PELAGIC COLD OCEAN MICROBIAL DYNAMICS AND SMALL-SCALE TURBULENCE INTERACTIONS WITH SPECIAL REFERENCE TO BACTERIA

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by

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Abstract. The marine microbial food web is a major source of biogenic carbon cycling within the world's oceans. Phytoplankton consume carbon dioxide and produce dissolved organic matter that is absorbed by the bacteria, thus stimulating bacterial growth and providing a valuable food source to micrograzers. It is believed that the energy of large scale turbulent events is propagated to ever smaller scales and can affect and influence the activity of microbial grazers. Little research exists today regarding this effect, and even less is known about how turbulence may affect the microbial food web in cold oceans in particular. Therefore, this investigation was designed to observe the combined effects of low temperature and small-scale turbulence on the microbial food web.

The role of bacteria and the microbial food web within a polar region was examined as part of a multi-year (1997-1999) seasonal study of the North Water polynya (NOW). Regions of the polynya were characterized into two distinct water masses: the silicate-rich Arctic water (SRAW) that flowed from the north and down the coast of Ellesmere Island and the Baffin Bay water (BBW) that flowed from the south and up along the coast of Greenland. Bacterial abundances were generally higher in the BBW region than the SRAW region of the polynya. Bacterial growth rates were found to be higher rates in the SRAW region of the NOW. It was also found that bacterial biomass was positively correlated with phytoplankton biomass and negatively correlated with both inorganic nutrients. Bacterial grazing mortality exceeded growth during high turbulence treatments and that bacterial production tended to be higher in the low turbulence treatment relative to the static and high turbulence treatments. These results thus suggest

that bacterioplankton are actively growing and are actively grazed within the NOW, that turbulence does have an effect on bacterial grazing mortality even at low ($\leq 1^{o}C$) temperatures and that there are regional differences in the pelagic food web structure and the patterns of biogenic carbon export in the NOW as the summer progresses.

In addition, an enclosure experiment was carried out with natural seawater of Logy Bay, Newfoundland to determine the effects of turbulence on heterotrophic and autotrophic growth in the presence and absence of micrograzers. The experiment was conducted in February and April, with water temperatures at $0^{o}C$ and $5^{o}C$, respectively. There was no difference in bacterial growth between the static and turbulent enclosures in either the presence or absence of micrograzers at both experimental temperatures. Heterotrophic nanoflagellate growth was found to be significantly higher at $0^{o}C$ in the presence of turbulence but only when micrograzers were absent. A similar pattern was found with the small autotrophic community at $0^{o}C$, as determined by chlorophyll *a* <5 μm, in which growth was significantly higher with turbulence but only when micrograzers were absent. Turbulence significantly enhanced growth rates of the large autotrophic community (>5 μm chl *a*) both in the presence and absence of grazers. These results suggest that turbulence effects are small under cold ocean conditions, but increase with the size of the organism. It thus appears turbulence could affect patterns of biogenic carbon export differentially, dependent upon the size structure of the plankton community.

DEDICATION AND THANKS

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PREFACE

This dissertation is a true example of personal and academic growth within a block of six years. How we think and what we discover along the way is certainly going to change from the beginning to the end because we never stop learning. No matter what age we may be, we continue to learn new things on a day-to-day basis, thus adding to, or altering our outlook on certain variables. This principle certainly applies to my dissertation as that not a day went by that something was changed, updated, re-analyzed or rewritten. This is due to my own growth and understanding of the field I have studied these last ten years. However, I cannot deny a great deal of it is also due to the change in supervision midway. As I grew more independent in my way of thinking in my area of research, and as I learned new methods through literary research and talking with others in my field, I grew farther apart from the way of thinking of my previous supervisor. In a bold step, I sought new supervision for this dissertation. I fortunately found a way to continue my work without too great of interruption, salvaging the work I had completed in the years before while exploring new ideas and trying new methods for the work yet to be done.

This dissertation is a product of change. It is my belief, as it has been many of my fellow graduate students, that a Ph.D. is merely a stepping stone to a career in science. Our Ph.D. is not, and does not have to be, what we do for the rest of our lives. Yes, it is a final step in our structured education, but by no means does having a Ph.D. mean we are at our capacity for learning. I believe I will always be a student of nature and thus, by

accomplishing this doctorate degree I have only shown to others that I am willing to learn. And learn more I shall.

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CHAPTER ONE

A BRIEF OVERVIEW OF THE ROLE OF THE OCEAN'S MICROBIAL FOOD WEB IN THE GLOBAL CARBON CYCLE AND OF THE THESIS RESEARCH OBJECTIVES

Abstract. The marine microbial food web is a major source of biogenic carbon cycling within the world's oceans. Phytoplankton consume carbon dioxide and produce dissolved organic matter that is consumed by the bacteria, thus stimulating bacterial growth and providing a valuable food source to micrograzers. It is believed that the energy of large scale turbulent events is propagated to ever smaller scales and can affect and influence the activity of microbial grazers. Little research exists today regarding this effect, and even less is known about how turbulence may affect the microbial food web in cold oceans in particular. Therefore, this investigation was designed to examine three main objectives concerned with the combined effects of low temperature and small-scale turbulence on the microbial food web. These objectives are: 1) To quantify summertime bacterial abundance, distribution, growth rates and grazing mortality rates in the North Water polynya; 2) To quantify the effects of turbulence on bacterial growth rates, grazing mortality rates and production in the North Water polynya; and 3) To assess the effect of turbulence on the microbial food web trophic interactions within the Labrador Current during winter.

1.1 Introduction

Of the nearly 7 gigatons carbon in anthropogenic CO_2 released in our atmosphere per year, it is estimated that ~ 2 gigatons is sequestered by our oceans alone, making our oceans the largest reservoir of freely exchangeable carbon on the planet (Siegenthaler and Sarmiento 1993; Figure 1.1). This exceeds the atmospheric reservoir by 50-fold (Ducklow and Fasham 1992). The predominant process within our oceans that is responsible for this regulation of CO_2 in our atmosphere is primary production.

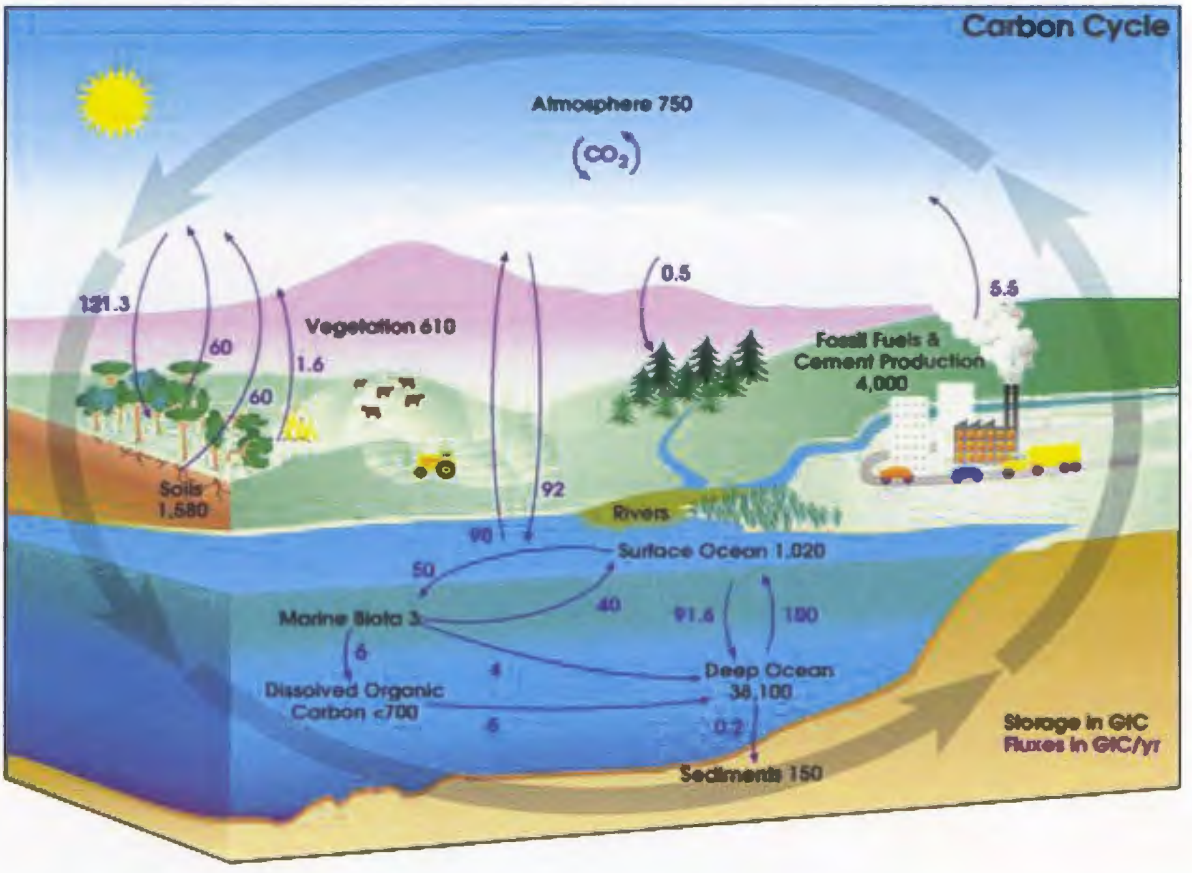


Figure 1.1 A pictorial representation of the global carbon cycle. Numeric fluxes for each transport mechanism signifies Gigatons of carbon per year. Image extracted from a website of the Earth Observing System (EOS) Program of NASA Goddard Space Flight Center (rst.gsfc.nasa.gov).

Net photosynthesis sets the upper limit for the biological pump that transfers atmospheric CO_2 into the ocean interior; however, it is the vertical export of particulate biogenic carbon particles to depth, derived via *bacterial production*, which serves as a principal factor controlling the carbon flux in our oceans (White *et al.*1991; Ducklow and Carlson 1992). *Bacterial production*, also called secondary production, is the synthesis of bacterial biomass mainly from dissolved organic matter, as well as other organic precursors. It is the bacteria that fuel much of the respiration, nutrient cycling and growth of other organisms within the ocean's interior. A conceptualization of the carbon cycled within the marine microbial food web is represented in Figure 1.2. Predator-prey interactions within the marine microbial food web strongly contribute not only to the recycling of biogenic carbon within the surface layer of the ocean, but also to the transfer of carbon to higher trophic levels (e.g., copepods → fish larvae → larger fish → mammals). Microheterotrophs, such as non-pigmented flagellates, are known to ingest bacteria and picoplankton (Fenchel 1982; Sherr and Sherr 1994), thus effectively repackaging and transferring a fraction of smaller-sized biogenic carbon, the bacterial biomass, that would otherwise not be available to larger metazoan grazers (Caron 1988), nor susceptible to sedimentation.

It is known that growth and mortality processes within microbial food webs are controlled by a variety of biological, chemical and physical factors. However, with the exception of light and temperature, no other physical variable has been extensively studied for its effects on the microbial food web. In order to obtain a full understanding of the factors regulating the carbon flux within the marine microbial food web, it is

necessary to determine how physical processes, such as small-scale turbulence, can potentially impact the pathways and rates of carbon transfer between trophic levels.

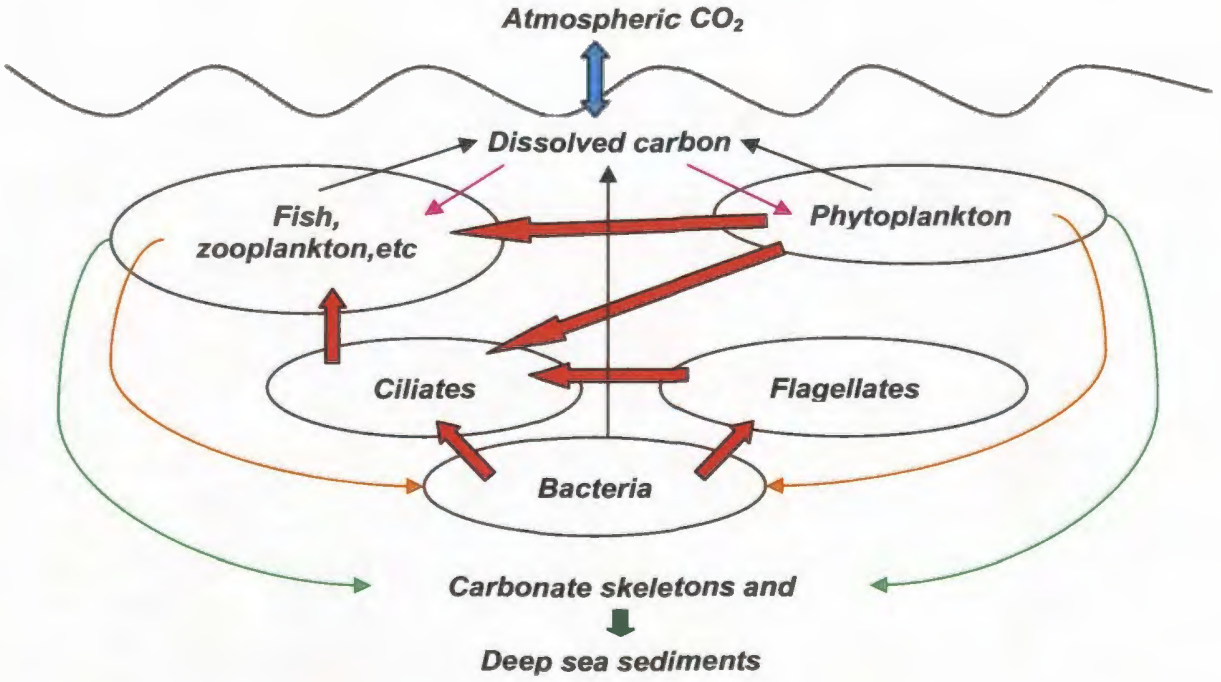


Figure 1.2. A representation of carbon cycling within the marine food web. Red block arrows represent the grazing patterns within the food web. Carbon is absorbed from the atmosphere into the water column and utilized for photosynthesis and calcification. All other arrows represent respiration (black), photosynthesis/calcification (pink), decay (orange) or sinking (green).

1.1.1 Small-scale turbulence and the marine microbial food web

The propagation of turbulent kinetic energy from the large- to small-size scales is an inherent characteristic of all aquatic systems. Mesoscale sources that create large turbulent eddies are oceanic features such as gyres, upwellings and fronts; breaking of surface and internal waves; and wind-driven convection, thermohaline intrusions and salt fingerings (Yamazaki and Osborn 1988). No matter how the turbulent energy originates,

all turbulent flows are affected by viscous shear stresses, which can decay turbulence rapidly. Large, fast-moving organisms, such as fish, live in an environment where inertia dominates and flow is turbulent. Whereas much smaller, relatively non-motile organisms, such as bacteria, live in a viscosity-dominated world where flow is laminar and cells are surrounded by a sheath of attached water molecules. Some organisms take advantage of both physical regimes. For example, Calanoid copepods demonstrate rapid bursts of speeds under turbulent conditions when avoiding predators but also exploit laminar flow conditions when feeding to detect, manipulate and redirect 'packets' of water containing food particles towards the mouth without ever touching the particles themselves (Koehl and Strickler 1981).

The Reynolds number, $\mathbf{R_e}$, is a useful metric for estimating where an organism lies along the laminar-turbulent continuum (Walsby and Reynolds 1980):

$$R_e = 2\, r\, \nu\, \rho\, \eta^{-1}$$

where $\mathbf{r}$ is the radius of the particle, $\boldsymbol{\nu}$ is the velocity of the particle, $\boldsymbol{\rho}$ is the density of the water and $\boldsymbol{\eta}$ is the viscosity of the water. Organisms with $\mathbf{R_e} < 1$ tend towards the laminar flow regime while organisms with $\mathbf{R_e}$ much greater than 1 tend towards the turbulence regime.

Surface ocean water of 34 ppt salinity at 0°C has a density 3% greater than at 20 °C which increases the $\mathbf{R_e}$ slightly, but more importantly 0°C water has 74% greater viscosity (CRC Handbook of Chemistry and Physics, 1996). This reduces the overall $\mathbf{R_e}$ at 0°C to 58% that of the same particle at 20°C, thus making cold oceans extreme areas

to test for micro-scale turbulence effects, which should be minimized due to these physical conditions.

Bacterio-, pico-, microzoo-, and some mesozooplankton experience life at low Reynolds numbers where inertia has little effect, so a large percentage of their energy is expended in just seeking out prey or nutrient particles. There has been an increased interest in the effects of small-scale turbulence on individual planktonic organisms, in which many believe small-scale turbulence can increase a predator's chances for encounter with prey by increasing the relative velocity of either organism. Much of the research has focused on the theory of a microorganism's increased relative velocity, which originated from the paper of Rothschild and Osborn (1988), who observed that fish larvae were growing successfully on concentrations of prey that were theoretically too low to result in the necessary encounter probabilities. Numerous other models were then published after the Rothschild-Osborn model, incorporating diffusion layers of protozoa (Lazier and Mann 1989) and behavioural components of predators (i.e., Kiørboe and Saiz 1995). Empirical studies thus far have shown that small-scale turbulence contributes to the development of small-scale patchiness (e.g., Squires and Yamazaki 1995), particle aggregation and disaggregation (e.g., Jumars *et al.* 1993; Kiørboe 1997), dispersion of plankton populations (e.g., Haury *et al.* 1990), and a variety of predator-prey interactions within the microbial and metazoan food webs (e.g., Sundby and Fossum 1990; Marrasé *et al.* 1990; MacKenzie and Leggett 1991; Saiz *et al.* 1992; Dower *et al.* 1997). The research on the impact of small-scale turbulence on microbial processes has been largely theoretical and there is little empirical data to test these theories (Browman 1996; Sanford

1997). Moreover, the number of reviews published recently on turbulence effects is greater than that of new empirical studies. The majority of those reviews have been primarily focused on just certain groups of organisms, e.g., copepods, and/or are largely theoretical themselves (Sanford 1997; Peters and Marrasé 2000). The effect of fluid motion on nutrient fluxes towards and away from cells has been reviewed by Jumars *et al.* (1993) and Karp-Boss *et al.* (1996). The effect of turbulence on phytoplankton has been reviewed by Kiørboe (1997), Thomas *et al.* (1997), and Estrada and Berdelet (1998), while the effects on zooplankton have been reviewed by Davis *et al.* (1991) and Dower *et al.* (1997), and most recently turbulence effects on planktonic protozoa has been reviewed by Peters and Marrasé (2000). Additionally, a few reviews have focused on the methods of generating and measuring turbulence in laboratory or mesocosm settings (Peters and Redondo 1997, Sanford 1997, Petersen *et al.* 1999). It is obvious that this is a lively area of research, but it is still in great need of empirical data to support or disprove the theories that have been developed. Based on the low $\mathbf{R_e}$ due to the high viscosity described above, the null hypothesis would be that turbulence would have no effect on bacteria and micrograzers in cold ocean conditions. However, the results in this study challenges that hypothesis and suggests that turbulence effects on bacteria and micrograzers needs to be reexamined in cold oceans.

The effects of turbulence on biological parameters have focused mainly on the physiology of the microorganisms, be it in terms of growth, nutrient uptake or feeding rates on particles, thus resulting in a very limited understanding of turbulence effects on plankton population dynamics and trophic interactions (Peters and Marrasé 2000).

Extending our knowledge in this field has been difficult due to both the lack of complete understanding of small-scale turbulence, one of the most difficult areas of fluid dynamics (Nelkin 1992), and the inability to compare the turbulence generated in the laboratory to natural oceanic turbulence (Osborn 1996). Peters and Marrasé (2000) reviewed 26 sources on turbulence effects on planktonic protozoa and found that, while many of the laboratory-generated turbulence levels are realistic of oceanic conditions or at least can be found in the ocean at certain locations or under certain conditions, the distribution of turbulence intensities that have been reported in lab studies is higher than average values of turbulence reported for oceanic conditions (see Figure 1a of Peters and Marrasé 2000). However, Peters and Marrasé (2000) believe this large difference may be artificially inflated because a) it is not easy to simulate low turbulent energy dissipation rates in a laboratory; b) field measurements have mostly been carried out under relatively calm conditions, thus average oceanic turbulence levels reported are lower than they would be if they included measurements under severe conditions (Peters and Redondo 1997); and c) most oceanic turbulence measurements have been made well below the upper surface mixed layer, in which the bulk of planktonic activity occurs. As more data are being gathered, especially from the upper section of the surface mixed layer with new microstructure profilers (Anis and Moum 1995, Moum *et al.* 1995), it appears that natural turbulence levels may be several orders of magnitude higher than previously reported (Peters and Marrasé 2000).

1.1.2 The use of enclosure studies

The study of microbial ecology within the ocean's pelagic photic zone has been extensive in the last few decades, but integrating results from enclosed experimental systems with results of observed natural systems has still proven to be difficult. Enclosure studies can be conducted under replicated, controlled and repeatable conditions. The same assemblage of natural populations can be sampled and studied for the whole period of an experiment, whereas constant water movement and large-scale mixing in the natural environment make the study of a particular natural assemblage of populations impossible. Specifically, an enclosure study allows us to identify the limiting factors affecting the growth rates and grazing losses of different organisms and to look for patterns of correlation between the distribution and abundance of those organisms. Furthermore, whether planned or expected, interactions observed during enclosure studies can provoke new hypotheses and insights on the ecosystem studied (Oviatt 1994).

Increasing the size of the enclosure from small bottles to several hundred liter containers, can minimize the chance of altering species richness and trophic dynamics, which may in turn influence patterns in the total productivity of a microbial community. Large enclosures can also reduce the effects of nutrient limitation, and thus allow longer incubation periods. It has been shown that bacterial community dynamics can change in small bottles incubated for periods longer than 24 h (Massana et al. 2001) or when predators are removed (Suzuki 1999).

An enclosure study may not be considered the perfect solution to mimicking the natural environment of the organisms being tested, because it is difficult to extrapolate

results from microcosms and mesocosms to nature due to the fundamental differences between model ecosystems and their natural counterparts. On the other hand, monitoring microbial predator-prey interactions in nature can be difficult due to the numerous parameters within an oceanic system that can cause temporal and spatial variability. Therefore, we become dependent upon the results of enclosure studies to help explain the physical, chemical and biological mechanisms controlling natural systems.

1.2 Research Objectives

This investigation was designed to achieve three main objectives to assist in filling the void of empirical studies in the area of combined effects of low temperature and small-scale turbulence on the marine microbial food web. These objectives, which are described further below, are: 1) to quantify summertime bacterial abundance, distribution, growth rates and grazing mortality rates in the North Water polynya; 2) to quantify the effects of turbulence on bacterial growth rates, grazing mortality rates and production in the North Water polynya; and 3) to assess the effect of turbulence on the microbial food web trophic interactions within the Labrador Current during winter.

1.2.1 Objective 1: To quantify summertime bacterial abundance, distribution, growth rates and grazing mortality rates in the North Water polynya.

Polynyas are recurring areas of open water in normally ice-covered seas. A habitual polynya in the Arctic is suspected to be an area of high biological productivity, as indicated by the continual presence of migrating or overwintering birds and marine mammals (Stirling 1997). This high density of birds and mammals in some Arctic

polynyas has led to the hypothesis that primary and secondary production may be elevated, consequently fuelling higher trophic levels and affecting regional biogeochemical cycles.

Polynya formation is driven by sensible-heat and/or latent-heat processes (Smith *et al.* 1990). A **sensible-heat polynya** is formed when the upwelling of warm (~2°C) deep water replaces surface waters that have been advected away from land by offshore winds, thus preventing the formation of new ice (Smith *et al.* 1990). In a **latent-heat polynya**, ice is continuously formed and transported away by winds or currents, thus preventing a build-up of ice. The wind that carries the ice away also mixes the water column, which restricts warming of the surface layer (Smith *et al.* 1990).

During the formation of a sensible-heat polynya, stratification may lead to an algal bloom and may promote heating of the surface layer. During the formation of a latent-heat polynya, an algal bloom may begin once algae within the deeper waters are brought to the surface by the vertical mixing. The season of biological productivity can be much shorter than that of a sensible-heat polynya due to the continuous water column mixing from the production of a latent-heat polynya.

The North Water polynya (NOW) is located in northern Baffin Bay, between the northwest coast of Greenland and eastern Ellesmere Island, Canada (Figure 1.3). The NOW is the largest recurring polynya in the Canadian high Arctic, opening to a maximum of ~80,000 km^2 (Dunbar 1981, Smith and Rigby 1981). The ice in the NOW does not consolidate in the winter, although the polynya is often 95% ice-covered (Steffen 1985). The polynya starts to expand along the Greenland coast and spreads

south and west in late March or early April, reaching its maximum extent by July. An ice bridge generally spans the northern part of Smith Sound during winter, preventing northern ice from entering the polynya (Dunbar 1981). There is no fast ice located in Smith Sound or Lady Ann Strait during the summer. These physical features of the NOW led Muench (1971) to hypothesize that the North Water was maintained by latent-heat processes since there was no significant upward transport of heat to the ice-water interface in winter. However, the discovery of "warm water cells" during winter along the Greenland coast (Steffen 1985), modeling efforts (Mysak *and* Huang 1992, Darby *et al.* 1994) and further hydrographical sampling (Bourke *and* Paquette 1991, Lewis *et al.* 1996), now indicate that the West Greenland Current does transport warm water into the region. Thus, it is likely that the NOW is maintained by a combination of latent- and sensible-heat processes.

Open waters in seasonally ice-covered seas undergo phytoplankton blooms and subsequent high secondary productivity, in part as a result of the ice-melt. The activity of bacterioplankton, or the grazing of bacterioplankton by protists and metazoans, is typically elevated during these blooms and can ultimately influence the flow of carbon between dissolved pools and higher trophic levels. The NOW provides a unique opportunity to examine the importance of bacterial activity in polar waters of varying physical and biogeochemical characteristics. It is hypothesized that despite the low temperatures of the NOW, the elevated production throughout the marine food web contributes to active bacteria-based food webs, assisting in overall energy and material cycling within the NOW pelagic food web.

Figure 1.3. The North Water polynya is located above the Arctic Circle in northern Baffin Bay, situated between Canada's Ellesmere Island and the northwest coast of Greenland.

1.2.2 Objective 2: To quantify the effects of turbulence on bacterial growth and grazing mortality rates and production in the NOW.

The seasonal sea-ice cover within a polynya can modify the physical dynamics of the upper water column. As ice retreats during the polar summer the upper water column becomes exposed to wind-induced turbulence. Since bacterial production can consume >60% of primary production via dissolved organic matter (Ducklow and Carlson 1992), there is considerable interest in determining the factors controlling and limiting the growth and mortality of bacterial populations in cold-water systems, such as the NOW. One controlling physical factor could be the turbulence induced by the reduction of ice cover in the polynya that is then cascaded to smaller scales (i.e. Kolmogorov length). An increase in turbulence within the water column can affect microzooplankton predator-prey interactions (e.g., Marrassé *et al.* 1990; Peters and Gross 1994; Shimeta *et al.* 1995) and, ultimately, trophic transfer efficiency within the microbial food web.

If the rate of growth of an osmotroph is limited by the availability of dissolved nutrients, then the movement of the cell relative to the surrounding fluid, e.g., from swimming, sinking or fluid shear, can replace nutrient-depleted water around a cell with nutrient-rich water to enhance rates of metabolism and growth. Bacteria are believed to be too small for fluid motion created by turbulence to increase the rate of solute supply to their surface (Lazier and Mann 1989, and references cited within), in which case the rate of solute uptake is largely dependent upon molecular diffusion. This has only been tested three times with natural populations of marine bacteria (Logan and Kirchman 1991; Moeseneder and Herndl 1995; Peters *et al.* 1998), and all with very different techniques

and inconsistent outcomes. Logan and Kirchman (1991) were the first to examine if fluid motion affected the substrate uptake of marine bacteria. Using a Couette cylinder, they showed that fluid shear did not increase the substrate uptake of suspended bacteria. Moesender and Herndl (1995) compared bacterial production (BP) in 14 ml Falcon tubes on a culture shaker with that of undisturbed cultures. They found no differences in BP between turbulent and stagnant conditions unless bacteria were in the presence of phytoplankton. Only then was BP was significantly higher in the stagnant condition. Peters *et al.* (1998) also found no difference in BP between turbulent and stagnant conditions when using the grid-stirring technique to generate turbulence. However, contrary to Moeseneder and Herndl (1995) results, Peters et al. (1998) found turbulence to increase productivity when bacteria were in the presence of a phytoplankton community. They attributed this difference to the method used in generating turbulence and the very small volumes utilized by Moeseneder and Herndl (1995). It should be noted that all three studies removed subsamples to inoculate with a radioisotope, which were then allowed to incubate in stagnant conditions. Also, to date, no study has examined the effects of turbulence on bacterial growth and production in a polar environment.

1.2.3 Objective 3: To assess the effect of turbulence on the microbial food web trophic interactions within the Labrador Current during winter.

Of all the research on turbulence and predator-prey encounters, no two experimental results or models absolutely agree upon how small-scale turbulence affects microorganisms and their encounter probabilities. However, all researchers share one underlying idea: if turbulence can truly influence physiological (e.g., growth and grazing) rates of microorganisms, then all previously published rates assessed under stagnant incubations may be under- or overestimated. Even though enclosure studies are widely accepted tools to examine food web dynamics, water column mixing is still often neglected in experimental design (Sanford 1997). A recent review of 360 aquatic enclosure studies revealed that only 56% included some form of mechanical mixing (Petersen *et al.* 1999) and even fewer of those studies actually quantified turbulence with standard physical parameters that would allow for comparisons among studies (Petersen *et al.* 1999).

Most turbulence studies regarding microbial food-web dynamics have been conducted within enclosures with volumes of 2L or less, and have observed effects only on individual species. It has been cautioned that a great deal of research is still needed to establish a firm link between turbulence and population dynamics (Dower *et al.* 1997), and that there is a need for an experimental link between microcosm studies and the open ocean. The present study includes an intermediate step by use of 300 L enclosures in order to observe larger microbial community effects and changes induced directly or indirectly by turbulence.

As noted above, it is has been shown that bacterial production is not significantly enhanced when subjected to turbulence unless larger plankton, i.e. phytoplankton and heterotrophic grazers, are present (Peters *et al.* 1998). Therefore, it is hypothesized that turbulence does not directly increase the growth and grazing rates of a microbial community smaller than 5 μm in the presence of lower temperatures (<5°C), but that bacterioplankton will display increased growth and abundance due to an increased supply of substrate supplied by the larger components of a microbial community benefiting from small-scale turbulence.

1.3 Summary

This study will: 1) quantify summertime bacterial abundance, distribution, growth rates and grazing mortality rates in the North Water polynya; 2) quantify the effects of turbulence on bacterial growth and grazing mortality rates and production in the NOW; and 3) assess the effect of turbulence on the microbial food web trophic interactions within the Labrador Current during winter.

These three objectives are all part of the larger question of carbon cycling within the marine microbial food web of cold ocean systems which affects the biological pump that influences CO_2 concentrations in the atmosphere.

CHAPTER TWO

BACTERIAL DYNAMICS OF THE NORTH WATER POLYNYA: DISTRIBUTION, GROWTH AND THE EFFECTS OF TURBULENCE ON GRAZING MORTALITY AND PRODUCTION

Abstract. The role of bacteria and the microbial food web within a polar region was examined as part of a multi-year (1997-1999) seasonal study of the North Water polynya (NOW). The objectives were for this study were to a) to characterize bacterial abundance and its relationship to short and medium-term indicators of primary production and b) assess the influence of turbulence on rates of bacterial growth, grazing mortality and carbon production in recently opened areas of water (July 1998).

Regions of the polynya were characterized into two distinct water masses: the silicate-rich Arctic water (SRAW) that flowed from the north and down the coast of Ellesmere Island and the Baffin Bay water (BBW) that flowed from the south and up along the coast of Greenland. Bacterial abundances were higher by an order of magnitude in the surface layer than below 50 m (i.e., 10^7 cells L^{-1}) during August 1997 and were generally higher in the SRAW region than the BBW region of the polynya. Bacterial abundance integrated over the upper 50 m of the water column ranged from 57 to 200 x 10^6 cells L^{-1}. Bacterial growth rates ranged from 0.06 to 0.28 d^{-1} in the surface layer (< 30 m) with the higher rates in the SRAW region of the NOW. Two dilution assay grazing experiments indicated moderately higher bacterial grazing mortality in the SRAW region at 0.21 d^{-1} relative to the BBW region at 0.17 d^{-1}. It was also found that bacterial biomass was positively correlated with phytoplankton biomass and negatively correlated with both nitrate+nitrite and phosphate concentration.

The effects of turbulence on the rates of bacterial growth, grazing mortality and thymidine uptake in recently opened areas of water in the polynya was tested. Intrinsic bacterial growth ranged from 0.15 to 0.78 d^{-1}, with the highest rate found at a southern-

most station. Grazing mortality ranged from 0 to 0.82 d^{-1}, with the grazing mortality exceeding growth during the high turbulence treatments at the two northern-most stations. Daily thymidine uptake rates ranged from 0.408 to 4.53 pmol L^{-1} d^{-1}, with the higher rates associated with the southern stations. It was also found that bacterial production tended to be higher in the low turbulence treatment relative to the static and high turbulence treatments.

These results thus suggest that bacterioplankton are actively growing and are actively grazed within the NOW, that turbulence does have an effect on bacterial grazing mortality even at low ($\leq 1^{\circ}C$) temperatures and that there are regional differences in the pelagic food web structure and the patterns of biogenic carbon export in the NOW as the summer progresses.

2.1 Introduction

The presence of seasonal ice cover in the North Water polynya (NOW) can reduce gas exchange between the ocean and atmosphere, which has major implications for the downward transport and potential sequestration of carbon into the ocean's interior. However, even in the cold temperatures of the Arctic, bacterial production and predator-prey interactions within the microbial food web still serve as the principle factors that vertically export and recycle biogenic carbon within the polar ocean. Studies have shown bacterial growth and production may be relatively high in polar regions (Kottmeier and Sullivan 1988; Anderson 1989; Rivkin 1991; Wheeler *et al.* 1996), which may be due to the greater availability of organic substrates (Yager and Deming 1999). Bacterivorous microzooplankton are abundant in the Central Arctic and are significant contributors to

the recycling of microbial carbon (Sherr *et al.* 1997). The high abundance of mesozooplankton in the Arctic Ocean (Wheeler *et al.* 1996) also suggests significant transport of biogenic carbon through grazing on large phytoplankton, organic aggregates and microzooplankton. Changes in the production of bacterioplankton or in the grazing rates of microzooplankton may thus influence the exchange of carbon dioxide between the atmosphere and ocean, the flow of biogenic carbon between dissolved pools and higher trophic levels, and the amount of material transported to depth.

Factors controlling the bacterial abundance, growth and grazing mortality were examined during August 1997 and July 1998 as part of the International North Water Polynya Study. It is hypothesized that despite the low temperatures of the Arctic, the elevated biological productivity found in the NOW contributes to active bacterial-based food webs. Reported herein are bacterial abundance, distribution, growth and grazing mortality in the NOW during August 1997. Also reported are the effects of small-scale turbulence on bacterial growth, grazing mortality and production from July 1998.

2.2 Methods and Materials

2.2.1 Vertical Profiles for water mass characterization and sampling at discrete depths

Sampling was conducted for estimation of bacterial abundance, spatial distribution, bacterial production and grazing mortality. Water was collected in the North Water polynya in the summer of 1997 while aboard the Canadian Coast Guard Icebreaker *Louis S. St. Laurent*, and summer of 1998 while aboard the Canadian Coast Guard Icebreaker *Pierre Radisson* (Figure 2.1, Table 2.1). Vertical profiles of salinity and temperature were measured with a Falmouth Scientific Instruments CTD and water samples were collected with a General Oceanics rosette system and 10-L Niskin bottles.

Stations were classified into three groups representing two water masses flowing into the polynya: silicate-rich Arctic water (SRAW) and Baffin Bay water (BBW), and an area of mixed (M) water characteristics. Tremblay *et al.* (2002a) characterized these two water masses through temperature and salinity profiles of the NOW during the 1998 expedition. Tremblay *et al.* (2002a) described the silicate-rich Arctic water mass as water associated with the Arctic outflow from the Canadian Basin, with low salinity at surface and a weak increase in temperature with salinity. The Baffin Bay water mass was described as water flowing up the east Greenland current from Baffin Bay with high surface salinities and a steep increase in temperature with increasing salinity.

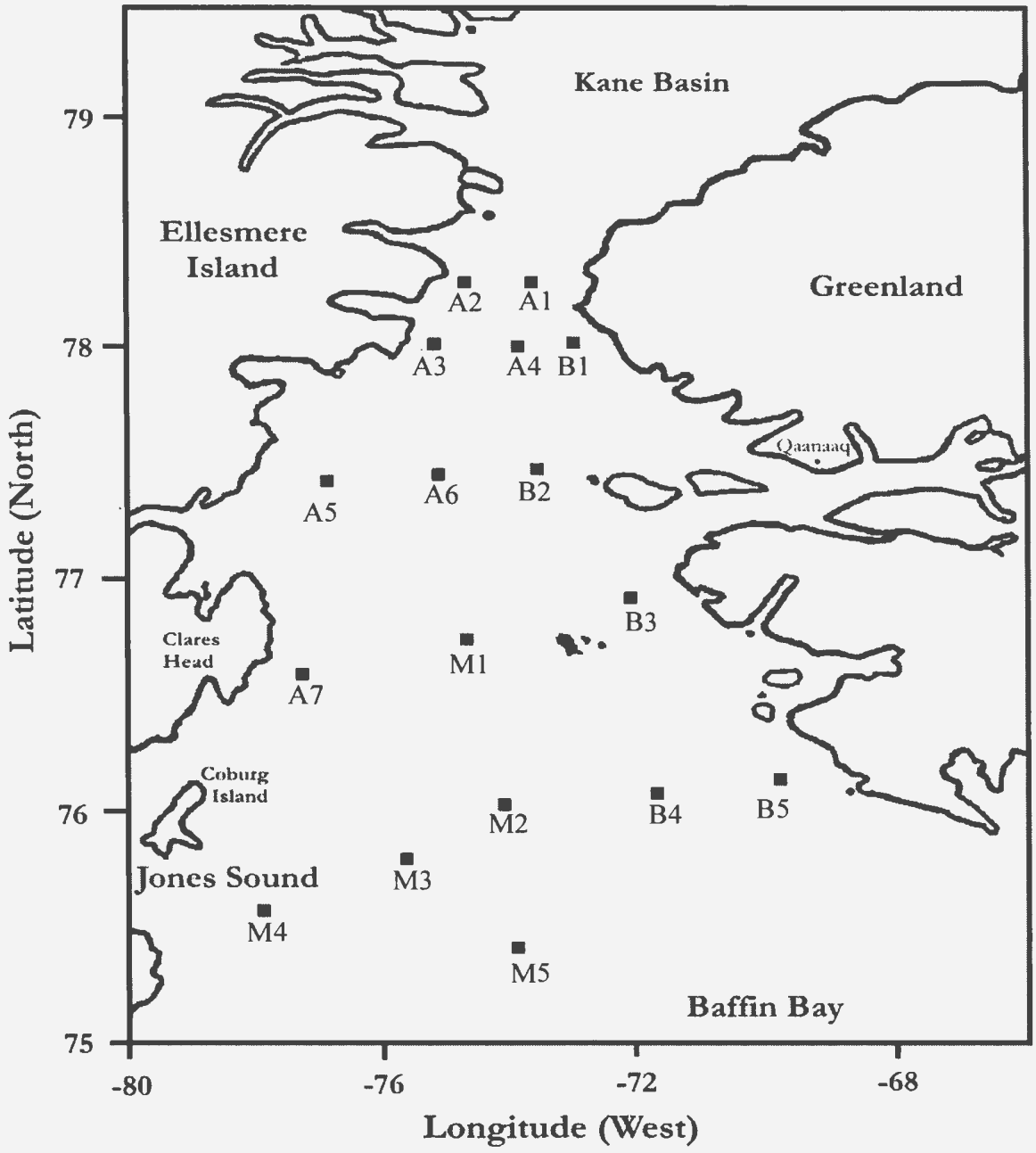


Figure 2.1 Map of the North Water polynya showing the sampling locations in August 1997 and July 1998. Stations with 'A' as a prefix represent stations within the Arctic water mass; 'B' prefix represent stations within the Baffin Bay water mass; 'M' prefix represents stations in an area of mixed water masses.

Table 2.1 North Water polynya station* sites. Temperature data are an average of temperatures at 10-20m depth at each station on the date of collection. Stations with 'A' as a prefix represent stations in the Arctic water mass; 'B' prefix represent stations in the Baffin Bay water mass; 'M' prefix represents stations in an area of mixed water masses. Temperature data was obtained from the NOW database (courtesy of B. Klein).

Station*	Collection Date	Latitude and Longitude	Temperature (°C)
A1	11 Jul 1998	78.3°N, 73.7°W	-1.05
A2	19 Aug 1997	78.4°N, 74.7°W	-0.92
A3	23 Aug 1997	77.9°N, 75.0°W	-1.40
A4	23 Aug 1997	78.0°N, 73.9°W	-1.38
A5	24 Aug 1997	77.3°N, 76.4°W	1.50
A6	24 Aug 1997	77.4°N, 74.9°W	--1.53
A7	21 Aug 1997	76.4°N, 77.4°W	-0.23
B1	15 Jul 1998	78.0°N, 73.3°W	-1.07
B2	23 Aug 1997	77.3°N, 73.6°W	0.02
B3	21 Aug 1997	76.9°N, 72.4°W	1.48
B4	22 Aug 1997	76.3°N, 71.9°W	1.62
B5	22 Aug 1997	76.3°N, 70.2°W	0.39
M1	19 Jul 1998	77.5°N, 74.3°W	1.00
M2	25 Aug 1997 6 Jul 1998	76.3°N, 74.2°W	0.55 -1.60
M3	26 Aug 1997	75.9°N, 75.7°W	0.83
M4	26 Aug 1997	75.5°N, 78.5°W	0.94
M5	25 Aug 1997	75.2°N, 74.9°W	1.20

*See Appendix for original station names.

2.2.2 Determination of bacterial abundance, bacterial distribution, chlorophyll concentrations and nutrient concentrations

Bacterial abundance and distribution within the polynya was quantified from samples collected during the August 1997 cruise. Bacterial abundance was determined by collecting 500 ml water samples from 10 depths in the upper 300m at 12 stations (A2, A3, A4, A6, A7, B2, B4, B5, M2, M3, M4 and M5: Table 2.1). All samples were immediately preserved with gluteraldehyde (1.5% final concentration) and stored in a cold room at ~5°C until analysis (Sherr and Sherr 1993). Bacterial abundance was later determined with the acridine orange direct count method (Hobbie *et al.* 1977). At least 300 cells from each filter were enumerated using a BH2-RFC Olympus epifluorescence microscope under a magnification of 1250X using blue-light excitation (BP440, DM455, AFC+Y475).

Inorganic nutrients (nitrate+nitrite, silicate, phosphate) and chlorophyll data from 1997 and 1998 depth profiles were obtained from the NOW database (courtesy of B. Klein, Université Laval). The inorganic nutrients were measured by an Autoanalyzer, and fluorometric chlorophyll *a* measurements were made using the acetone extraction method with correction for phaeopigments using the conventional acid ratio technique (Parsons *et al.* 1984).

2.2.3 Bacterial growth rates and grazing loss rates

Two different techniques were employed to measure bacterial growth rates and grazing losses within the North Water polynya: a grazer removal technique and a serial

grazer dilution technique. All bacterial abundances were determined by the acridine orange count method (Hobbie *et al.* 1977) as described in **2.2.2**.

2.2.3.1 Estimation of bacterial abundance using a grazer removal technique

A grazer removal technique was employed to estimate bacterial growth within the surface mixed layer where chlorophyll *a* levels were highest (between 0-50 m) at a select number of stations during August 1997. Niskin bottles were drained through silicon tubing into polyethylene buckets, which were gently poured into a larger Nalgene tub. Water was dispensed through silicon tubing capped with a 202 μm Nitex screen to eliminate macrograzers. Samples of 100 ml were then gravity-filtered through a 1 μm Nucleopore filter to remove micrograzers and then and then diluted with 400 ml of particle free water to minimize the potential effects of bacterial substrate depletion. Particle free water was prepared by gravity filtration through a 0.2 μm Gelman capsule. All sampling apparatus was rinsed with 5% HCl and deionized water (Milli-Q) prior to use, and all water was handled at $< 0^{\circ}C$.

Bacterial growth was monitored in samples obtained from Stations A1, A2, A5, A6, B3, M2 and M4. The bottles were incubated in the dark for 2-3 days at $-1.5^{\circ}C$ to minimize the effects of newly produced dissolved organic matter (Carlson *et al.* 1999; Ducklow *et al.* 1999). Subsamples of 50 ml were withdrawn each day and were immediately preserved with gluteraldehyde (1.5% final concentration). Bacterial growth rates (μ) were computed from the Model I least-squares linear regression slope of the time dependent changes in natural log (ln) transformed cell abundances.

2.2.3.2 Estimation of bacterial growth and grazing mortality using a serial dilution assay technique

Bacterivory by microzooplankton were determined by using dilution assay experiments (Landry and Hassett 1982) at one station each in the eastern (B3) and western (A5) regions of the polynya. The dilution-assay method is a technique that allows the rates of growth and grazing mortality of a microbial prey population to be estimated concurrently (Landry and Hassett 1982; Gallegos 1989; Paranjape 1990). Water was collected and macrograzers were removed in the same manner as described in **2.2.3.1**. The 202 μm-screened water was dispensed into eight, 4 L polycarbonate cubitainers and particle free water (PFW) was added to each cubitainer to obtain 8 target dilutions producing: 10%, 20%, 30%, 40%, 50%, 75%, 90% and 100% whole water. All 8 cubitainers were incubated in a cold room at -1.5°C with an irradiance of 3 μE $m^{-2}s^{-1}$ and were inverted every 4 to 6 h to minimize settling of particles.

At the initial (4h) and final sampling (52h), 250 ml samples were fixed with gluteraldehyde (1.5% final concentration) for the estimation of bacterial abundances by the AO method. Samples of 500 ml were fixed with 5% Lugols iodine for estimation of microzooplankton abundances. Replicate 50 ml subsamples of the preserved microzooplankton samples were allowed to settle for 48h and examined with a Zeiss Axiovert 35 inverted microscope under a total magnification of 200X. Microzooplankton were counted and grouped into taxonomic categories based on size, shape and morphology. In addition, 250 ml samples were collected in triplicate on 25 mm Whatman GF/F and 5 μm Poretics filters at a vacuum of <127 mm Hg to measure

chlorophyll *a*. Filters were stored in a -20°C freezer prior to chlorophyll *a* extraction. Chlorophyll *a* was extracted in 90% acetone for ~18 hours at -20°C. Chlorophyll *a* (Chl *a*) concentration was measured fluorometrically and corrected for phaeopigments using the conventional acid ratio technique (Parsons *et al.*, 1984) with a Sequoia-Turner fluorometer that was calibrated with pure Chl *a* (Sigma Chemical Co., St. Louis, MO, USA). Chl *a* concentration in the <5 μm fraction was calculated as the difference between total and >5 μm fractions.

Each cubitainer in the dilution series yielded an estimate of the observed growth rate (**k**, d^{-1}) of the bacteria and phytoplankton according to the exponential growth model given by Landry and Hassett (1982),

(Eq. 1) $$\mathbf{k = \ln (P_t/P_o)/t = \mu - g}$$

where **t** is the duration of the incubation in days and $\mathbf{P_o}$ and $\mathbf{P_t}$ are the initial and final prey abundance per litre. The intrinsic rates of prey growth (**μ**, d^{-1}) and grazing mortality (**g**, d^{-1}) are estimated by Model I linear regression of prey observed growth rate versus the whole seawater fraction. Intrinsic prey growth (**μ**) was determined from the y-intercept of the regression and grazing mortality (**g**) was determined from the slope of the regression.

2.2.4 Evaluating the effects of turbulence on bacterial dynamics

Turbulence effects on bacterial dynamics were investigated in shipboard experiments using a grazer removal technique at three levels of turbulence and by using the thymidine uptake technique for estimating bacterial metabolic activity, also at three levels of turbulence.

2.2.4.1 Turbulence effects on bacterial growth and grazing mortality during mid-summer

The effects of turbulence on bacterial growth and micro-grazing mortality (defined as those grazers passing a 10-μm Nitex screen) were quantified using the grazer removal technique during July 1998. Water was collected within the mixed surface layer (0 - 30 m) of stations A1, B1, M1 and M2 (Table 2.1) and drained into an acid-washed polycarbonate carboy. Estimates of bacterial grazing mortality (**g**, d^{-1}) were determined as the difference between intrinsic bacterial growth (**μ**, d^{-1}) in the nominally micrograzer-free conditions (*-micro*) and the observed bacterial growth (**k**, d^{-1}) in the presence of grazers (*+micro*).

(Eq. 2) $$\mathbf{g = \mu - k}$$

Micrograzer conditions (*+micro*) were established by filtering 5.4 L of collected water through a 10-μm Nitex screen to eliminate macro-grazers, and then gently transferring 1.8 L aliquots into three separate containers. The *–micro* treatment was established by diluting 900 ml of < 3-μm size-fractionated water with 4.5 L of 0.2-μm filtered PFW to prevent substrate limitation in the absence of grazers, which would normally recycle dissolved organic materials. Aliquots of 1.8 L of the diluted culture were then gently transferred into three more containers. Microscopic observations confirmed that heterotrophic and autotrophic nanoflagellate grazers were absent.

Three turbulence treatments were generated: high, low, and none (Table 2.2). The high level of turbulence treatment was generated within two containers by vertically oscillating plungers consisting of a plastic wand and a perforated polyvinyl chloride

(PVC) plate (plate size = 9.5 cm^2, perforation diameter = 2 mm, ~57% solidity). The plate was centred in each container with 2.5 mm clearance between the inside wall of the container and the edge of the plate. The vertical amplitude of the plunger motion was 3 cm, travelling in the upper half of the water column, and oscillating at a rate of 1 rotation per second (or Hz). This turbulence apparatus was kept in a cold room at a temperature of -1.5°C (for a further description of this apparatus, see Delaney 2003). The low level of turbulence was generated by a plankton wheel in which two containers were attached to a wheel rotating at a velocity of 0.06 rotation per second (Hz) immersed in a temperature-controlled water bath at -1.5°C. The zero level of turbulence treatment was maintained in two bottles nestled in a cushioned box to minimize any ship vibration, incubated in the same cold room as the high level turbulence treatment.

All treatments were incubated for 3 days in the dark. Subsamples of 20 ml were withdrawn every 24 h and were immediately preserved with gluteraldehyde (1% final concentration) so that bacterial abundances could be enumerated at a later date (AO method). Bacterial population changes in all treatments were determined by using Model I linear regression. Slopes were converted to growth rates (**k**) by log base e (= 2.302) and plotted together to permit graphic evaluation of statistical differences among treatments.

Statistical analyses were performed using SPSS and SigmaPlot software (SPSS, Inc. 2001). Replicate experiment data sets for each treatment (n=2) of each station were tested by a homogeneity of slopes procedure to determine if replicates could be combined, which always proved to be the case.

Table 2.2 Description of incubation methods and levels of turbulence for each incubation.

Incubation Method	Incubation Characteristics	Turbulence
Mechanical stirring	Containers stirred with a plunger at a rate of 1 Hz	**High**
Plankton wheel	Containers rotated on a wheel at a rate of 0.06 Hz	**Low**
Static	Containers in a cushioned box to minimize ship vibration	**None**

2.2.4.2 Turbulence effects on uptake of thymidine as an indicator of bacterial metabolic activity

The effects of turbulence on bacterial activity were assessed by estimating the rate of incorporation of [^{3}H] thymidine (TdR) in the grazer-free containers of each turbulence treatment. Each container (1.8 L) was amended with 10 nM TdR (final concentration). Aliquots of 50 ml were removed at time zero and after 48 h. The incubations were terminated by filtering triplicate 10 ml subsamples onto 0.2 μm polycarbonate filters, which were then rinsed 10 times with 1 ml ice-cold 5% trichloracetic acid and stored in a -40°C freezer until return to the laboratory for analysis. Samples were radioassayed using a Packard 2500 TR liquid scintillation counter. The incorporation of TdR (pM h^{-1}) was then ascertained by

(Eq. 3) $$pM\ h^{-1} = \frac{(DPM_F - DPM_I) \bullet (TdR\ concentration) \bullet (1000)}{(Total\ TdR\ activity\ ml^{-1}) \bullet (incubation\ h)}$$

where DPM_I and DPM_F represent the decays per minute at the initial and final incubation time and the total TdR activity is measured in an unfiltered water sample at the beginning of the incubation.

2.3 Results

2.3.1 Water masses and bacterial spatial patterns

Stations in the SRAW (west) region of the polynya (A1, A2, A3, A4, A5, A6) were typified by surface temperatures <0°C (Table 2.1), and generally higher silicate, nitrate+nitrite and phosphate concentrations (Table 2.3) relative to stations in the BBW (east) region of the polynya (B2, B3, B4, B5), which were typified by surface temperatures >0°C (Table 2.1) and generally lower silicate, nitrate+nitrite and phosphate concentrations (Table 2.3). Stations identified with mixed water masses (M1, M2, M3, M4 and M5) tended to have intermediate nutrient concentrations (Table 2.3).

2.3.2 Vertical distributions of bacterial abundance, nutrients and chlorophyll

A three-dimensional distribution of all bacterial abundance throughout the NOW is shown in Figure 2.2. The vertical distributions of bacterial abundance and inorganic nutrients of representative stations of each water mass are shown in Figures 2.3 a, b, c. Plots for all stations are provided in the Appendix (Figures A.2.1 to A.2.10). Bacterial abundance was greatest within the surface mixed layer (0 to 50 m) and decreased exponentially with depth concurrent with an exponential increase in nitrate+nitrite, phosphate and silicate concentrations at all stations. Bacterial abundance in the upper 50 m of the BBW region of the polynya varied from 78 to 99 x 10^6 cells L^{-1} (Table 2.3). Bacterial abundance in the SRAW region ranged from 97 to 200 x 10^6 cells L^{-1} (Table 2.3). Thus, mean values of bacterial abundances were 1.5-fold greater in the SRAW than the BBW region of the polynya. The bacterial abundance of the mixed stations varied from 52 to 99 x 10^6 cells L^{-1} (Table 2.3) with a mean value approximately one-half that of

the mean bacterial abundance of the SRAW. Nitrogen tended to be the most limiting nutrient in the surface waters. For example, both phosphorus and silicate were still at relatively high levels near the surface in the SRAW (Fig. 2.2a) and in the mixed water (Fig. 2.2c) while silicate was also approaching the limit of detection in the BBW (Figure 2.2b).

Table 2.3. Values of nitrate+nitrite, silicate, and phosphate content, bacterial abundance and chlorophyll *a* (Chl *a*) content in the North Water Polynya at 50m during August 1997. Stations are grouped according to two water masses flowing into the polynya: silicate-rich Arctic water (SRAW) and Baffin Bay water (BBW). The third grouping of stations are those stations within the mixed water masses. Values are integrated over the upper 50 m of the water column and dashed lines represent missing data. Temperature values at each station can be found in Table 2.1. Inorganic nutrients and Chl *a* raw data was obtained from the NOW database (courtesy of B. Klein).

Station	Nitrate + Nitrite (μM)	Silicate (μM)	Phosphate (μM)	Bacterial Abundance (cells x 10^6 L^{-1})	Chl *a* (μg L^{-1})
SRAW					
A1	---	4.5	0.6	---	0.42
A2	8.4	16.9	1.1	97.2	---
A3	---	11.3	1.0	167	---
A4	1.6	11.3	1.1	127	0.16
A5	---	14.2	1.0	---	0.26
A6	---	16.5	1.2	95.7	0.27
A7	---	8.0	0.9	200	0.41
Mean	**5.0**	**11.8**	**1.0**	**137.4**	**0.30**
BBW					
B2	---	9.7	0.8	78.0	0.18
B3	0.7	1.9	0.6	---	0.26
B4	10.8	7.9	0.9	98.9	0.14
B5	---	3.5	0.5	92.5	0.41
Mean	**5.8**	**5.8**	**0.6**	**89.8**	**0.25**
Mixed					
M2	5.5	7.9	0.8	99.0	0.13
M3	2.9	11.7	0.9	57.6	0.05
M4	---	7.4	0.9	56.9	0.28
M5	---	10.6	1.0	51.8	0.14
Mean	**8.4**	**9.4**	**0.9**	**66.3**	**0.15**

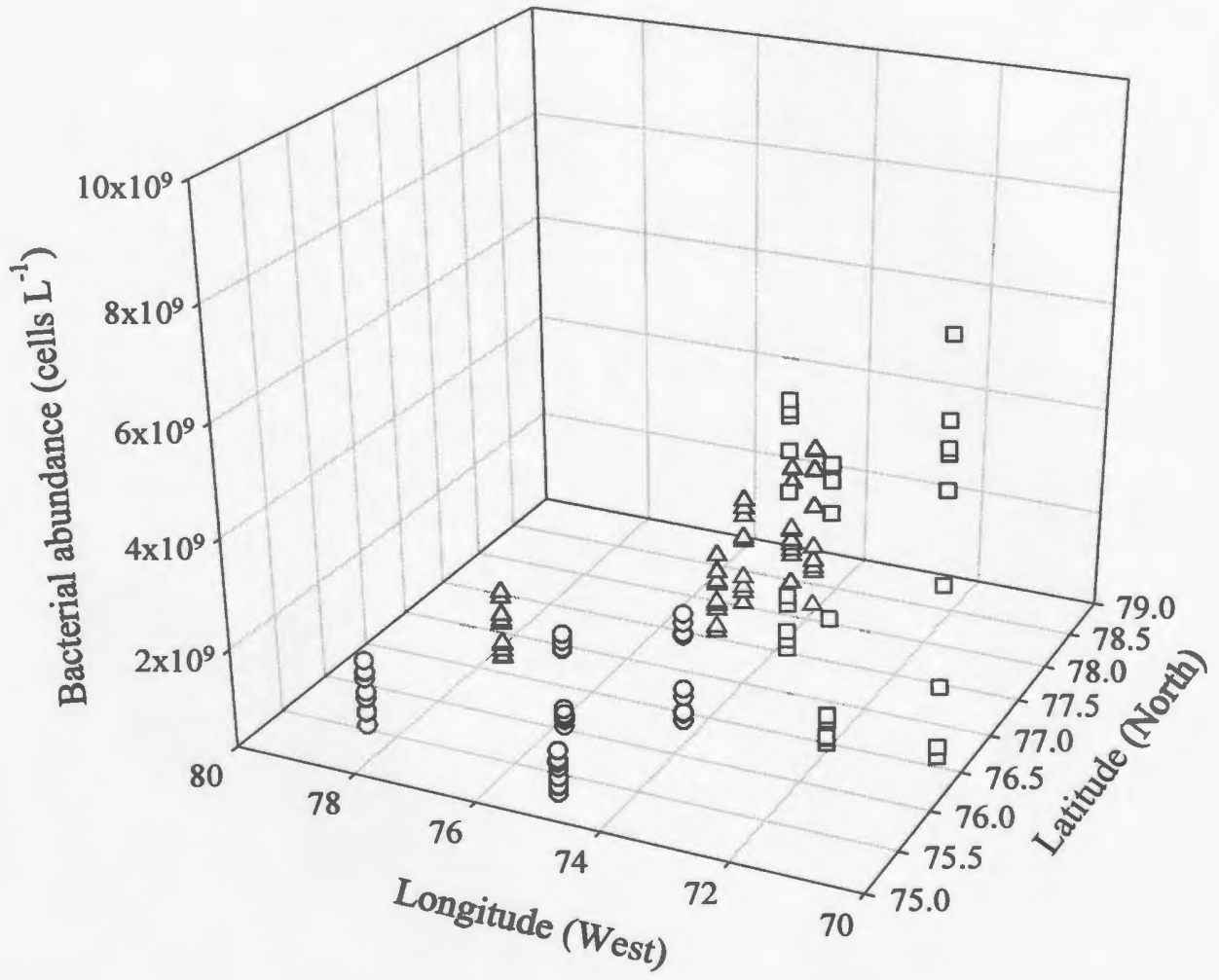
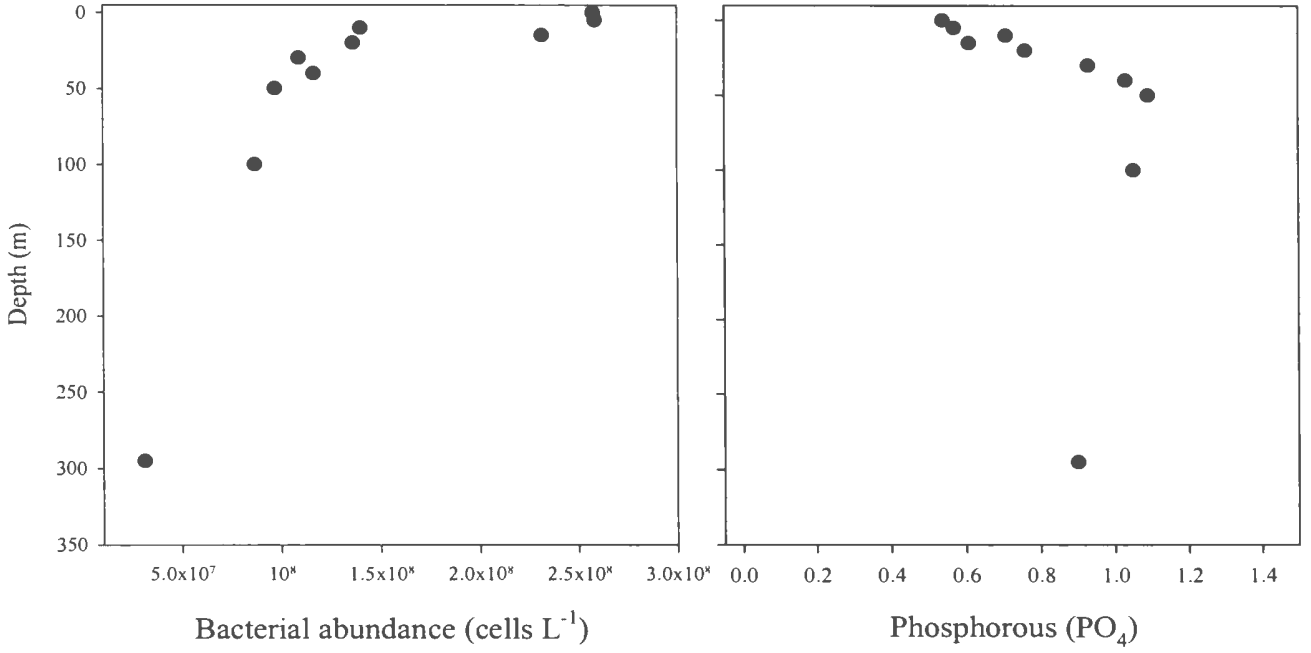


Figure 2.2. A three dimensional view of the bacterial abundance distribution at all station sites within the North Water Polynya in August 1997. Triangles (△) represent those stations in the Arctic water mass, squares (□) represent those stations in the Baffin Bay water mass, and circles (○) represent those stations in the mixed water masses region.



Station A2

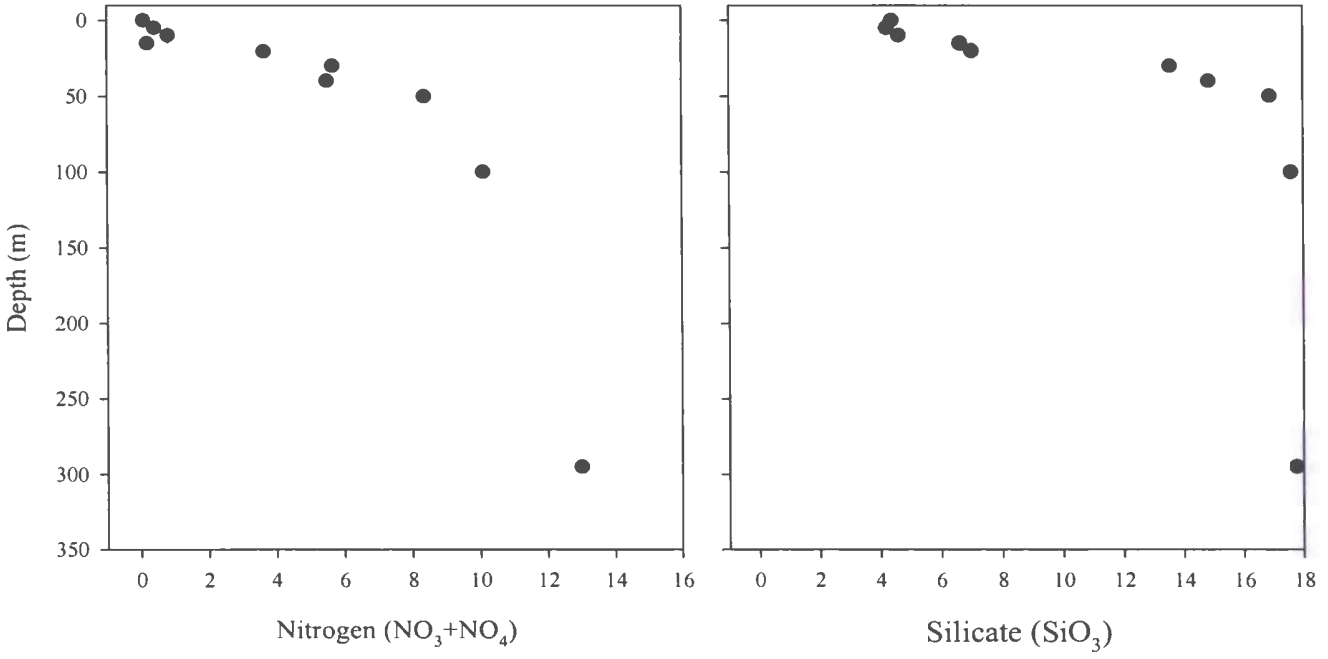


Figure 2.3a. Vertical profiles of bacterial abundance, phosphate and nitrate+nitrite of a representative station of the silicate-rich Arctic water mass region of the North Water polynya during August 1997. A full pictorial review of all stations sampled can be found in the Appendix.

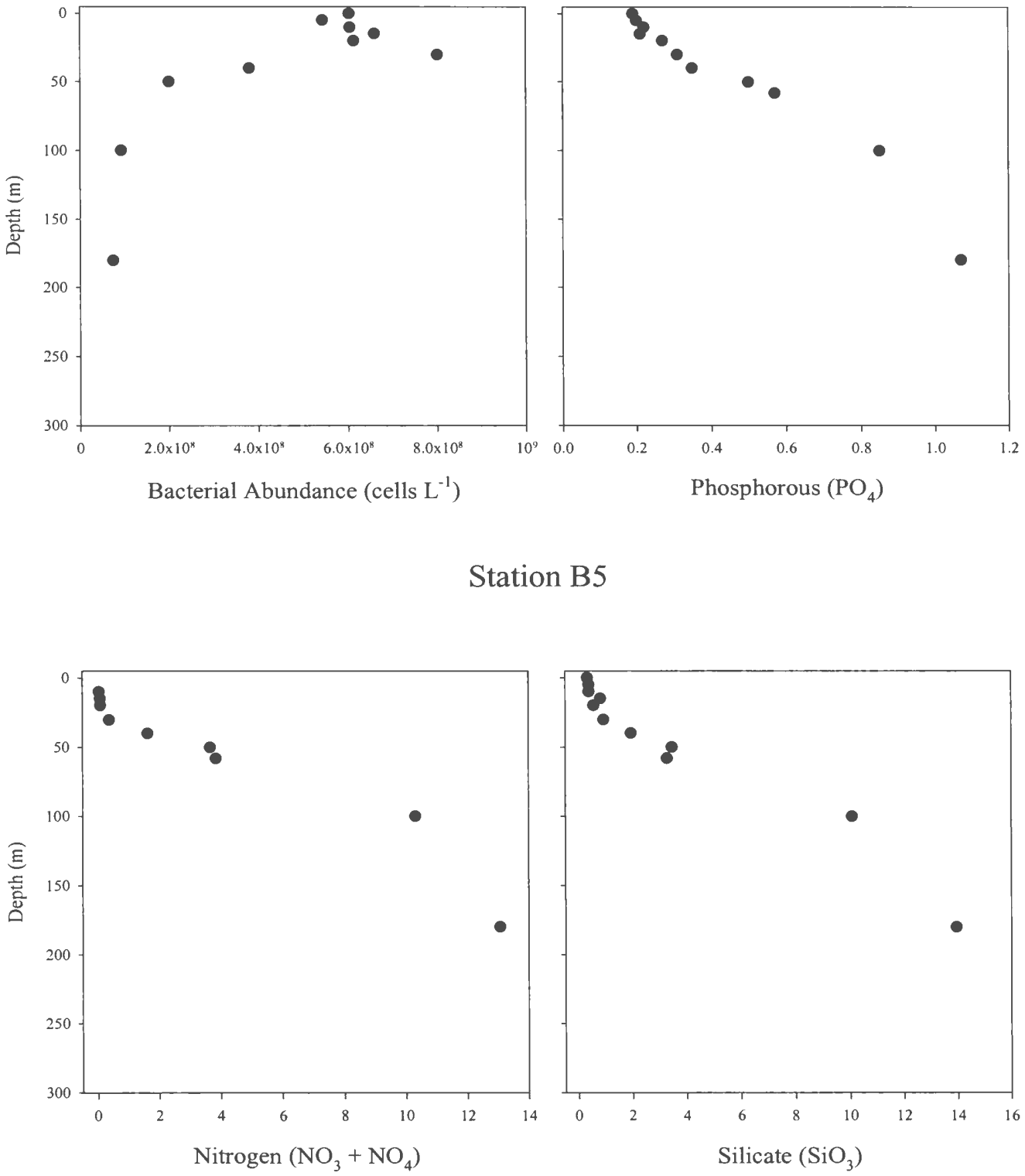
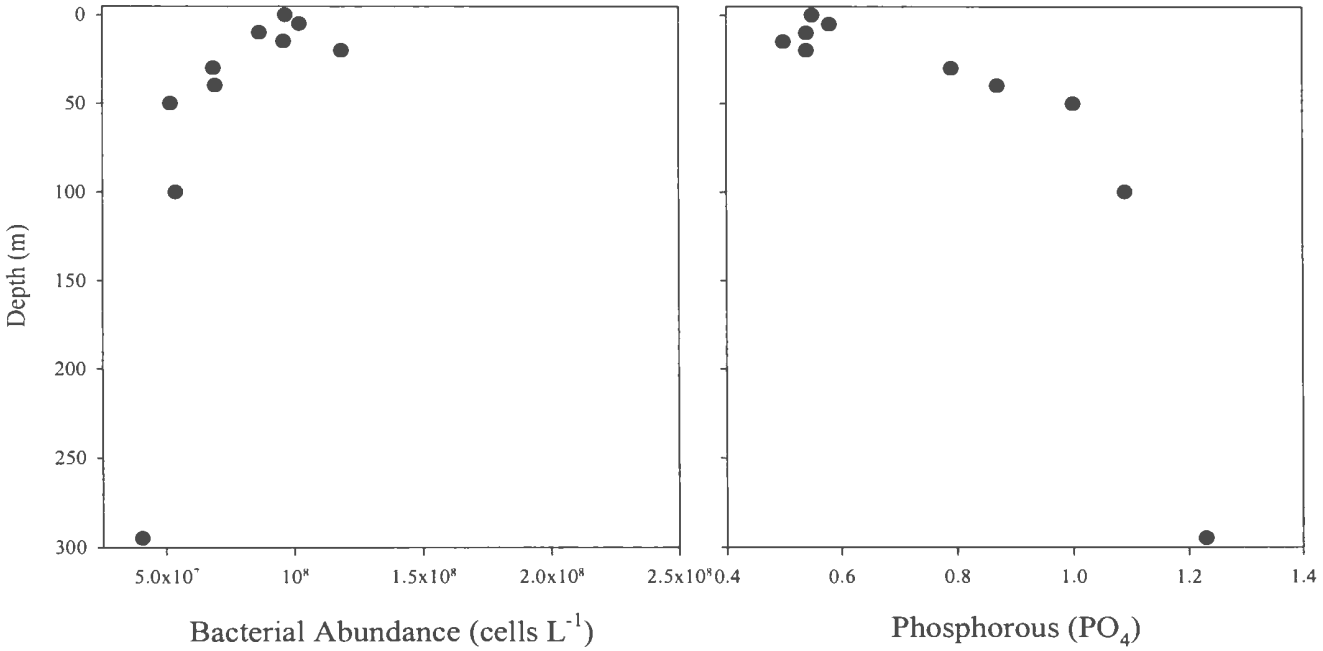


Figure 2.3b. Vertical profiles of bacterial abundance, phosphate and nitrate+nitrite of a representative station of the the Baffin-Bay water mass region of the North Water polynya during August 1997. A full pictorial review of all stations sampled can be found in the Appendix.



Station M5

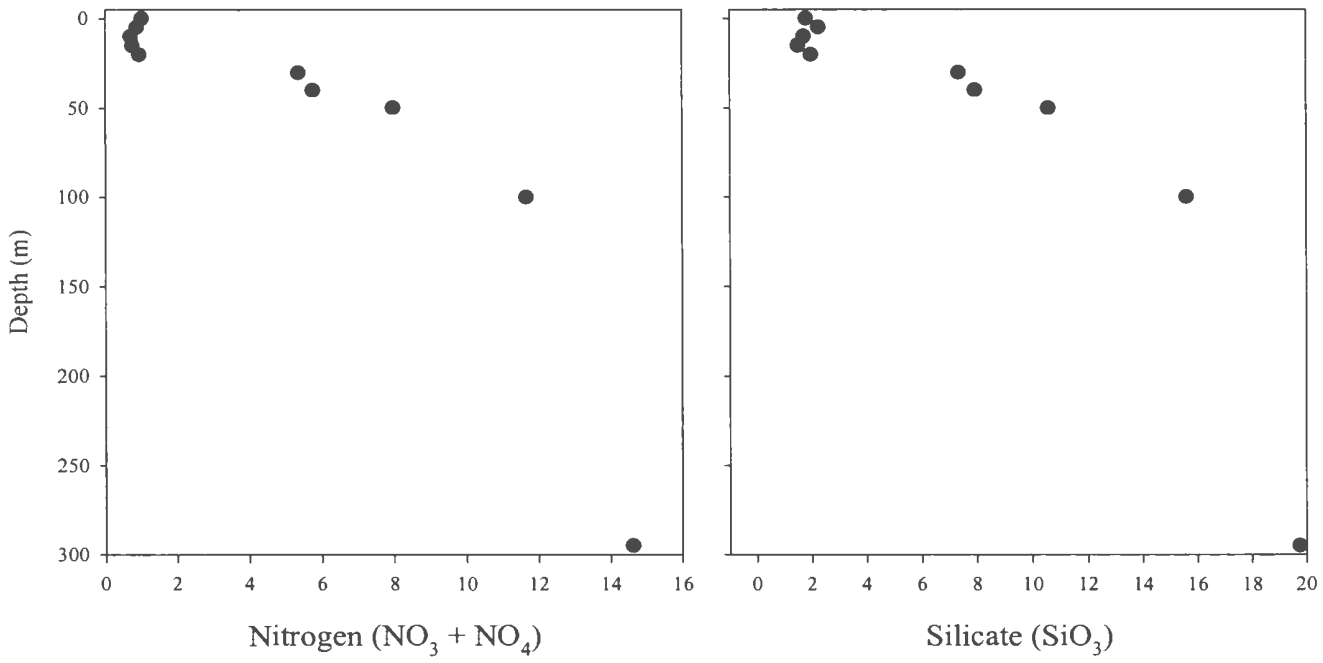


Figure 2.3c. Vertical profiles of bacterial abundance, phosphate and nitrate+nitrite of a representative station of the mixed water mass region of the North Water polynya during August 1997. A full pictorial review of all stations sampled can be found in the Appendix.

In addition, the log of bacterial abundance was plotted against the log of Chl *a* concentration for each water mass. Bacterial abundance was positively correlated with Chl *a* concentration in all regions with approximately 35% of the total variation explained in the SRAW region (Figure 2.4a). The positive bacteria-chlorophyll relationship was also significant in the BBW region (Figure 2.4b), with a total of 51.5% explained variance and a slope two-fold greater than that of the SRAW region. The mixed water mass also demonstrated a positive chl *a* to bacteria relationship with a slope similar to the SRAW region and a total explained variance of 69%, greater than that in both the SRAW and BBW regions. These observations suggest that the relationship of bacterial abundance with chlorophyll, and hence recent primary productivity, was weakest in the Arctic water-mass and strongest in the Mixed water mass and was characterised by the highest nutrient concentrations near-surface (see Figure 2.3). The correlations between log bacterial abundance and log nutrient concentrations indicate that the August bacterial abundance is more closely related to total nutrient drawdown (and hence total ecosystem production) than to recent chlorophyll concentration.

Table 2.4. Pearson correlation coefficients between the $\log_{10}$ of bacteria and the $\log_{10}$ of chlorophyll *a*, phosphorous, nitrogen and silicate within the North Water polynya.

Parameter	Correlation with log bacteria
Log chl *a*	0.630
Log phosphate (P)	-0.795
Log nitrate + nitrite (N)	-0.741
Log silicate (Si)	-0.748

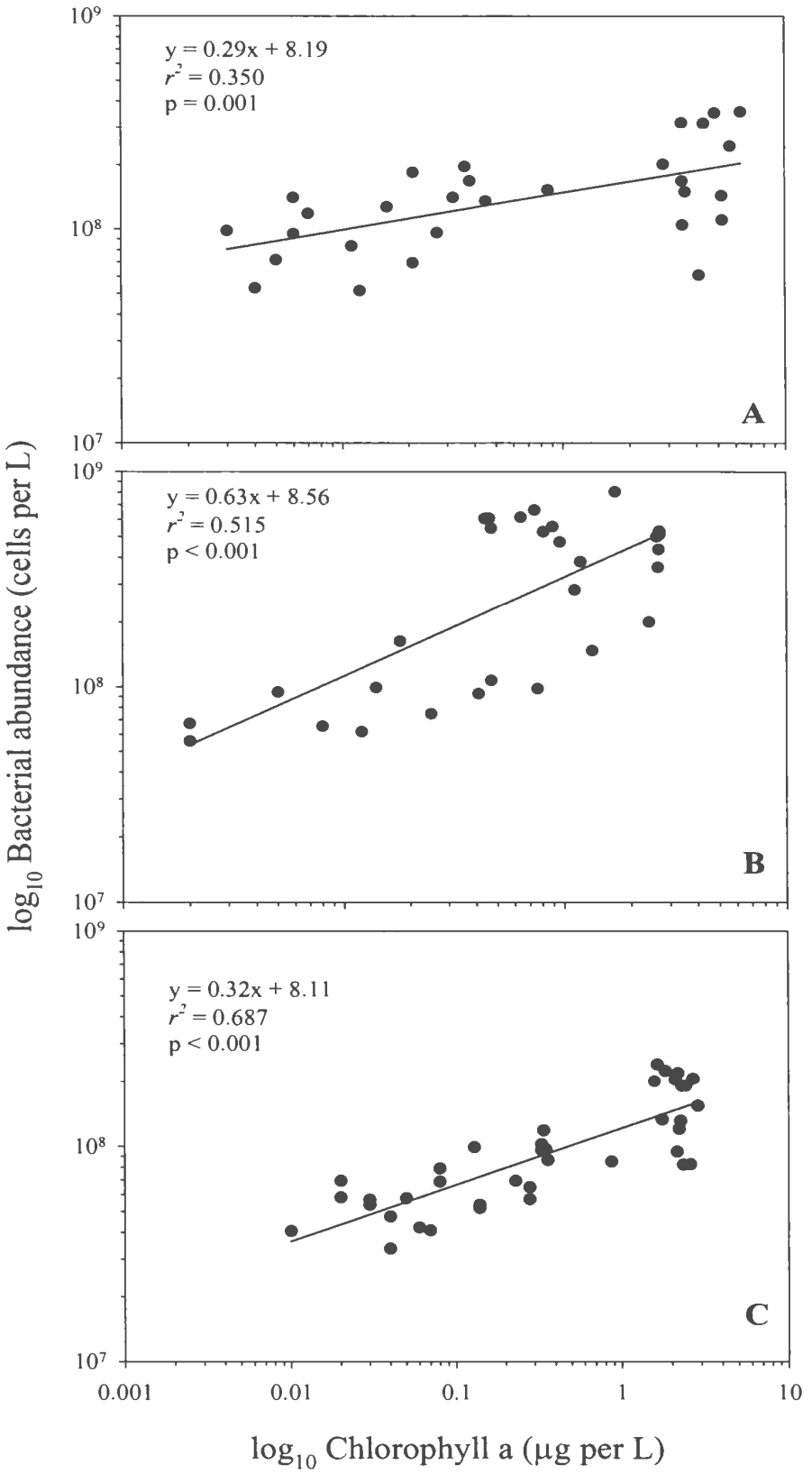


Figure 2.4 The relationship between $\log_{10}$ transformed chlorophyll a concentration and bacterial abundance (Model II regression) at the stations located in A) silicate-rich Arctic water mass, B) Baffin Bay water mass and C) mixed water masses region of the North Water polynya, August 1997.

2.3.3 Bacterial growth and grazing mortality within the NOW as determined by a grazer removal technique and *a serial dilution technique.*

Two methods were employed to determine bacterial growth rates and grazing mortality within the NOW during August 1997. It was found that the serial dilution technique as described by Landry and Hassett (1984) yielded higher bacterial growth and mortality rates than with a simple grazer removal technique. The results are presented below.

2.3.3.1 Bacterial growth and grazing mortality as determined by a grazer removal technique.

The rate of intrinsic bacterial growth (μ) determined in the upper 50 m during August 1997 ranged from 0.005 – 0.22 d^{-1} (Figure 2.4, Table 2.5), with higher rates associated with the stations in the SRAW and mixed water regions of the polynya.

Table 2.5 The calculated daily rates of observed growth (μ) and its corresponding doubling time at seven stations in the North Water polynya in August 1997 (see Figure 2.4).

Station	Doubling Time (d)	Observed growth μ (d^{-1})
A1	12.04	0.057
A2	7.17	0.097
A5	3.54	0.196
A6	138.63	0.005
B3	43.32	0.016
M2	3.13	0.221
M4	8.36	0.083

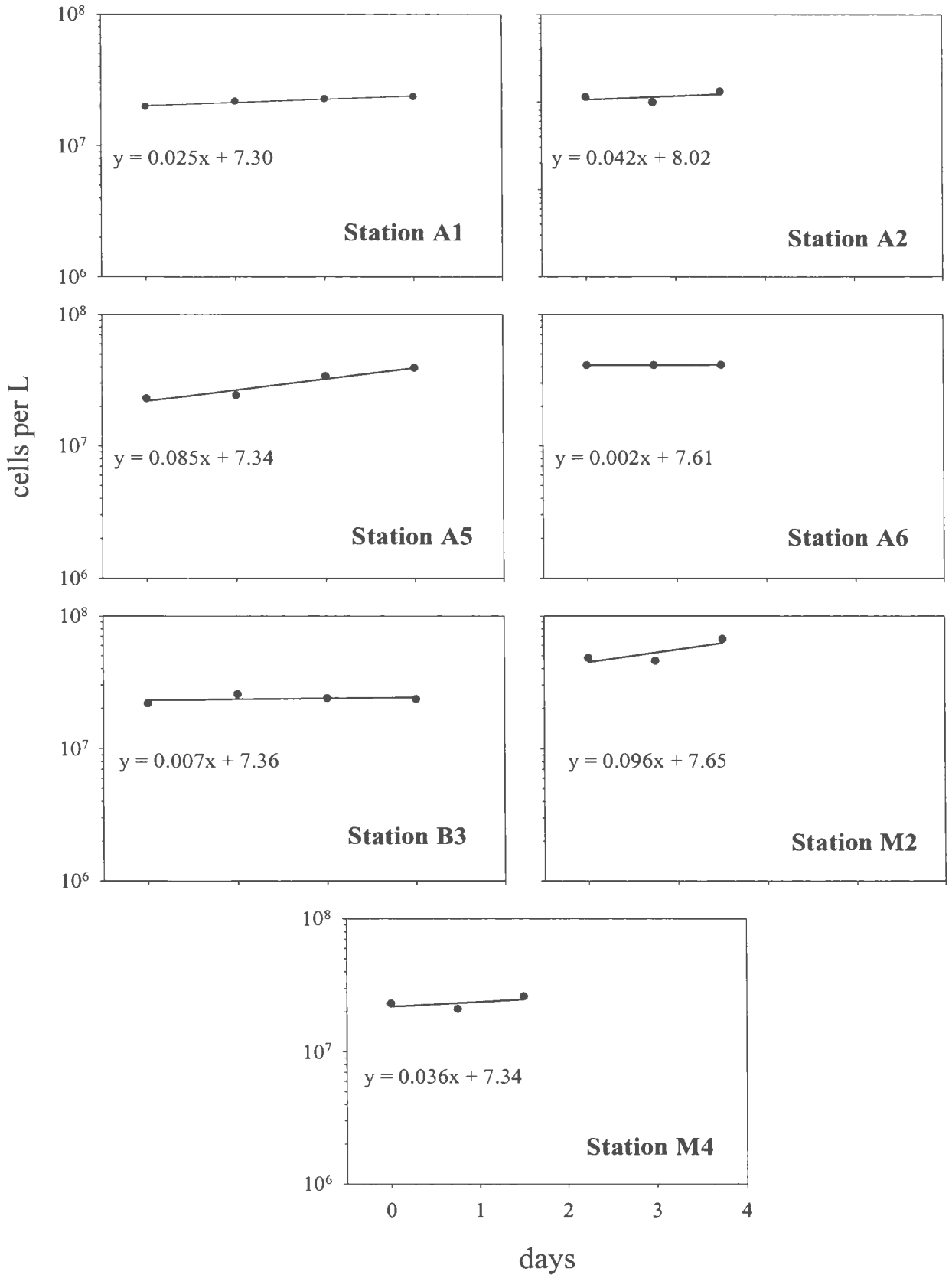


Figure 2.5 Bacterial rates of change at seven sites throughout the polynya in August 1997.

2.3.3.2 Bacterial growth and grazing mortality as determined by a serial dilution technique

Bacterial intrinsic growth rates (μ) determined from the serial dilution experiments were 0.22 ± 0.004 and 0.28 ± 0.003 d^{-1}, at a BBW (B3) and SRAW (A5) station, respectively, while the corresponding grazing mortality rates were 0.17 ± 0.006 and 0.21 ± 0.006 d^{-1} (Figure 2.5). The grazing mortality at Station A5 was 43% greater than that estimated by the grazer removal technique (see Table 2.5), while the grazing mortality rate measured at Station B3 was nearly 14- fold greater. Both experiments lasted four days. The serial dilution technique should be statistically more precise due to its higher number of observations per trial. There is also a procedural difference in that the grazer removal technique removed all particles greater that 1 μm while the dilution technique retained all organisms passing a 202 μm filter, thereby leaving most of the microbial community intact. These differences are analyzed further in the Discussion.

It was also observed that the microzooplankton communities of the dilution assay experiments were largely dominated by dinoflagellates >20 μm, predominantly of the genera *Gymnodinium*, *Gyrodinium*, *Ceratium*, and *Amphidinium*. The dinoflagellates outnumbered the ciliates two to one, which mainly consisted of tintinnids and oligotrichs. In addition, small heterotrophic nanoflagellates (<5 μm) were also a major component of the grazer community (~1000 cells ml^{-1}).

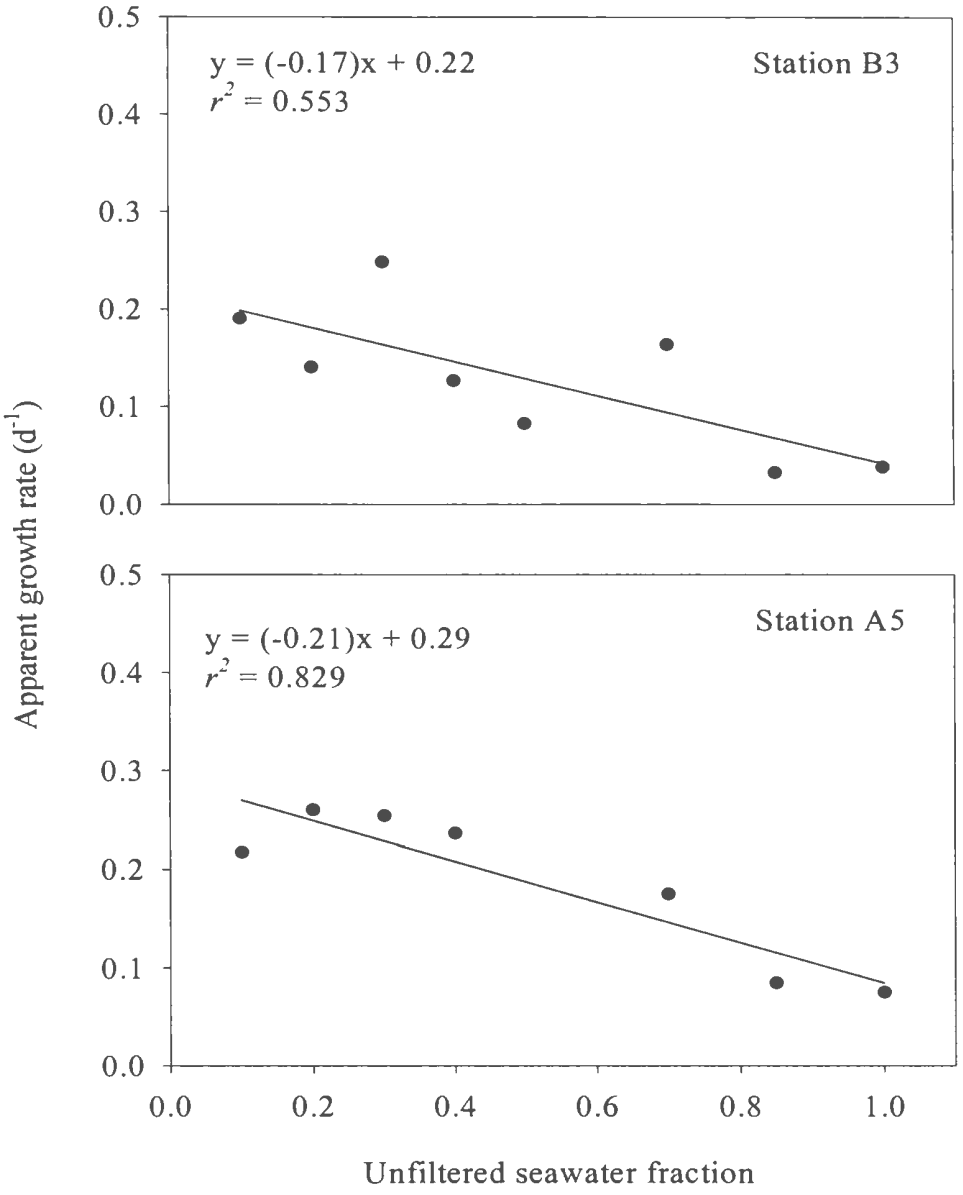


Figure 2.6 The relationship between bacterial observed growth rates (**k**) and fraction of unfiltered seawater at a station in the BBW water mass (B3) and SRAW water mass (A5) in the North Water polynya, August 1997.

2.3.4 Turbulence effects on bacterial growth and grazing mortality

The effects of turbulence on bacterial growth rates and grazing mortality rates were investigated using a grazer removal technique at three levels of turbulence. A

thymidine uptake technique for estimating bacterial metabolic activity was also used, testing three levels of turbulence.

2.3.4.1 Turbulence effects on bacterial growth and grazing mortality as determined by changes in bacterial population

In situ abundances of bacteria collected within the mixed surface layer of the stations A1, B1, M1 and M2 (Table 2.1) during July 1998 ranged from 2×10^8 to 1×10^9 cells L^{-1}, with the highest abundance associated with the station M2.

Table 2.6 The calculated daily rates of observed growth (**k**), intrinsic growth (**μ**) and grazing mortality (**g**) at four stations in the North Water polynya for three turbulence treatments: high, low and none (see Figure 2.6).

Station	Turbulence Treatment	Intrinsic Doubling time (d)	k (d^{-1})	μ (d^{-1})	g (d^{-1})
A1	High	4.70	-0.06	0.15	0.21
	Low	2.12	0.12	0.33	0.21
	None	2.25	0.09	0.31	0.22
B1	High	13.68	-0.37	0.05	0.42
	Low	1.55	-0.37	0.45	0.82
	None	1.84	0.03	0.38	0.34
M1	High	1.14	0.68	0.61	-0.07
	Low	1.03	0.21	0.67	0.46
	None	0.89	0.81	0.78	-0.03
M2	High	3.67	0.41	0.19	-0.22
	Low	1.19	0.50	0.58	0.09
	None	1.27	0.54	0.55	0.01

The slopes from the triplicates within each treatment were not significantly different ($p < 0.10$), therefore replicates were combined, resulting in one regression line per treatment (high turbulence, low turbulence and static, Figure 2.7). Intrinsic bacterial

growth (μ) at all four stations ranged from 0.05 to 0.78 d^{-1}, with the highest rate found at station M1 (Table 2.6). The rates of observed bacterial growth (**k**), where grazers were present, ranged from -0.37 to 0.68 d^{-1}. Among stations, the high turbulence treatment resulted in the lowest intrinsic growth rate amongst all three treatments, but only stations A1 and B1 showed statistically significantly lower growth in the high turbulence treatment ($p = 0.04$ and $p = 0.03$, respectively). Observed daily rates of bacterial growth (**k**) were lower than or approximately equal to μ, with the exception of the high and no turbulence treatments at station M1 and high turbulence treatment of station M2. Estimated grazing mortality (**g**) ranged from -0.22 to 0.82 d^{-1}, with the grazing mortality exceeding the intrinsic growth rate during the high turbulence treatments at stations A1 and B1 as well as the low turbulence treatment at station B1.

The observation of negative grazing rate estimates at stations M1 and M2 (see Table 2.6), although unexpected, is not without precedent. It has been previously noted in freshwater enclosure experiments (Lehman and Sandgren 1985) that the colonial diatom *Asterionella formosa* actually grew faster as the concentration of the predominant crustacean herbivore, *Daphnia pulex*, was increased. This was attributed to the *Asterionella* being relatively immune to the grazing (too large) while being able to benefit from the nutrients regenerated by species susceptible to grazing. The negative grazing rates observed in the present study might be due to a similar size-selectivity in grazing, perhaps in the reverse direction.

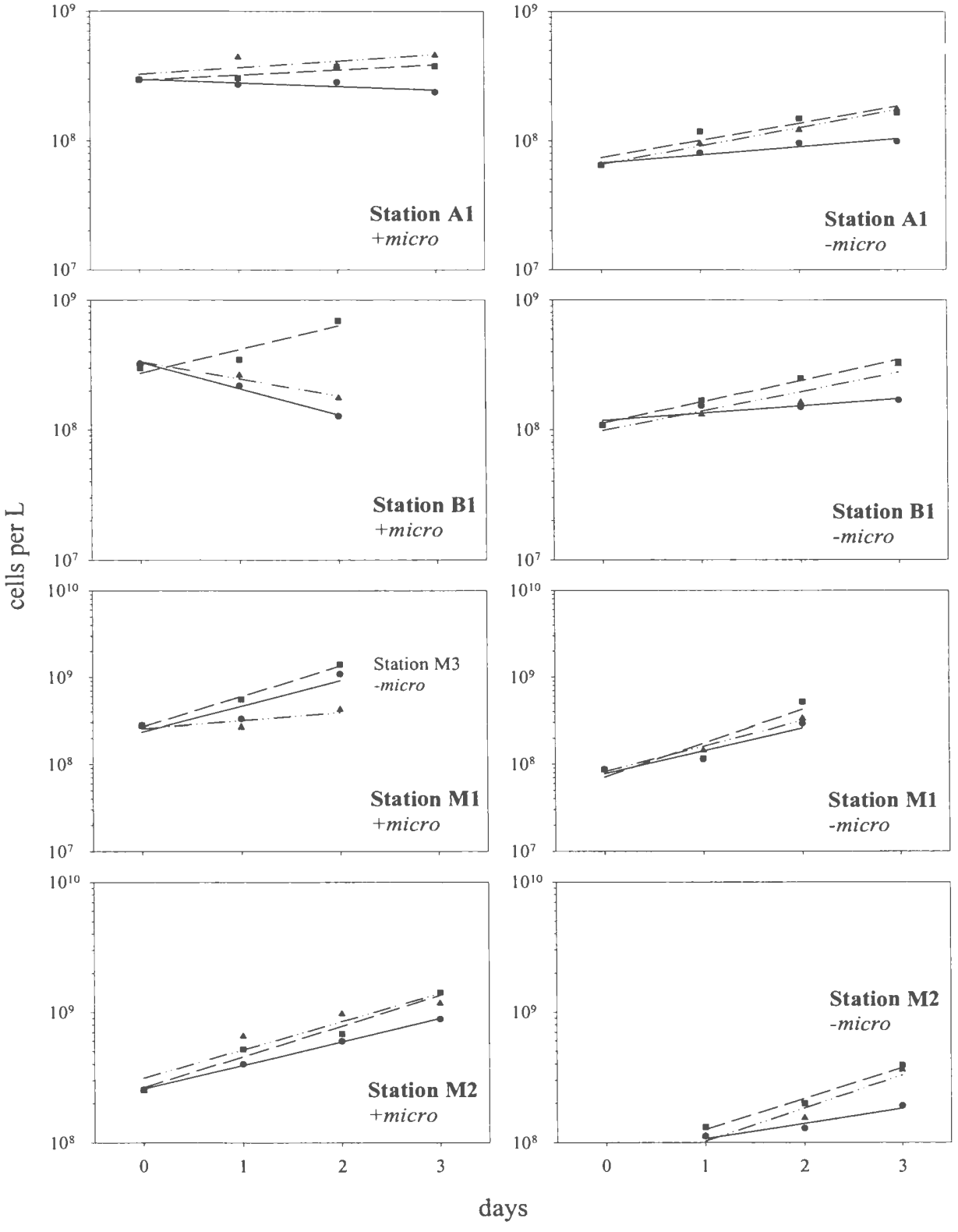


Figure 2.7 The daily change in the bacterial population under three turbulence treatments at four sites within the polynya during July 1998. Circles (●) represent high turbulence treatment, triangles (▲) represent low turbulence treatment and squares (■) represent no turbulence treatments. (Note: At Station M2, *-micro* treatment, sample was lost at the zero timepoint.)

2.3.4.2 Turbulence effects on bacterial thymidine uptake rates

The effect of turbulence on bacterial thymidine uptake was investigated at four stations under three turbulence treatments (high, low and none). Bacterial thymidine (TdR) uptake by bacteria ranged over an order of magnitude among stations: 0.408 to 4.53 pmol L^{-1} h^{-1}. At all four stations TdR uptake was typically higher under the turbulent than static treatment (Figure 2.8). Highest rates of uptake were related to the low turbulence treatment rather than the high turbulence treatment. Furthermore, the highest uptake rates were found to be associated with the southerly, mixed stations M1 and M2.

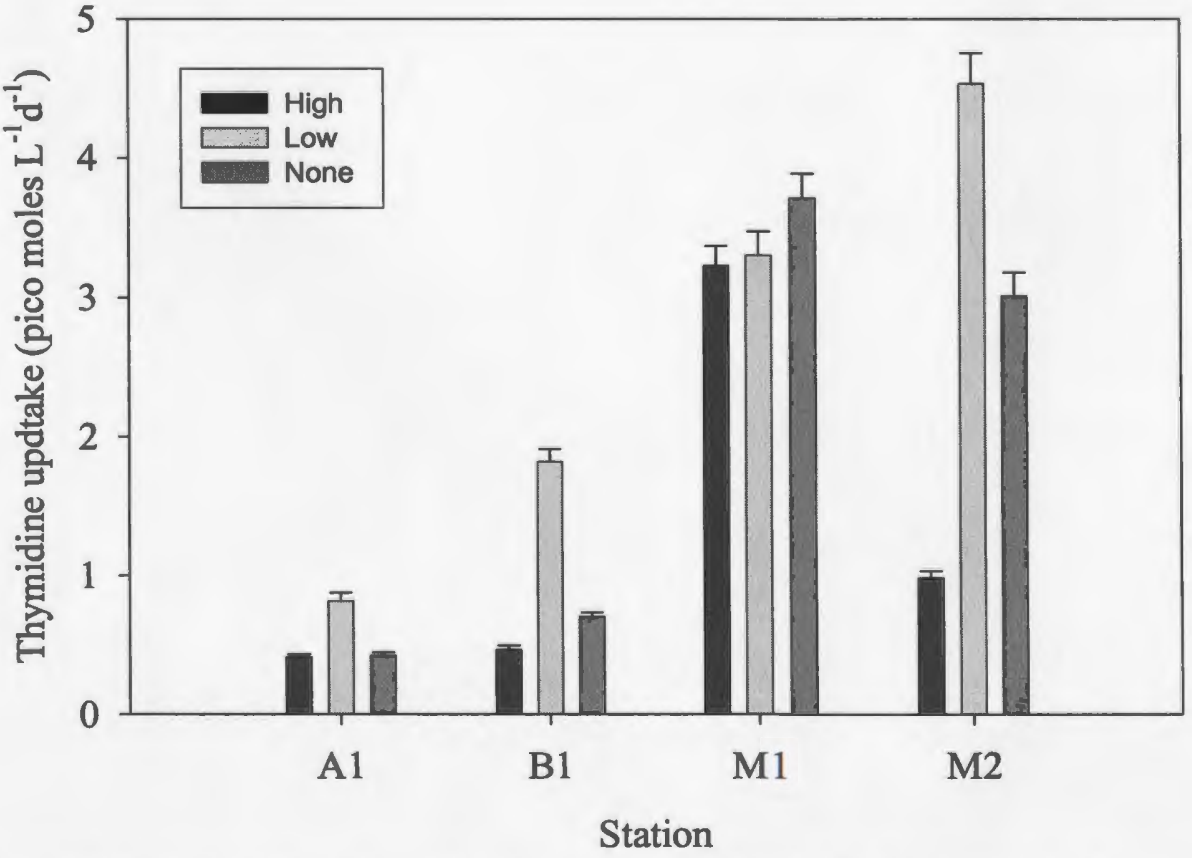


Figure 2.8 The tritiated thymidine rate of update by bacteria in the North Water polynya at four stations under three levels of turbulence: high turbulence, low turbulence and none.

2.4 Discussion

2.4.1 Bacterial distribution and growth during late summer

The North Water polynya is considered the most productive ecosystem above the Arctic Circle, as evidenced by the persistent presence of marine mammals and birds (Stirling 1997). It is apparent from this study that the polynya has an active microbial population within its highly stratified surface waters despite the low temperatures and high viscosity of the North Water. Furthermore, the bacterial abundances of the NOW equalled or exceeded summertime abundance values reported from most other Arctic environments (Table 2.7).

Table 2.7 Comparison of summertime bacterial abundances from the North Water polynya and other Arctic environments.

Water mass	Latitude and Longitude	Bacterial Abundance (L^{-1})	Reference
North Water polynya	75-79°N 75-78°W	0.5 – 22 x 10^8	This study
Northeast Water polynya	79-81°N 08-13°W	12 -58 x 10^8	Yager and Deming (1999)
Baffin Bay	69°N 53°W	4 – 25 x 10^9	Nielsen and Hansen (1999)
Resolute Passage	74°N 95°W	0.4 – 2.4 x 10^8	Pomeroy *et al.* (1990)
Greenland Sea	70-75°N 00-08°E	0.9 – 28 x 10^8	Borsheim (2000)
Arctic Ocean	79°N 108°W	0.1 – 5 x 10^8	Pomeroy *et al.* (1990)
Chukchi Sea	71-73°N 157-165°W	2 – 5 x 10^8	Cota *et al.* (1996)

The importance of bacteria relative to that of phytoplankton has been found to be similar in polar waters as it is in temperate and tropical waters (e.g., Thingstad and Marinussen 1990; Sullivan *et al.* 1990; Lochte *et al.* 1997). In all regions of the North Water during August 1997, bacterial abundance was coupled with phytoplankton abundance as estimated by chlorophyll concentration (Figure 2.4) with a stronger correlation in the BBW (r^2 = 0.515) than the SRAW (r^2 = 0.395). This positive correlation between bacteria and chlorophyll suggests that if bottom-up forces also regulate phytoplankton production, then bacterial abundances and production should respond to increases in phytoplankton nutrients, but high nutrients can reflect low primary production which is likely why the relation between bacterial abundance and nutrients with depth (Figs. 2.3a, b, c) are negative. Thus, bacterial abundance may be regulated by the supply of organic matter as reflected by chlorophyll stocks (Ducklow and Carlson 1992). If marine bacterial resources are mostly derived from phytoplankton exudates and nutrient recycling from food web interactions, i.e., sloppy feeding, then when phytoplankton abundance becomes limited, bacteria must recycle old organic matter and tend to grow more slowly than those bacteria growing on freshly degraded phytoplankton (Moriarty *et al.* 1998). When this happens, the microbial loop dominates and lower bacterial growth rates persist. The difference between the SRAW and BBW regions of the NOW could be attributed to the very water masses that describe them. Both groups of stations demonstrate a positive correlation between phytoplankton (chl *a*) and bacteria, but the SRAW region displays higher bacterial growth rates than the BBW region during late summer (Table 2.5). This could suggest that there is a different supply of nutrients

from the Arctic water being utilized by phytoplankton, which provides better substrate for bacteria in the west. In support of this, Table 2.3 showed higher inorganic nutrient concentrations at those stations associated with the Arctic water mass. To investigate these further, Pearson correlations were analyzed between bacteria, chlorophyll, salinity and inorganic nutrients for the SRAW and BBW regions (Table 2.8). It was found that there were significant negative correlations with the inorganic nutrients, than when bacteria were correlated with chlorophyll. It would appear that bacteria are responding immediately to the increased chlorophyll left by new photosynthate, but that the bacteria then respond to the inorganic nutrients as the season progresses. This emphasizes a characteristic of the microbial loop in that it is not just an immediate process, but a cumulative process as the season progress within the NOW.

Table 2.8 Pearson correlation coefficients between bacteria, phosphate, silicate, nitrate+nitrite, salinity and chlorophyll for the Baffin Bay water mass and Arctic water mass.

Water Mass	Bacteria: PO_4	Bacteria: SiO_4	Bacteria: NO_4+NO_3	Bacteria: Salinity	Bacteria: Chlorophyll *a*
BBW	-0.911	-0.800	-0.812	-0.894	0.535
SRAW	-0.714	-0.754	-0.815	-0.779	0.606
Mixed	-0.821	-0.821	-0.821	-0.782	0.685

Unfortunately, determining if this coupling of phytoplankton and bacteria are changed from earlier in the year during the shift of ice-covered to open water regions cannot be judged on the basis of this study alone. Tremblay *et al.* (2002) found that SRAW penetrated deep at the more southerly stations as the summer persisted, with strong SRAW cores in the south below the surface, thus combining with a mixture of

BBW and melt water. How the two water masses change and combine during the summer, may in fact have an effect on the phytoplankton-bacterial relationship in the NOW as the warm season progresses from April to August. It has been found that the horizontal distribution of bacteria in the North Water relates to the development and breakdown of the phytoplankton bloom in the North Water during summer (Middelboe *et al.* 2002). Studies have shown that the phytoplankton bloom originates along the Greenland coast in April to May, spreads toward the west and south, eventually reaching the more northerly region of the polynya by late June and July, then collapses later in July in response to nutrient limitation in the east and southern portions of the polynya (Mei *et al.* 2002, Tremblay *et al.* 2002). The results of this study coincide with those found by Middelboe *et al.* (2002), and Figure 2.10 demonstrates the relationship between $\log_{10}$ transformed chlorophyll *a* concentration and bacterial abundance at all sampled stations in the North Water polynya (Figure 2.9) during April 1998, May 1998, June 1998, July 1998 and August 1997.

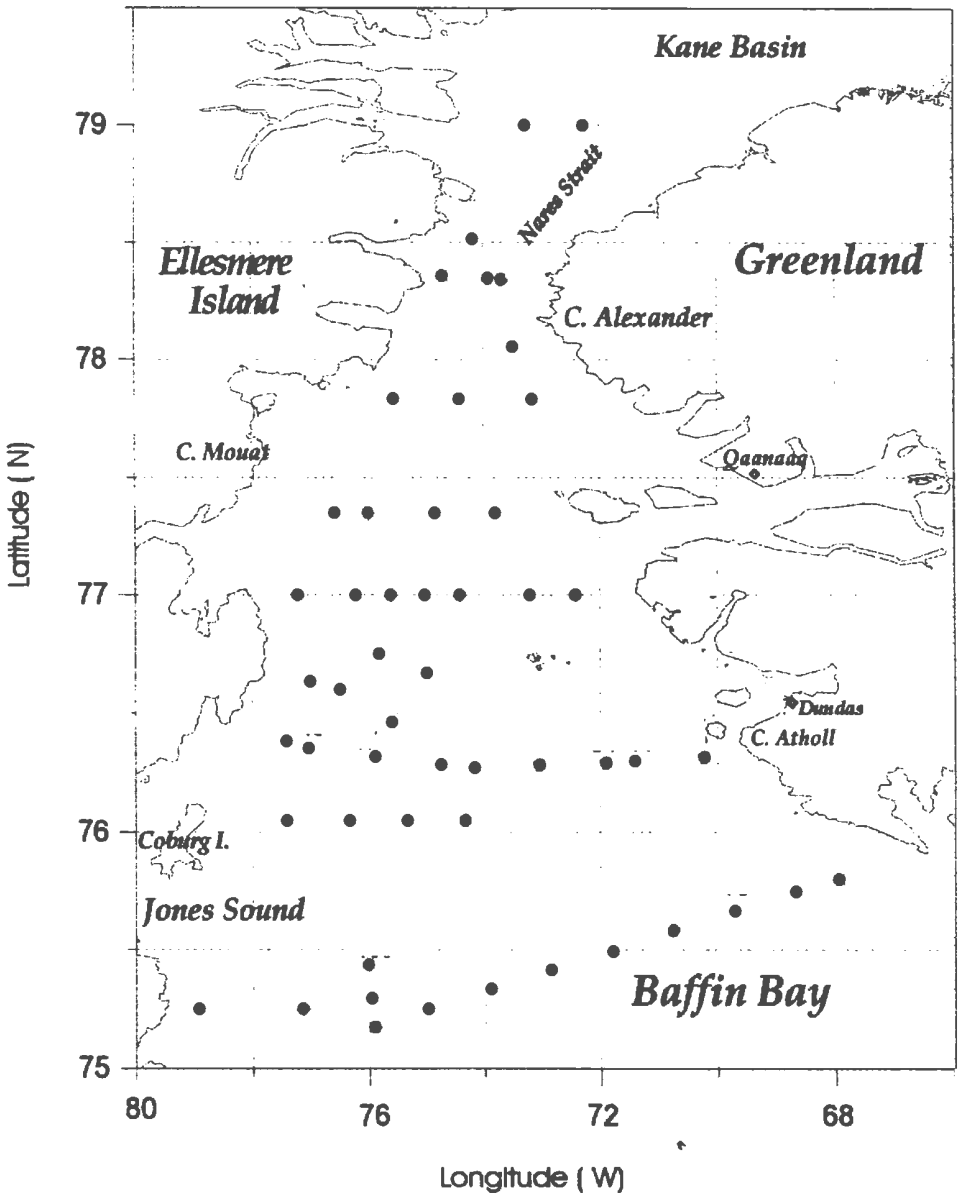


Figure 2.9 This is a map showing all station sites throughout the North Water Polynya during 1998 where bacterial abundance and chlorophyll content were measured (data represented in Figure 2.10.)

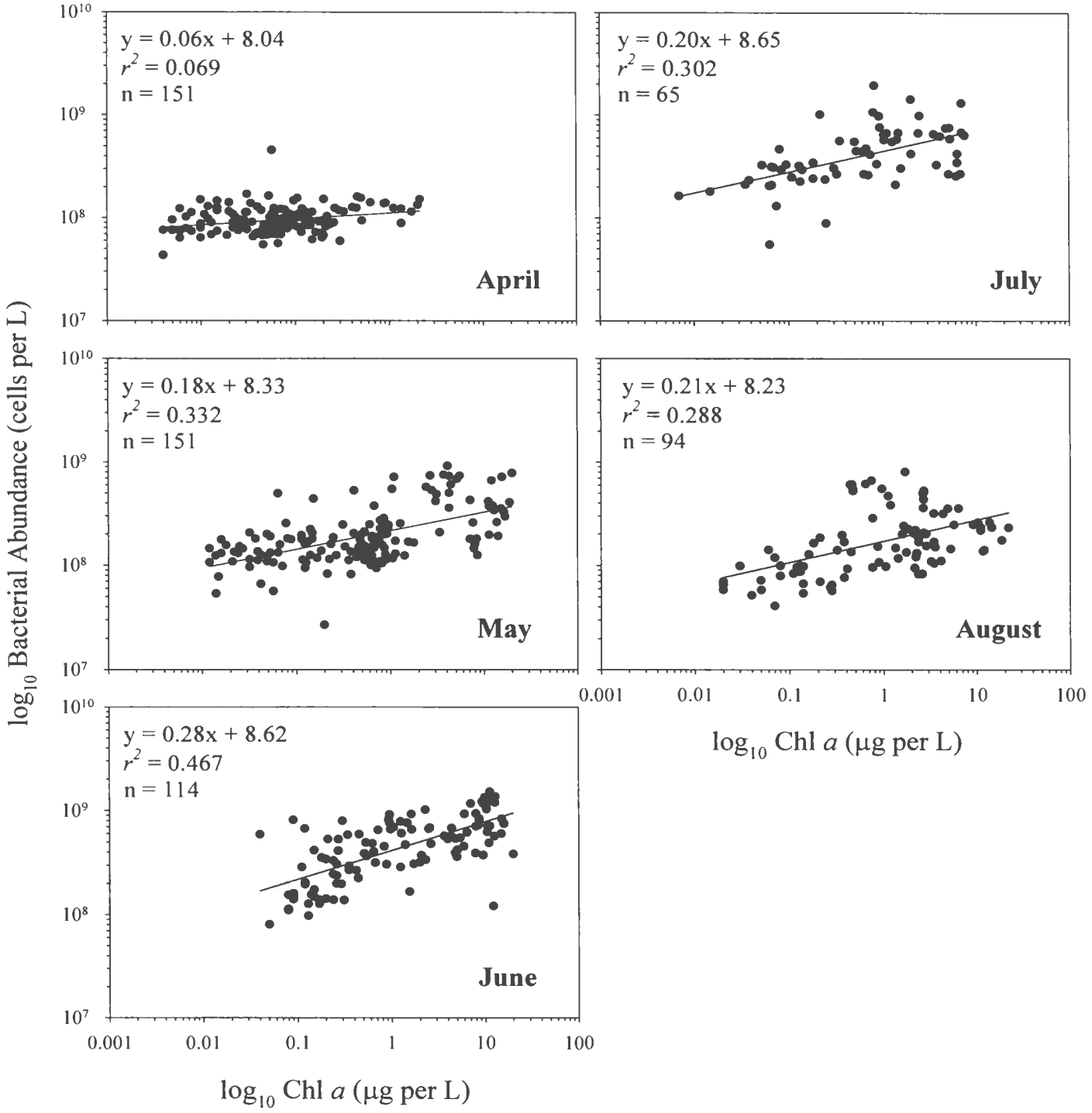


Figure 2.10 The relationship between $\log_{10}$ transformed chlorophyll *a* concentration and bacterial abundance at all sampled stations in the North Water polynya during April 1998, May 1998, June 1998, July 1998 and August 1997 to represent a seasonal change in the bacteria and phytoplankton coupling. This data collection and analysis originates from collaboration between Dr. JD Pakulski and M. Ptak Delaney.

2.4.1.1 A comparison of bacterial growth among methods

There were three different techniques employed to attempt to determine bacterial growth rates in the absence of grazers. The first technique employed the most extreme treatment of a 1-μm filter and produced the slowest mean doubling time of 7.2 days (Table 2.5) and a wide range among seven stations. The serial dilution technique employed a 202-μm Nitex filter and produce d a much higher and less variable growth rate, with a mean doubling time of 2.67 days, but at only two stations. The static treatment in July 1998 using a 10-μm filter produced a mean doubling time of 2.01 days at two A and B stations and an even higher doubling time of 1.38 days at the four mixed water stations. These data suggest that the extreme treatment of a 1 μm filter deprived the bacterial community of substrate while the 3 μm filter may have produced higher growth rates because it was earlier in the season than 1997 (July vs. August), or because it excluded some of the micrograzers, such as the dinoflagellates and ciliates (see Section **2.3.3.2**).

2.4.2 Bacterial grazing mortality during late summer

Microzooplankton play a central role in microbial systems because they are capable of grazing on a range of sizes of particles, including the ability to prey on smaller particles, such as bacteria, whereas most mesozooplankton are unable to capture such small particles efficiently (Burkhill 1995). With the possible exception of a few species of gelatinous zooplankton (i.e., *Oikopleura*, Deibel 1988), the only organisms capable of efficiently grazing bacteria and similarly small-sized primary producers are phagotrophic protists (Sherr and Sherr 1994) and dinoflagellates (Lessard and Smith 1985).

Microzooplankton thus act as trophic intermediates between the small bacteria, pico- and nanoplankton and the larger mesozooplankton (Gifford 1991; Froneman and Perissinotto 1996). Microzooplankton grazing is also quantitatively significant. Recent studies have shown that microzooplankton dominate grazing upon phytoplankton in the North Atlantic (Burkhill *et al.* 1993; Verity *et al.* 1993), sub-Arctic Pacific (Strom and Welschmeyer 1991) and in Antarctic waters (Garrison *et al.* 1991). Moreover, Taniguchi (1984) showed that absolute abundance of microzooplankton in the boreal Pacific and western Arctic waters was as high as those found in more temperate regions. Losses due to grazing in central Baffin Bay would amount to 9 to 15% the standing stock and 37 to 88% of production (Paranjape 1987). Furthermore, several studies of regions in the Arctic suggest that heterotrophic protists are the primary bacterivores in polar waters. Heterotrophic flagellates and ciliates were reported to be an integral component of pelagic food webs in the Bering and Chukchi seas (Anderson, 1989) and off the western coast of Greenland (Nielsen and Hansen 1995). Sherr *et al.* (1997) reported bacterivory rates of 0.03 to 0.9 μg C $L^{-1}d^{-1}$ in the central Arctic ocean, which is comparable to the present study of 0.74 and 1.32 μg C $L^{-1}d^{-1}$ (assuming 20 fg carbon $cell^{-1}$) in the SRAW and BBW regions of the NOW. Although nanoflagellates are thought to be the dominant bacterivore in planktonic systems, heterotrophic dinoflagellates are also known to feed upon bacteria (Lessard and Swift 1985, Sherr and Sherr 1987). More than 50% of the microzooplankton community in the present study were composed of heterotrophic dinoflagellates. This is consistent with the findings of Bursa (1961), who reported the predominance of heterotrophic dinoflagellate forms, such as *Protoperidinium* sp., *Gymnodinium* sp., and *Gyrodinium* sp.,

in the Canadian Arctic, constituting 73% of the Arctic microzooplankton community. Nielsen and Hansen (1995) also reported that heterotrophic dinoflagellates accounted for 50% of the microzooplankton biomass in Disko Bay, off the western coast of Greenland. Even though this study in the NOW did not formally investigate the role of dinoflagellates in the microbial food web, it is probable that direct consumption of bacteria by these larger consumers can significantly contribute, along with the remainder of the microzooplankton community, to the efficiency of trophic transfer of bacterial production in the North Water and to the overall polar marine food web.

2.4.3 Turbulence effects on bacterial growth, grazing mortality and production

The recently opened waters of the North Water polynya are characterized by high bacterial growth rates, but are limited by grazing under turbulent conditions. The polynya's bacterial community responded to the breakdown of the phytoplankton bloom in the sampled southern stations of July 1998. The results, of which, are higher rates of bacterial growth and production. At the northern stations (A1 and B1), where the bloom was still not completely developed in the middle of July, there was likely a limited release of organic carbon from the phytoplankton, in which bacteria could not sustain rates of growth and production as high as the other two stations.

The bacterial growth rates determined in the <3 μm condition by microscopic observation were significantly higher than the specific growth rates determined via the TdR uptake method. These higher rates may be considered as the potential rates of an active part of the sampled bacterial assemblage. It may be that a substantial fraction of the total bacterial assemblage is actually not growing (Zweifel and Hagström 1995,

Middleboe *et al.* 2002). A large fraction of non-growing cells would have a pronounced effect on the average specific growth rate estimated from TdR incorporation and total bacterial abundance, but a much smaller effect as seen during microscopic observation.

The effect of turbulence on grazing mortality of bacteria was not consistent among stations. Bacterial growth at stations A1 and B1 were significantly lower in the high turbulence treatment, but these stations also sustained higher rates of bacterial mortality than growth under the high turbulent treatment. Grazing mortality at Station M2 was negligible in the static and turbulence treatments, and at Station M1, it was negligible in the static treatment, but high under both turbulence treatments. This would suggest that grazers had some control over bacterial production in the northern region of the polynya, but little to no control in the southern region. These results coincide with the results of the dilution assay experiment, in which higher rates of bacterial mortality likely due to grazing losses were associated with stations found in the SRAW region. There is also a possibility that within the southern region of the polynya, the high bacterial biomass was maintained not only because of unlimited nutrient supply, but rather because of grazing pressure relief on the bacteria. Though it was not formally investigated in this study, their exists the potential that heterotrophic protists preferred more nutritious prey, such as nano- and pico-algae (Petersen *et al.* 1999)

It is difficult to explain the results of the daily TdR uptake rates: each of these rates was highest under the low turbulence treatment at all four stations. The lowest of the TdR uptake rates do relate to the more northerly stations (A1 and B1) where growth rates were low and mortality high. However, how the low turbulence treatment augments

the uptake rates than the other two treatments is undetermined. It would be expected that turbulence would have no effect on the TdR uptake since bacteria are too small to experience turbulent fluctuations in the water column. The only suggestion is that the gentle rotation of the plankton wheel maintained a homogeneous, or perfectly random Poisson distribution of particles, within the contained water sample, whereas the static sample allowed some settlement of particles and the high turbulence treatment created a clumped distribution of particles, or aggregation of particles. If the latter occurred, then it is possible that fewer bacteria were captured in the 10 ml subsamples used to test for TdR uptake.

2.4.4 Conclusion

The bacteria-based food webs and microbial trophic pathways within the North Water polynya have proven to be important in overall energy and material cycling in the Arctic marine food web. The relatively high bacterial biomass and the positive correlation to phytoplankton biomass indicate that bacteria are able to efficiently utilize and grow on the dissolved organic matter despite lower temperatures of the Arctic. Furthermore, turbulence in the NOW may have a degree of control on the carbon cycling within the marine microbial food web, but only at times when substrates and prey are limited. Therefore, the results of this study, as well as others, contribute to the growing realization that the polar microbial community contributes significantly to the overall biogeochemical cycle. Our results have also suggested that there are large regional differences in the pelagic food web structure and the patterns of biogenic carbon export in the North Water polynya during the summer.

Acknowledgements

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CHAPTER THREE

TURBULENCE EFFECTS ON COLD OCEAN MICROBIAL COMMUNITIES: AN ENCLOSURE STUDY

Abstract. There have been numerous studies on turbulence effects on macro-zooplankton during the last decade, but studies on microplankton have been fewer, sometimes contradictory, and conducted largely under temperate conditions. In the present study, an enclosure experiment was carried out with natural seawater of Logy Bay, Newfoundland to determine the effects of turbulence on heterotrophic and autotrophic growth in the presence and absence of micrograzers. The experiment was conducted in February and April, with water temperatures at 0°C and 5°C, respectively. There was no difference in bacterial growth between the static and turbulent enclosures in either the presence or absence of micrograzers at both experimental temperatures. Heterotrophic nanoflagellate growth was found to be significantly higher at 0°C in the presence of turbulence but only when micrograzers were absent. A similar pattern was found with the small autotrophic community at 0°C, as determined by chlorophyll *a* <5 μm, in which growth was significantly higher with turbulence but only when micrograzers were absent. Turbulence significantly enhanced growth rates of the large autotrophic community (>5 μm chl *a*), which was largely composed of diatoms, both in the presence and absence of grazers. These results suggest that turbulence effects are small under cold ocean conditions, but increase with the size of the organism. It thus appears turbulence could affect patterns of biogenic carbon export differentially, dependent upon the size structure of the plankton community.

3.1 Introduction

Concern about global warming has renewed interest in the role of the oceans in global carbon flux and in the effects of turbulence on oceanic microbial processes. The role of turbulence is of particular concern because logistics dictate that most studies of open ocean microbial communities must be conducted within enclosures. Enclosure studies are often utilized to investigate biological components of an oceanic system, but are either left unmixed or use mechanical mixing that may result in turbulence unrepresentative of natural conditions (Sanford 1997; Petersen *et al.* 1998; Peters and Marrasé 2000). Quantifying the effects of turbulence is thus essential to the accurate extrapolation of experimental results to predict natural ocean processes. Another limitation to our present understanding of turbulence effects is that studies have largely been conducted under temperate conditions. A recent review of turbulence effects studies by Peters and Marrasé (2000) reports a range of 7-28°C with a mean of 17°C, with little or no representation from extensive cold ocean environments.

Turbulence effects can be direct by enhancing the rate of physical transport of nutrients or prey to the recipient (e.g., Alcaraz *et al.* 1988; Meulbert *et al.* 1994; Shimeta *et al.* 1995), or even by inhibiting growth of some species (e.g. Thomas and Gibson 1992; Gibson and Thomas 1993). Turbulence effects can also be indirect, propagating across size fractions from larger to smaller organisms usually by means of trophic interactions. For example, direct turbulence-enhanced encounter rates by phagotrophs increases loss rates of their prey while indirectly enhancing organic substrates for bacteria and inorganic nutrient supplies for phytoplankton (Peters *et al.* 1998). However, reports

of turbulence effects on microplankton and nanoplankton are limited and frequently contradictory (Petersen *et al.* 1998; Peters and Marrasé 2000). Peters and Gross (1994) reported that small scale turbulence increased microplankton grazing rates on bacteria in the Gulf of Mexico, potentially limiting bacterial populations, whereas experiments on the microbial community of the northwest Mediterranean found that turbulence induced a shift by microheterotrophs to larger prey sizes thereby relieving grazing pressure on bacteria (Peters *et al.* 1998; Peters *et al.* 2002). Observations such as these make it clear that turbulence effects need to be investigated in a wide range of ecosystems under widely varying conditions before patterns can be expected to emerge.

The productive coastal waters of eastern Newfoundland typically have an annual surface temperature range of -2°C to 14°C (Kendaris 1980; deYoung and Sanderson 1995), with winter temperatures rarely exceeding 0°C. In the present study, both turbulence and microplankton abundance were manipulated in a factorial experimental design to determine their effects on the growth rates of bacteria, heterotrophic nanoflagellates and two size-fractions of autotrophs in Newfoundland coastal waters during winter and early spring.

3.2 Materials and Methods

Enclosure experiments were carried out in February and April 2001 at the Ocean Sciences Centre (OSC), Logy Bay, Newfoundland to compare cold ocean microbial community growth rates under turbulent and static conditions and in the presence and absence of micrograzers. Logy Bay is a section of relatively undeveloped coastline broadly open to the northwest Atlantic Ocean. Winter conditions of Logy Bay are characterized by the southward-bound Labrador Current with water temperature and salinity typically around 0°C and 32.6 ‰, respectively, with springtime temperatures rising to about 5°C (Kendaris 1980).

Experiments were conducted in large containers to try to minimize enclosure effects and wall growth during the incubations (Oviatt 1994; Chen *et al.* 1997). Enclosures were 0.56 m in depth with a diameter of 0.74 m. Ambient sea temperatures were maintained by placing the cylindrical enclosures within a flowing seawater tank that was supplied by fresh seawater continuously pumped from Logy Bay into the OSC (Figure 3.1). The flowing seawater maintained the temperatures of the experimental enclosures at 0°C throughout the incubation in February, and at 5°C in April. Incubations were conducted for 6 days under the natural diurnal light:dark cycle with incandescent irradiance of 100 $\mu E\ m^{-2}s^{-1}$.

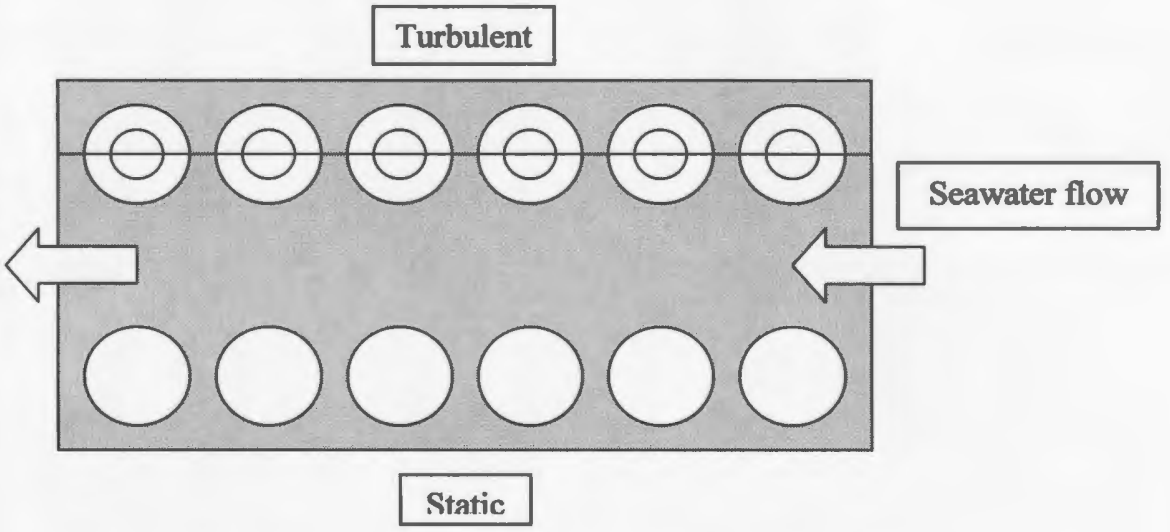
A factorial experimental design was employed with four treatments run in triplicate: static without micrograzers (**S** –micro), turbulent without micrograzers (**T** -micro), static with micrograzers (**S** +micro), and turbulent with micrograzers (**T** +micro). The enclosures with micrograzers were filled with raw seawater that was screened

through a 200 μm mesh sieve to remove macrograzers. Water for the micrograzer removal treatments was filtered through a 20 μm mesh sieve to remove most of the micrograzer community. After a 24 h acclimation period, enclosures were sampled 2h into the light cycle using a sample-rinsed non-toxic siphon tube that was moved throughout the water column to obtain an integrated sample. All water was gently siphoned into acid-washed (5% HCl), sample-rinsed, polycarbonate bottles.

Bacteria and heterotrophic nanoflagellate samples were fixed with gluteraldehyde (1% final concentration) and then filtered onto black 0.2 μm polycarbonate filters that were subsequently stained with acridine orange, mounted with Type A immersion oil and stored in a –30°C freezer for later microscopic analysis. Cells were enumerated at 1000x using epifluorescence techniques with a Zeiss Axiovert 35 inverted microscope equipped with a HBO 100W mercury lamp. Bacteria were enumerated from 10 random fields per filter and at least 12 random fields per filter were scanned for heterotrophic nanoflagellates.

Total autotrophic biomass was estimated by measuring the chlorophyll *a* concentration of replicate 250 ml samples filtered onto Whatmann 25 mm GF/F filters. Large autotrophic biomass (chl *a* >5μm) was determined from replicate 250 ml samples using 5μm Nucleopore filters and small autotrophic biomass (chl *a* <5μm) was then determined by the difference between that fraction and the total chlorophyll. Chlorophyll *a* was measured using a Turner Designs fluorometer after 24 h extraction in 90% acetone at –30°C, and with correction for phaeopigments by acidification.

A



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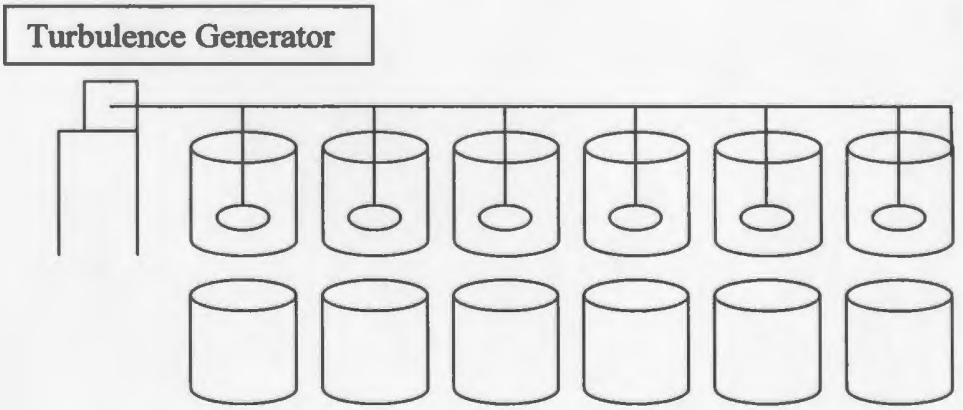

Figure 3.1 Schematic drawings of the experimental set-up with a A) top view and B) side view of the arrangement of static and turbulent cylindrical enclosures nestled within an inground flowing seawater tank.

Microphytoplankton and microzooplankton taxonomic composition and abundance were determined by phase-contrast microscopy. Subsamples of 200 ml were fixed with Lugol's iodine, filtered onto 5μm Nucleopore filters and then processed using the filter-transfer-freeze technique (Hews and Holm-Hansen 1983).

Turbulence was induced by a perforated PVC plunger of 0.27 m in diameter and 13.7% solidity, oscillating vertically at 2 rpm to produce a turbulence level representative of natural oceanic conditions. Vertical eddy diffusivity coefficients (K_z) for the enclosures were determined using the injected dye technique (Sanford 1997, Petersen *et al.* 1998) as:

Eq. 1) $$K_z = z^2 / (2T_m)$$

where z is the depth (cm) of the water column in the enclosure and T_m is the time (s) required for the dye to diffuse uniformly throughout the water column, which was determined using recorded output from a LICOR PAR sensor. The mean T_m of 102 s yielded a vertical eddy diffusivity in the turbulent enclosures of 15.4 ± 3.1 $cm^2\ s^{-1}$ while that in the static enclosures was negligible.

Statistical analyses were performed using SPSS and SigmaPlot software (SPSS, Inc. 2001). Replicate data sets (n=3) within each of the four treatments were tested for homogeneity of slopes of abundance vs. time prior to their combination for further analysis. Regression slopes from $\log_{10}$ cell abundance or chlorophyll versus incubation time were used to compare rates of

increase among treatments and to estimate doubling times (d) as:

Eq. 2) $d = (\log_{10} 2) / \text{slope}$

Regressions slopes and 95% confidence limits were converted to growth rates (log base e) and plotted together to permit graphic evaluation of statistical differences among treatments.

3.3 Results

Logarithmic plots of abundance and chlorophyll *a* versus incubation time were inspected for departures from linearity to evaluate if there was any evidence of acclimation time or nutrient depletion effects during the 6-day incubations. Constant growth rate throughout the incubation would result in an exponential increase in abundance or biomass with time which would be represented as a straight line response on a logarithmic scale. Acclimation effects would result in a lag phase during early incubation whereas nutrient depletion would result in diminished growth late in the incubation.

3.3.1 February Experiment - 0°C

Regression slopes of abundances versus time were positive and highly significantly different from zero ($p < 0.001$, Table 3.1) for bacteria, heterotrophic nanoflagellates and smaller autotrophs (chl *a* < 5μm) in both the absence (Figure 3.2) and presence (Figure 3.3) of micrograzers, indicating that these taxa were growing in each treatment. The larger autotrophic component (chl *a* > 5μm) exhibited a significant increase with time only in the **T** +micro treatment (Figure 3.4, Table 3.1). There were no obvious departures from a linear response late in the incubations, suggesting that the enclosures were sufficiently large to minimize resource depletion effects during the 6-day incubation. The heterotrophic nanoflagellates did appear to exhibit an initial lag effect in the micrograzer removal treatments, however, with no significant change in abundance

over the first two days (Figure 3.2). Consequently, regressions for this taxonomic category were calculated using only the day 2 - 6 data for all treatments.

Observed growth rates across all four treatments were highest for the smaller autotrophic component (chl *a* <5μm, Figure 3.2) with doubling times on the order of 2-3 days (Table 3.1). Heterotrophic nanoflagellates were growing more slowly, with doubling times of 4-7 days while bacterial doubling times ranged from 7 - 9 days (Table 3.1). In contrast, growth rates of the larger autotrophic component (chl *a* >5μm) were significantly greater than zero only in the turbulence treatment in the presence of micrograzers, with a doubling time of about 6 days (Table 3.1).

Table 3.1 Log_{10} regression slopes representing the observed daily rates of change (± std. err.) and the corresponding doubling time of four microbial components at 0°C under four treatments: static without micrograzers (S -micro), turbulent without micrograzers (T -micro), static with micrograzers (S +micro), and turbulent with micrograzers (T +micro).

Trophic Level	Treatment	Slope	*p*	Doubling time (d)
Bacteria	S -micro	0.039 ± 0.005	<0.0001	7.81
	T- micro	0.033 ± 0.005	<0.0001	9.08
	S +micro	0.034 ± 0.005	<0.0001	8.83
	T +micro	0.043 ± 0.005	<0.0001	7.05
HNF†	S -micro	0.067 ± 0.012	0.001	4.48
	T- micro	0.101 ± 0.012	0.0001	2.99
	S +micro	0.064 ± 0.012	0.0015	4.73
	T +micro	0.066 ± 0.011	0.001	4.59
<5µm Chl *a*	S -micro	0.089 ± 0.017	<0.001	3.38
	T- micro	0.125 ± 0.015	<0.001	2.41
	S +micro	0.151 ± 0.016	<0.001	1.99
	T +micro	0.149 ± 0.026	<0.001	2.02
>5µm Chl *a*	S -micro	-0.016 ± 0.017	0.3517	∞
	T- micro	0.021 ± 0.015	0.2110	14.20
	S +micro	0.012 ± 0.029	0.4796	24.18
	T +micro	0.052 ± 0.010	0.0003	5.79

† HNF daily rate of change based on regression of data from day 2 to day 6.

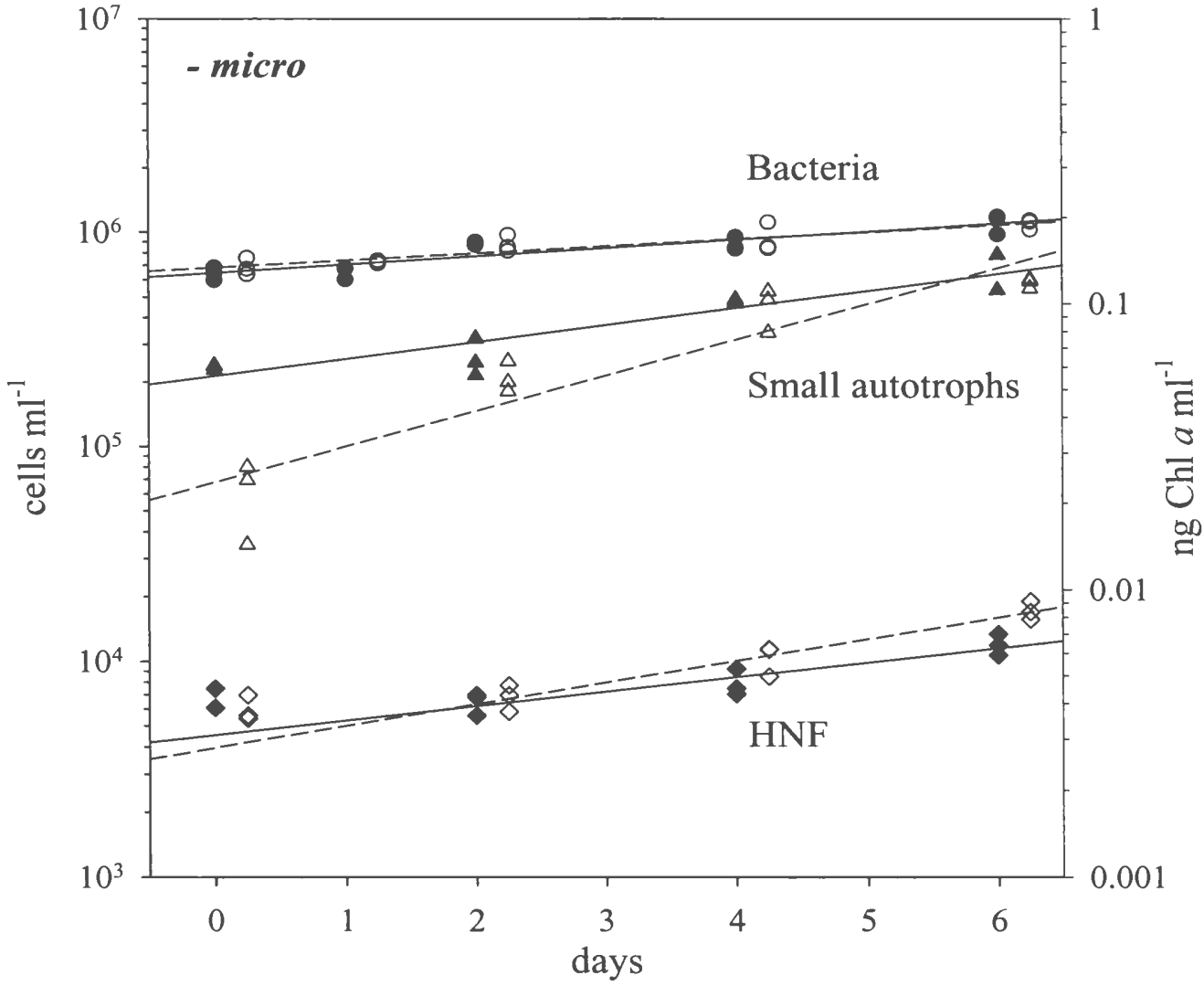

Figure 3.2 Temporal change in bacteria, heterotrophic nanoflagellates, and small autotrophs (chl *a* < 5μm) at 0°C in the absence of micrograzers under static (closed symbols, solid lines) and turbulent (open symbols, dashed lines) treatments. All data are presented for heterotrophic nanoflagellates, but regressions are only based upon days 2 - 6 due to the apparent lag phase during days 0 – 2 (see text).

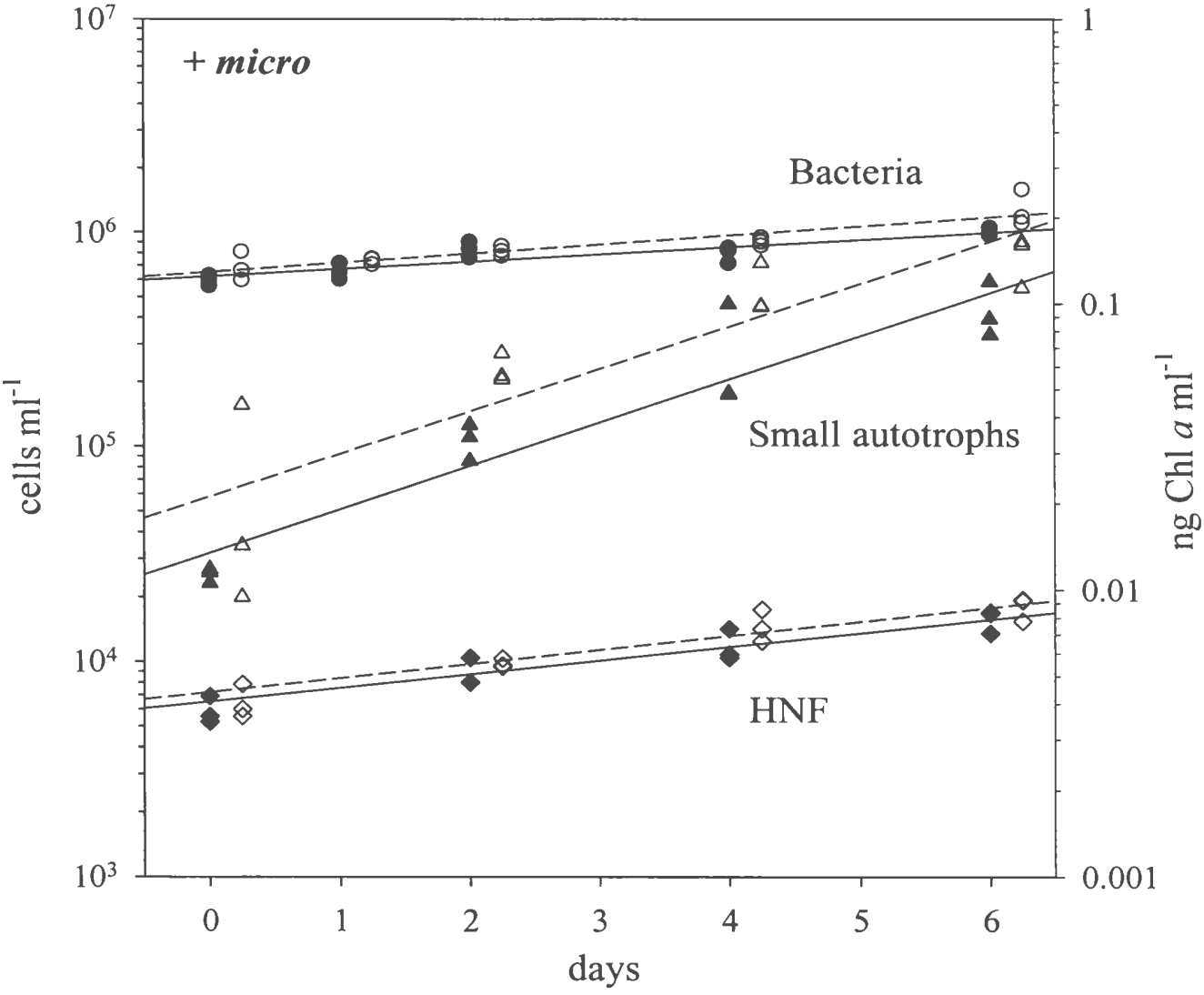

Figure 3.3 Temporal change in bacteria, heterotrophic nanoflagellates, and small autotrophs (chl *a* < 5μm) at 0°C in the presence of micrograzers under static (closed symbols, solid lines) and turbulent (open symbols, dashed lines) treatments. All data are presented for heterotrophic nanoflagellates, but regressions are only based upon days 2 – 6 due to the apparent lag phase during days 0 – 2 (see text).

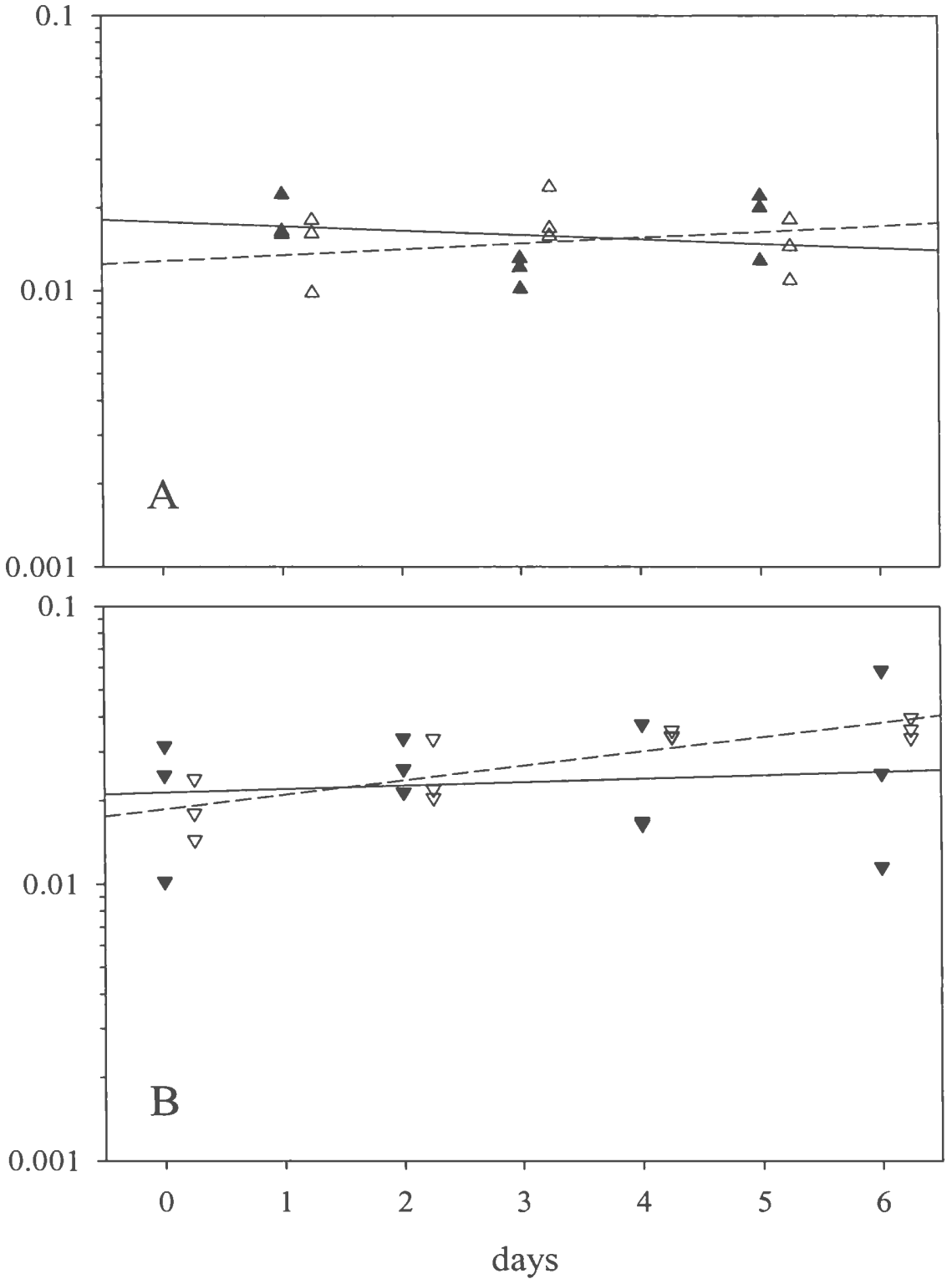

Figure 3.4. Temporal change in the large autotrophic community (chl *a* >5μm) at 0°C in the A) absence of micrograzers and B) presence of micrograzers under static (closed symbols, solid lines) and turbulent (open symbols, dashed lines) treatments.

Growth rates and their 95% confidence intervals were used to make statistical comparisons among treatments. The confidence limits for the bacterial growth rate of each treatment overlapped the observed growth rate in each of the other three treatments (Figure 3.5), thus indicating that none of the differences among growth rates were statistically significant at the $\alpha = 0.05$ level. A comparison of the heterotrophic nanoflagellate growth rates and their corresponding confidence intervals among the four treatments revealed that mean growth was higher only in the **T** -micro treatment (Figure 3.5).

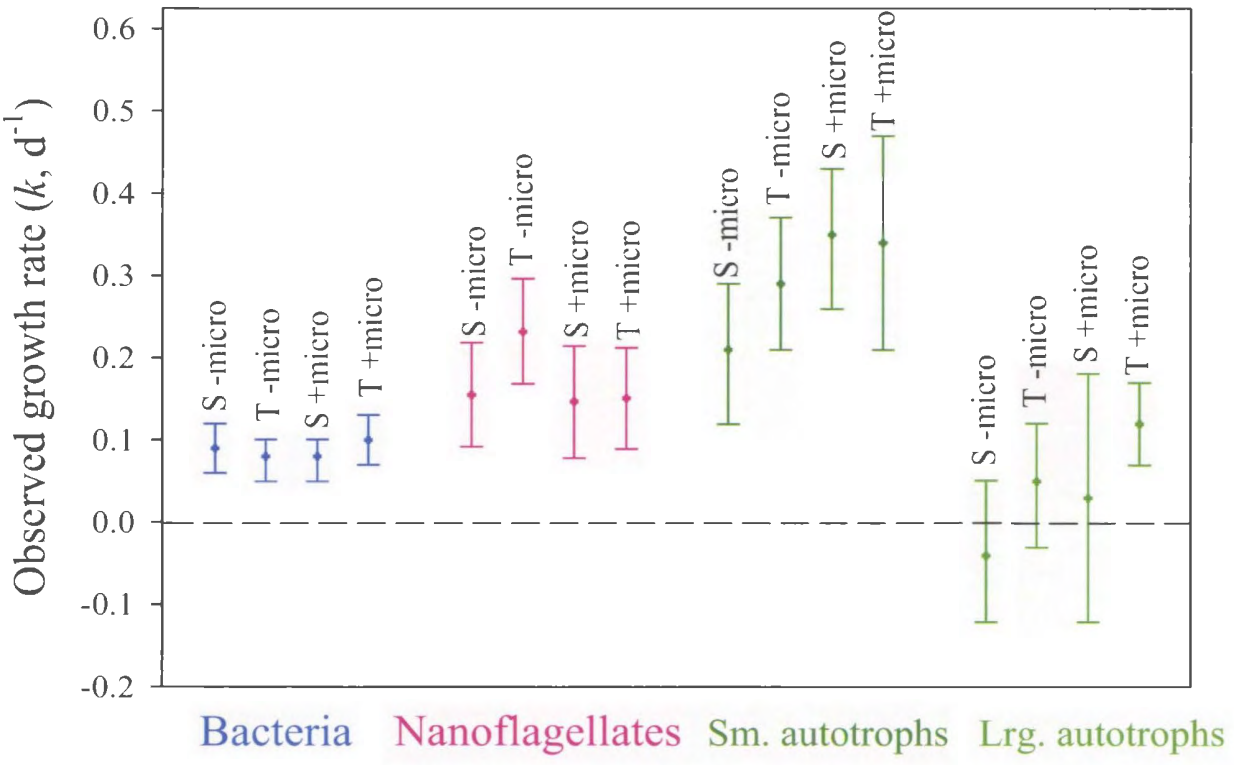

Figure 3.5. The observed growth rate (k, d^{-1}) with 95% confidence intervals for bacteria, heterotrophic nanoflagellates, small autotrophs (chl *a* <5µm) and large autotrophs (chl *a* >5µm) at 0°C under four treatments: static without micrograzers (**S** –micro), turbulent without micrograzers (**T** –micro), static with micrograzers (**S** +micro) and turbulent with micrograzers (**T** –micro).

The confidence limits of the small autotrophs (chl *a* < 5μm) rates of growth indicated that growth was significantly lower in the **S** -micro treatment relative to the other three treatments (Figure 3.4). Growth rates of the larger autotrophic component (chl *a* >5μm) were significantly higher in both turbulent vs. static treatment comparisons (**T**-micro vs. **S** -micro and **T** +micro vs. **S** +micro), however growth was significantly positive only in the **T**+micro treatment (Figure 3.5). Microscopic observations indicated that the larger autotrophs were predominantly diatoms of the genera *Thalassiosira* sp., *Coscinodiscus* sp., *Skeletonema* sp., *Fragilariopsis* sp., and a few unidentified pennate forms.

The dinoflagellates *Ceratium* sp. and *Gymnodinium* sp., and a silicate microflagellate, *Dictyocha* sp. also contributed to the larger autotrophic community, but were typically outnumbered 5:1 by the diatoms in the turbulent treatments. Total cell density of the larger autotrophic community was very low, less than 100 cells L^{-1}. Examination of the micrograzer community showed that it was largely dominated by oligotrich ciliates.

3.3.2 April Experiment - 5°C

Regression slopes were positive and significant (Table 3.2) for bacteria ($p < 0.001$), heterotrophic nanoflagellates ($p < 0.002$), and the smaller autotrophic component ($p < 0.1$) in both the absence (Figure 3.6) and presence (Figure 3.7) of micrograzers. One replicate was removed for each biological variable from the regression analyses due to non-homogeneity of slopes. The slopes of abundances vs. time were not homogeneous and it was thus necessary to eliminate one replicate in both the –micro and +micro

treatments prior to regression analysis. There were also three cases of departure from linearity in the logarithmic plots. Those cases demonstrated a decline in abundance on day 6 in the absence of grazers of both heterotrophic nanoflagellates (HNF, Figure 3.6) and larger autotrophs (Figure 3.8a). Consequently, the regressions excluded day 6 for these taxa. There were inexplicably high values for the large autotrophic component at time zero in the presence of micrograzers (Figure 3.8b), thus those data were also excluded from the regression for that taxonomic category (see Appendix for further illustration). The heterotrophic nanoflagellates exhibited decreasing abundance in the turbulent micrograzer removal (-micro) treatments on day 6 in all three replicates, thus regressions for this treatment were calculated using only data from days 0 - 4 (Figure 3.6). The larger autotrophic component also exhibited a decreasing effect in the -micro treatment, but only under static conditions of all three replicates. This regression, too, was then calculated using only day 0 – 4 data (Figure 3.8). In contrast, during the micrograzer present (+micro) treatment, the static condition exhibited a sharp decrease between days 0 - 2 before linearly increasing for the remainder of the incubation. Consequently, the regression for this data set was based upon days 2 – 6 (Figure 3.8).

Due to the variability among treatments, no one trophic group stands out from any other in representing the highest or lowest rates of observed growth. Bacterial rates of observed growth were consistent among all four treatments, with doubling times ranging 6 - 7 days (Table 3.2). Heterotrophic nanoflagellate growth was higher in the 5°C **S** – micro treatment than 0°C, but lower in the other three treatments, producing at doubling rates of 3 - 9 days (Table 3.2). The smaller autotrophic component (chl $a < 5\mu m$) showed

a similar response with observed rates of growth lower in the T -micro, S +micro and T +micro treatments than the S –micro treatment, as well as lower than those rates at 0°C. Doubling times for the smaller autotrophs ranged between 3 - 8 days (Table 3.2). The larger autotrophic component (chl *a* >5μm) showed the greatest difference between the 0°C and 5°C treatments, in which the S –micro, T –micro, and S +micro treatments at 5°C were significantly higher than their 0°C counterparts ($p < 0.01$), with doubling times between 5 - 7 days (Table 3.2).

Table 3.2. Log_{10} regression slopes representing the observed daily rates of change (± std. err.) and the corresponding doubling time of four microbial components at 5°C under four treatments: static without micrograzers (S -micro), turbulent without micrograzers (T -micro), static with micrograzers (S +micro), and turbulent with micrograzers (T +micro).

Trophic Level	Treatment	N	Slope	*p*	Doubling time (d)
Bacteria	S -micro	3	0.044 ± 0.008	0.001	6.77
	T- micro	3	0.051 ± 0.006	0.0001	5.92
	S +micro	3	0.044 ± 0.009	0.001	6.81
	T +micro	3	0.050 ± 0.007	0.0001	5.99
HNF†	S -micro	2	0.072 ± 0.006	0.0001	4.16
	T- micro	3	0.088 ± 0.016	0.001	3.41
	S +micro	2	0.034 ± 0.007	0.002	8.94
	T +micro	3	0.037 ± 0.005	0.0001	8.06
<5μm Chl *a*	S -micro	2	0.089 ± 0.011	0.001	3.39
	T- micro	3	0.069 ± 0.009	0.0001	4.36
	S +micro	2	0.075 ± 0.020	0.010	4.02
	T +micro	3	0.038 ± 0.020	0.102	7.97
>5μm Chl *a*	S -micro	2	0.043 ± 0.021	0.078	7.00
	T- micro	3	0.051 ± 0.009	0.0001	5.90
	S +micro	2	0.051 ± 0.013	0.017	5.90
	T +micro	3	0.059 ± 0.008	0.0001	5.08

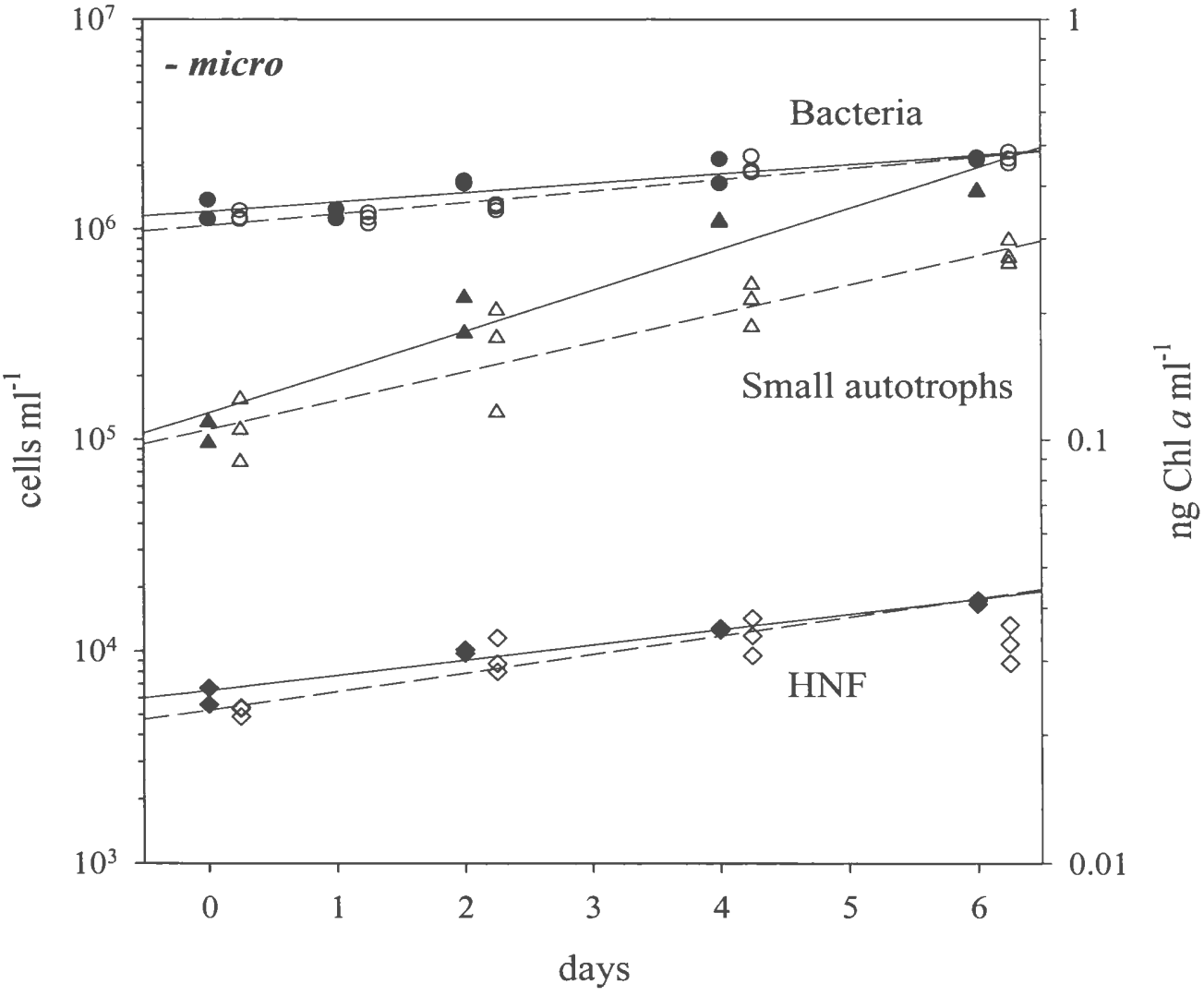

Figure 3.6. Temporal change in bacteria, heterotrophic nanoflagellates, and small autotrophs (chl *a* < 5μm) at 5°C in the absence of micrograzers under static (closed symbols, solid lines) and turbulent (open symbols, dashed lines) treatments. All data are presented for heterotrophic nanoflagellates, but regressions are only based upon days 0 – 4 for the turbulence treatment due to declining abundances on day 6.

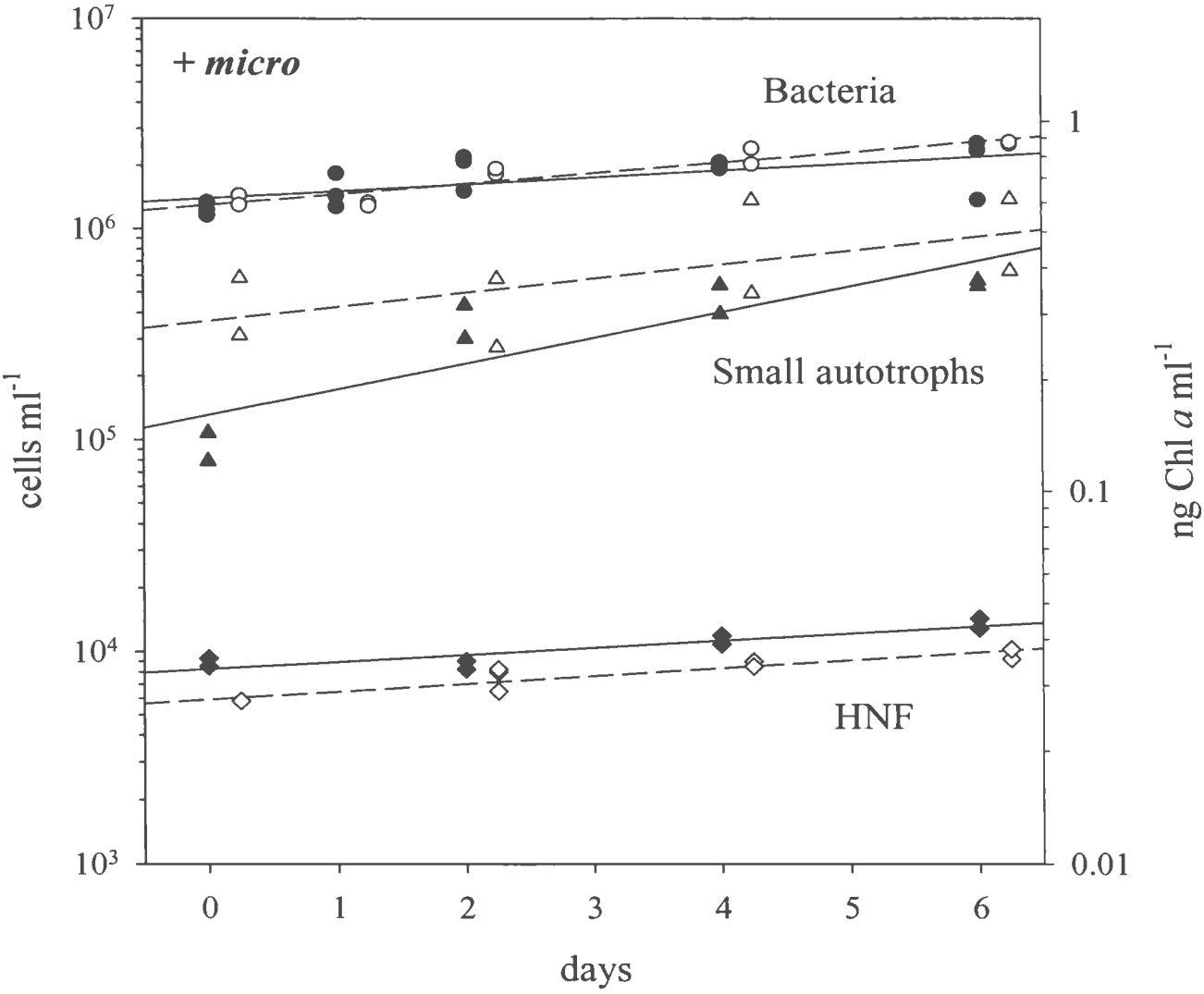

Figure 3.7. Temporal change in bacteria, heterotrophic nanoflagellates, and small autotrophs (chl *a* < 5μm) at 5°C in the presence of micrograzers under static (closed symbols, solid lines) and turbulent (open symbols, dashed lines) treatments. All data are presented for heterotrophic nanoflagellates, but regressions are only based upon days 2 to 6 for the static treatment, due to the apparent lag phase during days 0 – 2 (see text).

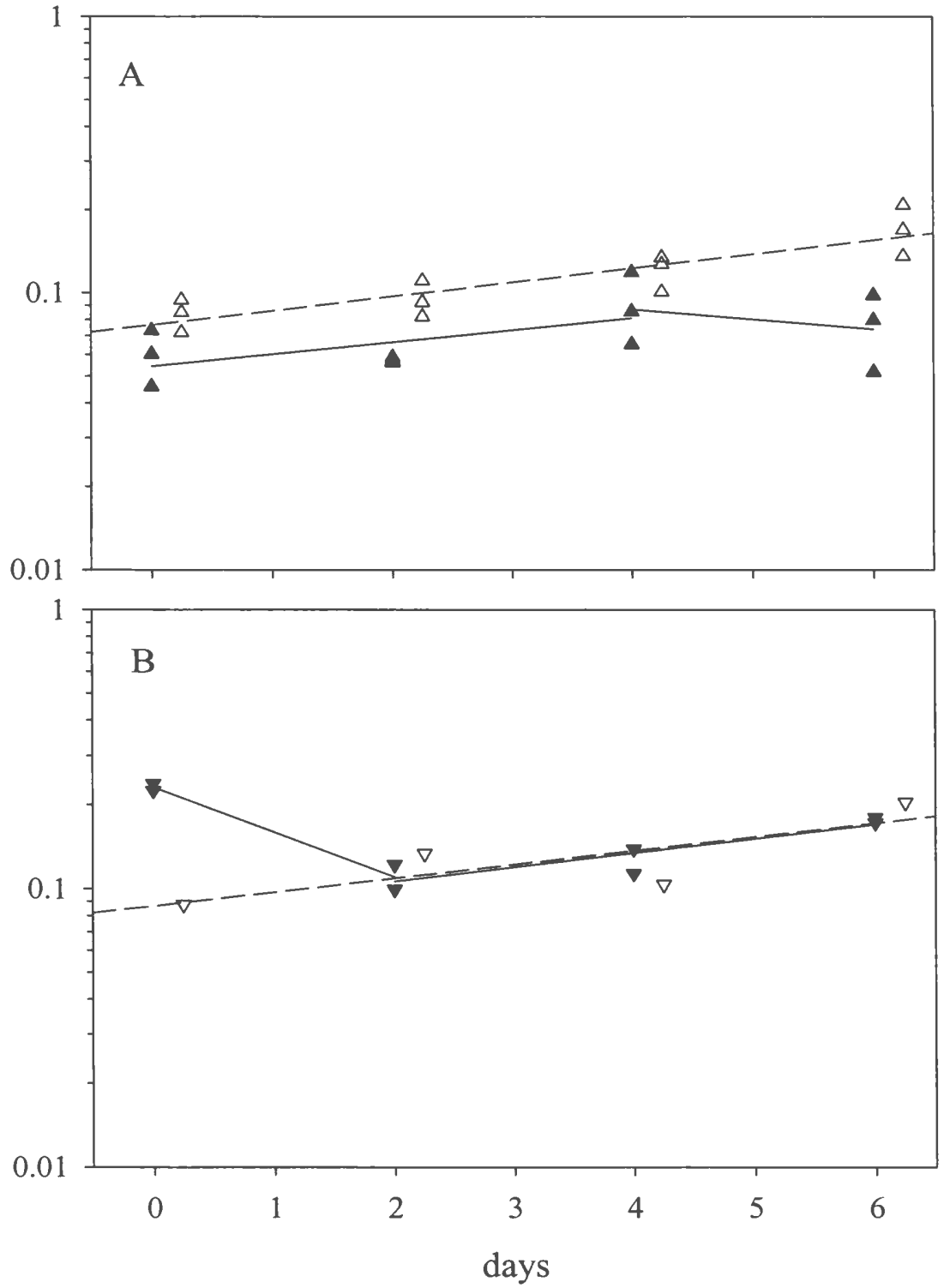

Figure 3.8. Temporal change in the large autotrophic community (chl *a* >5μm) at 5°C in the A) absence of micrograzers (–micro) and B) presence of micrograzers (+micro) under static (closed symbols, solid lines) and turbulent (open symbols, dashed lines) treatments. Data from day 0 – 2 in the static treatment and days 6 – 8 in the +micro treatment were excluded from regression analysis due to a lag phase and declining phase, respectively.

The confidence limits for the bacterial growth rate of each treatment overlapped the observed growth rate in each of the other three treatments (Figure 3.9) at 5°C, indicating that none of the differences among growth rates were statistically significant at the $\alpha = 0.10$ level. A comparison of the heterotrophic nanoflagellate growth rates and their corresponding confidence intervals among the four treatments revealed that mean growth was significantly lower in both the +micro treatments than both the –micro treatments (Figure 3.9).

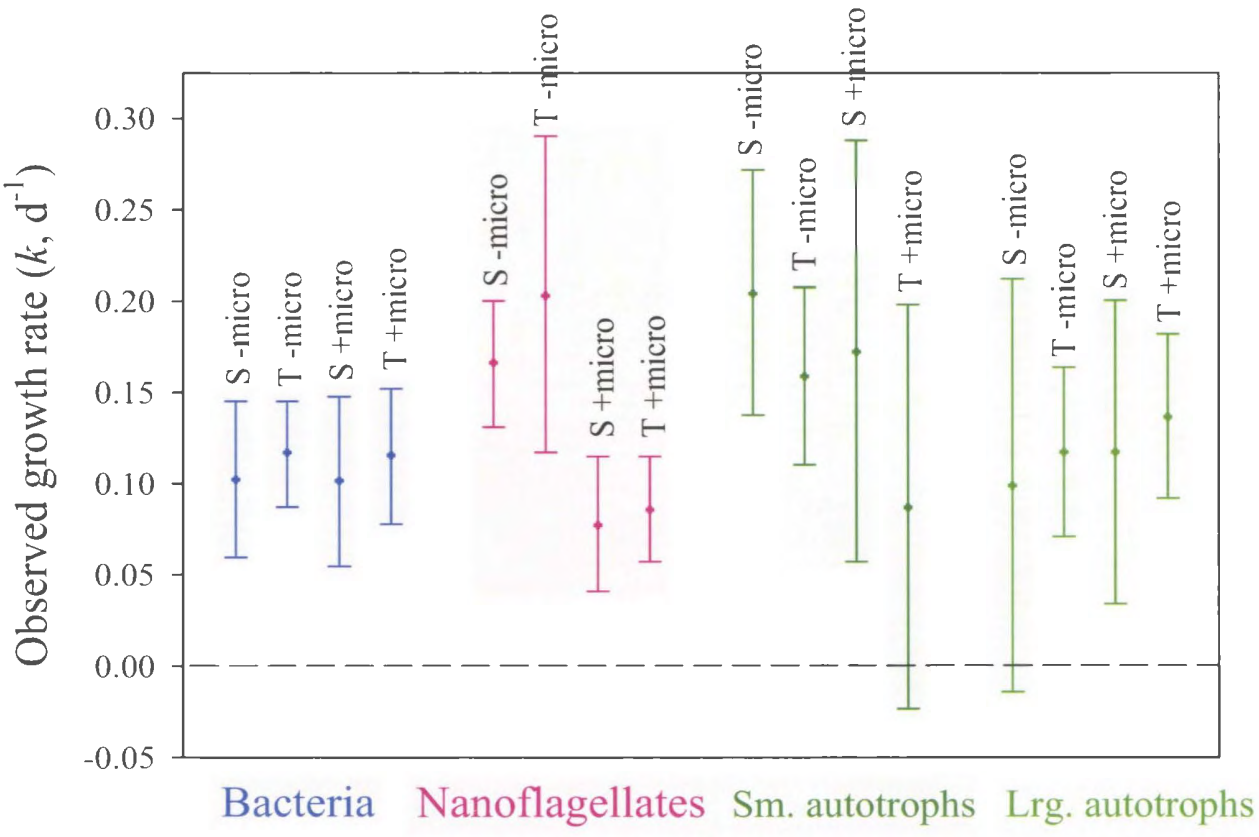

Figure 3.9. The observed growth rate (k, d^{-1}) with 95% confidence intervals for bacteria, heterotrophic nanoflagellates, small autotrophs (chl *a* <5μm) and large autotrophs (chl *a* >5μm) at 5°C under four treatments: static without micrograzers (**S** –micro), turbulent without micrograzers (**T** micro), static with micrograzers (**S** +micro) and turbulent with micrograzers (**T** +micro).

The confidence limits for the small autotrophic growth rates overlapped all growth rates of the four treatments, but with rates in both turbulent treatments lower than the static treatments. The confidence limits of the larger autotrophic growth rates overlapped in all four treatments, showing no significant differences among any of the treatments. Microscopic observations indicated that the autotrophs were predominantly diatoms of the genera *Thalassiosira* sp., *Chaetoceros* sp., *Skeletonema* sp., *Coscinodiscus* sp., *Rhizosolenia* sp., *Leptocylindrus* sp., and a variety of pennates. As to be expected during the spring, diatom abundances at 5°C exceeded those at 0°C, with abundances increasing 5- to 25-fold than those at 0°C. Diatom abundances also were 3-fold higher in the turbulent (-micro and +micro) than the static treatments at 5°C. The dinoflagellate *Gymnodinium* sp., silicate microflagellate, *Dictyocha* sp., and numerous cryptophytes also contributed to the autotrophic community, but were still dominated at least 3:1 by the diatoms. The micrograzer community at 5°C demonstrated a strong presence of oligotrich ciliates as well as some tintinnids, with abundances 2-fold to 5-fold higher than those found at 0°C, and at least 3-fold higher in the turbulent than static treatments.

3.4 Discussion

The present study manipulated both turbulence and micrograzers in a factorial design to investigate their effects on the growth rates of bacteria, heterotrophic nanoflagellates and two size fractions of autotrophs in cold ocean coastal waters during winter and early spring. At 0°C, turbulence had no effect on bacterial growth, weak effects on heterotrophic nanoflagellate growth and small autotrophs, but stronger effects on the growth of the larger autotrophic community. At 5°C, turbulence, again, had no effect on bacterial growth, a strong effect on heterotrophic nanoflagellate growth, a weak effect on small autotrophs, and no effect on the large autotrophs. The plankton community in the experimental enclosures was far smaller than the Kolmogorov microscale (L_v), which ranged around 0.5 mm for this study. Thus, it is unlikely for these planktonic organisms to have been directly subjected to turbulent eddy velocity gradients. Nevertheless, empirical evidence has clearly shown that phagotrophic microplankton respond to turbulence at sub-eddy scales, likely through mechanisms such as laminar shear effects (Shimeta *et al.* 1995; Peters *et al.* 1998). It has also been hypothesized that osmotrophic organisms, such as phytoplankton, could respond to fluctuations in the nutrient field at the Batchelor scale, which is 1-2 orders of magnitude smaller than the Kolmogorov microscale (Karp-Boss *et al.* 1996; Peters and Marrasé 2000).

These results demonstrate that neither turbulence nor micrograzer removal, singly or in concert, were sufficient to significantly increase bacterial growth under cold ocean experimental conditions. It was found that bacterial growth varied little among the four treatments with no trend favouring the turbulence treatments at either experimental

temperatures. However, under warmer environmental conditions, Peters *et al.* (1998) and Peters *et al.* (2002) found turbulence to indirectly increase bacterial growth. Peters *et al.* (1998) originally proposed that if phytoplankton growth increased, grazers of phytoplankton would benefit from increased food availability. This would then result in nutrient recycling, which in turn, provides bacteria with additional nutrient sources through phytoplankton excretion and sloppy feeding of those grazers of phytoplankton. Peters *et al.* (2002) later found that under turbulence, increased bacterial growth was likely due to the relaxed grazing pressure by heterotrophic nanoflagellates. With experimental temperatures at ~20°C, it would be probable that their results were a function of higher micrograzer growth and biomasses than those found in our present study, which would then invoke a higher and more significant response in the bacterial community during the presence of turbulence.

The experimental results at 0°C suggest that heterotrophic nanoflagellate growth is increased only when both turbulence and micrograzer removal act collectively. Growth was 1.5-fold higher in the **T** -micro treatment than the other three treatments, thus the turbulence and micrograzer removal effects were small, but additive. However, at 5°C, heterotrophic nanoflagellate growth was significantly lower in the +micro treatments than the –micro treatments, further suggesting that the presence of grazers do have a significant impact on the nanoflagellate population. Peters *et al.* (1998) had found an increase in heterotrophic flagellate growth, but only in the size-fractionated communities that eliminated potential grazers. Since nanoflagellates do not exist in nature without predators, our results and those of Peters *et al.* (1998) would suggest that

increased growth of heterotrophic nanoflagellates due to turbulence would be cancelled out by the presence of grazers.

The small autotrophic community demonstrated a similar pattern to that of the heterotrophic nanoflagellates at 0°C. Significant growth differences in the small autotrophic community would be expected due to the removal of micrograzers, thus reducing grazing pressure on the population. However micrograzer removal should also produce a negative growth effect due to reduced nutrient recycling. Since growth in the **T** -micro treatment was not significantly different from that in either of the micrograzer present treatments, our results suggest that enhanced nutrient transport under turbulent conditions compensated for any reduction in recycling rates. The observation that growth rates were not enhanced by turbulence in the presence of micrograzers (**T** +micro vs. **S** +micro) indicates that enhanced nutrient transport was insufficient to overcome the grazing losses when micrograzers were present. Finally, the observation that growth was significantly lower in the **S**-micro treatment suggests that both reduced nutrient recycling and reduced nutrient transport effects were small but additive, producing statistically detectable effects only when acting in concert.

The biomass of the large autotrophic community was low, typical of winter conditions. Growth was found to be significantly higher in the **T** +micro treatment than the other three treatments, suggesting that turbulence did increase nutrient transport to the larger phytoplankton cells in the presence of micrograzers. The increased growth of the larger autotrophic component under turbulence is consistent with other studies that have found a positive relationship between turbulence and chlorophyll *a* (Alcaraz *et al.* 1988;

Estrada *et al.* 1987) and primary production (Gervais *et al.* 1997). It has also been demonstrated in freshwater that large colonial diatoms *Asterionella*) can benefit from nutrients recycled by grazers at the expense of the smaller autotrophic community (Lehman and Sandgren, 1985).

In conclusion, it is important to expand our knowledge on how physical processes, such as turbulence, can impact the pathways of carbon transfer within the marine microbial food web. It is clear from this enclosure study that turbulence does have some control on the interactions of the marine microbial food web, and that low temperatures do not completely diminish the effect turbulence can have on those interactions. This study has shown that turbulence can contribute to the increased growth of larger phytoplankton, heterotrophic nanoflagellates and the smaller autotrophic community in a cold ocean system at $<5^{o}C$, however, the effects on the smaller organisms can be masked by grazing losses in the natural environment. Thus, it appears turbulence could affect patterns of biogenic carbon export differentially, being dependent upon the conditions of the marine environment.

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CHAPTER FOUR

CONCLUSION

In summary, this dissertation investigated two areas of cold ocean microbial dynamics and the effects of turbulence on the microbial food web and found the following:

4.1 Results of research objectives

4.1.1 Summertime bacterial abundance, distribution, growth rates and grazing mortality rates in the North Water polynya.

It was found that despite low temperatures the North Water has an active microbial population within its highly stratified surface waters and bacterial abundances of the NOW equalled or exceeded abundance values reported from temperate oceans and other Arctic environments. Within the North Water during August 1997, bacterial abundance was positively correlated with chlorophyll, indicating that the North Water's bacterial population is regulated by the supply of organic matter provided by the summer's phytoplankton bloom. Furthermore, there is a distinct difference in the bacterial dynamics between two regions of the North Water: a) the silicate-rich Arctic water (northern and western region of the polynya) where bacterial abundance, growth and grazing mortality was high; and b) the Baffin Bay water (eastern region) where bacterial abundance, growth and grazing mortality was low.

4.1.2 The effects of turbulence on bacterial growth and grazing mortality rates and production in the NOW.

In sampling the bacterial population at four stations within the North Water during July 1998, it was discovered that turbulence can have some control over the

bacterial biomass by increasing rates of bacterivory in the northern region. Bacterial abundance and growth were higher in the southern region of the polynya. It was also found that bacterial production was consistently higher in the low turbulent treatments relative to the static treatments. This would indicate that bacteria, though likely already exposed to an unlimited supply of nutrients, low levels of turbulence simply maintained a homogeneous mixture within the enclosure.

4.1.3 The effect of turbulence on the microbial food web trophic interactions within the Labrador Current during winter.

By manipulating both turbulence and micrograzers in a factorial design at 0° and 5°C, it was found that turbulence had no effect on bacterial growth at either temperature when in the presence of grazers. At 0°C, it was found that turbulence had weak effects on heterotrophic nanoflagellate growth and small autotrophs, but stronger effects on the growth of the larger autotrophic community. But at 5°C, turbulence had a strong effect on heterotrophic nanoflagellate growth, a weak effect on small autotrophs, and no effect on the large autotrophs. This would suggest that turbulence can contribute to the increased growth of larger phytoplankton, heterotrophic nanoflagellates and the smaller autotrophic community in a <5°C marine environment, however, the effects on the smaller organisms can be masked by grazing losses within a natural community.

4.2 Conclusion

It has been proven that cold-ocean microbes can significantly contribute to the global carbon cycle by facilitating remineralization of organic carbon, providing a

substantial food source for higher trophic levels, and can regulate the flux of particulate organic carbon between surface waters and the benthos. However, turbulence does not always have a definitive effect on the microbial food web dynamics at lower temperatures. The lower viscosity of the fluid, varying levels of turbulent activity, the presence of various grazers and other sources of prey, all contribute to a complex system that cannot be defined in one 'bottle' experiment. It is next to impossible to measure rates of microbial growth within nature, but as microbes are the base of the marine food web and are far more important than just sources of food for a higher trophic organism, we must resign ourselves to experimenting with these organisms in a controlled environment if we ever wish to fully comprehend this complex system.

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APPENDIX

Table A.2.1. For simplicity purposes, NOW97 and 98 station names were re-labeled to clarify those stations within the silicate-rich Arctic water mass (A-labelled stations), the Baffin Bay water mass (B-labelled stations) and those stations within the mixed water masses (M- labelled stations).

Station label	Actual station names from 1997-98
A1	N1
A2	N2
A3	25
A4	24
A5	28
A6	29
A7	S5
B1	E2
B2	22
B3	E1
B4	S2
B5	S1
M1	D2
M2	S4
M3	10
M4	12
M5	D1

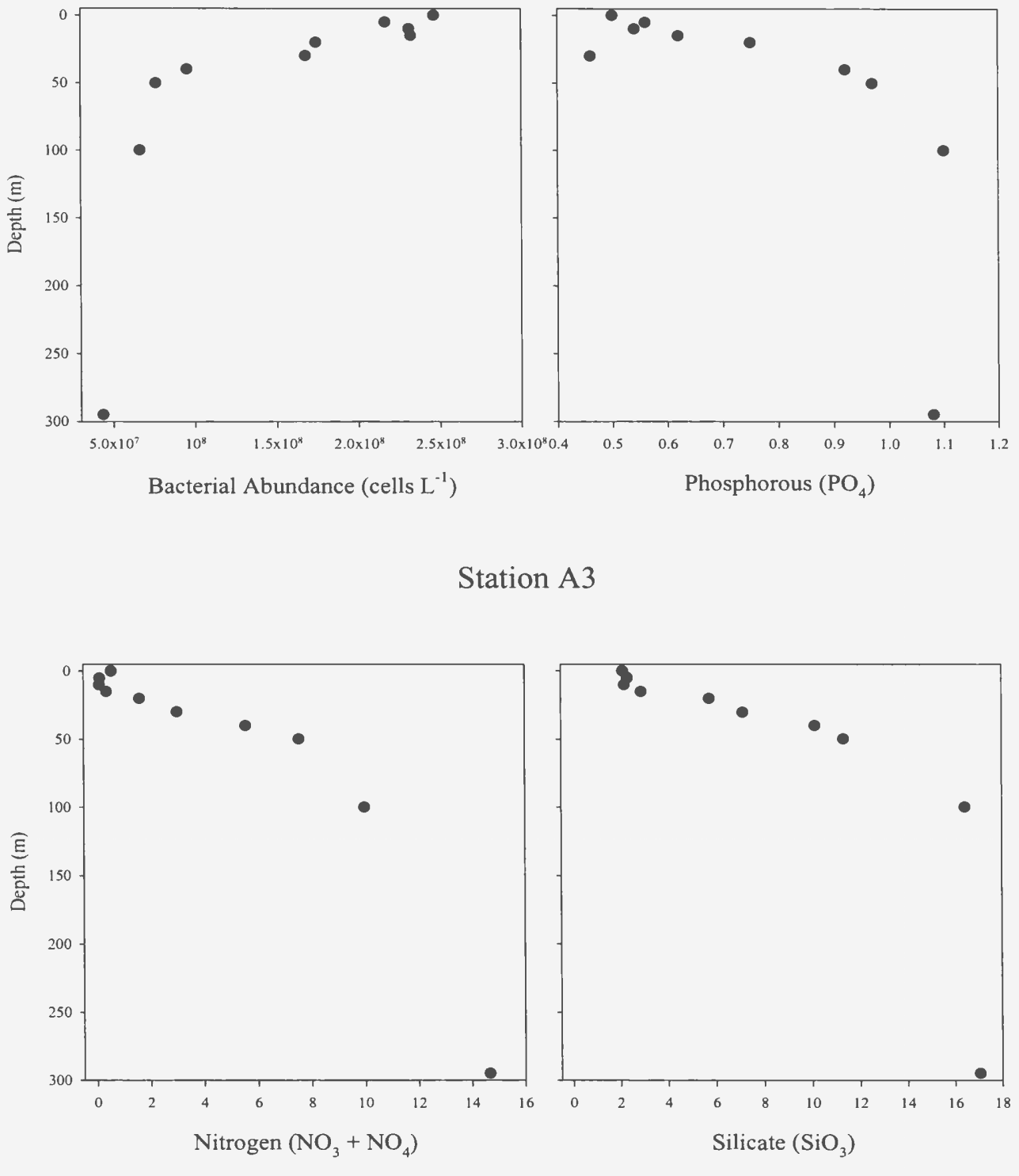


Figure A.2.1 Vertical profiles of bacterial abundance, phosphate, nitrate and silicate of station A3 of the North Water polynya during August 1997.

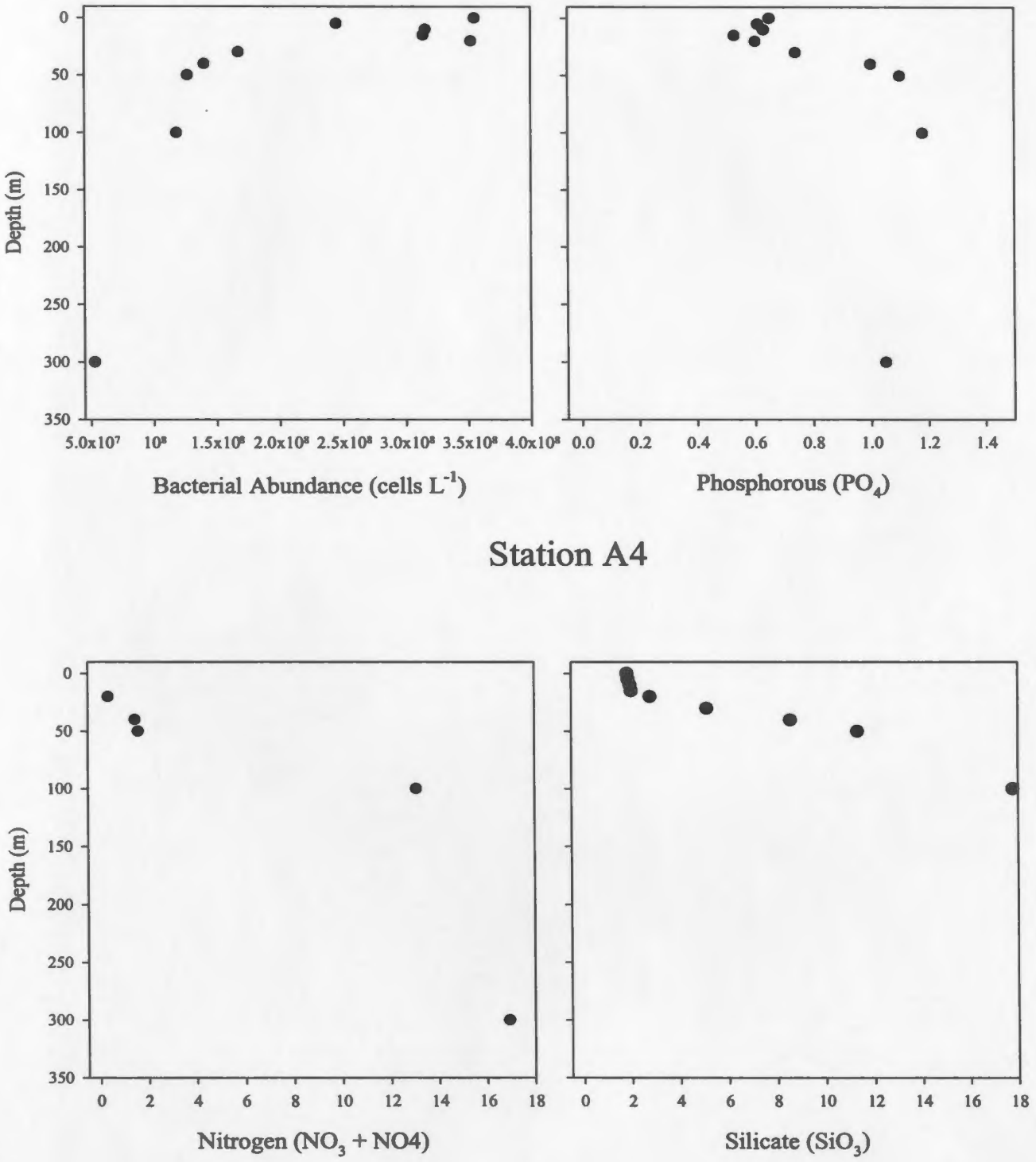


Figure A.2.2 Vertical profiles of bacterial abundance, phosphate, nitrate and silicate of station A4 of the North Water polynya during August 1997.

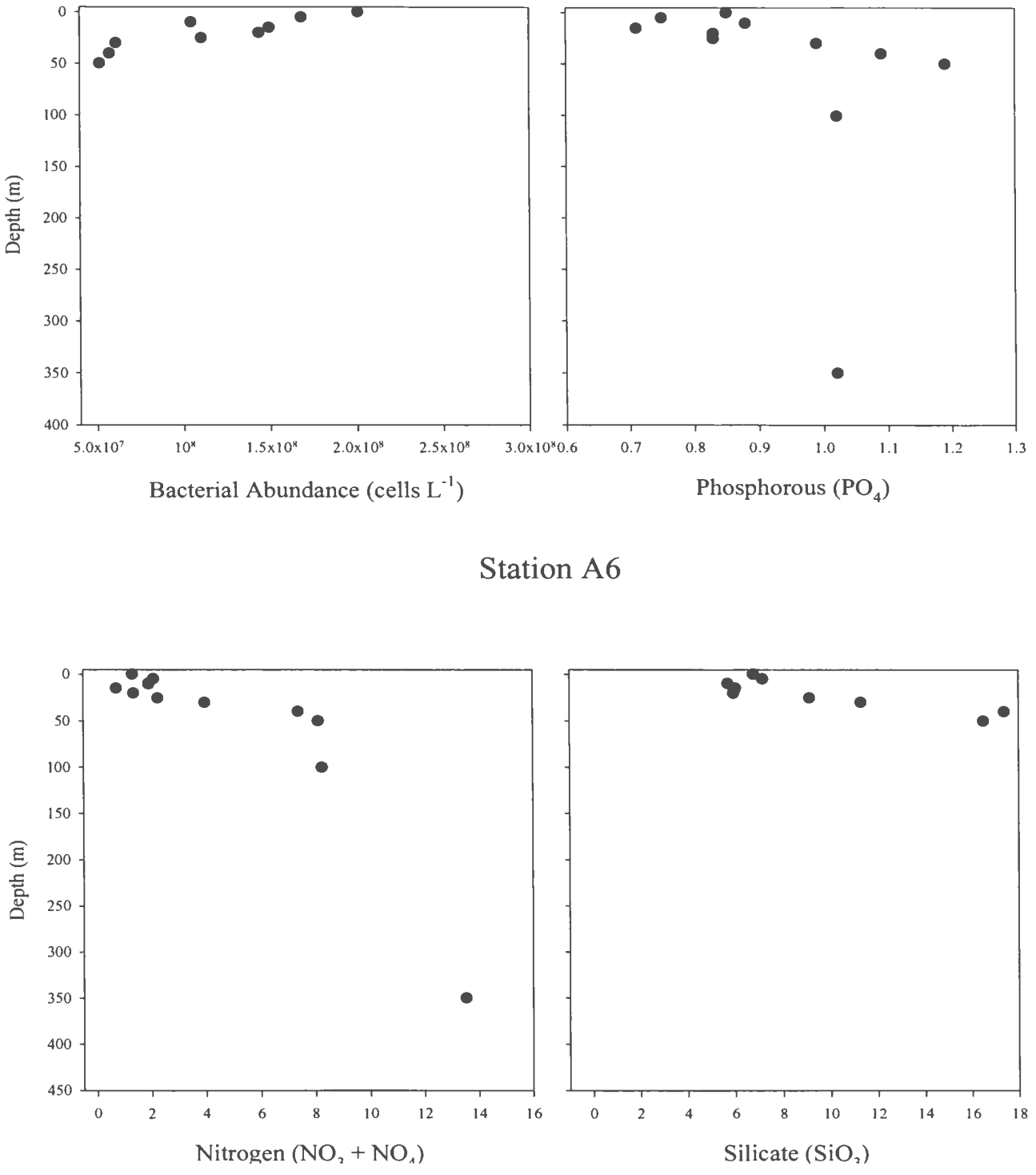


Figure A.2.3 Vertical profiles of bacterial abundance, phosphate, nitrate and silicate of station A6 of the North Water polynya during August 1997.

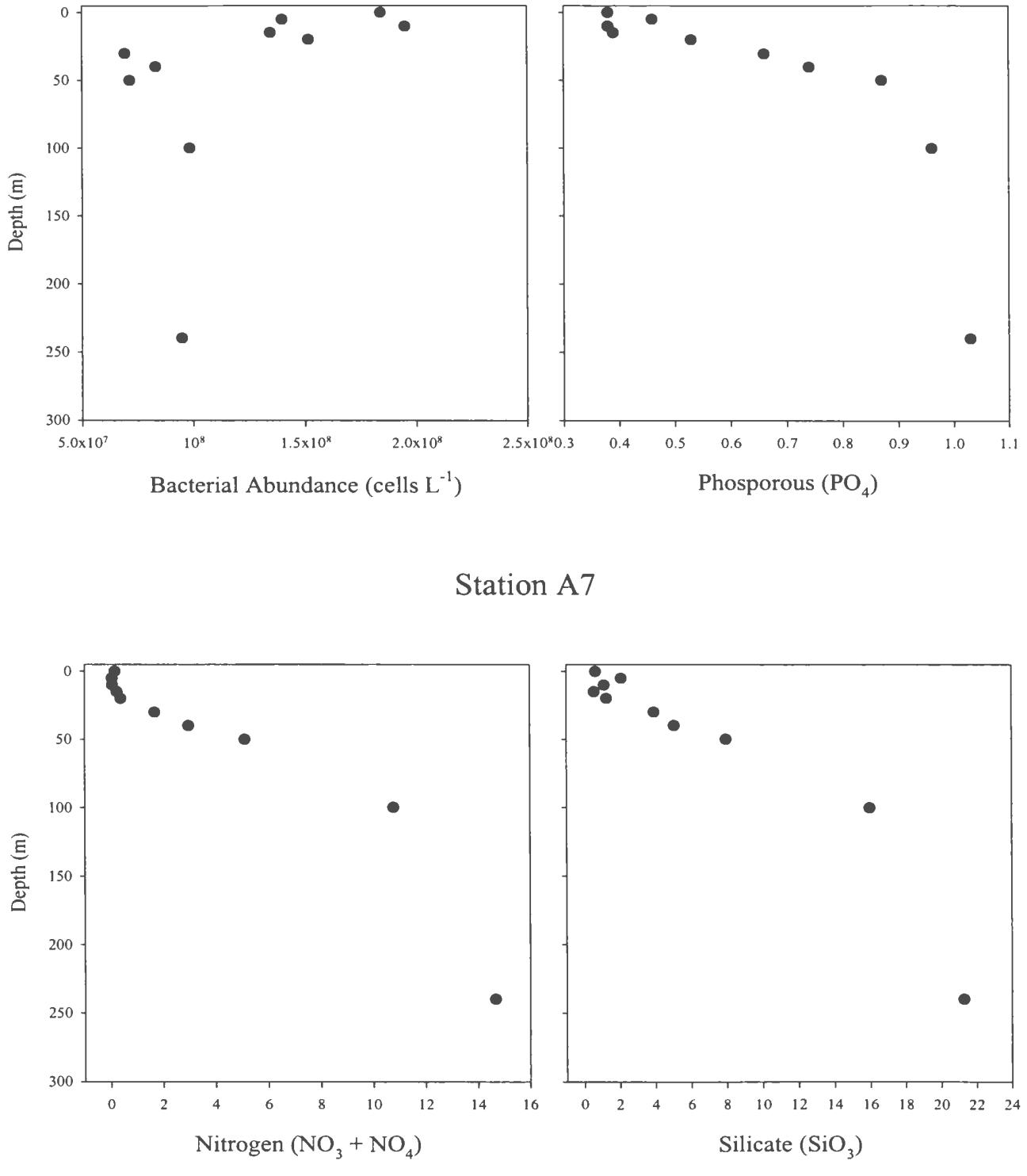


Figure A.2.4 Vertical profiles of bacterial abundance, phosphate, nitrate and silicate of station A7 of the North Water polynya during August 1997.

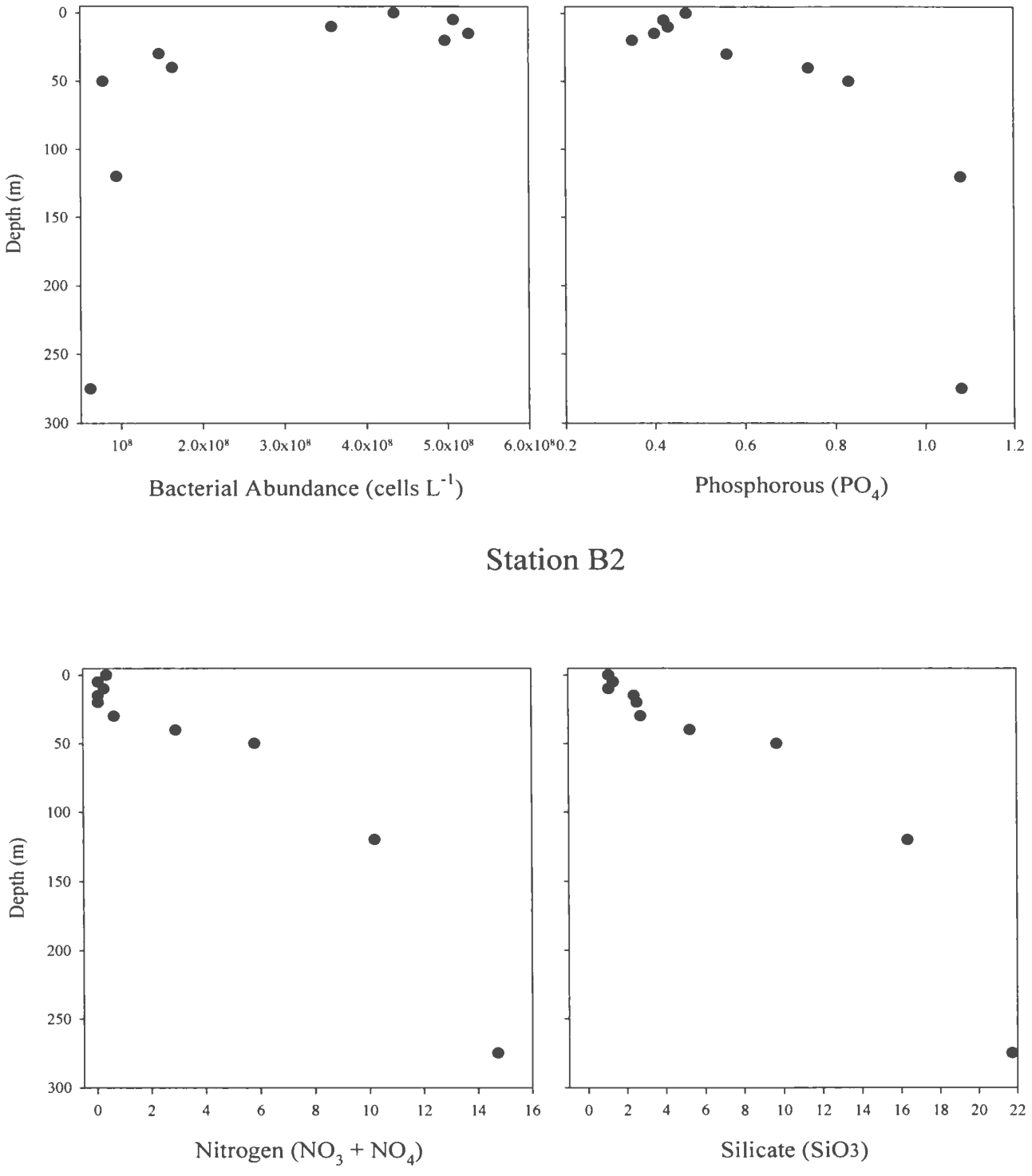


Figure A.2.5 Vertical profiles of bacterial abundance, phosphate, nitrate and silicate of station B2 of the North Water polynya during August 1997.

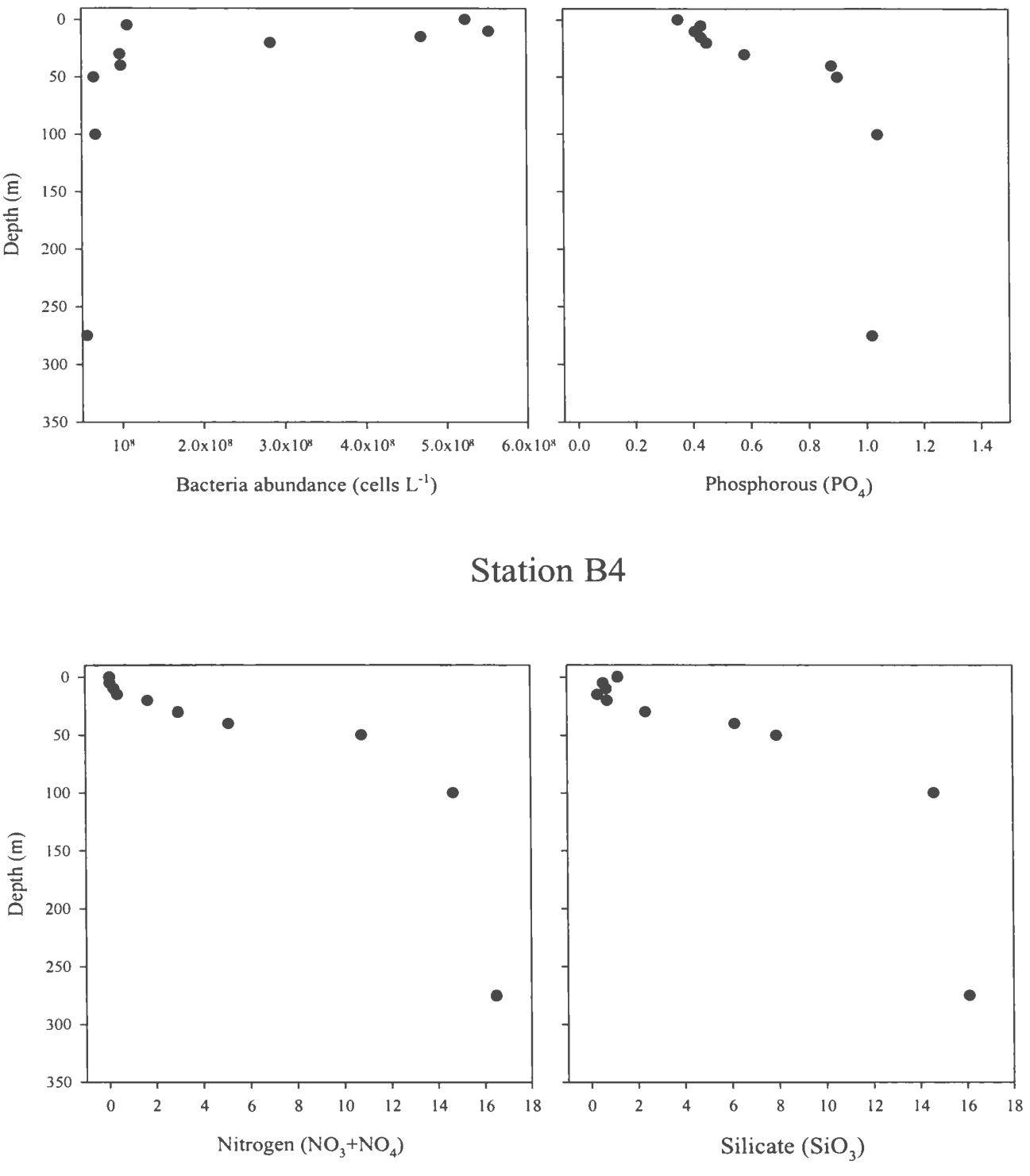


Figure A.2.6 Vertical profiles of bacterial abundance, phosphate, nitrate and silicate of station B4 of the North Water polynya during August 1997.

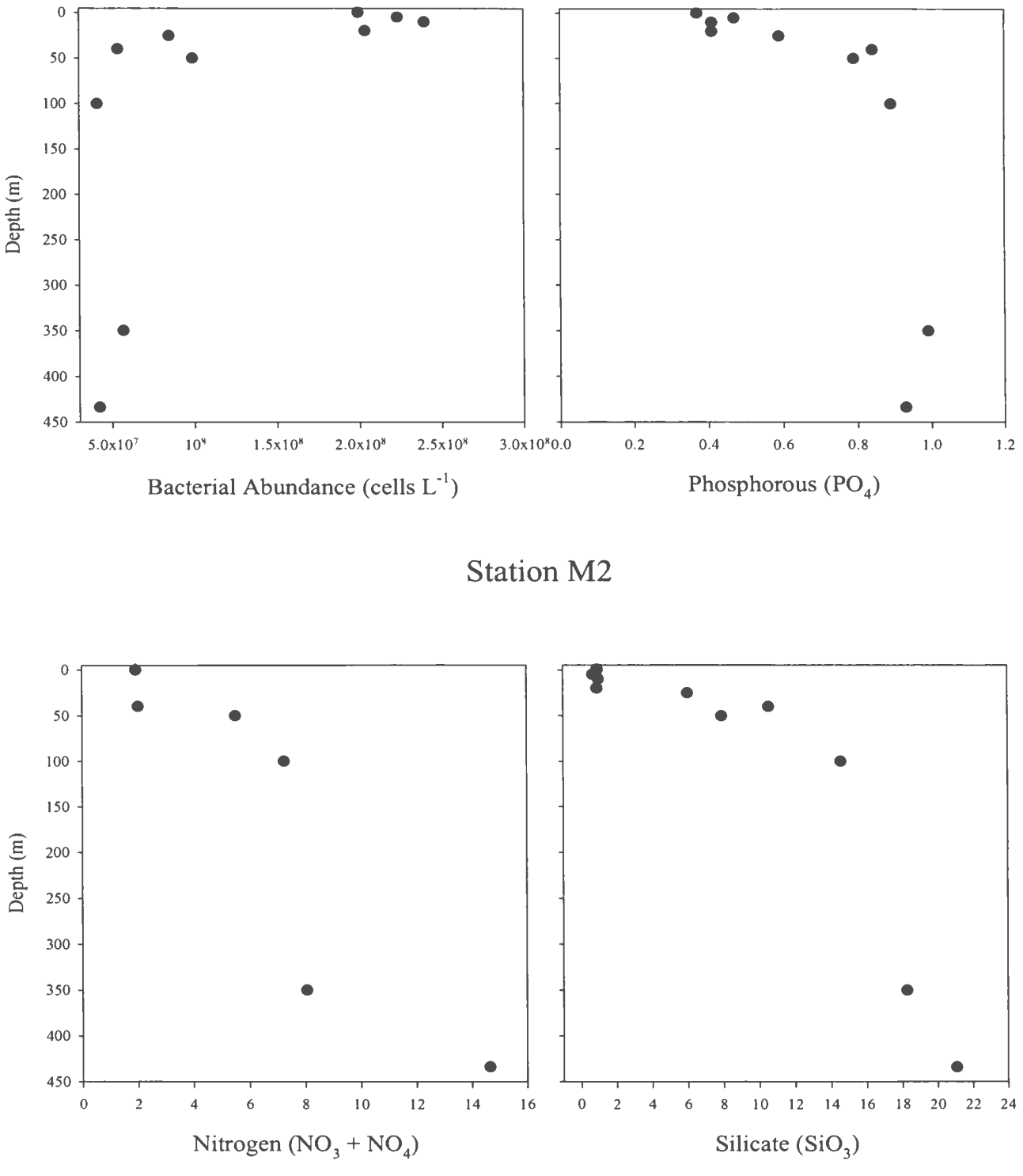
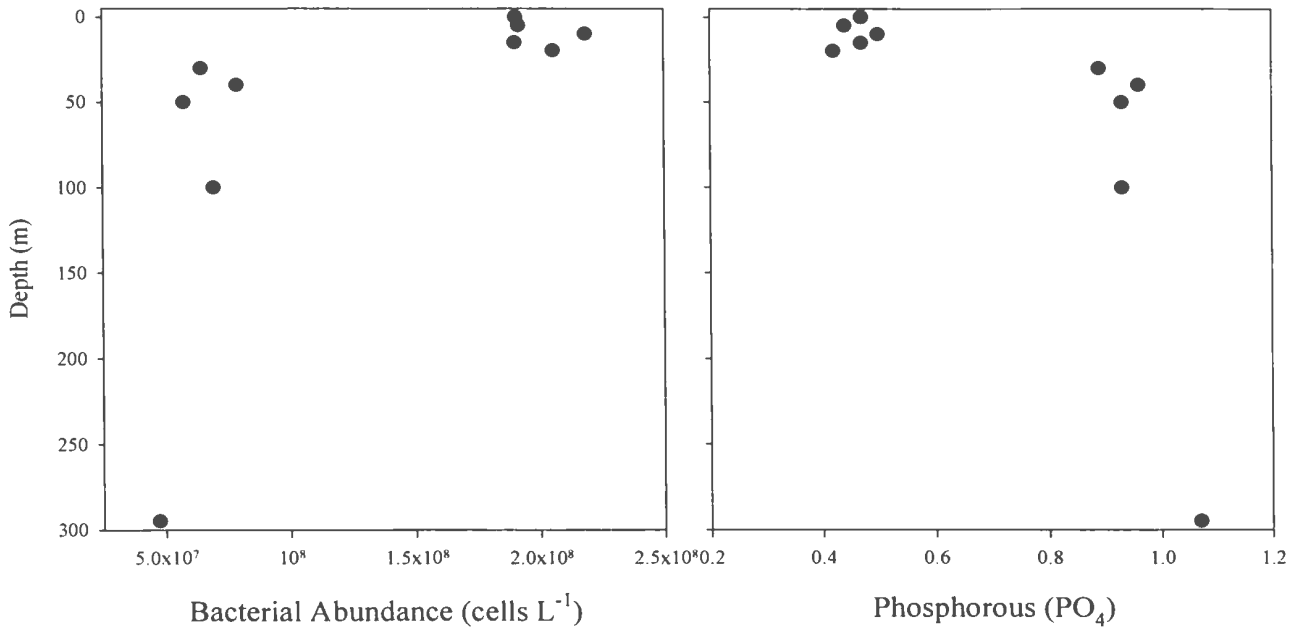


Figure A.2.7 Vertical profiles of bacterial abundance, phosphate, nitrate and silicate of station M2 of the North Water polynya during August 1997.



Station M3

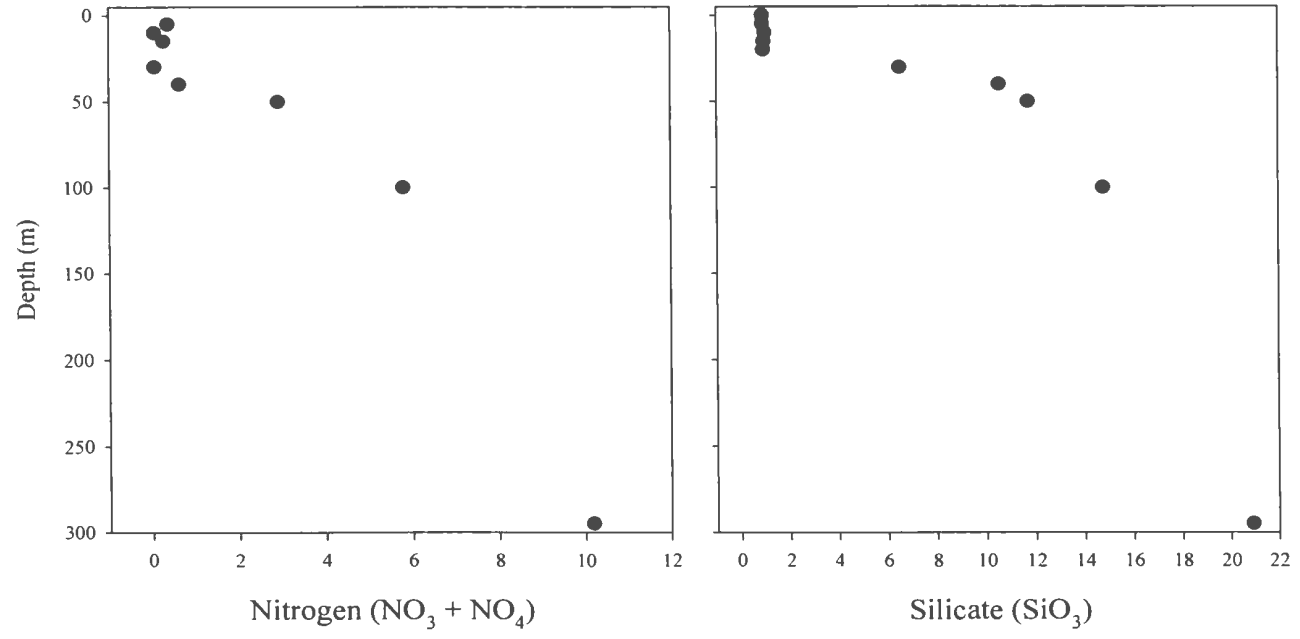


Figure A.2.8 Vertical profiles of bacterial abundance, phosphate, nitrate and silicate of station M3 of the North Water polynya during August 1997.

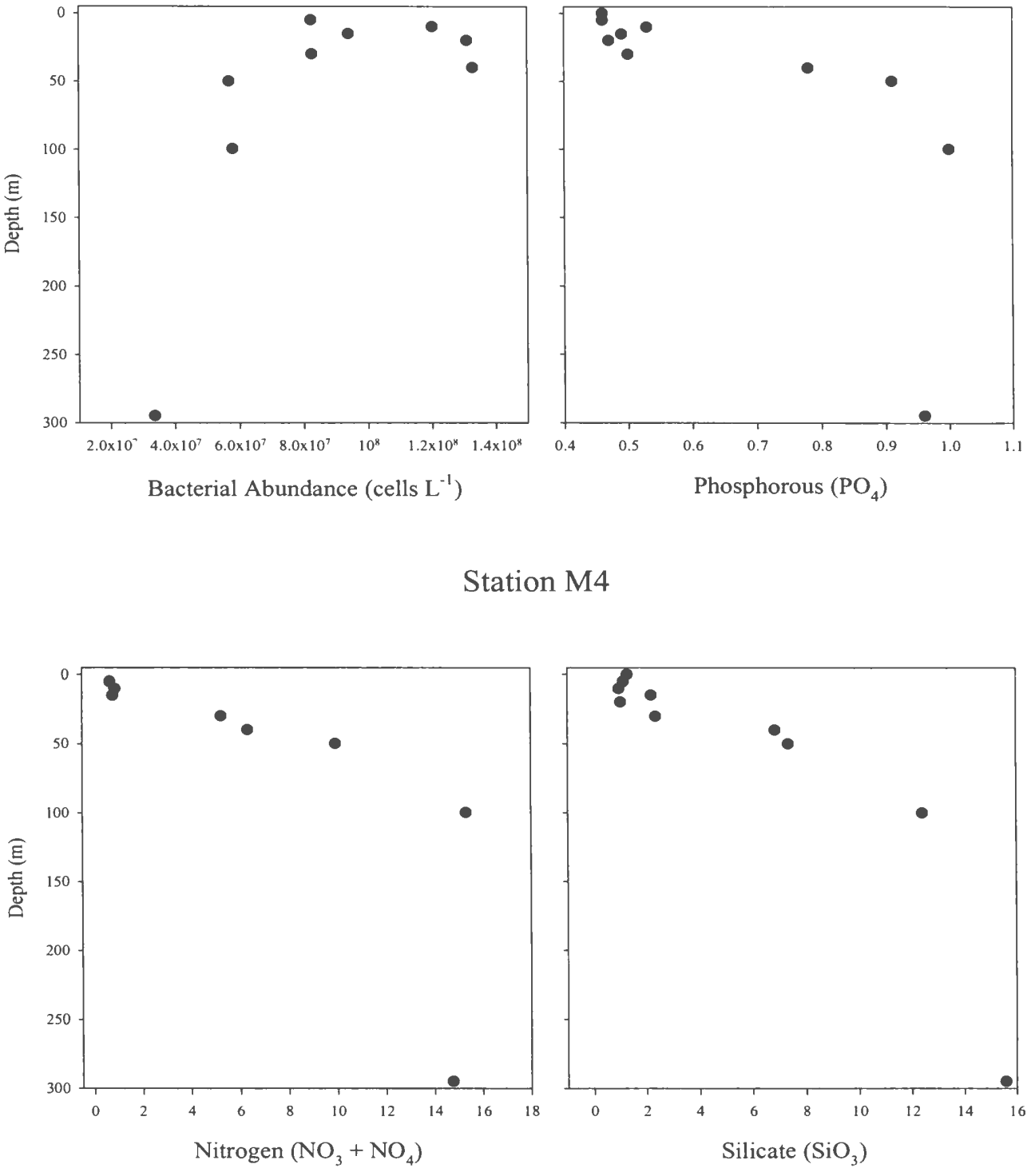


Figure A.2.9 Vertical profiles of bacterial abundance, phosphate, nitrate and silicate of station A4 of the North Water polynya during August 1997.

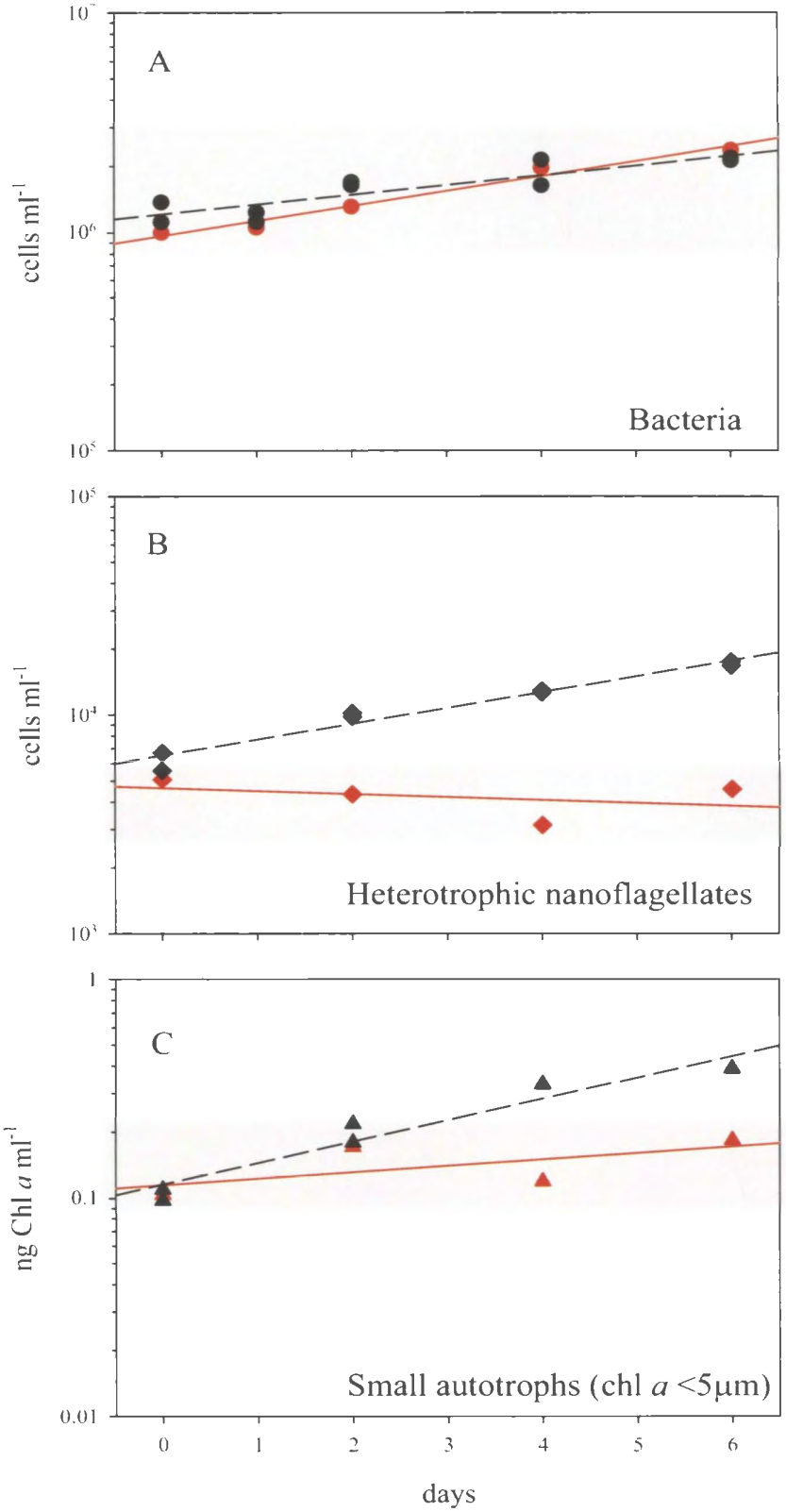


Figure A.4.1. Data points in red indicate the 5°C replicate experiment in the static without micrograzers (**S** –micro) treatment that deviated from the other replicates, thus were removed from regression analysis. Figure A represents one data set for observed bacterial growth, B represents data set for nanoflagellate growth, and C represents data for small autotrophic growth based upon <5µm chlorophyll.

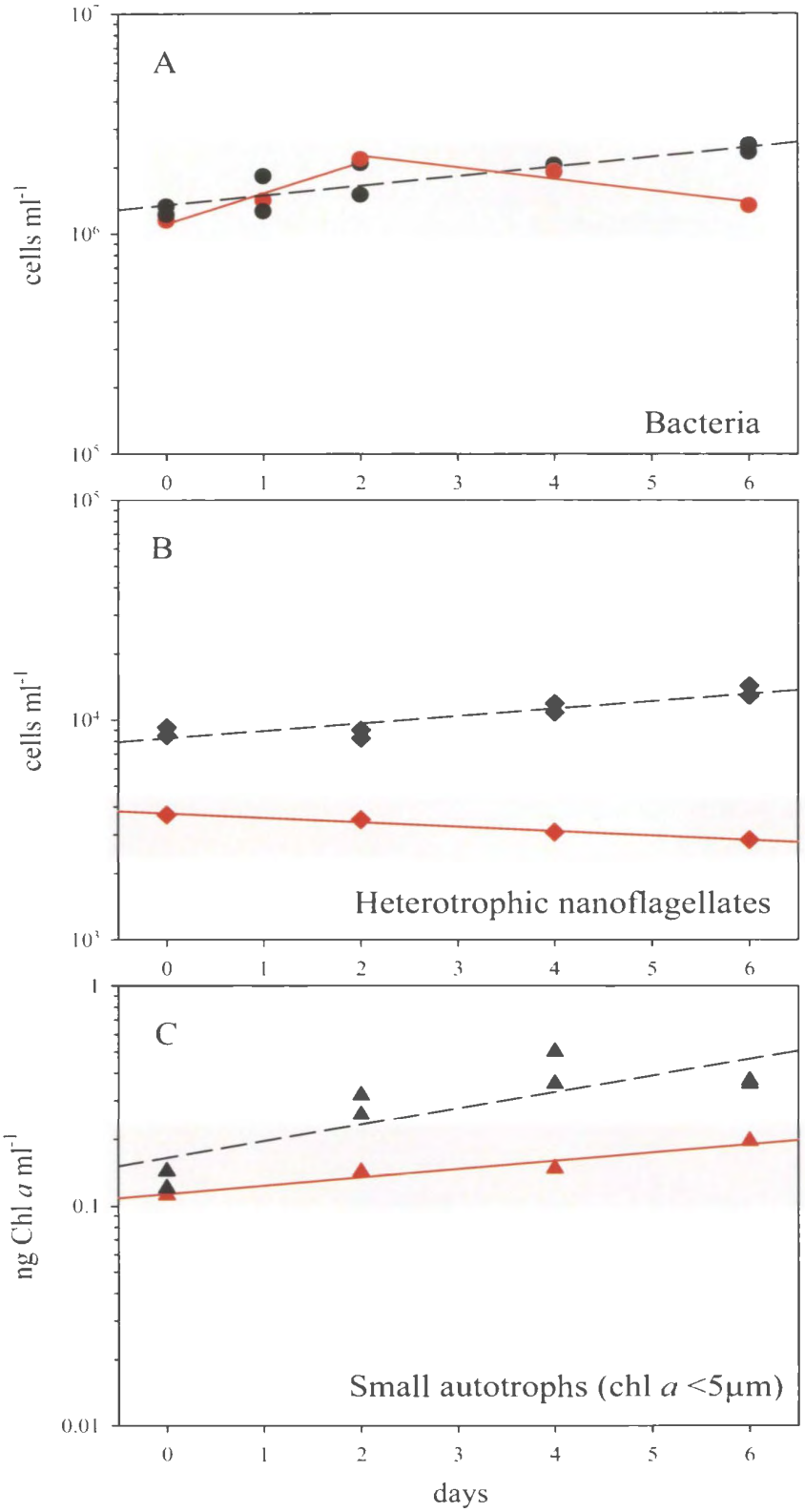


Figure A.4.2. Data points in red indicate the 5°C replicate experiment in the static with micrograzers (**S** +micro) treatment that deviated from the other replicates, thus were removed from regression analysis. Figure A represents one data set for observed bacterial growth, B represents data set for nanoflagellate growth, and C represents data for small autotrophic growth based upon <5µm chlorophyll.

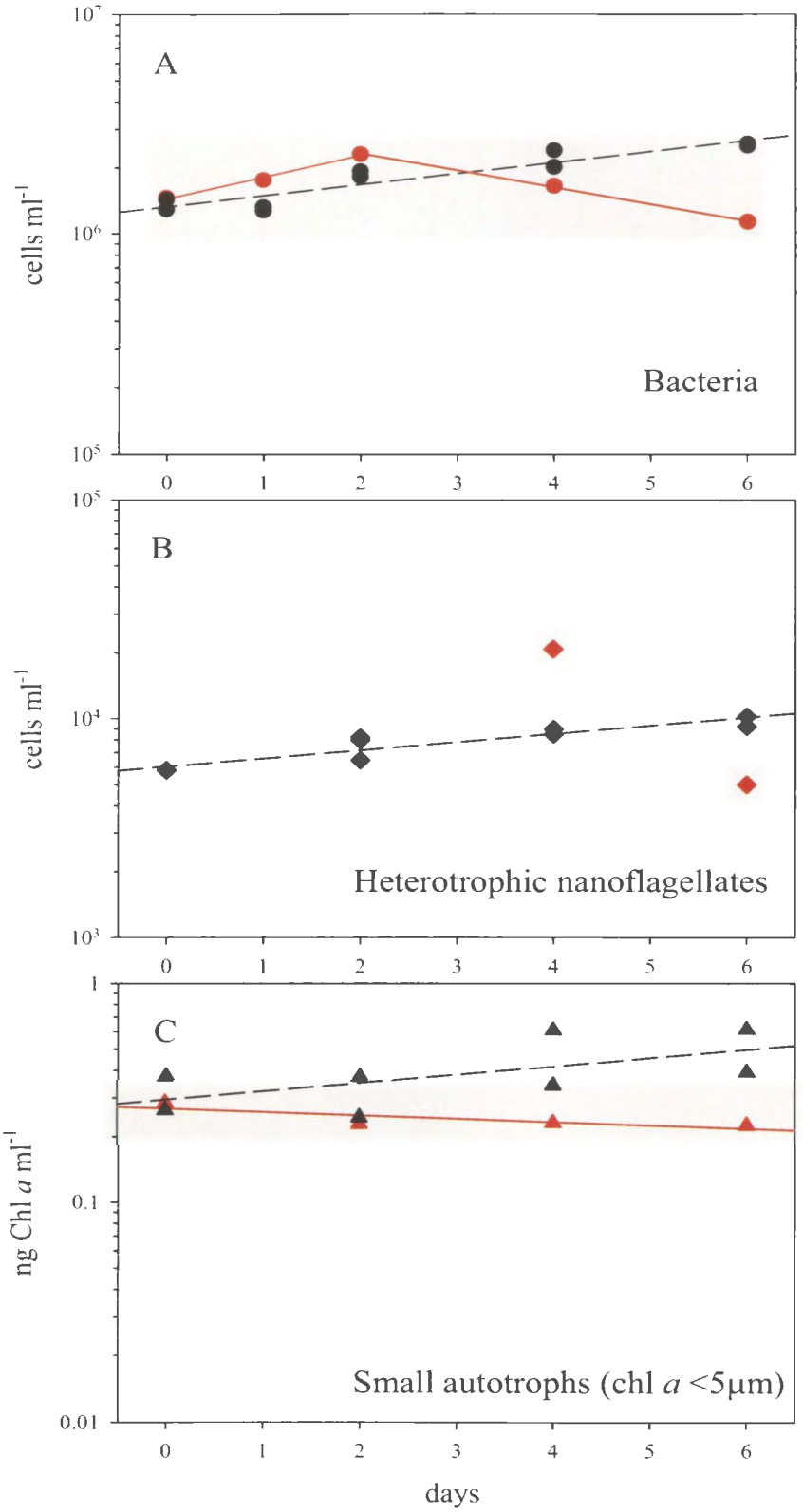


Figure A.4.3. Data points in red indicate the 5°C replicate experiment in the turbulent with micrograzers (**T** +micro) treatment that deviated from the other replicates, thus were removed from regression analysis. Figure A represents one data set for observed bacterial growth, B represents data set for nanoflagellate growth, and C represents data for small autotrophic growth based upon <5µm chlorophyll.