereas autotrophic picoplankton (< 2 µm) predominates there, it is very scarce in the Antarctic Ocean. In Antarctica the prevalent fraction is either nanoplankton (< 20 µm), in conditions of low production, or microplankton (> 20 µm) when there are blooms. In any case, it is diatoms that play the main role in both these size classes.

Matter circulates in two possible pathways, as follows :

— In a «microbial loop», with rapid recycling taking place principally within the euphotic layer itself. This type of system is a weak exporter of organic matter to the deep layers. The associated food web extends to copepods, with an intermediate level of protozoans.

— In a «classical» cycle, based principally on new production from mineral reserves welling up to the surface at the Antarctic Divergence. A large fraction of the organic matter is exported to deep water and the sediment. This food web is centered on krill.

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