Spatial and temporal variations of bacterioplankton in a subAntarctic coastal area (Kerguelen Archipelago)

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Abstract

Bacterial abundance and production were measured monthly for one year along cross-shore transects (seven stations each) carried out in 3 subAntarctic fjords of the Kerguelen Archipelago. 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 an annual cycle. All the sampling protocol was repeated two times during each cruise: at noon and midnight. During the entire sampling period temperature ranged from 2.1 to 7.4 °C, chlorophyll a concentrations varied by a factor of 10, bacterial abundance by a factor of 12 and bacterial production by a factor of 30. Over one day, all these parameters could vary by a factor of 4 between noon and midnight. A clear seasonality was observed for all the parameters. However, while variations of phytoplankton and bacterial production paralleled those of temperature, bacterial abundance is 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.

Keywords: Phytoplankton, Bacterioplankton, Seasonal changes, Diel changes, Spatial distribution, Kerguelen Archipelago, subAntarctica.

1. Introduction

Because the oceans are a significant sink for anthropogenic CO_2, a central objective of major biological oceanographic programs is to quantify, model and predict, at global and annual scales, the flux of biogenic carbon to 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 the coastal area, production, degradation and export of organic matter are disproportionate compared to the open ocean (Wollast, 1998). Furthermore, phytoplankton primary production to community respiration ratios exhibited 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, 2003, Delille et al., 1995, 1996). The information available concerning the patterns of energy flow through the lower food web in polar regions is still scarce and 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 everywhere set by phytoplankton, but the 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), while it has also been suggested that low concentration of iron could 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 sea (Billen and Becquevort, 1991, Fiala and Delille 1992, Delille et al. 1996, Ducklow et al., 2001).

Furthermore if the model could be valid in the oceans, in coastal areas the situation is likely to be more complex 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 (Behrenfeld and Falkowski, 1997). Although subAntarctic data are necessary for the construction of a global carbon budget for the Southern Ocean, investigations in the subAntarctic area have been much less numerous than similar Antarctic studies (Friedmannn, 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, Duclow 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, 2003 Helbling et al., 1995, Moline and Prézelin, 1996). 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 with intense temporal variability, perhaps the most extreme seasonality observed anywhere in the world ocean (Karl, 1993). Furthermore, variability in plankton biomass at the air-sea interface affects the partial pressure of CO_2 and related air-sea CO_2 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 coastal subAntarctic area during a whole year. This study was carried out in the frame of a project aiming to assess CO_2 dynamics in the surface waters the Kerguelen archipelago and estimate related air-sea CO_2 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 subAntarctic island However, from a strict oceanographic point of view, this archipelago is situated either in the Polar Frontal Zone (Sub-Antarctica) or Permanently Open Ocean Zone (Antarctica) depending of

the position of the Polar Front with regards 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, the Morbihan Bay (about 600 km²) opens to the ocean through the Royal Pass, which is 12 km wide and 40m 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 3km 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 *R.V. La curieuse* within a few minutes after sample collection.

Water samples for chlorophyll *a* analysis were prefiltered through a 200 µm mesh filter to remove larger detrital material and the larger biota. 1000 mL of seawater were filtered through a Whatman GF/F glass-fibre filters at a vacuum differential < 20 cm Hg. Pigments were extracted in 90 % acetone in the dark at least two hours (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 were determined by epifluorescence microscopy (Hobbie et al., 1977). Direct counts (AODC) were performed using an Olympus BHA microscope with acridine orange staining onto a 0.2 µm pore size black Nuclepore filter. A minimum of 500 fluorescing cells with a clear outline and definite cell shape were counted under oil immersion (x 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 the same geographic area, during “Antares” cruise, the saturation level of leucine uptake was reached slightly above 20 nmol L^{-1} (Jorma Kuparinen, personal communication).

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

$BCP = leucine_{inc} \times (100/7.3) \times 131.2 \times 0.86$

where $leucine_{inc}$ = moles of leucine incorporated, 7.3 = mol% of leucine in protein, 131.2 = formula weight of leucine, and 0.86 = conversion of 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 were 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. Measures analysis of variance (ANOVA) in Prism 4.00 (GraphPad) was used to analyse the differences between costal zone and offshore waters, and diel changes in specific zones.

3. Results

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

3.1. Spatial distribution

Spatial distribution of biological parameters of all transects carried out in the Morbihan Bay are presented in Fig. 3,4,5,6 & 7.

Chlorophyll a could vary 10 fold along a same transect (Fig.3, January 13). The highest values were then observed in the coastal zone (excepted the most coastal station). However opposite gradient 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). Maximum range of variation was observed in autumn (March 15).

Total bacterial abundance often decreased with the distance from the coast (February 5, August 17 and November 18) but this is not a general pattern.
Leucine incorporation showed strong spatial variation during the warmer periods (Fig.5). More than ten fold ranges were observed (December 12, January 13, February 5 & November 18). Like for bacterial abundance there was no clear general pattern. However, the greatest values were often observed in the more coastal station.
Within a given transect psychrotrophic heterotrophic bacterial abundance could vary more than 10 fold (Fig. 6). Despite the clear increasing gradient from the outer stations to the more coastal ones observed in 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 one.

3.2 Diel Changes

In the Morbihan Bay, chlorophyll *a* could vary 2 fold (t, $p=0.1$) between night and day (Fig. 3, January 13 & February 5). In both case phytoplankton biomass was lower during the night than during the day.
A comparison of noon and midnight data showed that bacterial abundance tend to be higher during the night relative to daytime (t, $p < 0.05$) at any given station of 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).
Excepted for the two transects realized 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).
One order of magnitude changes in the more psychrophilic heterotrophic bacterial abundance could occur at some stations between night and day (Fig. 7, December 12). The corresponding range was only of 5 fold for less psychrophilic ones (Fig. 6). Despite this difference there was a conspicuous resemblance between the data obtained under the 2 different incubation temperatures. There was no clear general pattern. Heterotrophic bacterial abundance could be higher (t, $p < 0.01$) during the day (April 12) or during the night (June 12). The two data sets were merged to compute seasonal averages.

3.3 Seasonal changes

For each transect, we have averaged the data of 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 variations with maximal values in 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 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 offshore. 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 not significant diel changes.

The seasonal pattern of bacterial production was rather similar to the one of chlorophyll *a*, with maximal values in summer and minimal ones in 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 the Morbihan Bay, bacterial production was higher in the coastal zone than offshore (ANOVA, $p < 0.05$), and was 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 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 $1.8 \times 10^5 \pm 7.3 \times 10^4$ to $2.4 \times 10^6 \pm 2.5 \times 10^5$ cells mL^{-1} at noon and from $4.4 \times 10^5 \pm 1.0 \times 10^5$ to $1.7 \times 10^6 \pm 3.1 \times 10^5$ cells mL^{-1} at midnight. Corresponding values in offshore zone ranged from $1.3 \times 10^5 \pm 6.2 \times 10^4$ to $1.4 \times 10^6 \pm 3.2 \times 10^5$ at noon and from $2.0 \times 10^5 \pm 4.2 \times 10^4$ to $1.8 \times 10^6 \pm 1.0 \times 10^4$ 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 summer and maximal values in winter. At noon heterotrophic bacterial abundance varied 16 fold in both coastal and offshore zone 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 $\mu g\ L^{-1}$) were lower than the values obtained previously during spring blooms in a coastal station of the Morbihan bay (generally between 7 and 20 $\mu g\ L^{-1}$, with a maximum around 50 $\mu g\ L^{-1}$, Delille et al., 1996, Delille et al., 2000) but were of the same magnitude as those observed around subAntarctic and Antarctic islands (Perissinotto et al., 1992, Whitehouse et al., 1993). In contrast, the data collected from 1990 to 1994 at the station Kerfix located in the Indian sector of the Southern Ocean, southwest off Kerguelen Archipelago showed lower concentration of phytoplankton with a maximum of 1.2 $\mu g\ L^{-1}$ (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 probably underestimate possible extreme variations, this observation highlights the differences between Antarctic and subAntarctic conditions. Even if the maximum values of chlorophyll *a* concentrations reported in McMurdo Sound (4 to 6 $\mu g\ L^{-1}$) are higher that the values observed around 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 phytoplanktonic biomass ranges from 4 to 100 $\mu g\ C\ L^{-1}$. However, C:chl *a* ratio between 40 (Li et al., 1993) and 89 (Eppley et al., 1988) are commonly used in open-sea environment (Pedros-Alio et al. 1999). If higher C:chl *a* ratio 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 crucial 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 for bacterial biomass estimation (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), for an assemblage of different species cell mass will remain dependent on cell volume (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 fgC cell-1. Using a median average bacterial cell mass of 60 fg C cell-1 (Bjørnsen 1986, Delille, 2003, Trousselier et al. 1997) 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 are 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 one in the surface coastal waters of the Kerguelen Archipelago. This contrast with the situation observed at Kerfix station in the offshore waters south-western of the archipelago, where bacterial biomass exceeds phototrophic biomass (Delille, 2003). These results agree well with the review of Gasol 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: 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 higher temperature and 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 able to grow at 0°C but with optimum temperatures >20°C (Delille and Perret, 1989); while even the small proportion of obligate psychrophiles have optimum temperatures greater than the environmental temperature. Lowered affinity for substrates will limit growth at low temperature (Nedwell 1999). However, temperature has been reported to have only a rather limited influence on Antarctic and subAntarctic 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 similude between the distributions of psychrophilic and psychrotrophic heterotrophic baccteria observed in the present data set confirm this assumption. Important regulating factors of the subAntarctic 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 reaches a maximum in January while bacterial abundance is at the 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 phytoplankton bloom, microzooplankton could consume 90% of local bacterial production. Seasonal variability could include periods of top-down and periods of bottom-up regulation (Gasol, 1994). Bacterivory 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 are only representative of

culturable bacteria, however, 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 assemblage 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 regulating factor of 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 as been reported in numerous area of the ocean. Such migration could have an impact on bacterivory. Algal metabolism (phytoplankon or macroalgae) obviously change between day and night (Mague et al., 1980). Variation in DOC excretion rate must play an important regulating role in 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 Søndergaard, 1984, Wheeler et al., 1989, Delille et al., 1997). No consistent pattern in the diel bacterial activity, however, can be deduced from 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 would 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 (days) 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 before to affect

significantly 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 allochtonous organic inputs. The montly sampling 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 may be insufficient to capture all the relationships between phytoplankton and bacteria (Staroscik and Smith, 2004).

5. Conclusion

Temperature variations are larger in subAntarctic 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 subAntarctic 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 in a lesser extend 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. 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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Figure captions:

Fig.1 Location of the sampling stations in the Kerguelen Archipelago.

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).

Fig.3 Spatial distribution of chlorophyll *a* concentration in surface seawater of the Morbihan Bay (thin black line : noon, thick gray line : midnight).

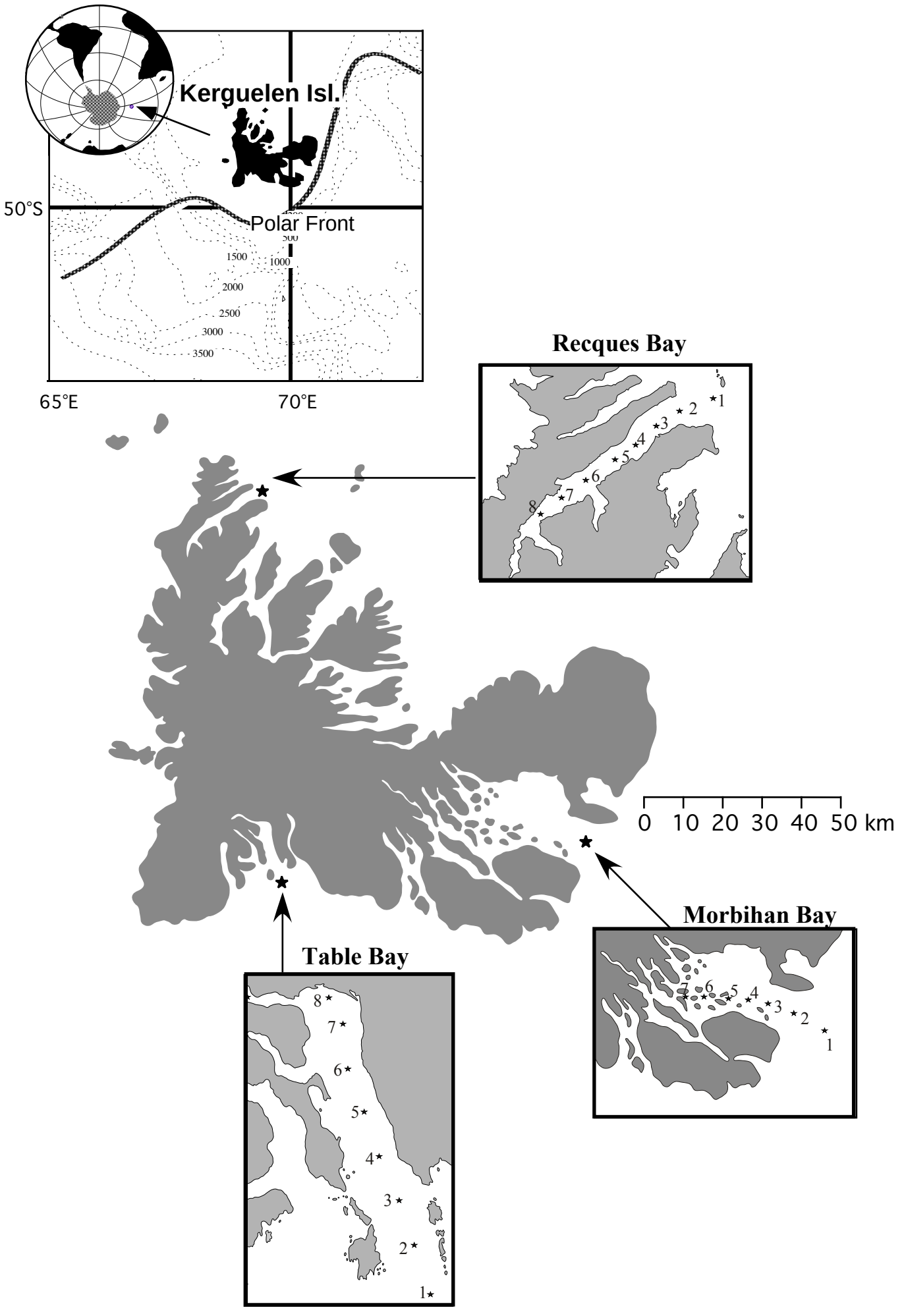
Fig.4 Spatial distribution of total bacterial abundance in surface seawater of the Morbihan Bay (thin black line : noon, thick gray line : midnight).

Fig.5 Spatial distribution of bacterial production in surface seawater of the Morbihan Bay (thin black line : noon, thick gray line : midnight).

Fig.6 Spatial distribution of "psychrotrophic" heterotrophic bacterial abundance in surface seawater of the Morbihan Bay (thin black line : noon, thick gray line : midnight).

Fig.7 Spatial distribution of "psychrophilic" heterotrophic bacterial abundance in surface seawater of the Morbihan Bay (thin black line : noon, thick gray line : midnight).

Fig.8 Seasonal changes in chlorophyll *a*, total bacterial abundance, bacterial production and heterotrophic bacterial abundance (thin black line : outside stations of Morbihan Bay, thick gray line : inside stations of Morbihan Bay, open triangles : outside stations of the Recques Bay, gray triangles : inside stations of Recques Bay, open circles : outside stations of the Table Bay, gray circles : inside stations of the Table Bay)


Kerguelen Isl.
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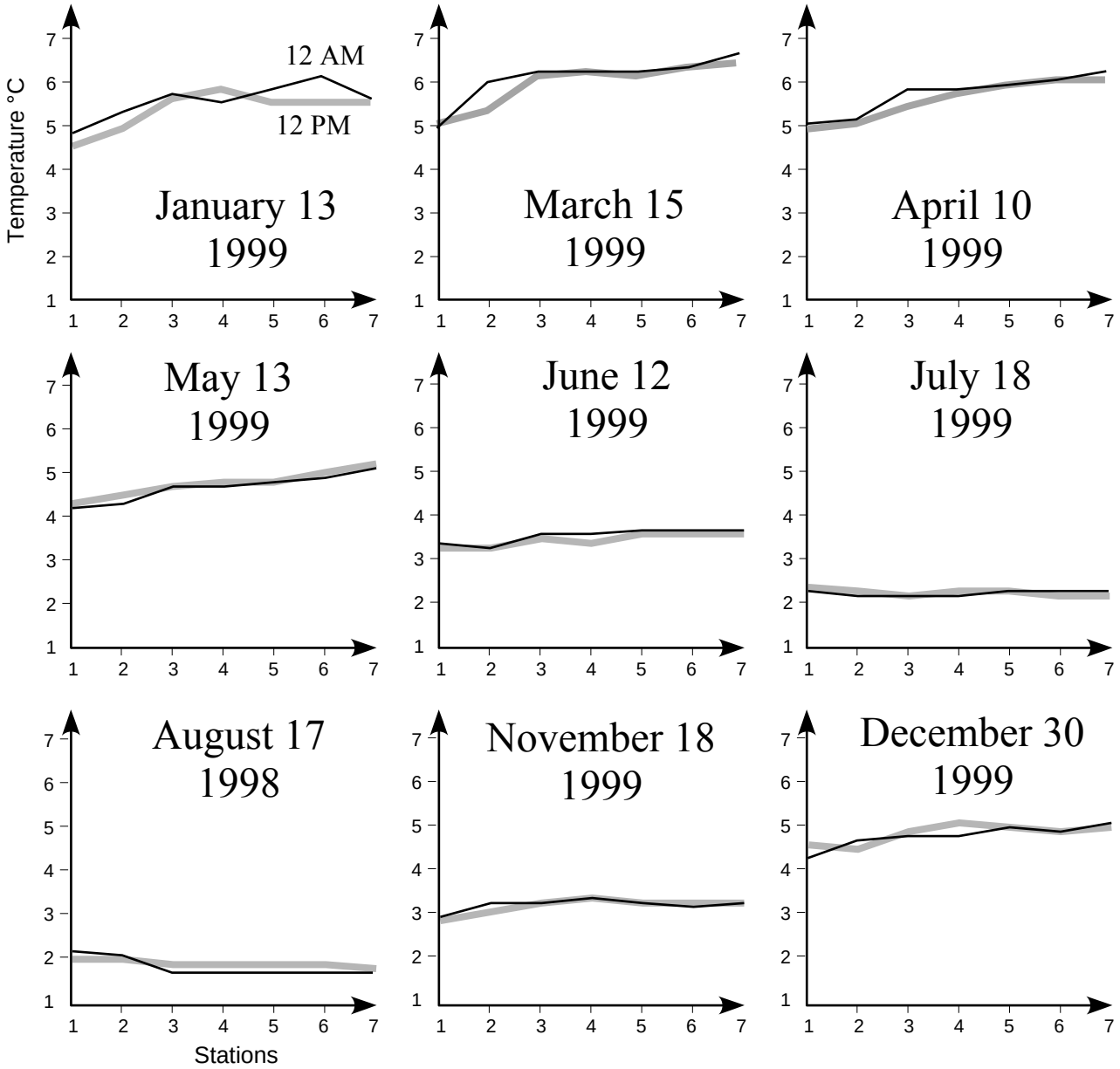
Temperature °C
12 AM
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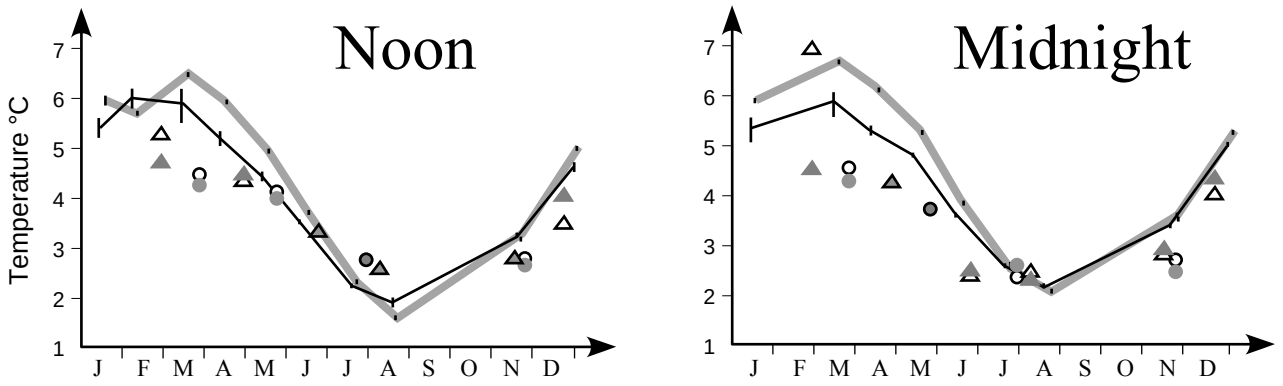
Temperature °C
Noon
Midnight
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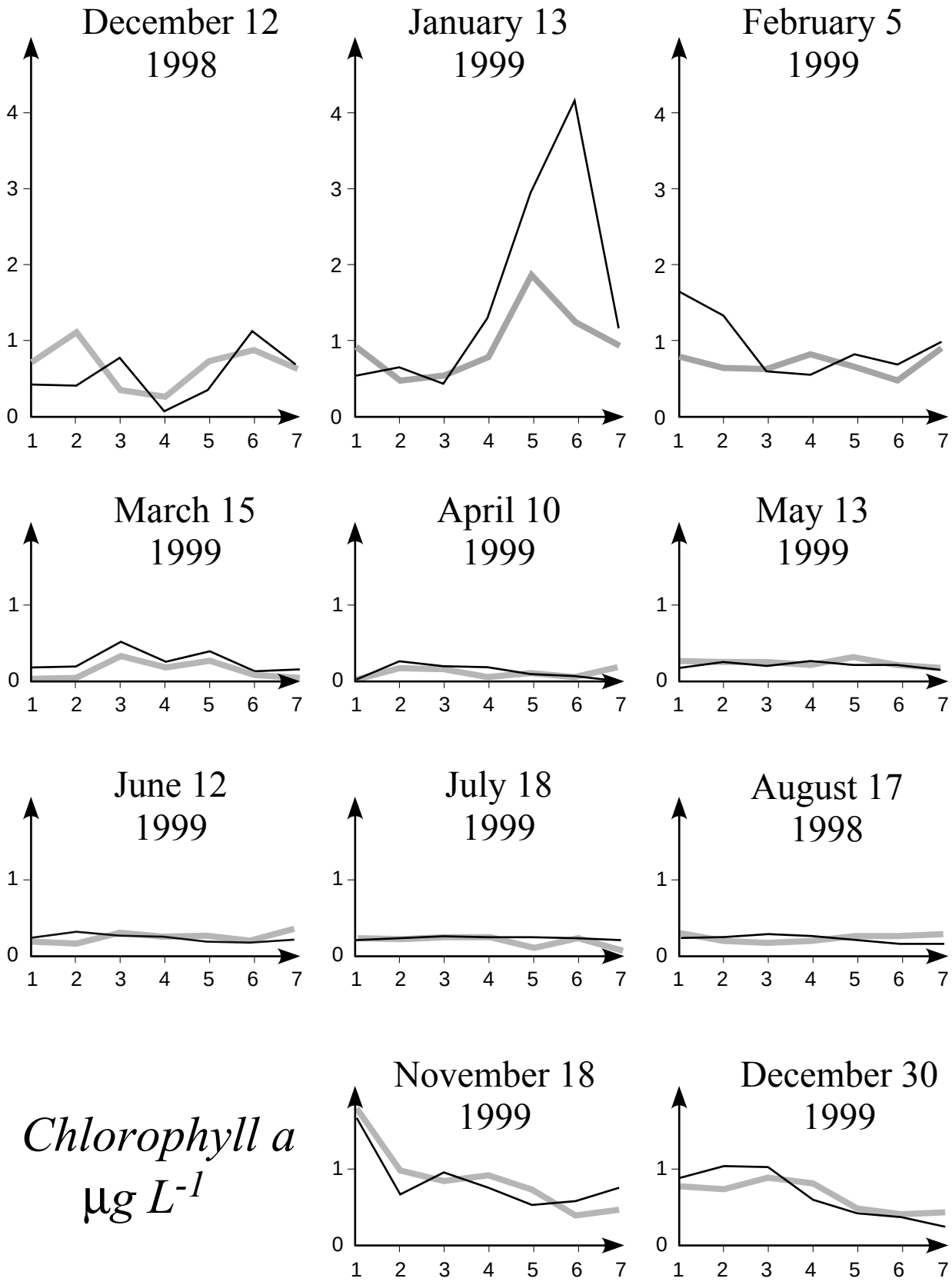
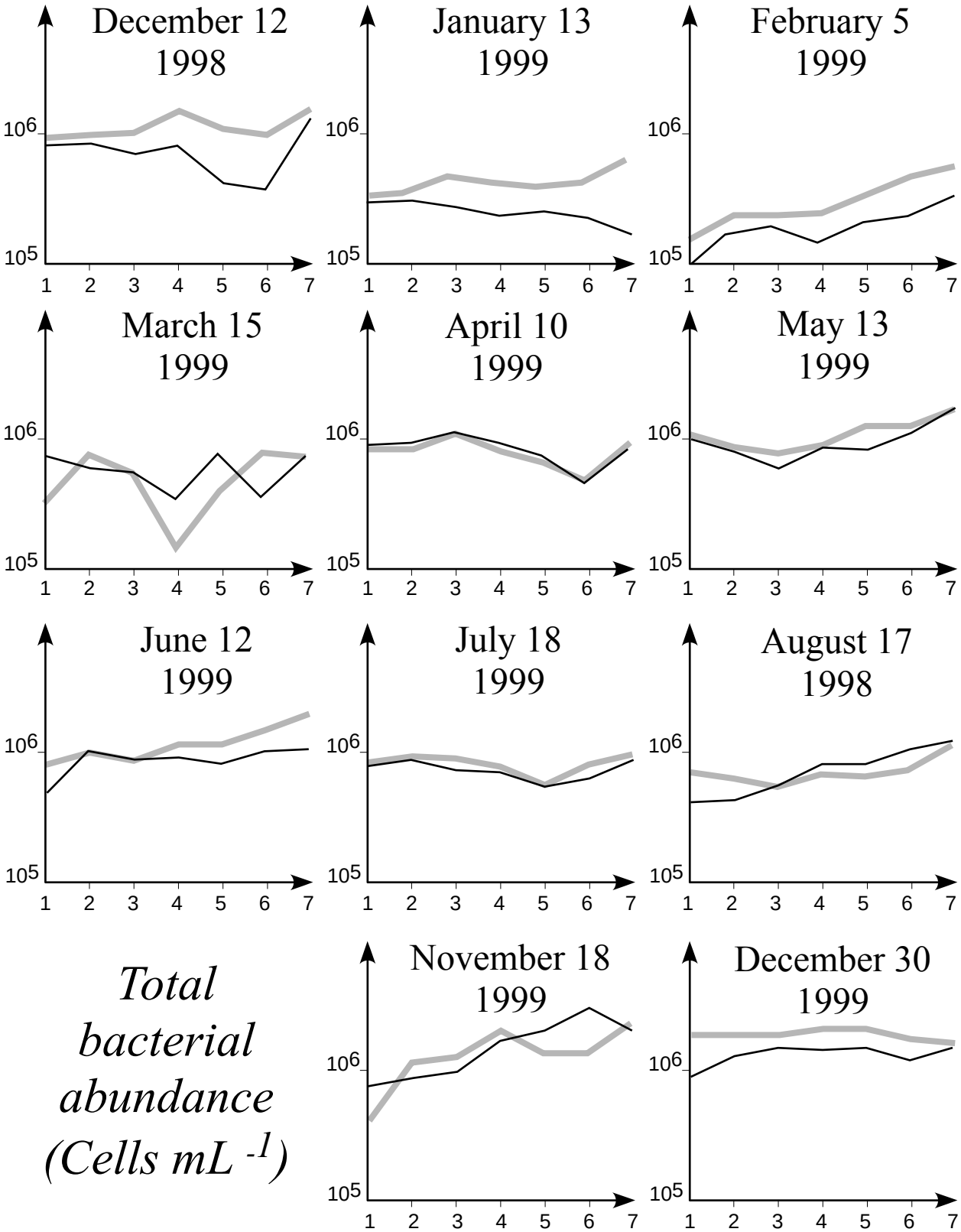
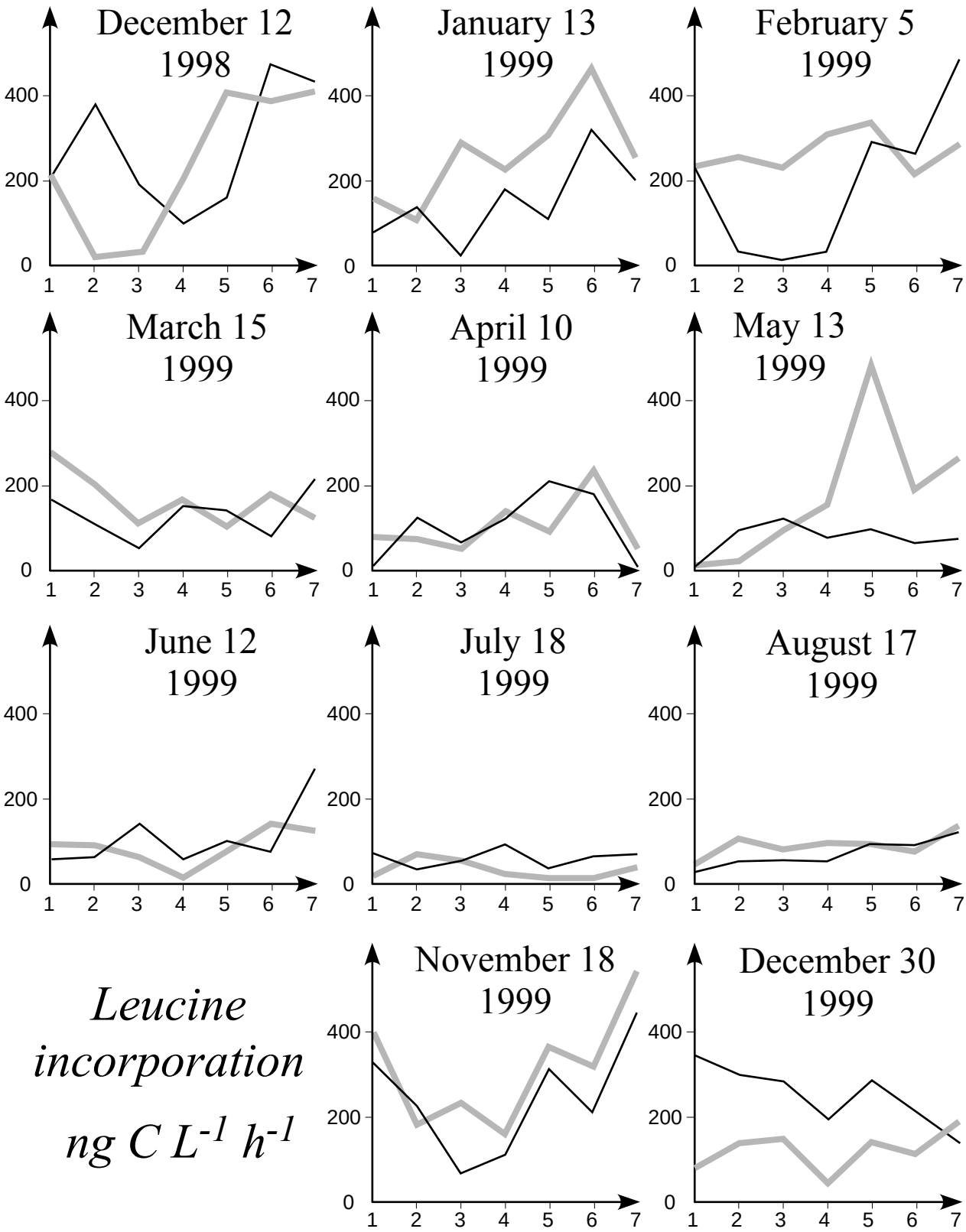
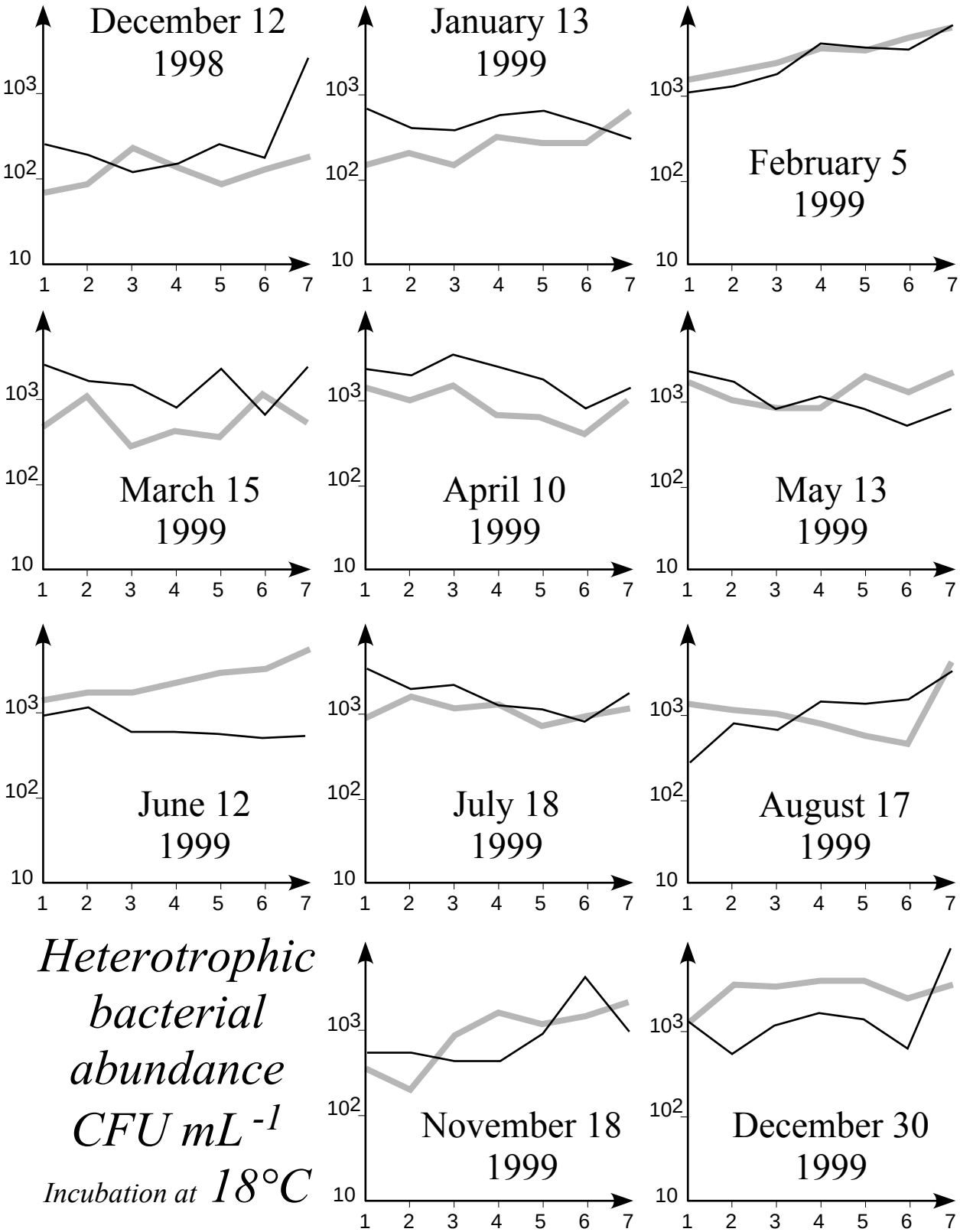


Chlorophyll a
μg L^{-1}



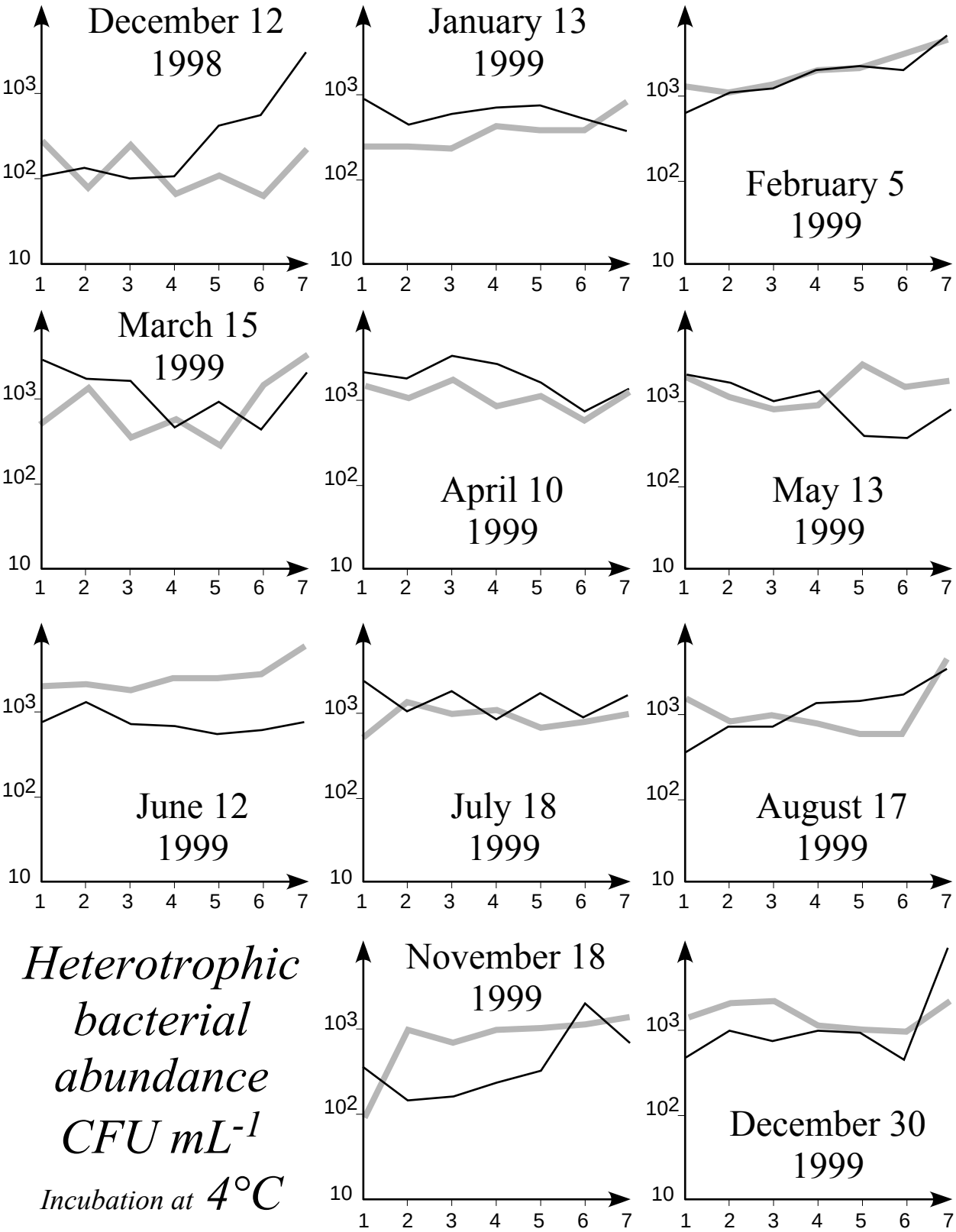
Total bacterial abundance (Cells mL $^{-1}$)


December 12
1998
January 13
1999
February 5
1999
March 15
1999
April 10
1999
May 13
1999
June 12
1999
July 18
1999
August 17
1999
November 18
1999
December 30
1999
0
200
400
1 2 3 4 5 6 7
Leucine incorporation
ng C L-1 h-1



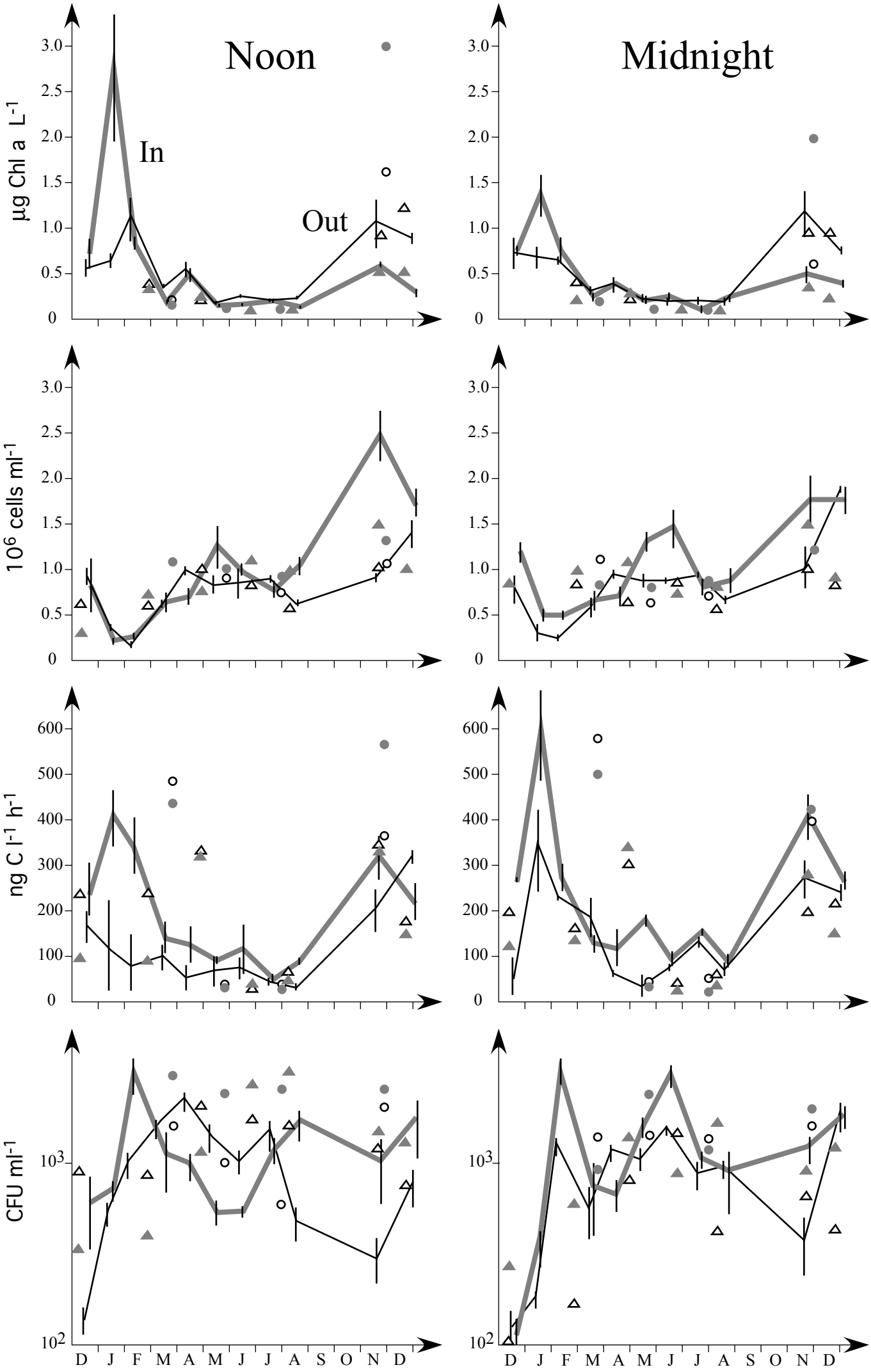
Heterotrophic bacterial abundance CFU mL^{-1}

Incubation at 18°C



Heterotrophic bacterial abundance CFU mL^{-1}

Incubation at 4°C


Noon
Midnight
In
Out
µg Chl a L-1
10^6 cells ml-1
ng C l-1 h-1
CFU ml-1
3.0
2.5
2.0
1.5
1.0
0.5
0
600
500
400
300
200
100
10^3
10^2
D J F M A M J J A S O N D