Spatial and temporal variation of bacterioplankton in a sub-Antarctic coastal area (Kerguelen Archipelago)

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Abstract

Bacterial abundance and production were measured monthly for one year along cross-shore transects in 3 sub-Antarctic fjords of the Kerguelen Archipelago (seven stations each). Mean values of the 3 most coastal (inside) and most offshore (outside) stations were used to describe the relationship between temperature, phytoplankton biomass, bacterial abundance and bacterial production over a one year annual cycle. The entire sampling protocol was repeated twice during each cruise: once at noon and once at midnight. Over the whole sampling period, the temperature ranged from 2.1 to 7.4 °C, while chlorophyll a concentrations varied by a factor of 10, and bacterial abundance and production varied by factors of 12 and 30, respectively. Within one day, all of these parameters sometimes varied by a factor of 4 between noon and midnight. A clear seasonality was observed for all of the parameters. However, while variations of phytoplankton and bacterial production paralleled those of temperature, bacterial abundance was low in midsummer and maximum in autumn. While no general pattern could be observed from the total data set, spatial gradients could interfere strongly with temporal changes.

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1. Introduction

Because the oceans are a significant sink of anthropogenic CO2, a central objective of many major biological oceanographic programs is to quantify, model and predict, at global and annual scales, the flux of biogenic carbon into deep waters. Bacterial assemblages have the potential to influence food web and biogeochemical cycles in aquatic systems (Cottrell and Kirchman, 2004; Staroscik and Smith, 2004). In coastal areas, production, degradation and export of organic matter are disproportionate compared to the open ocean (Wollast, 1998). Furthermore, ratios of phytoplankton primary production to community respiration exhibit high spatio-temporal variability (Gazeau et al., 2004). Indeed, seasonal changes in growth rates and respiratory demands of aerobic heterotrophic bacteria, which dominate total community respiration, can induce changes from autotrophy to heterotrophy (Hopkinson, 1985; Cho and Azam, 1988; Fuhrman et al., 1989; Griffith et al., 1990; Wiebe et al., 1993; Delille et al., 1995, 1996; Delille, 2003). The information available concerning the patterns of energy flow through the lower food web in polar regions is still scarce and is often contradictory (Anderson and Rivkin, 2001). Bacteria cannot be included convincingly in
scenarios describing trophic interactions of plankton communities.

The upper limit of bacterial abundance in the ocean is set by phytoplankton, but this limit is not always realized (Li et al., 2004). Since high nutrient–low chlorophyll Southern Ocean waters are characterized by high concentrations of inorganic nitrogen and phosphorus, bacterioplankton assemblages seem to be limited by
DOC (Karl et al., 1991; Ducklow et al., 2001). It has also been suggested that a low iron concentration could also be a limiting factor for bacterial growth (Tortell et al., 1996). Reviewing reports of phytoplankton and bacterial abundance and production, Cole et al. (1988) found significant correlations between bacterial and phytoplankton parameters, suggesting the ubiquity of a functional relationship between bacteria and phytoplankton. Since the latter excrete the organic substrates essential for bacterial metabolism, it can be assumed that bacterial dynamics are essentially controlled by phytoplankton dynamics (Smith et al., 1995). However, the model of Cole et al. (1988) is not a general rule in Antarctic seas (Billen and Becquevort, 1991; Fiala and Delille, 1992; Delille et al., 1996; Ducklow et al., 2001). Furthermore, even if the model was valid in the oceans, the situation would likely be more complex in coastal areas due to important sources of non-phytoplanktonic substrates (Ducklow and Kirchman, 1983; Bouvy et al., 1986; Alber and Valiela, 1994; Smith and Benner, 2005).

High latitude oceans account for about 10 to 20% of oceanic carbon production (Berhenfeld and Falkowski, 1997). Although sub-Antarctic data are necessary for the construction of a global carbon budget for the Southern

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**Fig. 2.** *Top:* Spatial distribution of surface seawater temperature in Morbihan Bay (thin black line: noon, thick gray line: midnight). *Bottom:* Seasonal changes in surface seawater temperature (thin black line: outside stations of Morbihan Bay, thick gray line: inside stations of Morbihan Bay, open triangles: outside stations of Recques Bay, gray triangles: inside stations of Recques Bay, open circles: outside stations of Table Bay, gray circles: inside stations of Table Bay).
Ocean, studies providing this data in the sub-Antarctic area have been much less numerous than similar Antarctic studies (Friedmann, 1993; Bernard and Froneman, 2005). Furthermore most of the previous studies of microbial distribution focused on short-term observations in a limited period of time (Lochte et al., 1997; Ducklow et al., 2001; Simon et al., 2004 and references herein). The seasonal variability in plankton biomass is poorly documented due to the scarcity of time series observations carried out over one or several years (Horne et al., 1969; Delille, 1990; Helbling et al., 1995; Moline and Prézelin, 1996; Delille, 2003). However, seasonal changes have to be understood in order to construct accurate carbon budgets (Platt et al., 1992; Priddle et al., 1992; Tréguer and Jacques, 1992). This is particularly true for the Southern Ocean which shows intense temporal variability, perhaps the most extreme seasonality observed anywhere in the world’s oceans (Karl, 1993). Furthermore, variability in plankton biomass at the air–sea interface affects the partial pressure of CO2 and related air–sea CO2 fluxes of the waters surrounding the Kerguelen Archipelago (Delille et al., 2000). The purpose of the research presented here was to document the spatial and temporal distribution of bacterioplankton biomass and production in surface waters of a coastal sub-Antarctic area throughout an entire year. This study was carried out in

Fig. 3. Spatial distribution of chlorophyll a concentration in surface seawater of Morbihan Bay (thin black line: noon, thick gray line: midnight).
the frame of a project aiming to assess CO₂ dynamics in the surface waters of the Kerguelen Archipelago and to estimate related air–sea CO₂ fluxes.

2. Material and methods

This survey was carried out from December 1998 to December 1999 in coastal surface waters of the Kerguelen Archipelago (Fig. 1). Usually, the Kerguelen Archipelago (69°30′E, 49°30′S) is cited in the literature as a sub-Antarctic island. However, from a strict oceanographic point of view, this archipelago is situated either in the Polar Frontal Zone (sub-Antarctica) or in the Permanently Open Ocean Zone (Antarctica) depending on the position of the Polar Front with regard to the archipelago (Delille et al., 2000). Waters of the archipelago are always free of ice. Cross-shore transects were carried out in two fjords and one large bay. Located in the southeast of the archipelago, Morbihan Bay (about 600 km²) opens to the ocean through Royal Pass, which is 12 km wide and 40 m deep. The fjords, Recques Bay and Table Bay, are located north and south of the archipelago, respectively. Recques bay is 14.5 km deep and 2 km wide while Table Bay is 10.5 km deep and 3 km wide and receives water from the Cook glacier.

Water samples were collected at 1 m depth using a Niskin bottle. Temperature was measured soon after sampling using a Hanna thermometer with an accuracy of ±0.2 °C. Other analyses were initiated onboard the
R.V. La curieuse within a few minutes of sample collection.

Water samples for chlorophyll $a$ analysis were prefiltered through a 200 μm mesh filter to remove larger detrital material and larger biota. 1000 mL of seawater were filtered through a Whatman GF/F glass-fibre filter at a vacuum differential of <20 cm Hg. Pigments were extracted in 90% acetone in the dark during at least 2 h (Neveux and Panouse, 1987). Chlorophyll $a$ concentrations were calculated by measurement of fluorescence using a Turner Designs fluorometer which had been calibrated against purified chlorophyll $a$ (Sigma).

Salinity was measured using a Guildline Portasal induction salinometer with an accuracy of ±0.003.

Total bacterial abundance was determined by epifluorescence microscopy (Hobbie et al., 1977).

Direct counts (AODC) were performed using an Olympus BHA microscope with acridine orange staining on a 0.2 μm pore size black Nuclepore filter. A minimum of 500 fluorescing cells with a clear outline and a distinct cell shape were counted under oil immersion (×1000) in a minimum of 10 randomly chosen fields.

Bacterial production was measured via the incorporation of 14C-leucine (Kirchman et al., 1985; Simon and Azam, 1989). Triplicate samples (10 mL) were amended with L-[U14C]-Leucine (specific activity 11.5 GBq mmol$^{-1}$, Amersham, final concentration 80 nmol L$^{-1}$). The samples and killed controls (10 mL water+0.5 mL of 100% TCA) were incubated for 2 h in the dark in flowing seawater tables. Incubations were terminated by the addition of TCA to a final concentration of 5%. In

**Fig. 5. Spatial distribution of bacterial production in surface seawater of Morbihan Bay (thin black line: noon, thick gray line: midnight).**
the same geographic area, during the “Antares” cruise, the saturation level of leucine uptake was reached at slightly over 20 nmol L\(^{-1}\) (Jorma Kuparinen, personal communication).

The results obtained were converted to bacterial carbon production (BCP, g) using the equation:

\[
\text{BCP} = \text{leucine}_{inc} \times \left(\frac{100}{7.3}\right) \times 131.2 \times 0.86
\]

where \(\text{leucine}_{inc}\) is the number of moles of leucine incorporated, 7.3 is the percentage of moles of leucine in protein, 131.2 is the formula weight of leucine, and 0.86 is the conversion factor for converting a gram of protein produced to a gram of carbon. Previous studies showed that this calculation is appropriate in the Southern Ocean (Pedros-Alio et al., 2002; Simon et al., 2004).

After tenfold dilutions in sterile aged seawater, viable heterotrophic platable bacteria were counted using the spread plate method with 2216 E medium (Oppenheimer and ZoBell, 1952, Marine Agar DIFCO). Each dilution was plated in triplicate. After inoculation (0.2 mL), the plates were incubated at 18 °C for 10 days (mesophilic/psychrotrophic assemblages) or 4 °C for 20 days (psychrotrophic/psychrophilic assemblages).

Diel changes were compared by means of paired \(t\)-test. An analysis of variance (ANOVA), conducted in Prism 4.00 (GraphPad), was used to analyse the differences between coastal zone versus offshore waters, and diel changes in specific zones.

**Fig. 6.** Spatial distribution of “psychrotrophic” heterotrophic bacterial abundance in surface seawater of Morbihan Bay (thin black line: noon, thick gray line: midnight).
3. Results

The temperature ranged from 2.1 °C to 7.4 °C over the sampling period (Fig. 2). In Morbihan Bay, salinity usually ranged from 33.42 to 33.68, but in a given transect, the maximum range of variation was 33.28 to 33.68 (February 5).

3.1. Spatial distribution

The spatial distribution of biological parameters of all transects carried out in Morbihan Bay are presented in Figs. 3–7.

Chlorophyll $a$ sometimes varied 10 fold along the same transect (Fig. 3, January 13). The highest values were then observed in the coastal zone (except for the coastal station that was closest to land). However opposite gradients were also observed (November 18 and December 30), and the concentrations were roughly low and constant during winter.

Within a given transect, total bacterial abundance varied less than 10 fold (Fig. 4). The maximum range of variation was observed in autumn (March 15). Total bacterial abundance often decreased with distance from the coast (February 5, August 17 and November 18) but this pattern was not consistent overall.

Leucine incorporation showed strong spatial variation during the warmer periods (Fig. 5). More than tenfold ranges were observed (December 12, January 13, February 5 and November 18). Like for bacterial abundance, opposite gradients were also observed (November 18 and December 30), and the concentrations were roughly low and constant during winter.

Heterotrophic bacterial abundance was then observed in the coastal zone (except for the coastal station that was closest to land). However opposite gradients were also observed (November 18 and December 30), and the concentrations were roughly low and constant during winter.

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![Graphs of temperature and salinity over time](image_url)

Fig. 7. Spatial distribution of “psychrophilic” heterotrophic bacterial abundance in surface seawater of Morbihan Bay (thin black line: noon, thick gray line: midnight).
abundance, there was no clear general pattern. However, the greatest values were often observed in the coastal station that was closest to land.

Within a given transect, psychrotrophic heterotrophic bacterial abundance sometimes varied more than 10 fold (Fig. 6). Despite the clear increasing gradient from the outer stations to the more coastal ones observed on February 5, like for other bacterial parameters, there were no general patterns in the spatial distribution. The spatial distributions of the psychrophilic heterotrophic bacterial assemblage (Fig. 7) paralleled those of the psychrotrophic assemblage.

3.2. Diel changes

In Morbihan Bay, chlorophyll $a$ varied up to 2 fold ($t, p=0.1$) between night and day (Fig. 3, January 13 and February 5), and phytoplankton biomass was lower during the night than during the day.

A comparison of noon and midnight data showed that bacterial abundance tended to be higher during the night than during the day ($t, p<0.05$) at all stations during summer transects (Fig. 4, December to February). Bacterial abundance could be 2 times higher
(t, \( p<0.05 \)) at midnight than at noon, as observed in December (December 12, 1998).

Except for the two transects conducted in December, leucine incorporation was conspicuously higher at midnight than at noon (t, \( p<0.005 \)) and could vary 5 fold (t, \( p<0.05 \)) between night and day (Fig. 5, May 13).

Differences of one order of magnitude between the abundance of the psychrophilic heterotrophic bacteria measured during the night and the day were observed at some stations (Fig. 7, December 12). The corresponding range was only of 5 fold for less psychrophilic bacteria (Fig. 6). Despite this difference, there was a conspicuous similarity between the data obtained under the 2 different incubation temperatures. There was no clear overarching pattern. Heterotrophic bacterial abundance was sometimes higher (t, \( p<0.01 \)) during the day (April 12) and, at other times, during the night (June 12). The two data sets were merged to compute seasonal averages.

### 3.3. Seasonal changes

For each transect, we averaged data from the 3 most coastal stations (inside) and offshore stations (outside) in order to distinguish clear seasonal trends. Results are shown in Fig. 8.

Chlorophyll \( a \) showed clear seasonal variation with maximal values occurring in the summer (January) and minimal values in winter. Chlorophyll \( a \) showed little contrast between coastal and offshore stations (ANOVA, \( p=0.17 \)). In the coastal zone, total annual ranges were 0.15±0.03/2.77±1.48 µg L\(^{-1} \) at noon and 0.11±0.08/1.38±0.47 µg L\(^{-1} \) at midnight. Corresponding values for offshore stations were 0.18±0.04/1.15±0.47 µg L\(^{-1} \) at noon and 0.20±0.08/1.19±0.53 µg L\(^{-1} \) at midnight. In the coastal zone, chlorophyll \( a \) varied 18 fold at noon and only 6.6 fold at midnight, and was larger at noon than at midnight (ANOVA, \( p<0.05 \)). In contrast, chlorophyll \( a \) varied less than 6 fold in the offshore zone with no significant diel changes.

The seasonal pattern of bacterial production was rather similar to that of chlorophyll \( a \), with maximal values occurring in the summer and minimal values in the winter. In the coastal zone, total annual ranges were 44±17/394±156 ng C L\(^{-1} \) h\(^{-1} \) at noon and 82±29/648±209 ng C L\(^{-1} \) h\(^{-1} \) at midnight. Corresponding values were 27±15/307±30 at noon and 45±14/336±106 ng C L\(^{-1} \) h\(^{-1} \) at midnight in the offshore zone. In Morbihan Bay, bacterial production was higher in the coastal zone than offshore (ANOVA, \( p<0.05 \)), and higher at midnight than at noon (ANOVA, \( p<0.005 \)).

The seasonal pattern of total bacterial abundance was more complex. A first maximum was observed in January, and then minimal values were measured in late summer (late January/February). A first increase was observed from February to June, followed by a small decrease in July and August. A second peak of abundance was observed in November. Total abundance was higher in the coastal zone than in the offshore zone (ANOVA, \( p<0.05 \)). Total annual abundance ranged from 1.8×10\(^5 \)±7.3×10\(^4 \) to 2.4×10\(^6 \)±2.5×10\(^5 \) cells mL\(^{-1} \) at noon and from 4.4×10\(^5 \)±1.0×10\(^4 \) to 1.7×10\(^6 \)±3.1×10\(^5 \) cells mL\(^{-1} \) at midnight. Corresponding values in the offshore zone ranged from 1.3×10\(^5 \)±6.2×10\(^4 \) to 1.4×10\(^6 \)±3.2×10\(^5 \) at noon and from 2.0×10\(^5 \)±4.2×10\(^4 \) to 1.8×10\(^6 \)±1.0×10\(^4 \) cells mL\(^{-1} \) at midnight. Thus, total bacterial abundance varied 13 fold at noon in the coastal zone and only 3.9 fold at midnight in the same area. In the offshore zone, total bacterial abundance varied 11 fold at noon and 10 fold at midnight.

The seasonal pattern of heterotrophic bacterial abundance differed greatly from that of temperature, chlorophyll \( a \) and bacterial production. Several small growth phases could be distinguished. However, minimal values were generally observed in the summer, and maximal values in the winter. At noon, heterotrophic bacterial abundance varied 16 fold in both coastal and offshore zones, while at midnight it varied 28 fold in the coastal zone and 14 fold in the more offshore area.

### 4. Discussion

The highest chlorophyll \( a \) values observed during the survey (2.77 µg L\(^{-1} \)) were lower than the values obtained previously during spring blooms in a coastal station of Morbihan bay (generally between 7 and 20 µg L\(^{-1} \), with a maximum around 50 µg L\(^{-1} \), Delille et al., 1996, 2000) but were of the same magnitude as those observed around sub-Antarctic and Antarctic islands (Perissinotto et al., 1992; Whitehouse et al., 1993). In contrast, the data collected from 1990 to 1994 at the Kerfix station located in the Indian sector of the Southern Ocean, southwest off Kerguelen Archipelago, showed lower concentrations of phytoplankton with a maximum of 1.2 µg L\(^{-1} \) (Fiala et al., 1998). In the present study, chlorophyll \( a \) varied 18 fold between winter and summer. This seasonal range is far below that observed in Antarctica by Anderson and Rivkin (2001). They reported a 1000-fold increase of chlorophyll \( a \) in McMurdo Sound between late August and early January. Even if our data correspond to mean values and thus might underestimate possible extreme variations, this observation highlights the differences between Antarctic and sub-Antarctic conditions. Even if the maximum values of chlorophyll \( a \) concentrations reported in McMurdo Sound (4 to 6 µg L\(^{-1} \)) are higher
than the values observed around the Kerguelen Islands during this study, the major difference lies in the minimal values, which were much lower in Antarctica, probably due to the sea-ice cover that is always absent in Kerguelen region. Using an average C:chl a ratio of 35, the phytoplankton biomass ranges from 4 to 100 μg C L⁻¹. However, C:chl a ratios between 40 (Li et al., 1993) and 89 (Eppley et al., 1988) are commonly observed in open-sea environments (Pedros-Alio et al., 1999). If higher C:chl a ratios were used, phytoplankton biomass values would increase and bacterial to phytoplankton biomass ratios would decrease accordingly.

In studies of carbon dynamics in aquatic microbial communities, the ability to convert bacterial abundance to carbon is needed in order to calculate bacterial biomass. Considering variability due to differences in bacterial species composition and bacterial growth conditions, it is not surprising to observe a wide spectrum of conversion factors. As a consequence of the low correlation between carbon per cell and cell volume, a constant cell mass would seem to be a logical choice in estimating bacterial biomass (Berger et al., 1995; Trousselier et al., 1997). Cell mass is, however, also subject to controversy. If, for some specific species, cell mass is quite constant during cell volume decreases associated with starvation (Trousselier et al., 1997), cell mass will remain dependent on cell volume for an assemblage of different species (Gazol et al., 1995; Pernthaler et al., 1996; Theil-Nielsen and Søndergaard, 1998). Considering all available observations, the extreme values of bacterial cell mass will be in the range of 20 to 120 fg C cell⁻¹. Using a median average bacterial cell mass of 60 fg C cell⁻¹ (Bjørsen, 1986; Trousselier et al., 1997; Delille, 2003), bacterial biomass would range from 8 to 15 μg C L⁻¹. This biomass is relatively high compared to the data available for the open Southern Ocean (Hodson et al., 1981; Cota et al., 1990; Goeyens et al., 1991; Delille, 1992, 2003), but is consistent with the values reported in the Bransfield Strait (4 to 28 μg C L⁻¹, Karl et al., 1991, 8 to 34 μg C L⁻¹, Vosjan and Olanczuk-Neyman, 1991), the southern Antarctic Pacific zone (9 to 82 μg C L⁻¹, Sazhin, 1993) and the Terre Adélie coastal area (1 to 30 μg C L⁻¹, Delille, 1993). Despite the uncertainties related to the use of questionable conversion factors, phytoplanktonic biomass seems to dominate the bacterial biomass in the surface coastal waters of the Kerguelen Archipelago. This is in contrast with the situation observed at Kerfix station in the offshore waters south–west of the archipelago, where bacterial biomass exceeds photosynthetic biomass (Delille, 2003). These results agree well with the review of Gazol et al. (1997) that reports that open-ocean communities support significantly more heterotrophic biomass in the upper layers than do coastal communities for a given autotrophic biomass.

Bacterial production is secondary production, or the synthesis of bacterial biomass, primarily from organic processors with some inorganic nutrients. The net effect is to move organic matter from one pool to another (Ducklow, 2000). In the Antarctic polar frontal region, Simon et al. (2004) reported bacterial production values ranging between 9 and 40 ng C L⁻¹ h⁻¹ during summer and autumn (December to May). The higher values observed in the coastal zone of Kerguelen Archipelago could be related to both a higher temperature and a larger availability of nutrients.

Salinity changes were too small to explain the differences observed in biological parameters. Many other factors act to control bacterial activity, two of which are temperature and substrate availability. The relative importance of these two factors is not well understood (Hoch and Kirchman, 1993). Substrate concentration and temperature interact in all bacterial populations at all temperatures and substrate concentrations (Pomeroy and Wiebe, 2001). The majority of the Antarctic microbial communities are of psychrotolerant types, which are able to grow at 0 °C though optimum temperatures are >20 °C (Delille and Perret, 1989); even the small proportion of obligate psychrophiles have optimum temperatures greater than the environmental temperature. Lowered affinity for substrates will limit growth at low temperatures (Nedwell, 1999). However, temperature has been reported to have only a rather limited influence on Antarctic and sub-Antarctic bacterioplanktonic populations (Delille et al., 1988; Vincent, 1988; Delille and Perret, 1989; Fukunaga and Russell, 1990; Vosjan and Olanczuk-Neyman, 1991; Nedwell and Rutter, 1994). The similarity between the distributions of psychrophilic and psychrotrophic heterotrophic bacteria observed in the present data set confirm this assumption. Important regulating factors of the sub-Antarctic bacterial communities are related to the available trophic sources (Delille and Bouvy, 1989; Delille and Perret, 1991). The bacterial assemblage in the Kerguelen coastal area showed strong seasonality. Both abundance and production varied with time but their variations were not parallel. Production reached a maximum in January, when bacterial abundance is at its lowest. In a temperate estuary, Coffin and Sharp (1987) observed that while bacterial production remained high over the summer months, bacterial abundance was kept low by microflagellate grazing. In the Arctic Ocean, Anderson and Rivkin (2001) reported that even if grazing losses of bacteria were insignificant immediately before and after the phytoplankton bloom, microzooplankton...
could consume 90% of local bacterial production. Seasonal variability could include periods of top-down and periods of bottom-up regulation (Gazol, 1994). Bacterivorous communities were not quantified in this study, but they may have contributed to the low summer bacterial abundance. In addition to grazing, the reduced rates of fall bacterial production may result from bacterioplankton having consumed enough of the available organic carbon to become substrate limited. Heterotrophic bacterial abundance is only representative of culturable bacteria, though it is a useful bacterial indicator corresponding to a small group of active bacteria that react immediately to the changes in their nutrient supply (Delille and Bouvy, 1989; Rheinheimer et al., 1989). The large development of heterotrophic assemblages during autumn and winter observed in the present study is thus a clear indication of the availability of organic substrates. Temperature is probably the most important factor regulating bacterial production during this period.

In contrast, the diel variations of temperature were certainly too small to explain the corresponding changes of bacterial biomass and production. Diel vertical migration of zooplankton has been reported in numerous areas of the ocean, and such migration could have an impact on bacterivory. Algal metabolism (phytoplankton or macroalgae) obviously change between day and night (Mague et al., 1980). Variation in DOC excretion rate must play an important regulating role in the diel variation of bacterial parameters. Diel variability of the growth of heterotrophic planktonic bacteria has been previously related to changes in phytoplankton and zooplankton activity (Riemann and Sondergaard, 1984; Wheeler et al., 1989; Delille et al., 1997). No consistent pattern in the diel bacterial activity, however, was observed in these studies. This holds true in the present study. This is presumably due to the fact that relationships between diel changes of phytoplankton, zooplankton and bacterioplankton activity are intricate and differ between aquatic environments. Short-term changes in bacterial abundance might be explained by a tight coupling to photosynthetic processes as well as by changes of water masses. Advection during diurnal cycles is a possible explanation for bacterial variability (Karner and Rassoulzadegan, 1995; Delille et al., 1997).

Concentrations of particulate and dissolved organic carbon vary spatially. This variation is driven by the inputs from both plankton and terrestrial sources. Plankton-derived organic matter is enriched in protein and labile polysaccharides, whereas terrestrial organic matter contains humic material and structural polysaccharides, such as cellulose and lignin, which are relatively resistant to mineralization by microbial processes (Delille and Perret, 1991; Benner, 2002). Terrestrial material does not play a major role because of the complex detrital processing cycle that would largely dissipate the carbon and energy (Peterson et al., 1994). The abundance and composition of POM and DOM could have short-term impacts on bacterial metabolism. Rates of constitutive enzymes can respond quite rapidly, on the order of minutes to hours, whereas days may be required for a rare ribotype to increase sufficiently in abundance in order to significantly affect DOM mineralization at the community level (Findlay, 2003).

Between these two extremes, the induction and synthesis of new enzymes occurs within hours (Kirchman et al., 2004). The response of bacteria to phytoplankton or any other organic matter availability changes is not instantaneous; rather, bacterial activity is dependent upon previous activity of phytoplankton or allochthonous organic inputs. The monthly sampling regime used in the present study would be therefore insufficient to capture all the relationships between bacteria and their trophic sources. Indeed, even a weekly sampling regime might be insufficient to capture all the relationships between phytoplankton and bacteria (Staroscik and Smith, 2004).

5. Conclusion

Temperature variations are larger in sub-Antarctic coastal area than in the surrounding open oceanic zone, with obvious consequences on the microbial loop. In contrast, the range of seasonal variations of phytoplankton is smaller in the sub-Antarctic coastal area than in the Antarctic one. This is probably related to the absence of ice cover. In Kerguelen fjords, low winter temperature seems to limit bacterial production and, to a lesser extent, bacterial abundance.

Changes in bacterial abundance are not necessarily related to changes in bacterial growth (Billen et al., 1990). Steady-state abundance is the balance between growth and mortality; hence, the loss rates due to bacterivory and viral lysis must be similar to cell growth. Even a small imbalance may result in large oscillations in bacterial populations (Anderson and Rivkin, 2001). Short-term changes could be as large as long term seasonal changes, and interactive effects of temperature and substrate supply could occur (Pomeroy and Wiebe, 2001). The data available do not allow us to decipher the main regulating factor. It is therefore likely that grazing, viral lysis, substrate availability and temperature adaptation all play a role in the regulation of bacterial communities.
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