

PHYTOPLANKTON STANDING STOCKS AT KERGUELEN ISLANDS (SUBANTARCTIC, INDIAN OCEAN): ANNUAL VARIATIONS IN RELATION TO ENVIRONMENTAL FACTORS

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ABSTRACT. – During a 15-month survey of standing stock phytoplankton at three coastal sites along Kerguelen Main Island, some hydrological as well as biological parameters differences between sites were noticed. The more sheltered site, at the head of the large Port-Raymond fjord (PRAY) on the north side of Morbihan Bay, was characterized by high and relatively stable salinity, a well defined cycle of phytoplankton biomass (up to 2 µg Chl *a* l⁻¹, November-January), and high ammonium concentrations following the phytoplankton bloom (January-February, up to 5 µM) that were probably also related to kelp degradation. At Port-Aux-Français (PAF), at the entrance of the Morbihan Bay, the salinity decreased with increasing water discharge in winter; the bloom, starting with the spring increase in water temperature, was intense and consisted of several short peaks in summer (late November-February, up to 11.2 µg Chl *a* l⁻¹ in 1992). The third site, at the head of the deep Portes-Noires fjord (PN), South Kerguelen, was characterized by frequent discharges from glacier-rivers, very low water temperature (min. 2°C in August, max. 5°C in January-March), low NH₄⁺ values (< 0.5 µM in winter), and a phytoplankton bloom apparently short and starting in February-March (up to 4 µg Chl *a* l⁻¹ in 1992). The ratio Chl *a*/Phaeo *a* also suggested that the phytoplankton productive period started later in the year at Portes-Noires fjord, in relation to its more exposed position. By comparison, in the offshore coastal waters (i.e. “KERFIX station”), the bloom was restricted to a short period (November-December) with low pigment maximum (up to 1 µg Chl *a* l⁻¹). The indented geomorphology of Kerguelen main Island, close to the Polar Front, allows the phytoplankton to develop actively in the inner fjords and bays, with nutrients supplied mainly from the oceanic Antarctic Divergence, but probably also from the kelp and epiphyte degradation and the flourishing macrofauna physiology. A geographical gradient in productivity was shown, from high biomasses in the Morbihan Bay, to a delayed cycle, low biomasses and nutrients, in the southern fjord with more direct open-ocean influence.

INTRODUCTION

In the open SW Sector of the Indian Ocean, the phytoplankton productivity was reported to be low, even in the spring time e.g. 0.17 µg Chl *a* l⁻¹ (Plancke 1977), 0.1-0.4 µg Chl *a* l⁻¹ (Jacques & Minas 1981), whereas higher values were linked to oceanic fronts, particularly the Polar Front (Taniguchi *et al.* 1986, Wefer & Fischer 1991, Tréguer & Jacques 1992). Recent long-term surveys, such as those reported in Louanchi *et al.* (2001, “KERFIX station”), demonstrated that offshore productivity of the Southern Ocean is higher than previously recorded.

Furthermore, a productivity increase was generally observed in the vicinity of Austral islands, particularly the Kerguelen and Heard Islands

(El-Sayed 1971), but also the Marion and Crozet Islands (El-Sayed *et al.* 1979). This enhance productivity may be linked to the Island Mass Effect (Doty & Oguri 1956, El Sayed *et al.* 1979, Perissinotto *et al.* 1992). However, another explanation could be an upwelling regime in the eastern part of the Kerguelen Plateau (Plancke 1977, Tréguer 1987). Recently, complex physical-biogeochemical interactions were shown to occur in the water masses off Kerguelen (Blain *et al.* 2001) and natural dissolved iron input, via the Kerguelen plateau, linked to favourable light-mixing regime, could cause an Island Mass Effect enhancement causing increased phytoplankton productivity.

Kerguelen Main Island, far from any continental influence and situated in this oligo- to mesotrophic oceanic context, exhibits diverse marine coastal

environments, from sheltered/semi enclosed bays to exposed deep fjords. This volcanic archipelago, close to the Polar Front (Park *et al.* 1998, Fig. 1) is characterized by a flourishing kelp canopy and a marine macrofauna that is particularly dense in the sheltered bays (polychaete mats, sea-urchins and large mussel beds), but also in exposed sites (sponges and dense epifauna invertebrates such as Gammaridae). This abundant and diversified secondary production may originate in the high phytoplankton production, and kelp degradation. This deeply indented Archipelago, benefits from an overall nutrient supply via the northward Antarctic Divergence (Tréguer 1987). Rough weather and water mixing may be unfavourable to oceanic phytoplankton development, but coastal productivity is more diverse. For example, near the Polar Front, at the 200 m deep “KERFIX station” (50°40’S, 68°25E) SW of Kerguelen, the phytoplankton biomass reached $1.2 \mu\text{g Chl } a \text{ l}^{-1}$ during short summer periods (maximum observed from November to December), with an inter-annual regular reproducibility (Fiala *et al.* 1998), while in the winter biomass production was low ($< 0.2 \text{ Chl } a \text{ l}^{-1}$). However, in the coastal environment, long-term studies conducted in the Morbihan Bay, a large embayment in the SE Kerguelen (“Z station”, 4 on Fig. 1), found a seasonal phytoplankton cycle (Delille *et al.* 1996, Razouls *et al.* 1997), with sporadic blooms from October to February and being particularly intense in spring (up to $28 \mu\text{g Chl } a \text{ l}^{-1}$; H Frass pers comm), but moderate winter values ($0.4\text{-}0.6 \mu\text{g Chl } a \text{ l}^{-1}$, Razouls *et al.* 1997). During

the phytoplankton bloom, silicate decreased for a short period at “Z station” (October to December) whereas NO_3^- and PO_4^- were never depleted.

The annual cycle of ammonium has not been studied in these areas, whereas, upon the nitrogen nutrients, NH_4^+ is the first compound to be assimilated by the autotrophic microalgae (Admiraal *et al.* 1987, and refs therein). Furthermore, only the Morbihan Bay received attention, whereas the Kerguelen main Island offers the possibility to study and compare sheltered and more open-ocean coastal environments. These last points motivated an annual survey of the phytoplankton standing stock at three well-defined locations, their comparison and relation to hydro-climatic parameters and particularly NH_4^+ variations, as a mean of evaluating the role of shelter or oceanic influence:

- 1) One site in the relatively sheltered Morbihan Bay, close to “Z station” in the vicinity of Port-Aux-Français (PAF, 1 in Fig. 1).
- 2) A more sheltered site at the head of the large Port-Raymond fjord (PRAY, 2 in Fig. 1), in the north of Morbihan Bay and
- 3) A site at the head part of the narrow and deep Portes-Noires fjord (PN, 3 in Fig. 1), connected to La-Table Bay, a large open-ocean indentation.

No CTD was available during that wintering stay, so that it was not possible to study the vertical profile (and time variation) in temperature and salinity at the three sites.

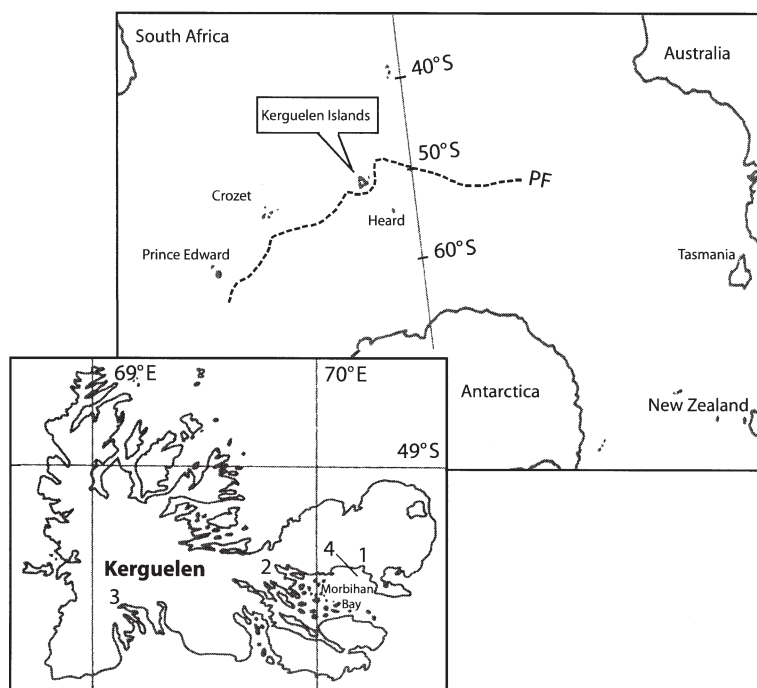


Fig. 1. – Kerguelen Archipelago position in Austral Ocean (Indian Sector) and Polar Front position in the vicinity of Austral islands (dotted line, according to Park *et al.* 1998). Kerguelen main Island sampling locations: 1) Port-Aux-Français (PAF), 2) Port-Raymond fjord (PRAY), 3) Portes-Noires fjord (PN), 4) “Z station”.

A first paper, based on results from the same period and time period (Riaux-Gobin & Bourgoin 2004) focuses on intertidal and subtidal microphytobenthos biomasses and comparison of the benthic and pelagic bloom patterns.

MATERIAL AND METHODS

Sampling occurred over 15 month period from December 1990 through March 1992. The sampling frequency differed slightly for the 3 sites, fortnightly for the Morbihan Bay at PAF and PRAY (with exceptions of rough weather), to monthly or even less frequently at PN, when rough conditions limited offshore boat travel.

NH_4^+ and salinity were analysed at the Kerguelen laboratory. Three surface water samples (between 30 to 40 cm below the surface) were collected (with no prefiltration) in twice rinsed borosilicate vials (100 ml capacity, 80 ml filled) for NH_4^+ measurements. The vials were kept in the dark for 6 hours until titration. NH_4^+ , in triplicate, was titrated manually with a KONTRON spectrophotometer, following Koroleff's method (1969 & 1976) and recommendations by Tréguer & Le Corre (1975). Results were expressed in μM . The precision of the method was 2% and standard deviation ranged from 0.004 to 0.41. Salinity was determined with a Autosal Guildline salinometer (precision 0.01 PSU). However, temperature was measured *in situ* with a manual thermometer (precision 0.1°C).

For pigment analysis, surface water samples (30 to 40 cm below the surface) were collected in pre-rinsed

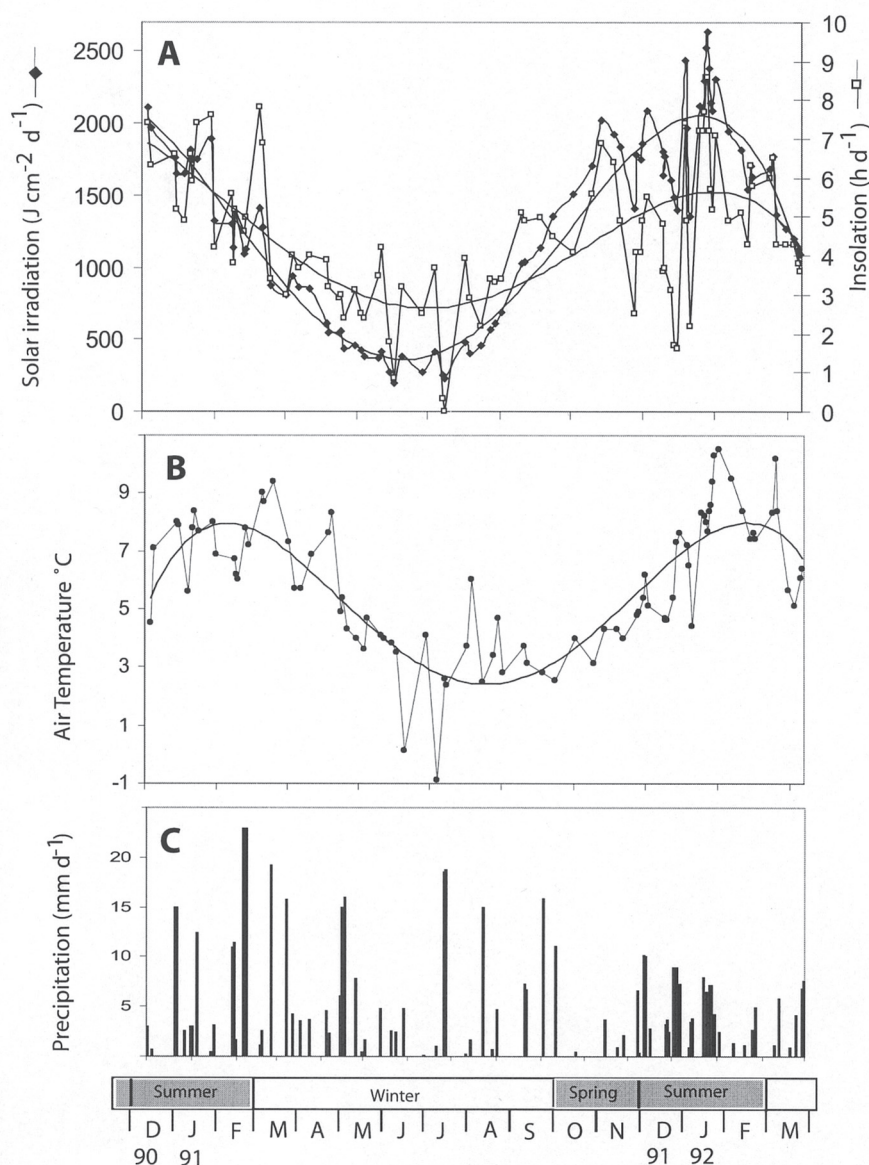


Fig. 2. – Meteorological conditions at each sampling date: A, solar irradiation and insolation B, air temperature C) precipitation. Each point represents the mean value of the preceding 5 days [polynomial curves (x^4) indicate the annual trend; $R^2 = 0.8892$ for solar irradiation, $R^2 = 0.6679$ for air temperature].

plastic 5 l containers, with no prefiltration. Four sub-samples (from 500 to 1000 ml) were filtered onto Whatman GF/F filters and stored frozen (-20°C) until pigment analysis (2-3 days delay). The methodology for fluorometric pigment analysis was performed under dim light conditions. Filters were manually homogenized in 7 ml 90% acetone and kept cool and dark for 2 h before pigment analysis. The sample was centrifuged at 3000 rpm for 5 min. The fluorescence of an aliquot of the supernatant was measured using a Turner Design Fluorometer (model 10.005h), before and after acidification with 80 μl 1N HCL. Chlorophyll *a* (Chl *a*) and phaeopigments (Phaeo *a*) concentrations were calculated according to Holm-Hansen *et al.* (1965) and Lorenzen (1966). Results were expressed in $\mu\text{g l}^{-1}$. The standard deviation for four replicate samples ranged, for Chl *a*, from 0.02 during low standing stock, up to exceptionally 0.53 during the 1992 bloom. This conventional method for pigment analysis using fluorometry implies that, in addition to measuring Chl *a*, it also includes Chlorophyllide *a*, iso and allomers of Chl *a*, while for

the Phaeo *a*, it groups phaeophytin *a*, phaeophorbide *a*, and other phaeophorbide *a*-like pigments. Moreover Chl *b* and high concentrations of degraded pigments interfere with these fluorometric measurements (Lorenzen & Jeffrey 1980, Redden *et al.* 1993).

To evaluate the short-term variations in phytoplankton productivity and ammonium, a day-to-day time-series was studied over 7 days in summer 1992 at the PAF site; samples were collected at the day-time high tide. A similar time-series was also conducted on intertidal sediments at the same time (Riaux-Gobin & Bourgoin 2004).

RESULTS

Hydro-Climatology

Indications of the meteorological conditions that prevailed on the sampling dates [calculated mean value on the preceding 5 days in: solar irradiation,

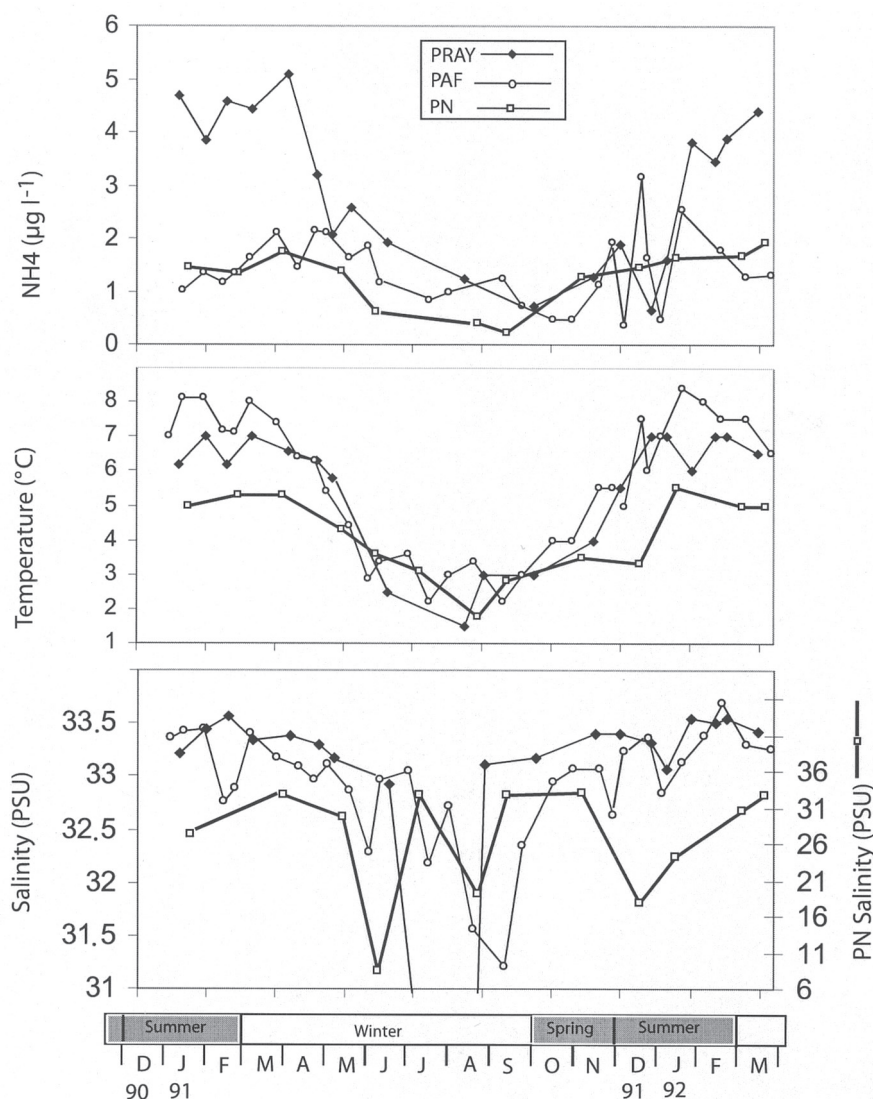


Fig. 3. – Surface water salinity, temperature and ammonium concentration, at the 3 studied sites (cf 1, 2 & 3 in Fig. 1). Note the break in scale for PRAY salinity.

insolation, air temperature and precipitation; the regression curves (see figure captions) indicate the annual trend] are given on Fig. 2. Wind speed (not illustrated) was often greater than 7 m s^{-1} (mean 9.2 , with maxima above 15), and for very short periods with wind speed less than 5 m s^{-1} (particularly in December 1991). Air temperature was quite temperate and stable (mean 5.9°C , σ 2.3°C) with an annual cycle exhibiting minima from June to September (mean 3°C) and maxima between January-February (mean $7-8^\circ\text{C}$). The insolation and solar irradiation exhibited their minimum and maximum respectively one month before those of the air temperature, with a sharp increase in September-October and a decrease in March. These last variables showed large inter-annual variations, with a deficit in November-December, followed by an exceptionally high solar irradiation at the end of December 1991, coupled with low precipitations. From the data, and the water temperature annual cycle at each site (Fig. 3), we tentatively defined a short spring period (October-November), a summer period (December-February), followed by a long winter period (March-September), keeping in mind that no well-defined delimitation existed between seasons.

The hydrology at each site, in relation to its geomorphology, showed slight differences (Fig. 3). The annual cycle in surface water temperature was

quite similar between PAF and PRAY but with 0.5 to 1°C in difference (PAF site being warmer). The increase in temperature started in late September and reached a maximum in December-January and the decrease started in February, more or less synchronized with the air temperature cycle (Fig. 2). PN was characterized by a variation reduced range and low maximum (around 5°C), but also by an apparent lag in the spring increase, only effective in December-January. Generally, salinities tended to have higher values during austral summer for every site (in accordance with Louanchi *et al.* 2001). However there was larger differences between sites (Fig. 3): large inputs of fresh and cold water at PN (from rivers taking their origin in the Chasles and Lamé glaciers); moderate freshwater inputs at PAF, probably from the Chateau River, with a direct relationship between temperature and salinity $y = 0.1975x + 31.814$ $R^2 = 0.522$); and if the August sampling characterized by a sudden fresh water input is deleted, relative stability at PRAY is noticed (see impact on pigments, Fig. 4).

Ammonium

In such austral environments, silicate and nitrate are present in abundance with silicate rarely being less than $10 \mu\text{M}$ even during the phytoplankton bloom (Louanchi *et al.* 2001, Tréguer *et al.* 1987).

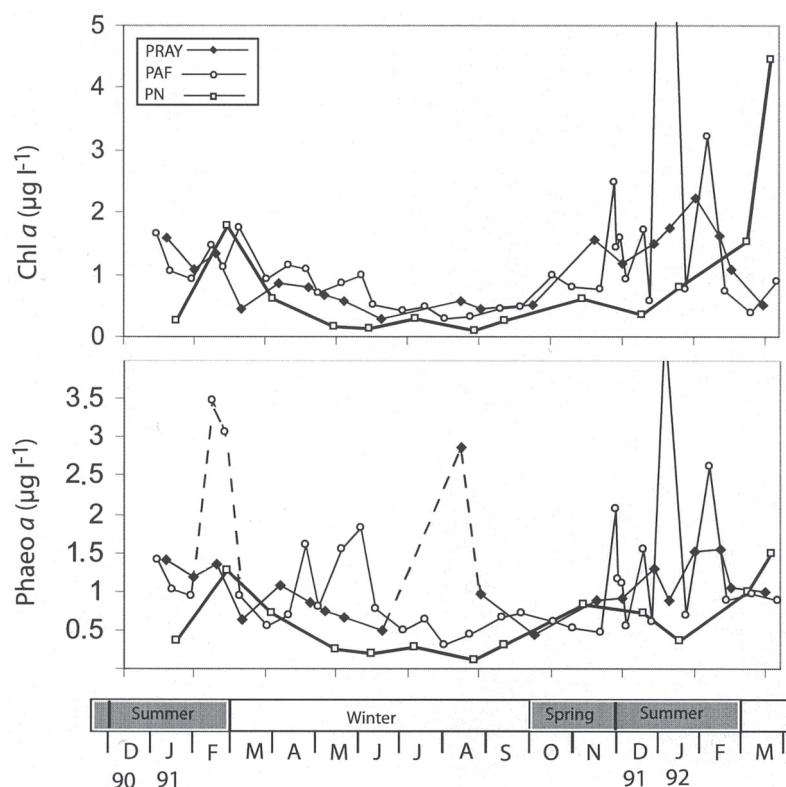


Fig. 4. – Surface water Chl *a* and Phaeo *a* contents, at the 3 studied sites (cf 1, 2 & 3 in Fig. 1). Note the break in scale for PAF in Chl *a* and Phaeo *a*.

Table I. – Comparison between the mean and standard deviation over the 15-month study, and the minimum and maximum recorded, for Chl *a*, Phaeo *a* and NH₄⁺, at the 3 studied sites. Chl *a* and Phaeo *a* expressed in µg l⁻¹. NH₄⁺ expressed in µM.

Site		Chl <i>a</i>	Phaeo <i>a</i>	NH ₄ ⁺
PAF	15-month mean	1.35 ± 1.80	1.21 ± 0.96	1.40 ± 0.66
	Min-Max	0.32-11.73	0.29-4.57	0.48-3.18
PRAY	15-month mean	1.03 ± 0.55	1.09 ± 0.52	2.90 ± 1.49
	Min-Max	0.29-2.24	0.51-1.55	0.67-4.59
PN	15-month mean	0.87 ± 1.20	0.60 ± 0.44	1.26 ± 0.55
	Min-Max	0.13-4.46	0.10-1.48	0.23-1.93

The annual cycle of nitrate, phosphate and silicate in Morbihan Bay was presented in Delille *et al.* (1996), so our study was restricted to NH₄⁺ survey. Large differences appeared between sites (Table I), with a general decrease in concentrations from May to November (Fig. 3). At PN the values were very low in winter (0.23 µM) and regularly reaching a maximum in summer (1.93 µM); at PAF the concentrations were highly variable during the summer, reaching around 2 µM after the bloom; at PRAY, NH₄⁺ exhibited the highest recorded marine values for Kerguelen (up to 5.1 µM in late summer), with lower values at the start of 1991 bloom (0.67 µM).

During the short-time sampling (day-to-day time series, from 15/01 to 21/01/1992) during the 1992

bloom (Table II), the concentrations varied from 1.73 to 3.17 µM. A strong negative relationship occurred between NH₄⁺ and Chl *a* ($y = -1.9374 x + 3.9021$ R² = 0.7482), and also between salinity and NH₄⁺ but to a lesser extent.

Chloropigments

The results concerning chloropigments (Chl *a* and Phaeo *a*) also showed well-defined differences between sites (Figs 4-5; Tabl. II); nevertheless a general trend appeared with low productivity from March to October followed by a more or less intense bloom. PN showed, in winter, the lowest biomasses recorded, and an annual cycle slightly

Table II. – Short term time series in chloropigments, temperature, salinity and NH₄⁺ measured on a daily basis at PAF (January 1992). Mean and σ on quadruplicate samples for pigments, and triplicate samples for NH₄⁺. Mean and σ on the series. Chl *a* and Phaeo *a* expressed in µg l⁻¹. NH₄⁺ expressed in µM. Nd = no data.

Date	15/01	16/01	17/01	18/01	19/01	20/01	21/01	Series	Mean ± σ
Sampling time	14h-14h30	14h30-15h15	16h30-17h15	17h15-17h45	17h30-18h	16h15-18h05	18h-18h30		
Chl <i>a</i>	0.75±0.08	0.51±0.06	0.42±0.01	0.80±0.04	1.02±0.06	0.86±0.02	1.00±0.01		0.88±0.23
Phaeo <i>a</i>	1.68±0.07	0.46±0.05	0.55±0.02	0.43±0.02	0.56±0.03	0.47±0.04	0.62±0.03		1.15±0.45
NH ₄ ⁺	2.09±0.08	2.96±0.36	3.17±0.145	2.22±0.11	2.16±0.035	2.60±0.10	1.73±0.11		1.91±0.51
S‰	32.775	33.484	32.196	nd	33.334	33.416	33.603		33.19±0.54
T°C	9.0	7.2	12.0	7.2	8.0	7.5	8.0		8.5±1.7

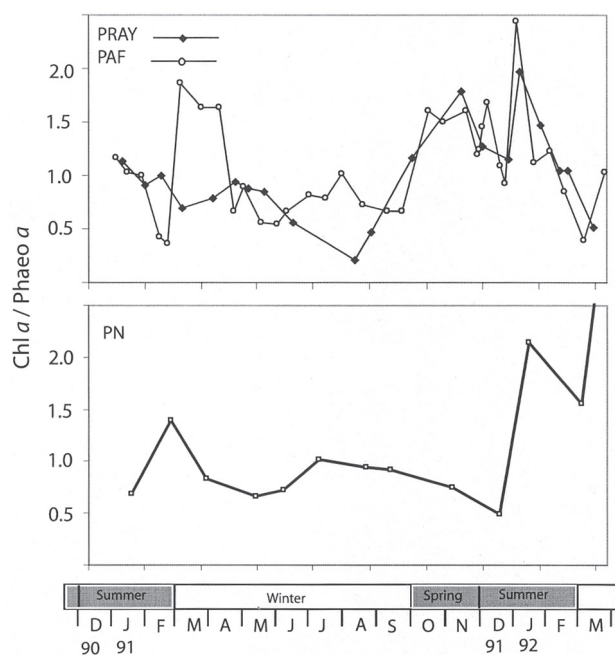


Fig. 5. – Surface water Chl *a* / Phaeo *a* ratio at the 3 studied sites (cf 1, 2 & 3 in Fig. 1).

different from the other sites, the bloom being delayed 2-3 months (Fig. 4). Some high Phaeo *a* values were linked to low salinities, such as at PAF in February 1991 or at PRAY in August 1991 (see dotted lines in Fig. 4) and were probably linked to sediment resuspension, detritic macroalgae particles or terrestrial inputs. The bloom at PRAY showed a regular increase but low concentrations (max. 2.24 $\mu\text{g l}^{-1}$) whereas the PAF bloom was characterized by several “pulsed” short outbursts, alternating with low values. In PAF and PRAY the bloom appeared in the same period (November to February). The Chl *a* / Phaeo *a* ratio (Fig. 5) also showed differences within sites, even if the sampling effort was not the same at each site, the high ratios, more or less representative of a production period, were seen in October-February for PRA and PAF and in January-March at PN, where the ratio was up to 3 in March 1992.

DISCUSSION

Ammonium is poorly documented in such far away environments, due to the lack of scientific equipments and therefore the difficulty of avoiding pollutions. Nevertheless, in the Austral Ocean, ammonium is preferred to nitrate, with a rapid cycling of N as ammonium (Glibert *et al.* 1982, Tréguer & Jacques 1992, Goyens *et al.* 1998). However, interaction between ammonium and nitrate uptake, as well as new and regenerated production strategies and changes, are complex (Dortch 1990, Semeneh *et al.* 1998).

When comparing NH_4^+ data available in the vicinity of Kerguelen (0 to 0.55 μM at the “KERFIX station”; Louanchi *et al.* 2001), the values recorded in the present study were very high, but were comparable to those previously found in the north of the Archipelago (1.7 to 3.9 in Baleiniers Golf coastal stations) whereas the Chl *a* reached 0.8-2 $\mu\text{g l}^{-1}$ (Tréguer 1987). No NH_4^+ data was available for the southern coast of Kerguelen. The present survey showed that at coastal inner sites a gradient appeared, linked to the more or less sheltered position of each site, with low NH_4^+ values at PN and very high at PRAY, nevertheless the general annual trend was comparable to that described in Louanchi *et al.* (2001): increase starting during the bloom period with higher values recorded after the bloom decreased. The high values in PRAY may be linked to the bloom decay, but also bacterial activity related to the degradation of the kelp canopy, and favoured by the sheltered position of the site. The dense macrofauna (particularly polychaete mats in the nearby sediments) may also be responsible for these high ammonium values. A surprising fact is that the phytoplankton biomass at PRAY is lower most of the year than that recorded at PAF. The kelp canopy, forming an impressive biomass [*Macrocystis pyrifera* (Linné) fronds grow 20 cm per day] may compete for nutrient stocks with the phytoplankton, and its degradation may generate high bacterial activity and ammonium formation. However, further investigations are needed to draw conclusions. A survey of heterotrophic bacteria in the water mass was done at “Z station” (Razouls *et al.* 1997) and showed no apparent coupling with temperature or phytoplankton, but survey of heterotrophic bacteria under the dense kelp-covered ecosystem was not available. Nevertheless, the results seem to favour an active recycling of nutrients in the more sheltered sites.

Concerning the standing stocks, the results confirm that productivity was higher in the Kerguelen’s Land coastal waters, but with a great variability. The bloom observed in 1992 in January-February, was more intense than in 1991, probably in relation with higher solar irradiation (Fig. 2). This variability may also be linked to the complex diverse trophic environments. The presence of flourishing mussel beds and dense mats of filter-feeding polychaete in some fjords, as well as intense and punctual outbursts of the copepod *Drepanopus pectinatus* (Razouls & Razouls 1990), or jelly-fish proliferation as noticed at PRAY on the 6 and 24 of January 1992, give proof that the primary productivity was higher a great part of the year in the inner marine indentations of Kerguelen Main Island. From the present results, three different situations can be suggested:

1) The annual phytoplankton cycle previously described at “Z station” (Morbihan Bay) represented one situation. Silicate concentrations, and to

a lesser extent nitrate concentrations, drastically decreased in October, sustaining a probable new phytoplankton production, then increased in February-March (Razouls *et al.* 1997, Delille *et al.* 1996). Our results at PAF confirm this cycle and the short-term sampling provided a proof that the brief peaks of Chl *a* in late summer were related to ammonium decrease, and probably of regenerated origin. Furthermore, such brief and intense phytoplankton blooms (lasting for 24-48 h) also have been observed (pers obs), but not sampled, in the vicinity of PAF, particularly in January 1988 and 1992, giving a greenish coloration (characteristic of chlorophycean and autotrophic flagellate blooms) to the surface water masses.

2) Another productivity pattern was observed in the sheltered fjord enriched with kelp canopy, such as at PRAY, with moderate phytoplankton productivity, regularly lasting from November to February, with high ammonium concentrations probably linked to kelp degradation and associated macrofauna.

3) The third pattern observed, concerned the southern fjord (PN), without kelp canopy, nor proliferating macrofauna, that exhibited a completely different productivity cycle, delayed in time, and with a high Chl *a*/ Phaeo *a* ratio during the bloom.

These observations also confirm that the high coastal productivity of Kerguelen originated in the geomorphology of the Archipelago, with its multiple indentations and fjords, in contrast with the coastal waters around Heard Island where the phytoplankton biomass is low (Tréguer 1987). Furthermore, if it is established that turbulence plays a major role in limiting phytoplankton growth in the offshore coastal waters of Kerguelen ("KERFIX station"), from the present set of data, the same conclusion can be made: the most sheltered inner locations are also the most productive.

A study of the floristic components of each situation described here would be useful to understand the diverse phytoplankton communities and complement the previous report by Hédoïn & Couté (1992) as well as a comparison with the offshore situation where new production dominates (Kopczynska *et al.* 1998, Fiala *et al.* 1998, Louanchi *et al.* 2001). Also of interest would be a study on the local recycling and/or export of these impressive phytoplankton biomasses.

CONCLUSION

During the 15-month survey of the phytoplankton productivity in Kerguelen Main Island coastal waters, a noticeable variability was shown between sites, in relation with shelter and geomorphology. As previously reported, the Morbihan Bay produc-

tivity was higher than at the offshore sites such as "KERFIX station". Nevertheless, if shelter seems to govern the productivity and annual cycle, the kelp cover and dense macrofauna in the inner sheltered fjords are in favour of an active nutrient recycling, an important ammonium accumulation and a probable regenerated production. In less sheltered sites, such as the deep Portes-Noires fjord, that shows a more direct relation with open ocean water masses, the annual cycle of water temperature, as well as productivity and ammonium availability, were delayed 1-2 month and characterized by lower values.

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