MICROZOOPLANKTON HERBIVORY AND BACTERIVORY IN THE NORTH WATER POLYNYA

HEATHER JANE BUSSEY

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by

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Abstract

Polynyas are regions of reduced ice cover in high latitude environments, which are ordinarily ice-covered. There are few comprehensive studies of microbial processes in polynyas although there are many of phytoplankton and metazoans which show their productivity is greater than surrounding regions. Here I report rates of growth of microbial prey and patterns of microzooplankton herbivory and bacterivory in the North Water Polynya (NOW), from April through July, 1998. Growth rates ranged from 0.0 to 1.1 day^{-1} for phytoplankton and 0.0 to 1.2 day^{-1} for bacteria. Highest bacterial grazing mortality was during July (1.3 day^{-1}) whereas for phytoplankton highest mortality was during late April (2.2 day^{-1}). Further investigation of protist size-dependent grazing, using high-resolution image analysis, indicated that microzooplankton were preferentially grazing small-sized bacteria. A substantial amount of carbon was channeled through the microbial food web in the NOW suggesting that microbial processes cycle large amounts of biogenic carbon in this polar region.

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Acknowledgments

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Introduction and Overview

1.1 Introduction to Microbial Food Webs

Characterising the interactions within and among the ocean's food webs is integral to understanding nutrient recycling and export from surface to depth. Food webs include phytoplankton, bacteria, microzooplankton and the animals at higher trophic levels, such as mesozooplankton, fish, marine mammals and birds (Steele 1974; Pomeroy 1974; Azam et al. 1983; Pace et al. 1984; Ducklow 1994). At each step in the food web, nutrients are transferred along food chains or released into the environment (i.e. regenerated). Excreted nutrients may be recycled back to phytoplankton or bacteria as dissolved inorganic or organic substrates via cell lysis, excretion or from sloppy feeding by zooplankton (Fenchel 1984; Goldman and Caron 1985; Porter et al. 1985; Sherr et al. 1986; Jumars et al. 1989). Hence, food web interactions are complex and have both direct and indirect consequences for nutrient cycling and utilisation.

High rates of bacterial growth during certain times of the year, have been reported in Arctic regions (Rivkin et al. 1996; Rich et al. 1997) suggesting that microbial communities are active in these regions. Few studies have concurrently studied the growth and grazer mortality of both phytoplankton and bacteria in high Arctic environments. The research presented here studies the interactions between bacteria, phytoplankton, and microzooplankton and the potential impact of microzooplankton grazing processes and food selection on carbon transfer through the microbial food web in the Arctic North Water Polynya. The primary objectives of this research were (1) to quantify the patterns and rates of bacterivory and herbivory of microzooplankton at

different locations in the North Water Polynya and at different times of the year, and (2) to determine the contribution of various prey types and size classes to the total carbon ration of microzooplankton. To address these objectives, the rates of growth and grazing mortality of phytoplankton and bacterial prey were measured using the dilution technique of Landry and Hassett (1982) at ten stations over the four month study period from April to July, 1998. Size selective grazing was examined using high-resolution image analysis to determine changes in bacterial cell sizes throughout the study.

North Water Polynya - What is Important About Polynyas?

A polynya is an oceanic region which remains relatively ice free during seasons and in locations where waters are normally ice covered (Smith et al. 1990). Polynyas have high biological productivity, relative to other polar regions, and attract a number of organisms, specifically birds and mammals that benefit from the availability of open waters for mating and spawning, as well as the enhanced food supply (Stirling 1997). Because of the high seasonal production there exists a greater potential for downward carbon flux which itself depends upon food web structure (e.g. Rivkin et al. 1996).

Polynyas are formed via two mechanisms; sensible and latent heat processes; which are important determinants of the biological processes occuring in them (Smith et al. 1990; Kawamura et al. 2001; Melling et al. 2001). Latent heat polynyas are formed when ice is carried away by winds or water currents as it is formed. In these polynyas, the continuous formation of ice which is constantly being carried away, results in a significant heat loss from the ocean to the atmosphere. Sensible heat polynyas are formed when warmer water from depth is upwelled to the surface thus preventing ice formation.

Heat is still lost to the atmosphere through the open water of the polynya. However, the supply of upwelled water is usually sufficient to prevent new ice from forming. Either latent or sensible heat processes allow early opening of polynyas in spring and both extend the duration of this opening. As the ice retreats, sunlight can penetrate the water column increasing phytoplankton productivity.

The North Water Polynya (NOW) is maintained by both latent and sensible heat processes (Barber et al. 2001) and is located in northern Baffin Bay and Smith Sound, situated between Greenland and Ellesmere and Devon Islands. It is the largest polynya in the Arctic and while the physical processes leading to the opening of the polynya have been fairly well documented, there has not been a detailed study of the biological properties. The International North Water Polynya Study was a four year study which examined the physical and biological coupling within in the North Water Polynya. The results reported here were collected and analysed as part of that study.

In the NOW Polynya, strong northerly winds in winter and spring drive ice southward and are also responsible for producing upwelling of relatively warm subsurface water. The phytoplankton bloom is initiated by the retreat of ice in April, initially on the Greenland side and later on the Canadian side. Warmer temperatures during this time, particularly on the Greenland side of the Polynya, also contribute to the early initiation of the bloom. Nutrients early in the bloom (April) are abundant throughout the Polynya and are depleted as the bloom progresses. Nutrient availability and self shading impose constraints on maximum phytoplankton accumulation. Until this point, growth of phytoplankton exceeds grazing by predators (which allows for the appearance

of the bloom). In the NOW Polynya, the bloom lasts around 1.5 months (Mei et al. 2002) from late April until mid-June.

Microbial Food Web Components

Microbial food webs have been found to be highly active in polar regions, during specific periods of the year, despite low water temperatures and low light conditions. The microbial food web is comprised of many organisms that vary over several orders of magnitude in size and that differ in trophic functioning. Phytoplankton, as the primary producers, form the base of the food web and ultimately provide higher trophic levels with nutrients and energy. Bacteria are also grazed and recycle nutrients back to the primary producers (Pace and Cole 1994). Heterotrophic bacteria are reliant upon dissolved organic carbon (DOC) exudates from phytoplankton either directly or indirectly through cell lysis or from grazing pathways (Larsson and Hagstrom 1979; Moran et al. 2001; Pomeroy and Wiebe 2001). Changes in bacterial biomass tend to follow changes in phytoplankton biomass i.e. if there is an increase in phytoplankton biomass there will be a corresponding increase in bacterial biomass, usually with a time lag of several days to weeks (Fenchel 1982; Griffith et al. 1982; Bird and Kalff 1984; Cole et al. 1988; Bjornsen et al. 1989; Servais et al. 2000; Pomeroy and Wiebe 2001). This is because bacteria respond to the changing or, in particular, the increase in nutrients, specifically carbon, released by phytoplankton. This relationship is much weaker in polar regions than in more temperate oceans (Karl et al. 1991; Rivkin 1991). There is also some evidence that bacteria and phytoplankton may compete for limiting inorganic nutrients (Caron et al. 2000).

While growth rates of microbial food web components are influenced by light, nutrients and temperature (Azam et al. 1983; Ducklow and Carlson 1992; Rivkin et al. 1996; Caron et al. 2000; Pomeroy and Wiebe 2001) it is the loss factors that ultimately determine the size of standing stocks (Wright 1988; Banse 1992). Grazing mortality, of phytoplankton and bacteria, is one of the most important loss factors to be considered (Sanders and Porter 1988; Fuhrman 1992) and may account for >100% of daily production (Sherr and Sherr 1994). High grazing rates combined with active recycling of nutrients means that large amounts of primary production can occur without net accumulation of biomass (Gallegos et al. 1996).

Bacteria and autotrophic picoplankton are small and are not effectively grazed by some crustacean-dominated mesozooplankton or larger sized organisms in the ocean (Sherr and Sherr 1984; Sherr et al. 1986; Fortier et al. 1994; Calbet and Landry 1999). Small organisms, such as microzooplankton, (< 200 μm) are more efficient bacterivores (Landry and Hassett 1982 and references cited within; Waterhouse and Welshmeyer 1995) and can have high growth and grazing rates (Heinbokel 1978a; Goldman and Caron 1985; Banse 1992; Azam et al. 1983). Hence, both bacteria and phytoplankton can be grazed by microzooplankton, which can then be grazed by higher trophic levels, thus transferring nutrients through the food web. Because these small cells do not sink directly from the surface layer they are otherwise retained in the upper ocean and the nutrients they contain will not be exported to the deep ocean. Grazing by microzooplankton may also result in decreased export from surface waters due to an increased contribution to recycled nutrients as metabolic by-products from respiration (Legendre and LeFevre

1995; Kuipers and Witte 1999). Consequently, microzooplankton are not only predators of bacteria and phytoplankton but also are crucial to nutrient recycling and export in the ocean (Porter et al. 1985).

Microzooplankton, such as heterotrophic ciliates and flagellates, ingest a significant fraction of large phytoplankton biomass, which may decrease sinking of biogenic carbon due to an increase in recycling or through inefficient trophic transfer. Heterotrophic dinoflagellates are of particular importance in polar waters as they may constitute greater than 75% of protozoan biomass in these waters, compared to a much smaller fraction in lower latitude ocean environments (Lessard 1991). As a result, the relative contribution of these protozoa to carbon flux may be more important in high latitude regions. Phagotrophic protists are important bacterivores and herbivores, and as prey for larger metazooplankton (Porter et al. 1985; Sherr et al. 1986; Vezina and Platt 1988; Sherr et al. 1997). Predation on these protists by metazooplankton potentially contributes to export of nutrients from the surface layer by contribution to the sinking flux through fecal pellet loss and vertical migration of these predators (Gonzalez 1992; Fortier et al. 1994).

Grazing efficiency of many mesozooplankton is dependent upon the size of available food resources (Uitto 1996). As noted above, most metazoans are not able to efficiently consume small cells, such as bacteria and pico-phytoplankton. Large copepods, for example, cannot efficiently ingest particles smaller than 5-10 um (Morales et al. 1991; Fortier et al. 1994). The non-crustacean macrophages, such as salps and appendicularians are able to capture and ingest small cells. Grazing by both salps and appendicularians

repackages these small cells into fast sinking particles either by incorporation of carbon into houses which become discarded or into fecal pellets (Fortier et al. 1994). Appendicularians in particular have been found to be important consumers of small phytoplankton in the North Water Polynya and may account for losses up to 10% of primary production (Acuna et al. 2002). Grazing by these macrozooplankton are important as they may be responsible for channelling the nutrients from small phytoplankton into downward export. Also these animals may compete with microzooplankton for food resources during the bloom of small phytoplankton (Acuna et al. 2002).

Food Selection

Microzooplankton are able to graze both bacteria and phytoplankton as food resources i.e. they may either be bacterivores or herbivores. Feeding modes may depend on food availability, location and season. Sherr and Sherr (1994) suggest that for ciliates, herbivory may be more important than bacterivory as a carbon flow pathway in marine food webs. Herbivores, including < 20 μm flagellates, > 20 μm ciliates and heterotrophic dinoflagellates, have been found to consume 25-100% of daily phytoplankton production (Sherr and Sherr 1994). Froneman and Perissonotto (1996) suggested that these herbivorous microzooplankton selectively graze phytoplankton (also Verity 1986; Burkhill et al. 1987; Legendre and LeFevre 1991) resulting in the significant decrease in small cells. Seasonal shifts in the community size structure of phytoplankton have also been recorded by Garrison et al. (1993), with large cells found during winter and small cells dominating the summer assemblage. These herbivores may control phytoplankton

populations either by grazing standing stocks directly or, more indirectly, by contributing to resource availability and growth conditions.

Microzooplankton are also important grazers of bacteria (Caron et al. 1982; Fenchel 1982, 1984; Epstein and Shiaras 1992). Heterotrophic or mixotrophic microflagellates, the most important group of bacterivores in the ocean (Azam et al. 1983; Fenchel 1984; Landry et al. 1984; Kuuppo-Leinikki 1990), may graze 25 to 100% of daily bacterial production (Pace 1988; Sherr and Sherr 1994). Selective grazing on certain sizes of prey may shift the size distribution of the prey, i.e. to either small or large bacterial cells (Caron et al. 1982; Epstein and Shiaris 1992; Kuuppo-Leinikki 1990; Jimenez-Gomez et al. 1994; Lebaron et al 1999; Hahn and Hofle 2001)

Size-selective ingestion of ciliates and dinoflagellates by copepods has been documented in laboratory studies of population dynamics (Uitto 1996; Levinsen et al. 1999). Levinsen et al. (1999) reported that small ciliates were cleared at a higher rate than large ciliates, yet it was the large size dinoflagellates which appeared to be preferrably grazed. In contrast, Stoecker and Egloff (1987) found higher clearance rates on large ciliates rather than small ones. Hence size selective feeding may occur throughout the food web, influencing community structure at more than one trophic level. In addition, different species and different life stages may be grazing different types and size classes of prey making the detailed analysis of size selective feeding much more complex.

Bacterial Response

Size selective grazing on bacteria has mostly been examined in freshwater systems. Gude (1979) carried out one of the first studies which examined the impact of

grazers on bacteria and found that grazing by protists can modify the structure of bacterial communities. Two responses are observed: 1) the formation of large spiral-shaped or filamentous bacteria and 2) the increase of single-celled bacteria which are protected from grazing due to their small size. Filamentous bacteria also fall outside the size range available to most bacterial grazers (Chrzanowski and Simek 1990; Gonzalez et al. 1990). More recent studies have also shown that bacteria are able to develop more complex, grazing-resistant morphologies, such as filaments or aggregates (Jurgens et al 1997; Hahn and Hofle; 2001 and references cited within). Chrzanowski and Simek (1990) also indicated that the distribution of bacterial cell types shifts under heavy grazing pressure leaving an abundance of cells which are so-called "grazing-resistent". del Giorgio et al. (1996) have lent support to this idea suggesting that bacteria can escape grazing through cell inactivation which results in smaller cells that have some protection from grazing.

Other studies suggest that the size of bacteria is controlled only by substrate supply not predation pressure (Krambeck 1984; Palumbo et al. 1984; Psenner and Sommaruga 1992). Posch et al. (1999) suggested that bacteria react to grazing pressure not by increasing cell size but by actively dividing. Remineralization of nutrients, or release of substrate by predators during intense grazing, contributes to a positive feedback on the bacterial prey itself. So, the effect of grazing on size distribution of bacterial cell sizes results in an increased number of either very small or very large cells.

Size selection by grazers is proposed to account for differences in cell size observed between natural populations and cultures (Ammerman et al. 1984; Sherr et al. 1992). This selectivity has both direct and indirect effects on the microbial community

dynamics including directly cropping stocks of a certain prey size class while indirectly regenerating nutrients. Actively growing bacteria appear to be the preferred prey of microbial predators (Gonzalez et al. 1993; Sherr and Sherr 1994; Lebaron et al 1999; Posch et al. 1999; Sherr et al. 2002). Increased predation on these actively growing bacteria may be compensated for by increased cell division of the bacteria, thus resulting in higher demands for the nutrients which assist in maintaining the prey stocks (Chrzanowski and Simek 1990; Posch et al. 1999). Hence, understanding the grazing processes of the microzooplankton is important in determining the flow of nutrients and energy throughout the ocean.

Explaining Food Web Interactions

Several food web models have been introduced which deal with the interactions between small cells and larger grazers and how these interactions contribute to nutrient recycling and export. Two examples are the microbial food web (Sherr and Sherr 1988) and the microbial loop (Azam et al. 1983). The structure of these trophic pathways, including size distributions of both prey and predators, influences the vertical particle flux from the surface of the ocean.

In the microbial loop model, bacteria take up dissolved organic matter and are then grazed by small heterotrophic flagellates and ciliates. As a result, when flagellates, or other predatory microzooplankton, increase in biomass, the biomass of their bacterial prey generally decreases (Azam et al. 1983). These flagellates can in turn be grazed by larger microzooplankton so that some of the energy originally released by phytoplankton is incorporated into the main food chain. In the microbial loop, bacteria are both

controlled by microzooplankton and nourished by nutrient excretion by microzooplankton and other organisms (Azam et al. 1983; Porter et al. 1985; Rassoulzadegan 1993; Legendre and Le Fevre 1995; Legendre and Rassoulzadegan 1995; Moller and Nielsen 2001). The microbial loop is also considered to be a part of the larger microbial food web (Sherr and Sherr 1988).

In contrast, the microbial food web has been presented to include autotrophic microorganisms. Here ciliates graze on the flagellates that are grazing the pico-phytoplankton (Azam et al. 1983). In this case carbon may be either recycled, through respiration, or repackaged, through grazing, and therefore channelled to higher trophic levels. There is very little export of nutrients in a system dominated by the microbial food web i.e. the more carbon which gets respired, less is available for vertical export (Legendre and LeFevre 1995).

The atmosphere-ocean CO_2 flux has been connected to the structure and dynamics of the planktonic food web (Vezina and Platt 1988; Rivkin et al. 1996). Processes of export and sequestration of carbon have been termed the "biological pump" (Legendre and Le Fevre 1995). Drawdown of organic or inorganic carbon found in the immediate ocean-surface interface influences uptake of CO_2 from the atmosphere. Phytoplankton play a direct role as a sink for atmospheric CO_2 and are responsible for uptake of half the carbon dioxide from the atmosphere. The carbon in the surface layer is then replenished by diffusion of atmospheric CO_2 into the ocean. Biological activity will respond to climate changes hence any feedback effects between processes of export and

sequestration and climate must be quantified by studying the food web interactions in the ocean's surface.

Food Webs in Polar Regions

Up to 20% of total primary production over the globe occurs in high latitude oceans (Longhurst et al. 1995; Rivkin et al. 1996). Bacteria in polar regions largely depend upon carbon originating from phytoplankton sources, accordingly changes in bacterial production and biomass should follow changes in phytoplankton production and biomass. Furthermore, while early studies suggested that microbial activity in polar regions is low, more recent findings indicate that microbial activity during certain times of the year may in fact be similar to that in temperate regions (Thingstad and Martinussen 1991; Rivkin et al. 1996; Rich et al. 1997; Pomeroy and Wiebe; 2001).

Seasonal variation in light, ice cover and temperature complicate food web interactions, including availability of prey, grazing control and nutrient recycling. Polar oceans are ice covered throughout most of the year which means that the light levels which penetrate the water column are often low and variable. The low water temperatures in polar regions also play a role in marine food web processes. The "cold ocean paradigm" suggested that at critically low sea water temperatures bacterial growth and activity are suppressed (Pomeroy and Deibel 1986). Later studies indicate that it is also nutrient availability, not only temperature, which determines growth rates and therefore abundances of stocks (Rivkin et al. 1996; Pomeroy and Wiebe 2001). Pomeroy and Wiebe (2001) suggest that temperature-substrate interactions differ depending on the temperature regime - polar versus temperate. In particular, bacteria which exist in low

temperature require higher levels of substrate to achieve the same level of growth. Some researchers have also found that low temperatures may be responsible for low phytoplankton grazing mortality (Caron et al. 2000, and references within).

In polynyas, which are seasonally ice-covered, the dissolved CO_2 accumulated by phytoplankton during the summer cannot be returned to the atmosphere during the winter because of ice cover (Barber et al. 2001). In addition, because of higher growth efficiencies of microplankton in polar regions, less carbon is respired and more is incorporated into bacterial biomass (Rivkin and Legendre 2001). In both of these cases there is greater potential for export and sequestration of carbon. Thus, previous models of carbon flux developed using studies from temperate oceans may have underestimated carbon export.

Carbon Cycling In Polar Regions

Characterisation of microbial processes is crucial for models of oceanic carbon flux and for characterising the interactions between oceanic and atmospheric processes (Huntley 1992; Livingston and Bowles 1992). As techniques have been developed which allow for the quantification of phytoplankton and bacterial biomass, as well as production, more studies of carbon flux through the microbial loop have arisen (Vezina and Platt 1988; Zubkov et al. 2000). Rates and volumes of carbon cycling and carbon export are suggested to be a function of food web structure (Michaels and Silver 1988). For example, grazing by microzooplankton contributes more to nutrient recycling rather than export (Michaels and Silver 1988; Longhurst and Harrison 1989; Verity et al. 1993; Edwards et al. 1999).

1.2 Methodology

Theory of the Dilution Assay

Microzooplankton grazing rates on bacteria and phytoplankton can be determined using dilution assays (Landry and Hassett 1982). This method concurrently estimates the rates of apparent growth and grazing mortality of prey in a microbial community. Growth and grazing rates are calculated from changes in cell numbers (bacteria) or photopigment concentration (phytoplankton) over time in a series of seawater samples variously diluted with filtered seawater. Inherent in the dilution approach are several assumptions: prey growth is exponential and is independent of dilution; grazers do not respond to decreased food levels i.e. rate of grazing is a linear response directly proportional to dilution effect on predator abundance, not to changes in prey concentration; the grazer population is not influenced by manipulation. It is also assumed that the decrease in cell numbers is as a result of grazing and not as a result of other loss processes such as viral mortality.

While the technique was originally developed to estimate grazing on phytoplankton, it has been used to assess growth and grazing mortality of bacterial prey (Landry and Hassett 1982; Bautista et al. 1993, Jimenez-Gomez et al. 1994; Landry et al 1994; Rivkin et al. 1998; Putland 2000). The interpretation of the dilution model is more complex for bacterial prey due to differing nutrient requirements for bacteria than for phytoplankton. While phytoplankton respond to changing light levels and nutrients, growth rate can be kept constant by incubations carried out in neutral low light conditions and through the addition of saturating limiting inorganic nutrients. Bacteria, however, respond to changing ambient organic nutrient levels.

The exponential model of population growth is the basis for the dilution model whereby

$$1) \qquad r = NGR = \ln (P_t/P_o)/t = \mu - g$$

Here **r** is the net growth rate (NGR), observed over incubation time interval (**t**), in days. NGR can be calculated as the difference between instantaneous rates of population growth (μ) and grazing mortality (**g**) (Landry 1993) and $\mathbf{P_o}$ and $\mathbf{P_t}$ are the initial and final prey stock, estimated from chlorophyll *a* concentrations or bacterial cell counts. Growth rates calculated for each individual sample within a dilution series is the apparent growth rate or AGR. Instantaneous rate of prey growth (μ d^{-1}) and mortality due to grazing (g, d^{-1}) is estimated from Model I linear regression of AGR, from the lowest percent dilution of RSW to 100% RSW, versus dilution for each prey type. In the ideal model the instantaneous rate of prey growth, which is prey growth in the absence of grazing mortality, is the ordinal intercept of the regression, and grazing mortality is the absolute value of the negative slope.

In this study, the dilution approach was modified in several ways. Prey AGR was regressed against actual dilution factor (ADF) rather than the target dilution factor (TDF). TDF is subject to measurement errors and changes in the grazer viability so ADF was calculated from chlorophyll concentrations,

$$2) \qquad ADF = \text{Chl } a_o(X_i) \,/\, \text{Chl } a_o\,(X_o)$$

where **Chl $a_o(X_i)$** is chlorophyll *a* concentration at time zero at dilution factor X_i. **Chl $a_o(X_o)$** is the chlorophyll *a* concentration at time zero of the unmodified experimental bottle. ADF is used rather than TDF as a more accurate measure of realised prey dilution.

Microzooplankton grazing impact on different prey is determined through the calculation of daily net growth rates for microbial prey types (NGR), percentage of ingested prey (%Ps), and rate of ingestion of microbial prey carbon (Ic, ug C l^{-1} day^{-1}) using the formulae below

3) $NGR = \mu - g$

4) $\% Ps = (((C_o e^{\mu} - C_o) - (C_o e^{(\mu - g)} - C_o))/C_o) * 100$

5) $Ic = C_o e^{\mu} - C_o e^{(\mu - g)}$

where $\mathbf{C_o}$ is prey carbon (μg C l^{-1}) at time zero calculated from bacterial and phytoplankton biomass integrated to 100m (Klein unpublished, Rivkin unpublished). Here it is assumed that clearance rate by microzooplankton is uniform throughout the 100m water column.

Published and generally accepted carbon conversion factors were utilised to convert prey abundances to carbon. Bacterial carbon was estimated using 20 fg C $cell^{-1}$ (Kirchman et al. 1993; Zubkov et al. 1998) and chlorophyll *a* was converted to carbon assuming a C:Chlorophyll *a* ratio of 55 (Booth et al. 1993).

There are several limitations and possible sources of error associated with the dilution method. Firstly, this approach is very labour intensive involving much time and

effort for set-up and manipulation. For simplicity, the following limitations will be discussed point-wise:

1. Filtration Effects: Contamination of the diluted samples may be incurred during experimental handling. This may include changes in the bacterial population which would increase the nutrients available to prey in the case of cell breakage and consequent nutrient enhancement. Gasol and Moran (1999) discuss in more detail the filtration effects on sea water used in dilution assays including not only changes in abundances, but changes in community structure (size selection) as well as potential stimulation of bacterial activity. Furthermore, the filtrate cannot be assumed to be bacteria-free even following filtration (Wright and Coffin 1984; Li and Dickie 1985; Gasol and Moran 1999) and pore size of the filter must be chosen carefully. Pico-bacteria which pass through the filter may proceed to grow very quickly in an environment enriched by nutrients from cell breakage due to filtration.

2. Population Effects: Grazer population estimates may be inaccurate if community structure changes during the incubation time (Dolan et al. 2000), if grazers are damaged during sample handling, or if the protists are food limited. Conversely, following filtration to obtain <202 μm water, removal of large predators reduces grazing pressure on the remaining protists. These protists, now growing unchecked, may now graze bacteria more vigorously than would be occurring naturally (Jurgens et al. 1994;Vaque et al. 1994).

3. Nutrient Conditions: Nutrient limitation or differential nutrient availability among dilutions may affect prey growth rates, as may changes in irradiance levels.

a) Because phytoplankton have different energy requirements than bacteria, interpretation of growth rates measured using the dilution model is more complex (Landry 1993). Phytoplankton are dependent upon light (both quantity and quality) as a source of energy. Since the light regime in the upper 50 m can be highly variable any simulated intensity would not be an accurate proxy for the *in situ* light levels. Incubating in low light levels minimizes any potential enhancements of growth. However, growth rates of phytoplankton may be enhanced through the increased levels of organic nutrients by cell breakage during filtration (Ferguson et al. 1984; Vaque et al. 1994). Results must be viewed with caution.

b) In the conditions which include high volumes of filtered seawater, the diluent has been filtered to remove all particles greater than 0.2 μm. In this case, there will be less regenerated nutrients because of lower rates of remineralization (Gude 1986; Neuer and Cowles 1994; Vaque et al.1994). The prey may become nutrient limited in dilution of high FSW. Tremaine and Mills (1987) defended the technique by indicating that because there are fewer cells present, there is also less competition for available nutrients. Conversely, in dilutions containing higher dilutions of raw sea water, consumers with more available food may grow at a faster rate (Landry et al. 1995). Again, the complex food web interactions within experimental containers can make the interpretation of results of dilution grazing experiments difficult.

4) Changes in Cell Size: The dilution approach measures growth rates based on changes in cell numbers and does not account for changes in cell biovolumes. Where individual cells may increase in size, as with bacterial populations, measurement of cell

sizes in addition to cell numbers would assist in more accurate determination changes in the structure and characteristics of sub-populations.

Despite the limitations of the technique, Tremaine and Mills (1987) rigorously tested each of the assumptions of the dilution method and found that the model, and its assumptions, are generally valid. They also determined that rates obtained correlated closely with other more direct methods of measuring growth and grazing dynamics. Furthermore, the limitations of this technique are well recognised by biologists studying the interactions of grazers and prey and it is now widely used to measure growth and grazing mortality values.

1.3 Summary

Microbial processes in Arctic environments have not been well researched. Studies which measure rates of growth and grazing of microbial prey often do not study both phytoplankton and bacteria as potential prey. There are several methods which exist to study growth and grazing mortality rates of microbial prey. However, there are few studies which address these processes in combination with a size selective study to further examine grazing processes within the microbial food web.

The research in the following Chapters deals with the interactions taking place between microzooplankton grazers and their phytoplankton or bacterial prey. In Chapter two, the dilution approach (Landry and Hassett 1982) was used to determine growth and grazing mortality of bacteria and phytoplankton throughout the North Water Polynya. Chapter three introduces a new method of studying size selective grazing by microzooplankton on bacteria by using samples collected using the dilution approach

combined with image analysis measurements. Hence, this study encompasses both the interactions between bacteria,phytoplankton, and microzooplankton and the potential impact of microzooplankton grazing processes and food selection on carbon transfer through the microbial food web in the Arctic North Water Polynya.

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Co-authorship Statement

This work was conducted as a component of the multidisciplinary International North Water Polynya Study. Logistics and cruise planning was carried out by my supervisor and supervisory committee prior to my entrance of the Graduate Program. I have made substantial contributions to (a) conducting experimental processes (b) the analysis and interpretation of the data, and to (b) drafting the manuscript. Various groups were responsible for specific sets of measurements. All data or information which was obtained from other sources has been acknowledged or referenced. This manuscript represents original material, has never been published before, and is not under consideration for publication elsewhere.

Chapter 2

Microzooplankton Herbivory and Bacterivory in the North Water Polynya

2.1 Introduction

High latitude regions are characterised by distinct seasonal variations in temperature, and ice cover. As a result there are seasonal changes in biological components including biomass, growth and grazing mortality rates of bacteria and phytoplankton as well as other microbial food web components. Although, bacteria in polar oceans can exhibit growth rates during some months, which are as high as those in more temperate regions, their biomass remains relatively constant suggesting that growth and loss processes are closely balanced (Thingstad and Martinussen 1991; Rivkin et al. 1996; Rich et al. 1997; Pomeroy and Wiebe 2001; Rivkin and Legendre 2001). Polynyas are of particular interest because the seasonality of ice cover in these regions results in high primary productivity and hence an increased number of birds and mammals that are drawn to the open water for feeding and mating (Stirling 1997).

The microbial food web is an integral component of organic carbon cycling pathways in these high latitude oceans. One of the key components of the microbial food web are the microzooplankton (< 200 μm). Because most crustacean metazoans are not considered to be efficient consumers of small prey in the ocean, grazing processes of microzooplankton predators, on bacteria and phytoplankton, may be the main pathway that efficiently repackages this carbon into a form available to larger metazoan grazers (Sherr and Sherr 1984; Sherr et al. 1986; Uitto 1996; Calbet and Landry 1999). Microzooplankton consume a large proportion of primary production in the ocean and

have been suggested to consume large amounts of bacteria as well, thus placing constraints on prey population size (Verity 1986; Burkhill et al. 1987; McManus and Fuhrman 1988).

The North Water (NOW) Polynya is located in northern Baffin Bay and Smith Sound, between Greenland and Ellesmere and Devon Islands. This is the largest polynya in the Arctic and while the physical processes, which lead to the opening of the polynya, have been fairly well documented (Smith et al. 1990; Kawamura et al. 2001; Melling et al. 2001), the biological properties of this polynya are poorly defined. As a component of an international study of the NOW polynya, the primary objectives of this research were (1) to quantify the patterns and rates of bacterivory and herbivory of microzooplankton at different locations in the North Water Polynya and at different times of the year, and (2) to determine the contribution of different prey to the total ration of ingested carbon by microzooplankton. To address these objectives, the rates of growth and grazing mortality of phytoplankton and bacterial prey were measured over the four month study period from April to July, 1998.

2.2. Methodology

Sampling Site

Samples were collected aboard the Canadian Coast Guard icebreaker *Pierre Radisson* from early April 1998 to late July 1998 as a component of the multidisciplinary International North Water Polynya Study. A total of 30 experiments were carried out at ten stations in the North Water Polynya, some of which were visited several times over the season (Table 2.1, Figure 2.1). Stations were selected at the East and West ends of each transect, as well as in the middle of the longer transects (Figure 2.1).

Experimental Design

Microzooplankton grazing impact on bacteria and phytoplankton was examined using a modified dilution assay, as described by Landry and Hassett (1982). This approach concurrently estimates the rates of growth and grazing mortality of a microbial community and assumes that 1) prey growth is exponential and independent of dilution, 2) the rate of grazing is a linear response, directly proportional to dilution effect on predator abundance, not to changes in prey concentration and 3) the grazer population is not influenced by the manipulation.

Sample collection depth was selected based on the structure of the water column. Water for dilution experiments was collected at the depth of the chlorophyll *a* maximum, if present. Otherwise samples were taken at the midpoint of the upper mixed layer. Water samples for the determination of *in situ* prey abundances were normally collected at six to eight depths spanning the upper 200m of the water column. Water for the particle free diluent (i.e. water which has been filtered free of any microbial components) was

collected from below the upper mixed layer (Bird and Karl 1999; Rivkin et al. 1999; Putland 2000) where nutrient concentrations are typically high (Tremblay et al. 2002 and refs cited within). This nutrient enriched water ensures that the growth of microbial prey will not be nutrient limited during the experiments.

Water for experiments was collected in 10-L Niskin bottles (Brooke Ocean Technology Limited, Dartmouth, Nova Scotia) mounted on a General Oceanic rosette sampler that was equipped with a CTD profiler (ICTD, Falmouth Scientific Inc.), and a Seatech fluorometer. Water was drained from the Niskin bottles through an attached tube into the collection container. The end of the tube remained below the surface of the water to minimise turbulence and damage to delicate microorganisms. Subsamples were also collected for the determination of bacterial abundance in the sea water prior to any manipulation. Particle free sea water (PFW) was prepared by gravity filtration through 0.2 μm Gelman capsule filters which drained into a separate collection container. This PFW was then gently combined with <202 μm size fractionated sea water (prepared by gentle gravity flow of water through a Nitex screen with mesh pore size 202μm (thus removing any large zooplankton) into 4-litre polycarbonate bottles at eight target dilutions of 10, 25, 37.5, 50, 62.5, 75, 90, 100%. Gasol and Moran (1999) determined that 0.2 μm filter was effective in removing most of the bacterial cells in the water (i.e. 2% - 26% of the bacteria were found in the filtrate following filtration through 0.2 μm polycarbonate filters). Bottles were mounted on a plankton wheel rotating at 1 rpm and were incubated at *in situ* temperatures and in low light conditions for ~48 hours. Gelman filters and Nitex

screening (used for <202 μm filtered sea water) were rinsed with distilled water and sea water before use.

Sampling Dilution Assays

Initial samples were collected directly from the rosette and immediately preserved for quantification of bacterial abundance prior to experimental manipulation. After the set up of the experiment, subsamples for chlorophyll *a*, bacteria and microzooplankton abundances were collected after a pre-incubation period of four hours, and again at the end of the experiment. The equilibrium period was incorporated into the experimental design because an initial change in prey abundance has been observed following mixing of dilutions. Samples for chlorophyll *a* were collected onto 25mm GF/F (i.e. > 0.7μm) and 5 μm Poretics filters (> 5.0 μm) and stored at -20° C until analysis. Samples for bacteria, and protists were collected into 500 ml Nalgene bottles and preserved with gluteraldehyde (2% final concentration). Preserved samples were stored in the dark at about 4° C.

Sample Analysis

Chlorophyll samples were analysed within 12 months of collection. Chlorophyll *a* was extracted overnight in 90% acetone at -20° C and fluorescence was measured using a Sequoia-Turner fluorometer equipped with a wide-band filter set. The fluorometer was calibrated using pure chlorophll *a*. The chlorophyll *a* concentration in the <5 μm size fraction was determined as the difference between total (GF/F) and > 5 μm size fractions.

Abundances of bacteria were determined from water samples preserved in 2% glutaraldehyde within 18 months of collection. Bacteria samples were filtered onto 25mm diameter, 0.2 μm black polycarbonate filters, stained with acridine orange (Hobbie et al. 1977) and counted on a BH2- RFC Olympus epifluorescence microscope at a magnification of 1250x using blue-light excitation (BP440, DM455, AFC+Y475). Flagellates were preserved and counted using the method described in Lovejoy et al. (2000). All the slides for each individual experiment were made and counted at the same time so that counts within an experiment were consistent and comparable (Putland and Rivkin 1999). A minimum of 300 cells per filter (10 or more random fields counted; CV~20%) were counted for determination of bacteria.

Bacterial carbon was estimated using 20 fg C $cell^{-1}$ (Kirchman et al. 1993; Zubkov et al. 1998) and chlorophyll *a* was converted to carbon assuming a C:Chlorophyll *a* ratio of 55 (Booth et al. 1993).

Statistical Analysis of Results

Rates of prey growth and mortality were determined using Model I linear regression (Sokal and Rohlf 1995) of the apparent growth rate versus actual dilution factor for each type of prey. Net growth rate (NGR) of each prey type was determined as the difference between growth rate and grazing mortality rates (i.e. NGR = μ- g). Results were analysed using parametric and nonparametric tests for significant differences in prey growth rates (absence of grazing), μ; rates of mortality due to grazing, *g*, of a microbial prey population; net growth rates; and ingestion of carbon. A univariate Analysis of

Variation of the general linear model was carried out to examine trends of μ, g, and NGR between regions and months. To test for relationships between rates obtained and other biological properties such as biomass estimates, regression analyses were performed. Tests using the general linear model were carried out to determine whether observed rates could be logically grouped based on location.

Regression analyses were run using SPSS statistical software to determine the relationship between growth and grazing mortality rates and other environmental variables (i.e. nutrients such as nitrate+nitrite, phosphate, silicate and dissolved organic carbon).

2.3. Results

2.3.1. Station Information

Table 2.1 summarises the physical and biological characteristics of the stations sampled. Chlorophyll data were provided by Dr. Bert Klein (Université Laval, Québec, QC). The locations of the stations within the Polynya are presented in Figure 2.1. The polynya was separated into North, East and West regions. These regions were selected based on differences in water mass, phytoplankton and bacterial distributions through the polynya in June 1998 (Bacle 2000; Rivkin et al. 2000 unpublished; Tremblay et al. 2002).

2.3.2. Biological Characteristics

Areal chlorophyll *a* concentrations (courtesy of Dr. Bert Klein) ranged from ~5 to > 700 mg m^{-2} (Table 2.1) and large-sized phytoplankton (> 5 μm) were dominant. Bacterial abundances ranged from 76 to 886 x 10^{11} cells m^{-2} (Table 2.1).

Phytoplankton and bacterial biomass measured from initial experimental samples ranged from ~ 3 to 398 μgC L^{-1} and 1.6 to 17.7 μgC L^{-1} respectively during this study (Table 2.1). Highest phytoplankton biomass was seen from late May through late June whereas bacterial stocks continued to increase from June through July (Figure 2.2a and 2.2b).

Flagellate abundances were determined in the ambient water samples and are shown in Table 2.2. The abundances reported here are the *in situ* number of protists. There are no data on microzooplankton concentrations within the experimental bottles. Sample storage problems during shipping back from the polynya resulted in the development of gluteraldehyde crystals which interfered with enumeration of the protists. Heterotrophic flagellate abundances were provided by Dr. Connie Lovejoy (Université Laval, Québec, QC) and range from 1440 - 952 000 cells L^{-1} with the maximum occurring early in June (Figure 2.2c).

2.3.3. Growth and Grazing losses

Thirty grazing experiments were conducted during this study. Tables 2.3 to 2.6 show the rates of growth and grazing mortality for three size classes of phytoplankton (> 0.7μm, >5 μm, <5μm) and bacteria as measured by the dilution experiments. These experiments were conducted at the ten stations from April through July. As can be seen in the Tables, some of the stations were repeatedly sampled during the study. Experiments where there was a positive grazing slope (i.e. greater mortality at low predator abundance) were not further analysed since they violate the assumptions of the

dilution approach. The significance of μ and g, determined from regression analyses, is indicated in the tables. Net growth rates (NGR =μ-g) are calculated and included in the Tables.

Phytoplankton

Total Phytoplankton (> 0.7 μm) - Growth rates of total phytoplankton (Figure 2.3 (a)) were low (< 0.05 d^{-1}) in the beginning of the study period, prior to the bloom. Rates increased during mid-April and remained between 0.15 to 0.54 d^{-1}, until June when they decreased again. Growth rates were highest at station 35, in the Western region of the Polynya, during late-April (0.54 d^{-1}, $\alpha = 0.10$). Rates were low generally during early June until mid-July (0 to 0.14 d^{-1}). However, an experiment conducted on July 17 (JD = 198, See Table 2.1 for Julian day equivalents for remaining dates in text) at station 40 (Eastern region) resulted in a growth rate of 0.25 d^{-1}. Over 60% of these growth rates were significant i.e. $p < 0.05$.

Grazing mortality for phytoplankton (>0.7 μm) was highest from mid-to-late April (range from 0.24 to 0.56 d^{-1}). Rates of grazing mortality during May and June ranged from 0.04 to 0.18 d^{-1}.

Large Phytoplankton (> 5 μm) - Growth and grazing mortality trends for the large (>5 μm) size fraction of phytoplankton (Figure 2.4) were similar to those for total phytoplankton. Growth rates began to increase mid-April and peaked mid-May at station 14 in the north western region, with a rate of 1.14 d^{-1}, which is higher than growth rates measured for total chlorophyll.

Grazing mortality of large phytoplankton was also highest at station 14 (1.26 d^{-1}). Grazing mortality was high mid-April (0.47 d^{-1}) at the beginning of the bloom. Rates were consistent and low (<0.15 d^{-1}) from mid-May to late July.

Small Phytoplankton (< 5 μm) - Growth rates of small phytoplankton (<5 μm) during April were variable with a seasonal average of 0.40 d^{-1}. However, from May until early June, rates increased from 0.48 to 1.00 d^{-1} ($\alpha = 0.05$). Growth rates decreased from mid-June through July (Figure 2.5, Table 2.5).

Grazing mortality of small phytoplankton (<5 μm) were highest during mid-April (> 1.50 d^{-1}) in the western region of the polynya (station 44 and 49). Rates were variable during May and June (mean 0.5 d^{-1}). The highest grazing mortality during May was determined for station 2, located in the North. Mortality rates remained > 0.30 during July.

Bacteria

Bacterial growth rates (Figure 2.6, Table 2.6) were low during April throughout the Polynya and ranged from 0.10 to 0.58 d^{-1}. During May, growth rates increased and ranged from 0.11 to 1.21 d^{-1}. Growth rates decreased again during June through the beginning of July with values relatively consistent throughout the Polynya (0.01 to 0.54 d^{-1}). During July growth rates increased (from 0.54 to 1.23 d^{-1}). The highest bacterial growth rates observed were at station 54 (1.21 d^{-1}) and station 40 (1.23 d^{-1}) during late May and mid-July, respectively. Both these stations are located in the south east region of the Polynya. These were the highest growth rates for any of the prey measured.

Rates of grazing mortality ranged from 0.20 to 0.58 d^{-1} in April. They remained from 0.02 to 0.91 d^{-1} during May, however in June these rates decreased and were 0.13 to 0.36 d^{-1}. In July, grazing mortality rates increased to 1.32 d^{-1} - the highest grazing mortality measurement for this study.

2.3.4. Statistical Analysis

The high number of non-significant regressions computed during this study prompted further evaluation of growth rates. A grazing mortality rate which is non-significant indicates that there is no grazing mortality occurring and the dilution slope is essentially zero. Therefore, the mean of the apparent growth rates should equal the originally obtained growth rate (i.e. obtained from the y-intercept of the extrapolated regression line). This mean AGR was calculated for those experiments with a non-significant regression slope but which resulted in a y-intercept which was significantly different from zero.

For those experiments where the mean AGR was much different from the μ, the original dilution plots were examined. Upon examination of the original dilution plots differences could be explained by extreme scatter in the AGR's in the dilution plot. Alternatively, some plots included points which could be considered outliers which resulted in the non-significant regression and resulted in the difference between mean AGR and actual μ. For the purposes of this study, the actual values obtained from the dilution approach will be presented and discussed. However, the limitations of the approach are recognised.

Rigorous statistical analysis was carried out to determine if growth and grazing mortality rates were different among regions and seasons. ANOVA's were performed by month and prey, to test among regions. Prey growth and grazing mortality was examined by region separated by month.

The differences in phytoplankton rates of growth and grazing mortality among regions were not significant ($p>0.05$). Spatial trends observed throughout the polynya are presented in the results section as contour plots (Surfer(Win32) , Version 6.04). It should be noted that the plots presented in the following section are intended for visual representation of the rates obtained in this study and are not presented for data analysis.

Regression analysis of growth and grazing mortality of phytoplankton indicates a significant correlation of phytoplankton (>0.7 μm) growth rates on nitrate+nitrite ($p < 0.05$, $r^2 = 0.49$) but not on silicate, phosphate or dissolved organic carbon.

The differences in rates of growth and grazing mortality of bacteria among regions were not significant ($p > 0.05$). Regression analysis of bacterial growth and nutrients indicates some dependence of bacteria on nitrate+nitrite ($p < 0.1$, $r^2 = 0.45$) and dissolved organic carbon ($p < 0.05$, $r^2 = 0.37$) but not on silicate or phosphate. Grazing mortality of bacteria was weakly correlated with dissolved organic carbon concentration ($p < 0.1$, $r^2 = 0.23$).

2.3.5. Spatial and Seasonal Analysis

2.3.5 i) Spatial Analysis Differing physical characteristics seen throughout the Northwater Polynya drive changing biological characteristics in the North, East and West. The regional differences can be seen in both chlorophyll and bacterial distributions. Fig

2.7 shows the changing spatial patterns in phytoplankton biomass (as measured by chlorophyll concentrations). During April, chlorophyll *a* concentrations were low throughout the Polynya. The south eastern region of the Polynya showed the first increase in chlorophyll concentrations during May which then spread north and westward as the season progressed into June. Chlorophyll concentrations, throughout the polynya, decreased again during July.

Bacterial abundances were low during April and May although cell numbers increased slightly in the south western region of the Polynya during May (Figure 2.8). Cell numbers peaked in June in the north western region of the Polynya, and decreased again during July except in the south eastern region of the Polynya.

Flagellate abundances (Figure 2.9) showed similar patterns to phytoplankton with low abundances in April that first increased in the south eastern region of the Polynya in May. Highest abundances were reported for the northeastern region of the Polynya in June. No data was available for July.

Phytoplankton growth and grazing morality Growth rates and grazing losses were measured for total chlorophyll (i.e. > 0.7 μm) and for the two size fractions of chlorophyll, >5 μm and <5 μm.

Growth rates of the total phytoplankton community (Figure 2.10) were highest in the south western region of the Polynya during April. They increased to the north and east as the season progressed. Growth rates appeared to decrease throughout the Polynya during June with higher rates in the south western area until July. Growth increased again

in the northeastern region of the Polynya during July. Only April and May are shown in Figure 2.11 (there are insufficient data to create plots for June and July) for phytoplankton >5 μm. However we again saw the first increase in the south western region of the Polynya extending north into May. The small phytoplankton (<5 μm) (Figure 2.12) appeared to be growing most rapidly during April in the western region of the Polynya. Growth rates remained high during May extending throughout the Polynya and culminating during June in the north. There were insufficient data to create a contour plot for July.

Grazing mortality rates of total phytoplankton (Figure 2.13) were highest in the south western region of the Polynya during April. In the other months, grazing mortality rates never reached levels observed in the south west during April. Phytoplankton >5 μm (Figure 2.14) showed similar spatial patterns in rates of growth and grazing mortality (Figure 2.11) during April and May. Spatial patterns in grazing mortality of small phytoplankton (<5 μm) (Figure 2.15) also followed growth rates with highest rates in the south west, spreading throughout the Polynya during May with main focus across the south and central Polynya and culminating in the North during June.

Bacterial growth and grazing mortality Growth rates of bacteria (Figure 2.16) were low throughout the Polynya during April. During May, rates in the south eastern region of the Polynya were high. The spatial pattern was similar during June although rates were lower throughout. July saw growth rates increasing in the north eastern region of the Polynya and decreasing to the south east and south west.

In contrast to other microbial prey, grazing mortality of bacteria (Figure 2.17) during April was elevated in the North. During May rates were higher in the north as well as in the south east. Rates were very low throughout the Polynya during June. During July there only appeared to be active grazing in the central eastern region of the Polynya.

2.3.5. ii) Seasonal Analysis Spatial patterns of growth and grazing were generally similar within each prey type/size class. However, statistical analysis (ANOVA) of the results indicated that due to the high variance in these parameters, differences among regions were not significant in the Polynya. Therefore, mean monthly rates were calculated and used to describe general seasonal trends. Means were only calculated for those experiments with a positive grazing value (i.e. a negative regression slope). Figures 2.18 and 2.19 show these seasonal patterns for each prey. For months with fewer than three rates measured, boxes were not presented but the mean rates are indicated. The following section describes each prey type separately beginning with phytoplankton.

Phytoplankton growth and grazing mortality Total phytoplankton (>0.7 μm) mean growth rates (as seen in Figure 2.18) were highest during April (0.38 d^{-1}) and decreased during June and July when rates were lowest (<0.08 d^{-1}). When size fractions were examined separately, growth rates of the large size fraction (> 5 μm) were moderate during April (0.28 d^{-1}), and peaked during May (0.45 d^{-1}). Mean values were not presented here for June as only one value was reported. Only two values were reported for July so the mean calculated was 0.11 d^{-1}. The small size fraction (< 5 μm) exhibited the highest

growth rates during May (0.52 d^{-1}) and rates remained above 0.26 d^{-1} during June and July.

Mean grazing mortality (Figure 2.19) of total phytoplankton was greatest during April (0.46 d^{-1}) and lowest during May and June (0.11 d^{-1} and 0.09 d^{-1} respectively). Size fractions showed different trends than for total phytoplankton. For the large size fraction, a grazing mortality of 0.27 d^{-1} was measured during April. It increased only slightly to 0.29 d^{-1} during May, and declined to 0.14 d^{-1} during July (see Table 2.4). Grazing mortality on the smallest size fraction of phytoplankton exceeded that of the large size fraction during all four months of the study beginning with a mortality of 0.75 d^{-1} during April, slowly decreasing to 0.37 d^{-1} during July.

Bacterial Growth and Grazing Mortality Mean bacterial growth rates were lowest during April (0.25 d^{-1}) increased to 0.3 d^{-1} during May and remained above 0.3 d^{-1} for the duration of the study (Figure 2.18). The maximum mean growth occurred during July (0.49 d^{-1}).

Mean grazing mortality of bacteria (Figure 2.19) was high at the beginning of the study with a rate of 0.40 d^{-1} during April. This rate remained high until June when mortality declined to 0.20 d^{-1}. Rates rebounded in the final month of study to 0.46 d^{-1}.

2.3.6. Net Growth Rates Net growth rates, the difference between growth rate and grazing mortality (NGR = μ-g), are indicative of net prey dynamics. No significant differences between growth or grazing mortality rates among regions within the Polynya

were found (ANOVA). Thus, monthly net growth rates (NGR) were calculated for examination of general trends (Fig 2.20).

Phytoplankton During April, mean NGR of total phytoplankton (>0.7 μm) was -0.03 d^{-1}, with grazing mortality essentially balancing growth. Growth exceeded grazing mortality during May resulting in a positive net growth rate (0.20 d^{-1}). Growth and grazing mortality were again in balance during June resulting in a NGR of -0.03 d^{-1}. Grazing mortality continued to increase slightly into July resulting in a net growth rate of -0.07 d^{-1}.

Large and small size fractions of phytoplankton showed different trends in net growth rates. Net growth of large phytoplankton was near to zero during April, rising to 0.16 d^{-1} during May. No data were available for June however net growth decreases again during July to -0.03 d^{-1} (calculated from Table 2.4). Grazing mortality of small phytoplankton exceeded growth throughout the study with net growth remaining negative from April until July. NGR was lowest during April (-0.35 d^{-1}), rising to -0.08 d^{-1} during May. Net growth decreased again during June (-0.14 d^{-1}) and returned to -0.08 d^{-1} again during July.

Bacteria Mean net growth rates of bacteria were negative during April (-0.14 d^{-1}) indicating that grazing mortality exceeded growth at this time. Rates increased during May (0.06 d^{-1}) and continued to increase during June as growth was greater than grazing mortality (0.14 d^{-1}). July saw net growth of bacteria decrease again, resulting in a final mean net growth rate of 0.04 d^{-1}.

2.3.7 Ingestion

While net growth and grazing mortality give an indication of prey dynamics, prey-specific carbon ingestion values are dependent on the size of the standing stocks of each prey type and are more representative of carbon flow within the community. Calculated ingestion is an important parameter for understanding carbon cycling and export in the upper ocean. Ingestion was only calculated for those experiments showing significant grazing mortality rates, hence no data was presented for large phytoplankton which had both non-significant results and some positive regression slopes. Because there were no differences among regions of the Polynya, polynya-wide results were compiled and examined.

The ingestion of phytoplankton (> 0.7 μm, 0.18 - 59.9 μg C $L^{-1}day^{-1}$) was generally greater than ingestion of bacteria (0.45 - 39.9 μg C $L^{-1}day^{-1}$) throughout the study period (Fig 2.21), except for the very last experiment in July. During May, ingestion of phytoplankton was up to 4-fold higher than bacteria.

Percent Prey Stock Ingested

To provide the trophic level context for these ingestion rates, the percent of the total prey standing stock which was ingested was computed for phytoplankton (> 0.7 μm, and <5.0 μm) and bacteria (Figure 2.22). Again, the percent of prey stock ingested was only calculated for those experiments showing significant grazing mortality rates, hence no data is presented for large phytoplankton.

Total phytoplankton (i.e. > 0.7 μm) was ingested at a higher rate than bacteria, however the percent of prey standing stock that was consumed was the lowest of the three prey types shown (Figure 2.22). In fact, the percent of total phytoplankton prey stock consumed was less than 25% throughout the study period. Small phytoplankton were being vigorously grazed throughout the study with the percent of prey stock consumed remaining above 25% throughout the study. The percent of total prey standing stock ingested was highest for bacteria with percentages ranging from 11% to 250%. The two highest percentages were found at station 54 (May 26, JD = 146) and station 40 (July 17, JD = 198) which are both located in the eastern region of the Polynya.

2.4 Discussion

Biological Characteristics of the North Water Polynya

The North Water polynya is covered by seasonal ice for much of the winter months, until April when ice break-up begins. Due to the early opening of this Arctic region, the polynya is an important feeding ground for zooplankton, fish and other apex predators. As the ice cover recedes, and nutrients and irradiance are high, a phytoplankton bloom develops.

According to Klein et al. (2002) and Mei et al. (2002) annual phytoplankton production in this polynya is among the highest reported for polar seas. Mei et al. (2002) showed that large sized phytoplankton dominated the total phytoplankton biomass and accounted for 57% to 86% of the biomass during April and May respectively. In July, both total and large size phytoplankton decreased. In this case, maximum biomass of phytoplankton appeared to be limited by nutrient availability. Self shading may also be

responsible for the reduction in phytoplankton biomass. In addition, both higher salinity and higher temperatures appear to correlate with high chlorophyll concentrations which are found on the Greenland side of the polynya (Mei et al. 2002). These characteristics are in contrast to the cooler, less saline conditions found on the Canadian coast of the polynya.

Klein et al. (2002) also reported a distinct regional separation of phytoplankton biomass and primary production. Biomass increased first in the East and then spread North and West until the peak of the bloom (see Figure 2.7). Maximum values differed for each of the four regions and biomass tended to consist of larger size fractions in the North, East and West. The regional differences in biomass suggests that prey growth and grazing may also show regional differences leading to a spatial study of these dynamics.

Bacterial abundances in late spring and summer were equal to or greater than numbers from both temperate regions as well as other Arctic regions. Patterns in bacterial abundance followed ice and chlorophyll distribution (Rivkin et al. unpub. data). Results of bacterial abundance measurements also corresponded to grouping of stations into regions of North, East and West. The highest bacterial abundances were found following the decline of the phytoplankton bloom (Figure 2.2 and 2.8). This may be a response of the bacterial community to enhanced substrate availability, especially organic carbon, associated with the decline of phytoplankton (Bjornsen et al. 1989). Studies have reported a time lag of ten to fifteen days before the response of bacteria to the declining phytoplankton population (Lancelot and Billen 1984). It is these differences in biomass of phytoplankton and bacteria among regions within the polynya which were expected to

drive grazing mortality rates. Hence, regional differences in microzooplankton herbivory and bacterivory were expected.

Nutrient availability is important in controlling phytoplankton production. Tremblay et al. (2002) reported than nutrient levels were highest in the NOW polynya during April. These nutrients, particularly nitrate and phosphate, show a clear seasonal pattern as concentrations of these nutrients decreased as the bloom progressed. Areas of nutrient depletion (Appendix A) spread as the bloom progressed from the eastern Greenland side to the western, and northern Canadian side. Initially nutrients were high, then were utilised and depleted during the bloom. At this time, grazing activity can exceed growth thus further reducing the phytoplankton biomass and terminating the bloom.

Microzooplankton Herbivory and Bacterivory

Dilution Experiment overview: Explanation of outlier values

Grazing dynamics generally follow prey concentrations, since grazing is usually directly dependent upon the availability of prey. There are some exceptions whereby herbivory rates may be underestimated if there is an overabundance of prey available. In this case each predator would feed at a constant rate regardless of prey concentration violating the assumption of dilution experiments that grazing mortality rates depend on prey concentration. This response is known as saturated feeding (Landry and Hassett 1982). In contrast, if prey concentrations are very low then an opposite response would occur and microzooplankton may respond by decreasing their rate of feeding, i.e. they would exhibit a threshold feeding response (Landry and Hassett 1982). It is unlikely that

the microzooplankton in our study were displaying a threshold feeding response as ambient prey concentrations were fairly high in the case of both bacteria and phytoplankton, particularly once prey concentrations increased during May. The second basic assumption of dilution experiments (i.e. no nutrient limitation of prey) was avoided within sampling containers, by using water taken from the deep ocean which was nutrient rich (Tremblay et al. 2002).

The interpretation of dilution experiments may not always be straightforward and may not follow the methods of analysis as first presented by Landry and Hassett (1982). For example, if the relationship between growth rate and dilution is non-linear, an alternate interpretation of the dilution theory is necessary. In some instances, μ may increase disproportionately in dilutions with higher volumes of filtered seawater such that linear regression is an inappropriate method to assess grazing pressure. There are two possible interpretations (Elser and Frees 1995) where either the grazing pressure in the lower dilutions is underestimated, or the prey concentrations were high enough to saturate the grazing rates. Both circumstances could result in the underestimation of grazing pressure.

A positive regression slope may also result from nutrient recycling caused by grazing. One possible explanation is that in the higher dilutions of raw seawater, grazer abundance is higher hence there is increased grazing pressure which supplies limiting nutrients in the experimental bottle. This in turn results in a growth increase of the prey. Such positive grazing responses were excluded from analysis due to the fact that the cause of the response may be difficult or impossible to pinpoint.

An increase in grazer density in undiluted samples may result in a nonlinear response (Gallegos 1989; Landry et al. 1993; Landry et al. 1995). In such cases, the NGR computed using simple linear regression may be underestimated because of the implications of changes in grazer concentration (Gallegos 1989). Dolan et al. (2000) also found that changes in the grazer community may affect grazing rate estimates from the dilution approach. Since we do not have intact samples we are unable to assess this source of variability.

In the literature, experiments resulting in growth rates that were negative or not significantly different from zero often were not included in the analysis of the dilution experiments or were not discussed (Gifford et al. 1995; Gallegos et al. 1996; Rivkin et al. 1999). Negative growth rates violate the critical assumption that prey growth occurs during the incubation. Since negative prey growth has no physiological relevance, we have assigned it a value of zero (Rivkin et al. 1999) and suggest that the prey populations may actually be in a state of physiological decline (Neuer and Cowles 1994). This may have been due to the presence of contaminants in the filtered seawater or the physiological state of the prey.

Quite often, dilution experiments result in non-significant regression slopes (Landry et al. 1995; Kuipers and Witte 1999; Dolan et al. 2000). In the research presented here, when an experiment resulted in a non-significant regression slope, the mean AGR was determined to test whether it was a better measure of growth rate rather than using the y-intercept. In many cases the two values are similar and the cases where they are very different can be explained by high scatter or possible outliers which may be driving the

regression. Recognising the limitations of the approach, actual results obtained were discussed, in general terms, and polynya-wide arithmetic means were used to examine seasonal trends for each prey type.

Spatial and Seasonal Analysis

Spatial Analysis

Although chlorophyll *a* and bacteria standing stock biomass show similar spatial patterns in the NOW, the same patterns were not observed for growth, grazing mortality and ingestion. Using a general linear model analysis of variance, it was found that differences among regions were not significant for either growth and grazing mortality for all prey types examined. Moreover ingestion did not show significant differences among regions. There does appear to be general trends that are associated with changing seasons. This suggests that in this case, grazing dynamics are dominated by factors other than prey concentrations and there must be other reasons for the apparent uncoupling of grazing and prey concentrations. There may be top down control by mesozooplankton on the microzooplankton which is not measured by the experiments presented here.

Contour plots are presented to examine spatial patterns throughout the North Water Polynya. Ducklow et al. (1995) tested the effects of small data sets on gridding results in Surfer contouring plots by creating contour plots using a full data set and a reduced data set. They found that the two contour plots were very similar and the means of the residuals were not significantly different ($p>0.5$). By consecutively removing data points from an independent data set, we too determined that while detail is decreased upon removal of data points, the same general trends still remain.

While phytoplankton biomass first increased in the south eastern region of the polynya, grazing mortality on total phytoplankton was highest in the south western region of the polynya at this time. Booth et al. (2002) reported a bloom of large centric diatoms in the NOW, during this period. This bloom was followed by a bloom of smaller diatoms. While large phytoplankton dominated the total phytoplankton biomass, grazing mortality of the small size fraction (<5 μm) was the highest. This may be because the large diatoms are too large to be effectively grazed by the microzooplankton population. The dominance of large phytoplankton are typical of spring blooms at high latitude and generally results in low levels of recycling and high transfer to high trophic levels (Legendre and LeFevre 1989; Archer et al. 2000). Grazing of the small phytoplankton however, is a potential source of regenerated nutrients for the system. These smaller diatoms in the North Water are able to sustain their population up to three months, despite decreasing nutrient concentrations (Booth et al. 2002).

Bacterial biomass was highest in the Polynya in June, when bacterivory was at a minimum (Fig 2.8 and 2.17). This peak in biomass followed an increase in growth in May. Microzooplankton, in the Polynya, were still feeding herbivorously at this time. Increased grazing mortality on bacteria occurred once phytoplankton populations began to decline and bacteria were the more abundant prey source available to the microzooplankton.

Because grazing does not appear to be dependent on or correlated with prey biomass there must be other factors driving grazing dynamics or the prey biomass distributions. Changes in feeding may occur as a result of changing prey size, as the cells

themselves may be responding to changing or decreasing nutrient availability, or as a result of changes in the size distribution of the predators resulting in differential grazing. Grazing responses by microzooplankton may also be delayed resulting in an uncoupled response. Other studies have shown that appendicularians appear to play an important role as grazers of small phytoplankton (Acuna et al. 2002) and therefore may compete with microzooplankton for the small prey. Changing nutrient concentrations may also be impacting the prey distributions as may temperature differences between regions within the Polynya.

Seasonal Analysis

Microzooplankton mediated grazing mortality of phytoplankton did not always balance growth. In this case, biomass increases and a bloom occurs. Figure 2.20 shows the appearance of the bloom in May for phytoplankton where net growth was positive. During June and July, rates of herbivory (i.e. grazing mortality) appeared to be sufficient to control the bloom progression and net growth rate decreases. Nutrient depletion may also contribute to the eventual decrease in phytoplankton biomass.

Bacteria

The NGR for bacteria remains very low until May. During June, bacterial growth exceeds its grazing pressure in a type of delayed coupling whereby bacterial growth may be stimulated upon the decrease in growth rates of phytoplankton. This can occur when there is an increase in the availability of organic substrates in the water column, and there is more carbon originating from phytoplankton cells (Bjornsen et al. 1989).

Size dependence of grazing rates

Through size fractionation, we were able to estimate growth and grazing mortality of the total phytoplankton community, and the <5 μm and > 5 μm size fractions. Growth and grazing mortality were highest for the small phytoplankton rather than the large phytoplankton. This indicated that microzooplankton were preferably grazing the smaller size fraction of available phytoplankton prey despite a dominance of large phytoplankton making up the total phytoplankton biomass. The smaller prey were also growing at a much faster rate than the larger phytoplankton yet did not replace large phytoplankton as the dominant group. Results presented here indicate that they were being controlled by vigorous grazing.

Microzooplankton Carbon Ingestion

Small phytoplankton (< 0.5 μm) were ingested at a higher rate than bacteria and accounted for a large percentage (from 33% to 117%) of the phytoplankton standing stock which was grazed. Bacteria became more important as a food source for microzooplankton later in the season as indicated by the increasing ingestion rates through July, combined with decreasing ingestion of phytoplankton. This occurs as a result of changing prey fields (Table 2.1, Figure 2.2) and the microzooplankton are simply grazing the prey which is most readily available to them.

2.5 Summary

A major export pathway of microbial carbon from the upper ocean is through grazing. Here, as the season progressed, grazers switched from herbivory early in the season to bacterivory later in the season. This indicated a change in grazing by microzooplankton from herbivory during the phytoplankton bloom when phytoplankton prey were abundant and of high nutrient quality, to bacterivory as the phytoplankton bloom declined and cells became nutrient limited. Alternatively, the grazer community may have switched from protists which preferably grazed phytoplankton to those which grazed bacteria. The small phytoplankton were growing most quickly and were most vigorously grazed in the Polynya and the large phytoplankton were not as important as prey for protists. These large phytoplankton are grazed by other predators but the majority sinks from the water column ungrazed. Grazing did not appear to be sufficient to control the overall phytoplankton bloom so it is more likely that growth was controlled by nutrient supply in the North Water Polynya. The bloom decline appeared to be correlated with the decrease in available macro-nutrients.

Microzooplankton are an important link between small cells and larger metazoan grazers. Small organisms do not normally sink from the surface and as such have often not been considered in models of carbon flow in the ocean. Grazing by microzooplankton on small phytoplankton is an indirect path which channels this organic carbon to mesozooplankton. Quantifying the contribution of various carbon sources to microzooplankton ingestion is important in determining carbon transfer through the microbial food web, respiratory losses, and potential carbon export to higher food chains.

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Table 2.1 :Characteristics of stations sampled in the North Water Polynya, for determination of growth and grazing mortality rates during April through July, 1998. Regional designation can be seen in Figure 2.1 (N = North, E - East , W - West). Depth reported is the sampling depth. Bacteria and chlorophyll values reported for each station are integrated through the upper 100m.

Date 1998	Julian Day (JD)	Station Number	Latitude (°N)	Longitude (°W)	Region	Depth (m)	Temp (°C)	Int. Bact. Abundance (10^{11}cells m^{-2})	Int. Total Chl (mg m^{-2})
April 8	98	2	78.36	74.71	N	24	-1.5	na	na
April 9	99	2	78.36	74.71	N	24	-1.5	na	na
April 13	103	2	78.36	74.71	N	75	-1.2	81	6
April 17	107	22	77.35	76.58	W	56	-1.8	211	6
April 19	109	35	77.00	75.03	W	53	-1.8	92	12
April 21	111	44	76.38	77.41	W	53	-1.7	76	5
April 22	112	49	76.28	74.75	W	26	-0.7	99	18
April 27	117	27	77.35	73.80	E	23	na	132	83
May 2	122	40	77.00	72.42	E	20	-1	na	na
May 9	129	2	78.36	74.71	N	25	-1.4	110	55
May 13	133	14	77.83	75.55	N	40	-0.8	377	70
May 15	135	18	77.83	73.15	N	40	-0.7	217	578
May 16	136	27	77.35	73.80	E	40	-0.5	174	63
May 18	138	22	77.35	76.58	W	90	-0.8	121	30
May 25	145	40	77.00	72.42	E	30	-0.2	118	210
May 26	146	54	76.27	71.91	E	15	-0.5	249	591
May 28	150	44	76.38	77.41	W	35	-0.4	677	441
June 5	156	49	76.28	74.75	W	15	-1.4	750	712
June 7	158	2	78.36	74.71	N	37	na	na	na
June 10	161	14	77.83	75.55	N	15	-1.5	495	331
June 11	162	18	77.83	73.15	N	10	-1.1	703	724

Table 2.1 continued

Date 1998	Julian Day	Station Number	Latitude (°N)	Longitude (°W)	Region	Depth (m)	Temp (°C)	Int. Bact. Abundance (10^{11}cells m^{-2})	Int. Total Chl (mg m^{-2})
June 12	163	27	77.35	73.80	E	10	-1.1	271	532
June 14	165	22	77.35	76.58	W	16	-1.1	694	278
June 19	170	40	77.00	72.42	E	16	-0.5	779	480
June 21	172	54	76.27	71.91	E	35	-0.4	806	113
June 24	175	44	76.38	77.41	W	22	0.4	na	na
July 6	187	54	76.27	71.91	E	22	-0.8	na	na
July 9	190	44	76.38	77.41	W	21	-1	494	146
July 12	193	2	78.36	74.71	N	9	-0.7	336	181
July 17	198	40	77.00	72.42	E	14	-0.4	886	87.5

Note : na = data not available for these stations. Chlorophyll data courtesy of Dr. B. Klein
Int. Bact. Abundance = Integrated Bacterial Abundances, integrated to 100m.
Int Total Chl = Integrated Chlorophyll Biomass , integrated to 100,

Table 2.2: Flagellate abundances at stations where grazing experiments were conducted in the North Water Polynya from April through July, 1998. Regions are defined in Figure 2.1 Depth reported is the sampling depth.

Date	Station Number	Latitude (°N)	Longitude (°W)	Region	Depth (m)	Flagellate Abundance (cells L^{-1})
April 8	2	78.36	74.71	N	24	na
April 9	2	78.36	74.71	W	24	na
April 13	2	78.36	74.71	N	75	94 400
April 17	22	77.35	76.58	W	56	2 980
April 19	35	77.00	75.03	W	53	na
April 21	44	76.38	77.41	W	53	1 440
April 22	49	76.28	74.75	W	26	na
April 27	27	77.35	73.80	E	23	142 000
May 2	40	77.00	72.42	E	20	na
May 9	2	78.36	74.71	N	25	80 900
May 13	14	77.83	75.55	N	40	97 100
May 15	18	77.83	73.15	N	40	124 000
May 16	27	77.35	73.80	E	40	91 100
May 18	22	77.35	76.58	W	90	na
May 25	40	77.00	72.42	E	30	301 000
May 26	54	76.27	71.91	E	15	419 000
May 28	44	76.38	77.41	W	35	na
June 5	49	76.28	74.75	W	15	453 000
June 7	2	78.36	74.71	N	37	na
June 10	14	77.83	75.55	N	15	499 000
June 11	18	77.83	73.15	N	10	na
June 12	27	77.35	73.80	E	10	524 000
June 14	22	77.35	76.58	W	16	190 000
June 19	40	77.00	72.42	E	16	447 000
June 21	54	76.27	71.91	E	35	64 900
June 24	44	76.38	77.41	W	22	na
July 6	54	76.27	71.91	E	22	na
July 9	44	76.38	77.41	W	21	na
July 12	2	78.36	74.71	N	9	na
July 17	40	77.00	72.42	E	14	na

Note : na= data not available for these stations. Data on flagellates courtesy of Dr. C.Lovejoy.

Table 2.3 : Rates of growth (μ, d^{-1}) and grazing mortality (g, d^{-1}) for total phytoplankton (> 0.7 μm), measured as extracted chlorophyll *a*, in the North Water Polynya during 1998. SE is the standard error of the mean, μ or g. N is the number of observations per experiment. Net growth rate (NGR) is the difference between positive growth and grazing mortality measurements (μ-g).

Date 1998	Station	r^2	μ (d^{-1})	SE	g (d^{-1})	SE	N	NGR
April 8	2	0.35	-0.29 **	0.11	-0.27	0.15	8	nc
April 9	2	0.26	0.05	0.04	0.06	0.05	6	-0.01
April 13	2	0.01	0.00	0.06	-0.24	0.1	7	nc
April 17	22	0.00	0.05	0.03	-0.01	0.05	6	nc
April 19	35	0.37	0.54 *	0.22	0.56	0.32	7	-0.02
April 21	44	0.03	0.02	0.23	-0.15	0.34	8	nc
April 22	49	0.41	0.40 **	0.16	0.45	0.25	7	-0.06
April 27	27	0.10	0.10	0.08	-0.09	0.11	8	nc
May 2	40	0.20	0.15 ***	0.01	-0.02	0.01	7	nc
May 9	2	0.39	0.34 ***	0.06	0.18	0.1	7	0.16
May 13	14	0.68	0.32 ***	0.03	0.17 **	0.05	7	0.15
May 15	18	0.65	0.46 ***	0.02	0.08 **	0.03	7	0.37
May 16	27	0.01	0.29 **	0.09	0.04	0.13	8	0.26
May 18	22	0.13	0.15	0.11	0.13	0.15	7	0.02
May 25	40	0.08	0.32 ***	0.06	0.06	0.09	8	0.25
May 26	54	0.69	-0.10	0.03	-0.11	0.04	6	nc
May 28	44	0.21	0.11	0.15	-0.27	0.21	8	nc
June 5	49	0.36	-0.11 *	0.04	-0.12	0.07	8	nc
June 7	2	0.03	0.14 *	0.07	-0.05	0.11	8	nc
June 10	14	0.09	0.06	0.04	0.04	0.05	8	0.02
June 11	18	0.12	0.01	0.08	0.14	0.12	8	-0.14
June 12	27	0.23	0.10 **	0.04	0.08	0.06	8	0.02
June 14	22	0.00	0.16 ***	-0.03	-0.01	0.04	8	nc
June 19	40	0.56	0.14 **	0.03	0.12 *	0.05	6	0.02
June 21	54	0.08	0.00	0.06	0.07	0.1	8	-0.07
June 24	44	0.74	0.14 ***	0.02	-0.09	0.03	7	nc
July 6	54	0.77	0.06 **	0.02	0.13 ***	0.03	8	-0.07
July 9	44	0.02	-0.24	0.28	0.16	0.5	8	nc
July 12	2	0.02	0.00	0.16	0.08	0.24	8	-0.08
July 17	40	0.95	0.25 ***	0.02	0.23 ***	0.03	6	0.02

Note: nc = NGR not computed
Reported significance levels are designated as : * $\alpha < 0.1$, ** $\alpha < 0.05$, *** $\alpha < 0.01$.
g reported in the table is the regression slope multiplied by -1. Statistics reported for g correspond to slope measurements. Negative growth values assumed to be zero for statistical analyses.

Table 2.4 : Rates of growth (μ, d^{-1}) and grazing mortality (g, d^{-1}) rates of large phytoplankton (> 5µm), measured as extracted chlorophyll *a*, in the North Water Polynya during 1998. SE is the standard error of the mean, μ or g. N is the number of observations per experiment. Net growth rate (NGR) is the difference between positive growth and grazing mortality measurements (μ-g).

Date 1998	Station	r^2	μ (d^{-1})	SE	g (d^{-1})	SE	N	NGR (d^{-1})
April 8	2	0.01	-0.29	0.23	-0.08	0.35	7	nc
April 9	2	0.04	0.06	0.23	0.11	0.28	5	-0.04
April 13	2	0.07	0.00	0.11	0.14	0.20	8	-0.13
April 17	22	0.03	0.01	0.19	-0.13	0.29	8	nc
April 19	35	0.44	0.41 *	0.19	0.45	0.25	6	-0.04
April 21	44	0.00	0.28	0.19	-0.03	0.31	7	nc
April 22	49	0.34	0.51 **	0.19	0.46	0.29	7	0.05
April 27	27	0.20	0.40 **	0.15	0.22	0.20	7	0.18
May 2	40	0.05	0.06	0.09	-0.07	0.13	7	nc
May 9	2	0.67	0.22 ***	0.01	-0.09***	0.03	8	nc
May 13	14	0.34	1.14 **	0.43	1.26	0.72	8	-0.12
May 15	18	0.00	0.31 ***	0.08	0.01	0.12	8	0.30
May 16	27	0.00	0.35 ***	0.04	0.00	0.05	8	0.35
May 18	22	0.27	0.10 *	0.05	0.10	0.07	8	-0.01
May 25	40	0.76	0.17 ***	0.03	-0.19 ***	0.04	8	nc
May 26	54	0.09	-0.17	0.10	-0.10	0.14	7	nc
May 28	44	0.03	0.35 ***	0.09	0.06	0.14	8	0.29
June 5	49	0.30	-0.1 *	0.05	-0.13	0.08	8	nc
June 7	2	0.03	0.15	0.15	-0.09	0.22	8	nc
June 10	14	0.33	0.03	0.03	-0.07	0.05	7	nc
June 11	18	0.00	0.16 **	0.06	-0.01	0.08	7	nc
June 12	27	0.06	0.01	0.08	-0.08	0.12	8	nc
June 14	22	0.09	0.19 ***	0.03	-0.03	0.04	8	nc
June 19	40	0.74	-0.02	0.02	0.11 ***	0.03	8	-0.11
June 21	54	0.25	-0.14 **	0.05	-0.10	0.07	8	nc
June 24	44	0.75	0.08 **	0.02	-0.12 **	0.03	6	nc
July 6	54	0.14	-0.59 *	0.29	-0.41	0.42	8	nc
July 9	44	0.61	-0.56 ***	0.13	-0.70 **	0.13	8	nc
July 12	2	0.24	0.00	0.07	0.15	0.11	8	-0.15
July 17	40	0.69	0.22	0.03	0.14	0.05	6	0.09

Note: nc = NGR not computed
Reported significance levels are designated as : * $\alpha < 0.1$, ** $\alpha < 0.05$, *** $\alpha < 0.01$.
g reported in the table is the regression slope multiplied by -1. Statistics reported for g correspond to slope measurements. Negative growth values assumed to be zero for statistical analyses.

Table 2.5 : Rates of growth (μ, d^{-1}) and grazing mortality (g, d^{-1}) rates of small phytoplankton (< 5 μm), measured as extracted chlorophyll *a*, in the North Water Polynya during 1998. SE is the standard error of the mean, μ or g. N is the number of observations per experiment. Net growth rate (NGR) is the difference between positive growth and grazing mortality measurements (μ-g).

Date 1998	Station	r^2	μ (d^{-1})	SE	g (d^{-1})	SE	N	NGR (d^{-1})
April 8	2	0.01	-0.08	0.48	-0.08	0.82	4	nc
April 9	2	0.20	0.16	0.20	0.15	0.23	6	0.01
April 13	2	0.04	0.24	0.21	0.23	0.44	7	0.01
April 17	22	0.01	0.06	0.15	0.07	0.24	8	-0.01
April 19	35	0.25	0.33	0.30	0.38	0.38	7	-0.05
April 21	44	0.33	1.13	1.20	2.16	2.18	4	-1.03
April 22	49	0.28	0.48	0.49	1.50	1.40	5	-1.02
April 27	27	0.08	-0.41	0.56	-0.56	0.87	7	nc
May 2	40	0.03	-0.17	0.17	-0.10	0.28	6	nc
May 9	2	0.16	-0.60	0.59	-0.71	0.95	5	nc
May 13	14	0.53	0.48 ***	0.11	0.50 *	0.21	7	-0.02
May 15	18	0.11	0.65 ***	0.13	0.18	0.23	7	0.47
May 16	27	0.07	0.28	0.38	0.38	0.56	8	-0.10
May 18	22	0.46	0.52	0.28	1.03 *	0.46	7	-0.50
May 25	40	0.52	0.67 **	0.23	0.93 *	0.39	8	-0.26
May 26	54	0.06	-0.04	0.08	-0.06	0.11	7	nc
May 28	44	0.15	-0.14	0.32	-0.56	0.54	8	nc
June 5	49	0.20	-0.11	0.07	0.12	0.10	8	-0.12
June 7	2	0.90	1.00 ***	0.14	1.42***	0.24	6	-0.42
June 10	14	0.24	0.12	0.08	0.18	0.13	8	-0.06
June 11	18	0.02	-0.25	0.29	0.17	0.45	8	-0.17
June 12	27	0.54	0.29 **	0.09	0.35 **	0.13	8	-0.06
June 14	22	0.09	0.08	0.04	-0.06	0.08	8	nc
June 19	40	0.51	0.37 **	0.09	0.31 *	0.15	6	0.06
June 21	54	0.19	0.07	0.16	0.30	0.28	8	-0.23
June 24	44	0.05	.34 **	0.10	-0.07	0.15	7	nc
July 6	54	0.69	0.31 ***	0.08	0.43 **	0.12	8	-0.12
July 9	44	0.00	-0.23	0.36	-0.10	0.68	8	nc
July 12	2	0.17	-0.48	0.44	-0.60	0.60	7	nc
July 17	40	0.94	0.26 ***	0.02	0.30***	0.03	6	-0.04

Note: nc = NGR not computed
Reported significance levels are designated as : * $\alpha < 0.1$, ** $\alpha < 0.05$, *** $\alpha < 0.01$.
g reported in the table is the regression slope multiplied by -1. Statistics reported for g correspond to slope measurements. Negative growth values assumed to be zero for statistical analyses.

Table 2.6 : Rates of growth (μ) and grazing mortality (g) for bacteria measured in the North Water Polynya during 1998. SE is the standard error of the mean, μ or g. N is the number of observations per experiment. Net growth rate (NGR) is the difference between positive growth and grazing mortality measurements (μ-g).

Date 1998	Station	r^2	μ (d^{-1})	SE	g (d^{-1})	SE	N	NGR
April 8	2	0.99	-0.26 ***	0.02	-0.72***	0.04	5	nc
April 9	2	0.36	-0.88 *	0.43	-1.13	0.62	8	nc
April 13	2	0.56	0.22	0.22	0.96	0.49	5	-0.74
April 17	22	0.00	0.10	0.15	0.02	0.25	7	0.08
April 19	35	0.02	0.58	1.03	0.32	1.29	5	0.25
April 22	49	0.50	0.11	0.07	0.28**	0.12	8	-0.17
April 27	27	0.13	-0.05	0.17	-0.22	0.23	8	nc
May 2	40	0.48	-0.26	0.29	-0.89	0.54	5	nc
May 9	2	0.18	0.18	0.20	0.38	0.37	7	-0.21
May 13	14	0.08	0.11	0.22	0.27	0.36	8	-0.16
May 15	18	0.03	0.21 *	0.09	-0.05	0.13	7	nc
May 16	27	0.00	0.30	0.19	0.04	0.30	7	0.26
May 18	22	0.70	0.36 **	0.12	0.61 **	0.18	7	-0.25
May 25	40	0.00	0.05	0.21	-0.04	0.32	8	nc
May 26	54	0.87	1.21 ***	0.11	0.91***	0.16	7	0.30
May 28	44	0.00	0.47**	0.16	0.02	0.24	8	0.44
June 5	49	0.39	0.47 **	0.14	0.36	0.20	7	0.12
June 7	2	0.02	-0.02	0.27	-0.15	0.40	8	nc
June 10	14	0.13	0.19	0.13	0.20	0.21	8	-0.01
June 11	18	0.05	0.26	0.20	0.17	0.30	8	0.10
June 12	27	0.24	0.41 **	0.13	0.19	0.17	6	0.22
June 14	22	0.50	0.16 ***	0.03	0.13 **	0.05	8	0.03
June 19	40	0.23	0.54 ***	0.09	0.16	0.15	6	0.38
June 21	54	0.00	0.20	0.13	-0.02	0.17	7	nc
June 24	44	0.76	-0.15	0.10	-0.67 ***	0.15	8	nc
July 6	54	0.02	0.20 *	0.10	0.05	0.14	7	0.15
July 9	44	0.48	0.01	0.03	0.12 *	0.05	8	-0.11
July 12	2	0.70	0.54 ***	0.06	0.35 ***	0.09	8	0.19
July 17	40	0.75	1.23 ***	0.21	1.32**	0.38	6	-0.09

Note: nc = NGR not computed
Reported significance levels are designated as : * $\alpha < 0.1$, ** $\alpha < 0.05$, *** $\alpha < 0.01$.
g reported in the table is the regression slope multiplied by -1. Statistics reported for g correspond to slope measurements. Negative growth values assumed to be zero for statistical analyses.

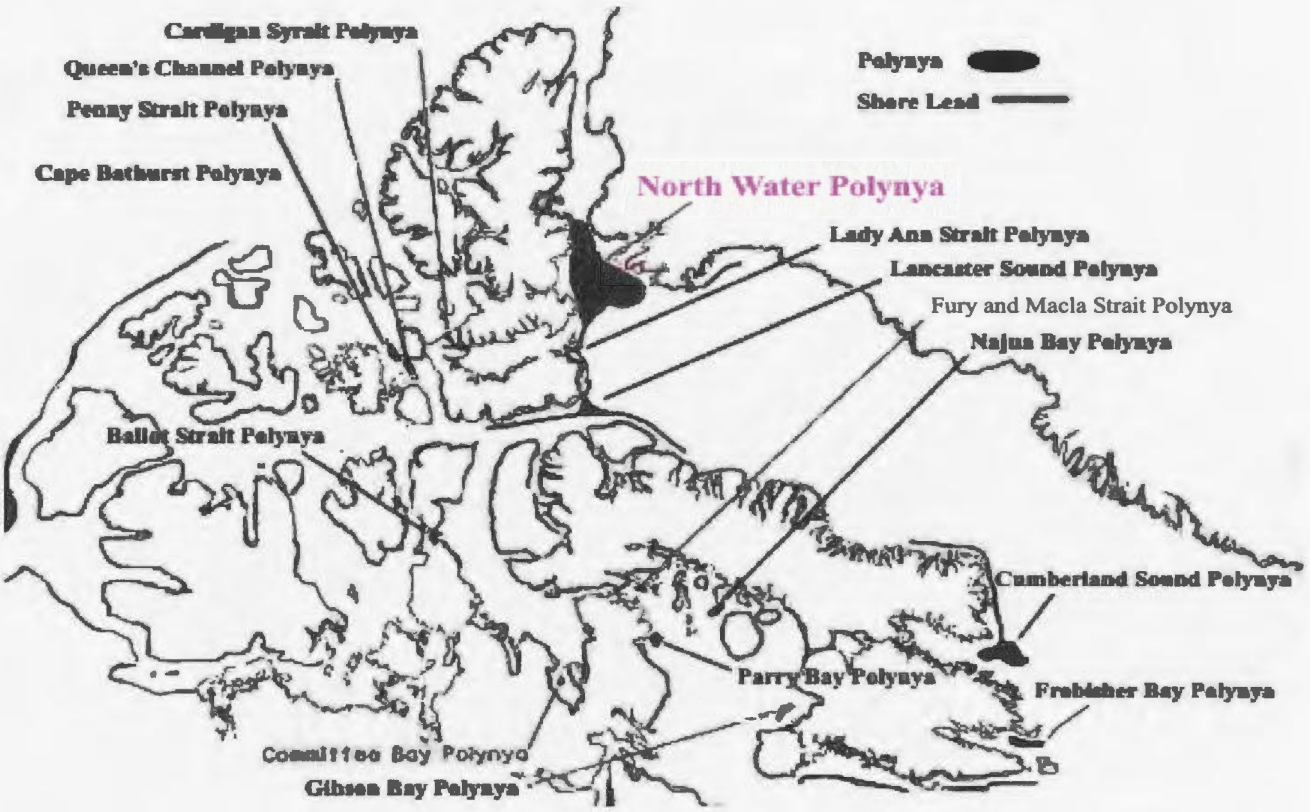

Figure 1.1 Geographical location of the North Water Polynya relative to other polynyas in the Arctic.

Map source: http://www.fsg.ulaval.ca/giroq/now/

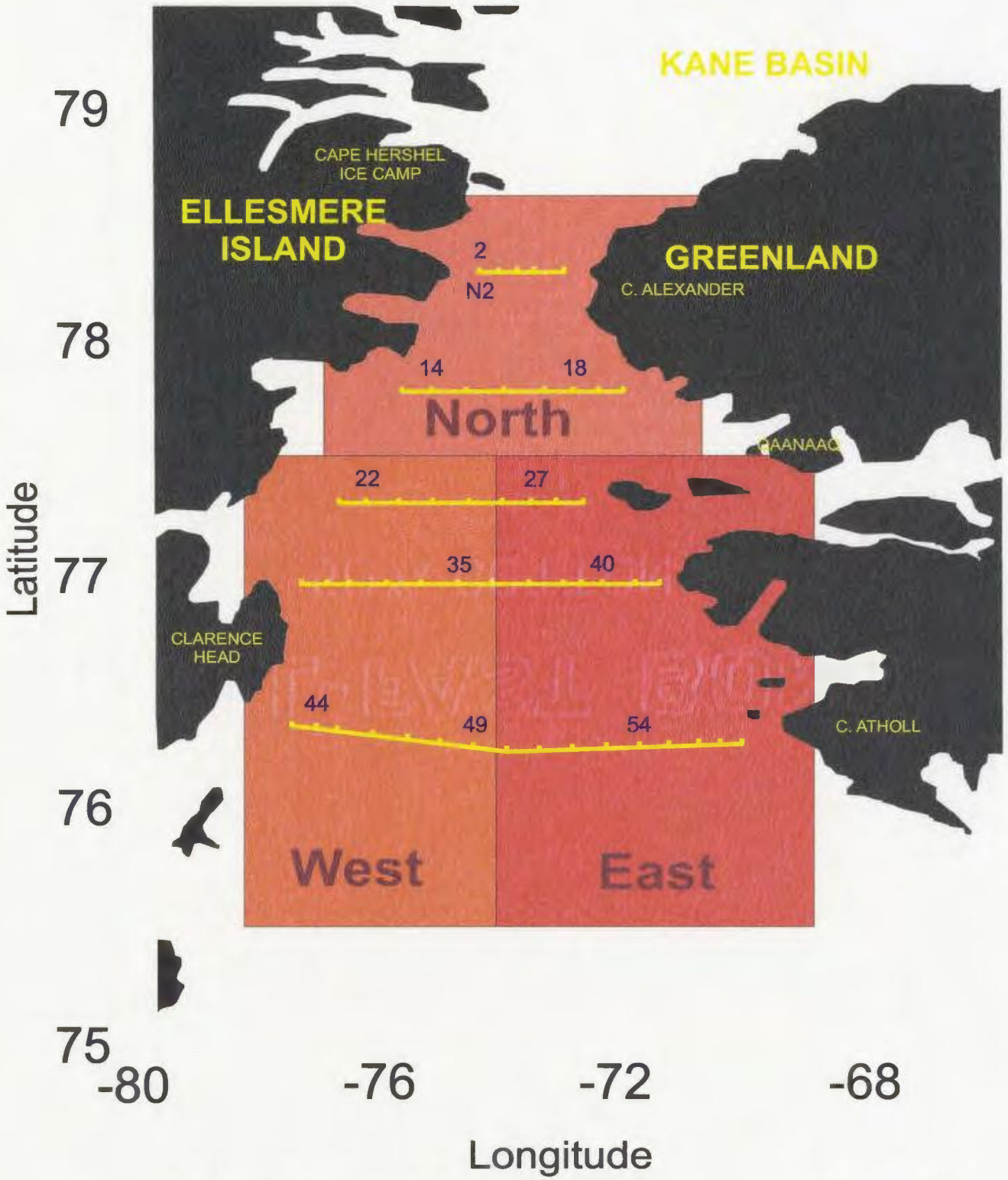

Figure 2.1 Map of the North Water Polynya showing transects with stations sampled for microzooplankton grazing experiments.

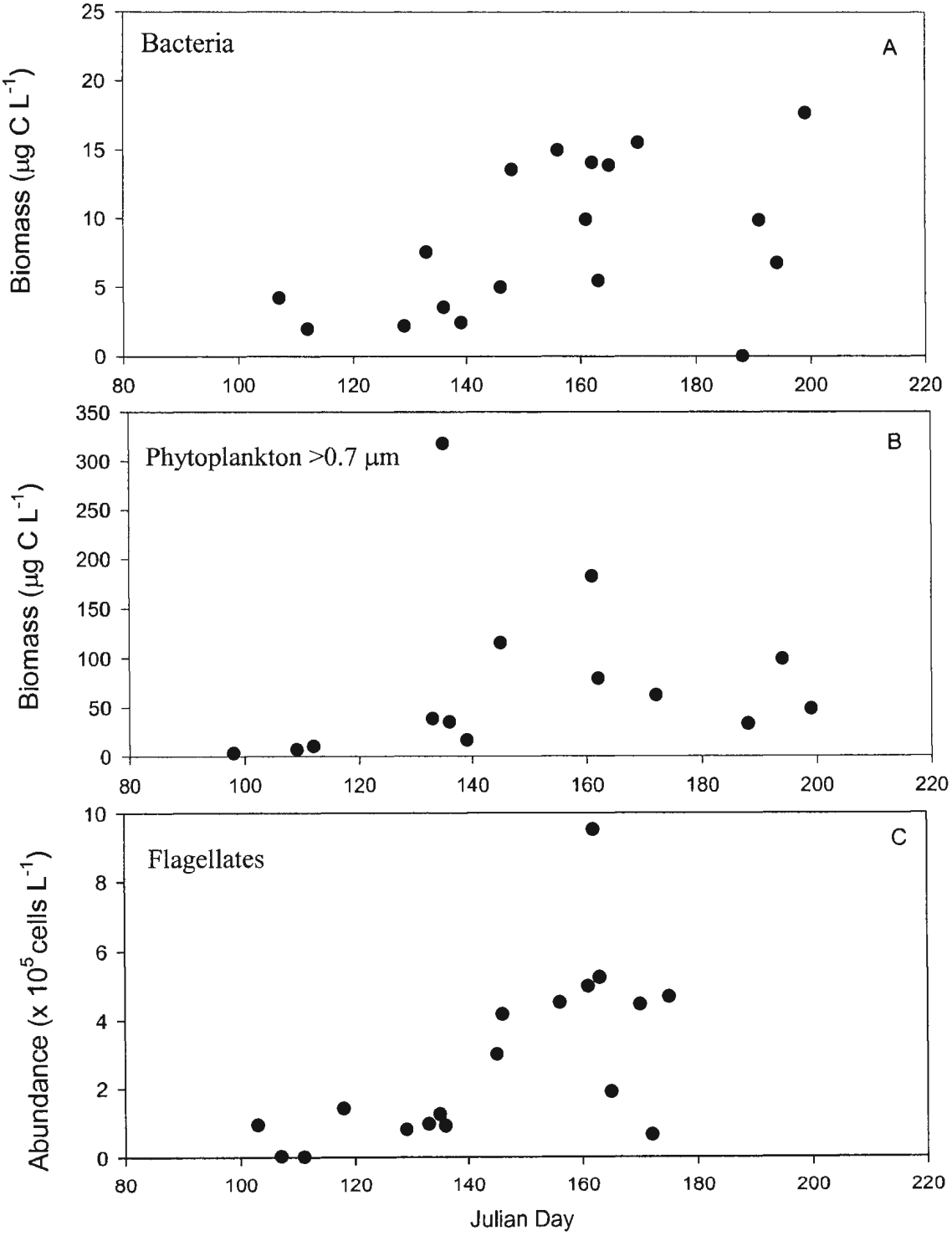

Figure 2.2 Bacteria (A) and total phytoplankton (>0.7µm) (B) biomass, and heterotrophic flagellate (C) abundance in the North Water Polynya at stations where dilution experiments were conducted from April through July,1998.

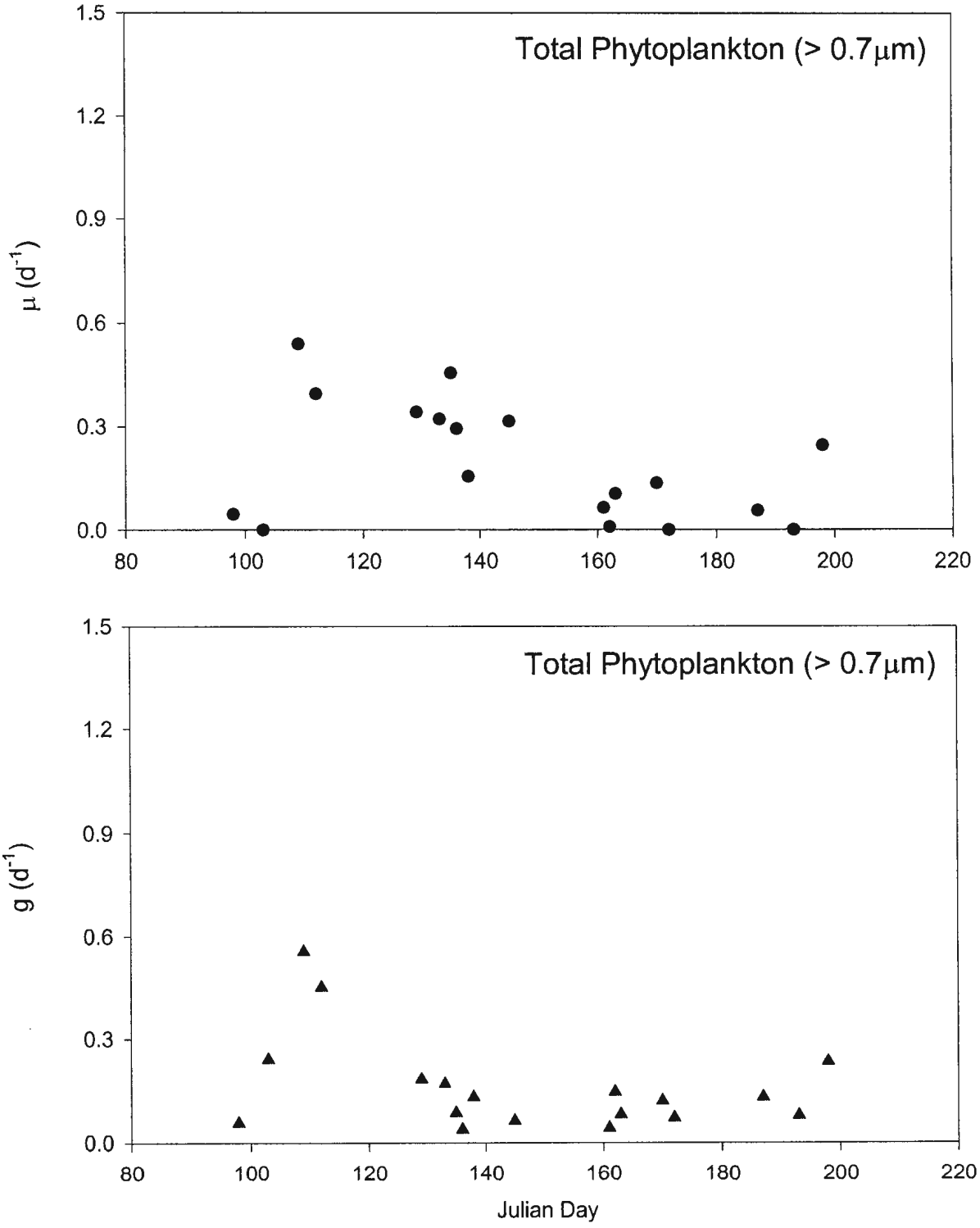

Figure 2.3 Phytoplankton (> 0.7 μm) growth (μ) and grazing mortality (g) rates measured in the North Water Polynya from April 8 through July 17, 1998.

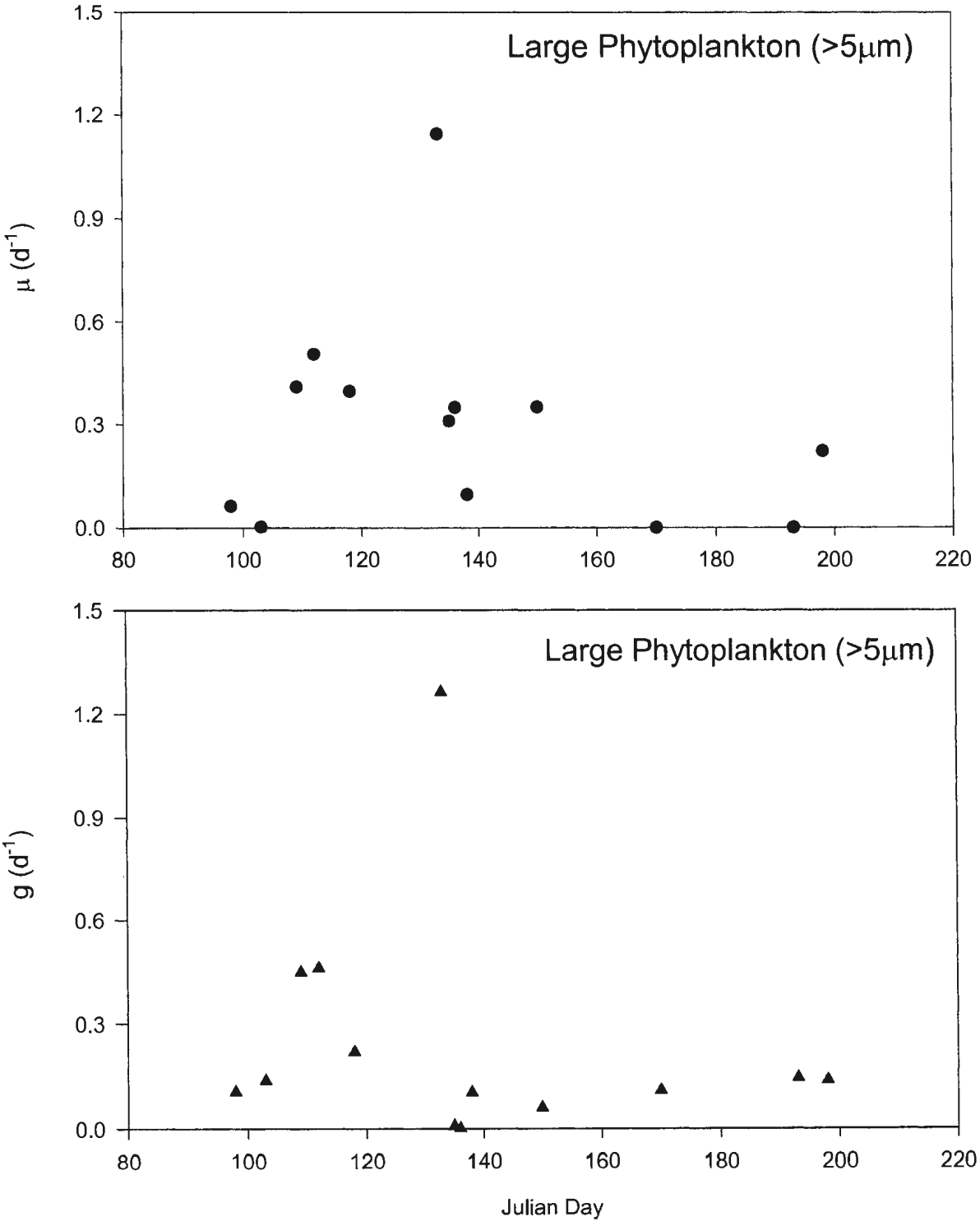

Figure 2.4 Large phytoplankton (>5 μm) growth (μ) and grazing mortality (g) rates measured in the North Water Polynya from April 8 through July 17, 1998.

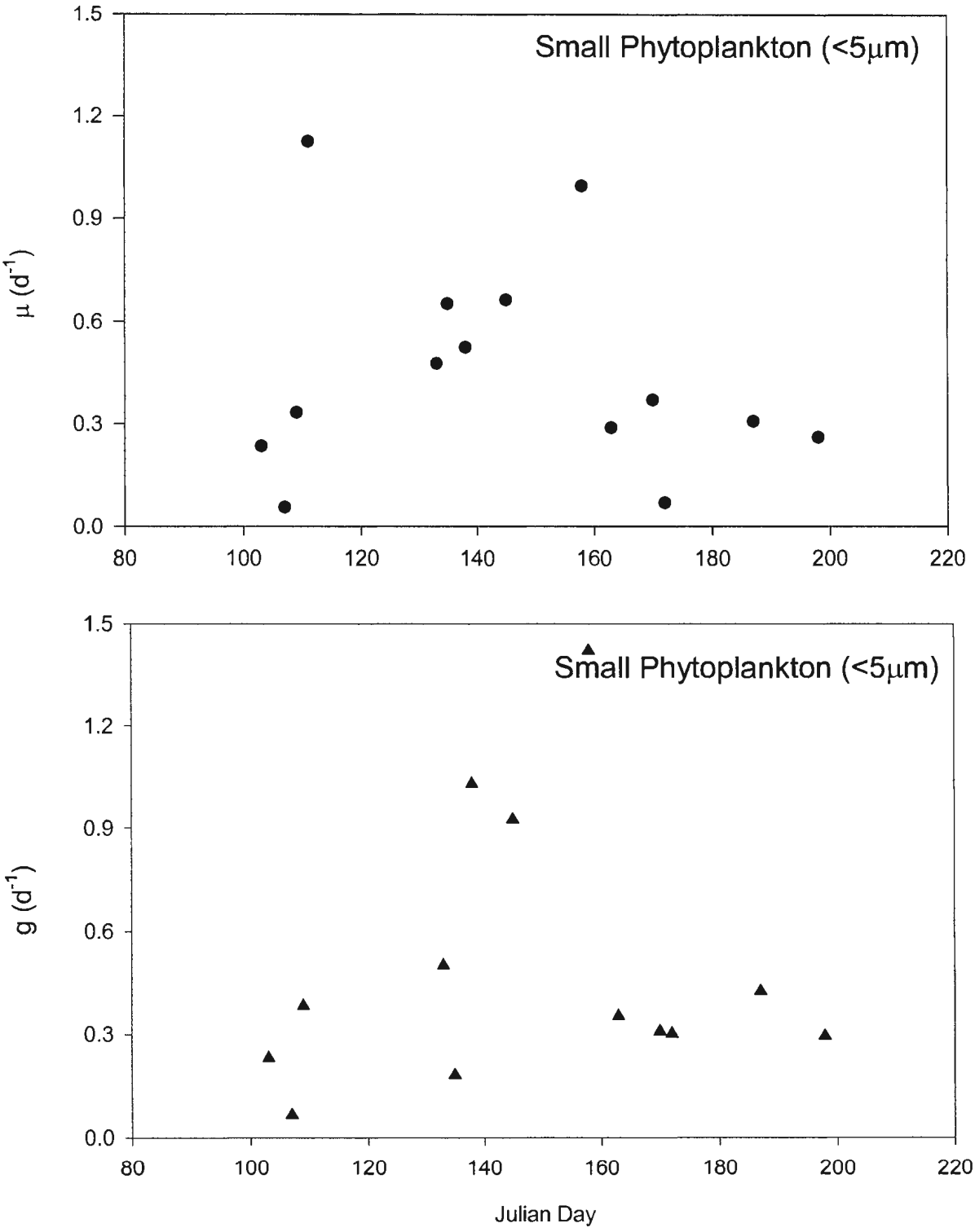

Figure 2.5 Small Phytoplankton (<5 μm) growth (μ) and grazing mortality (g) rates measured in the North Water Polynya from April 8 through July 17, 1998.

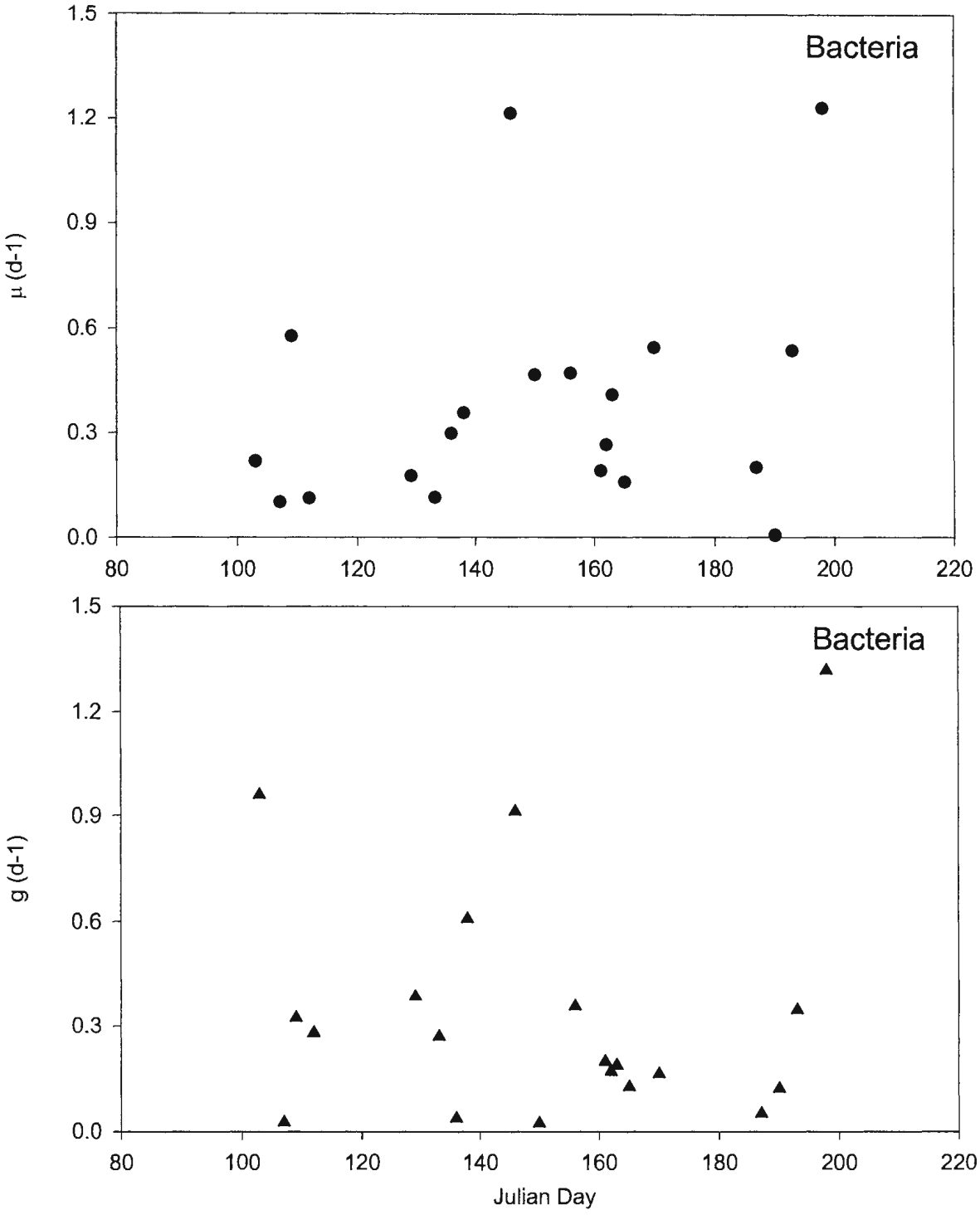

Figure 2.6 Bacterial growth (μ) and grazing mortality (g) rates measured in the North Water Polynya from April 8 through July 17, 1998.

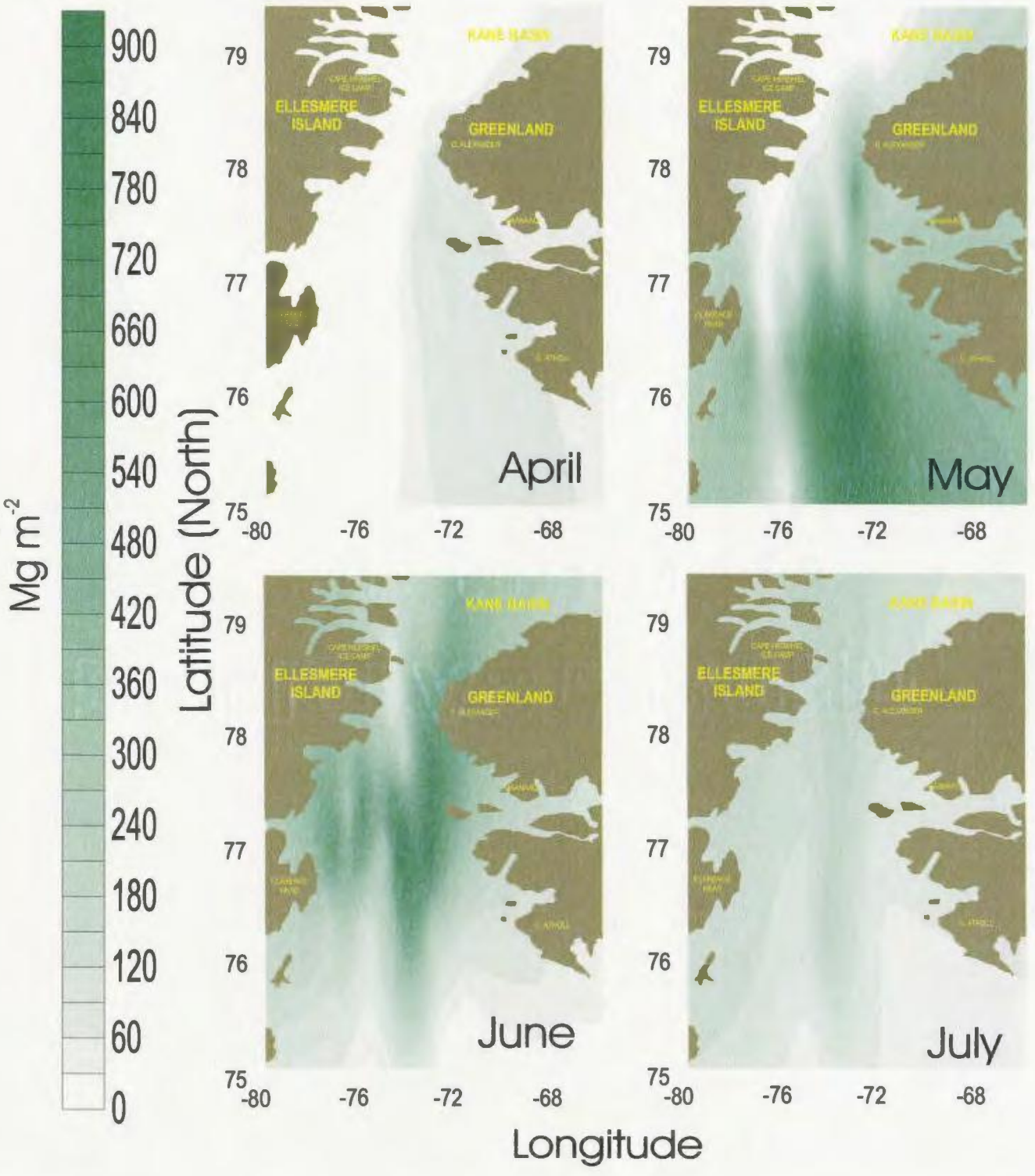

Fig. 2.7 Contour plots of spatial distributions of phytoplankton (>0.7μm) biomass, integrated to 100 m, during April, May, June and July.

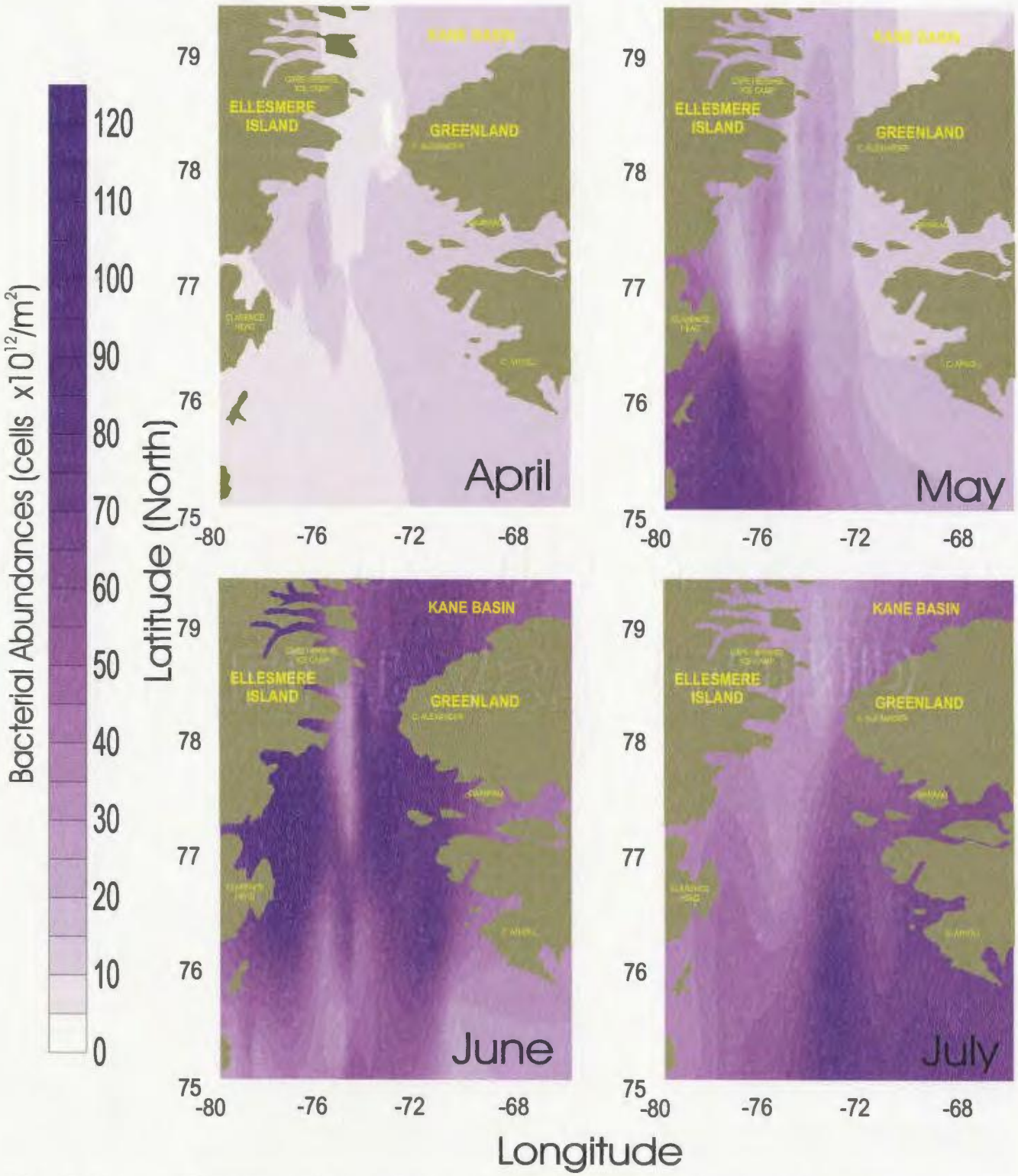

Fig. 2.8 Contour plots of spatial distributions of bacterial abundances, integrated to 100m, in the North Water Polynya during April, May, June and July, 1998.

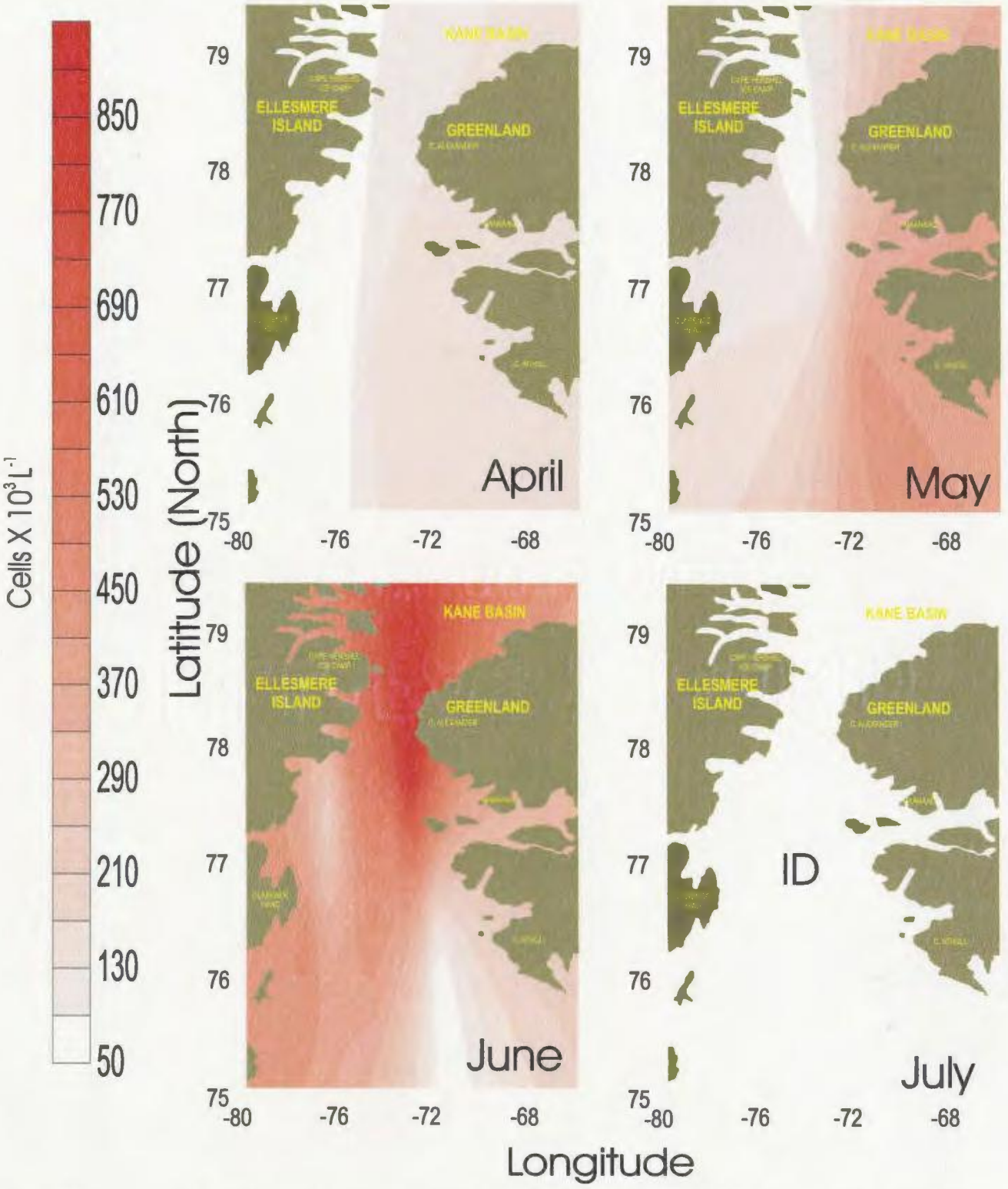

Fig. 2.9 Contour plots of spatial distributions of flagellate abundance in the North Water Polynya in April, May, June and July 1998

Note: "ID" means insufficient data points to create contour plots

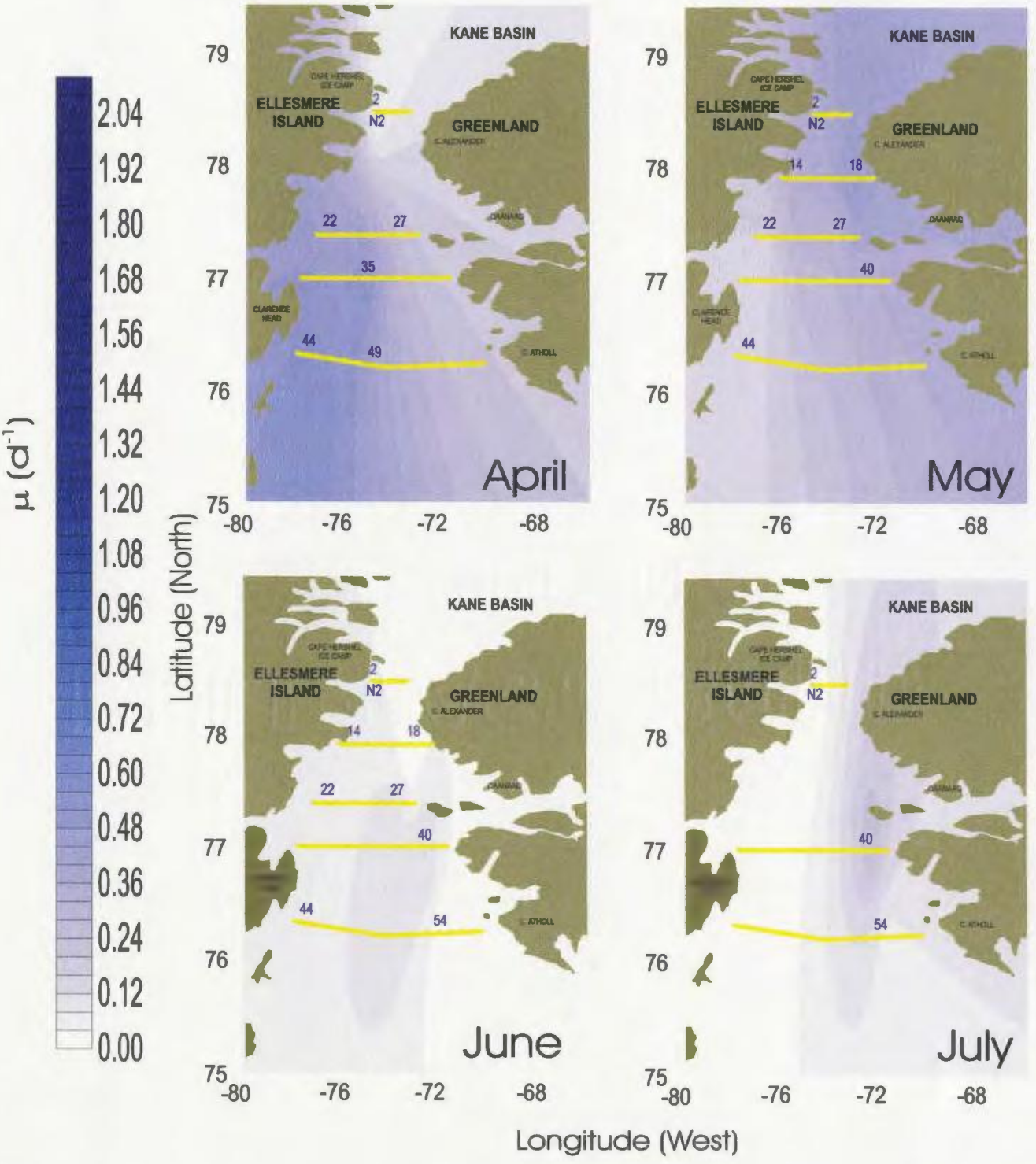

Fig. 2.10 Spatial patterns of growth rates (μ) of phytoplankton (> 0.7 μm) throughout the North Water Polynya during April, May, June and July, 1998.

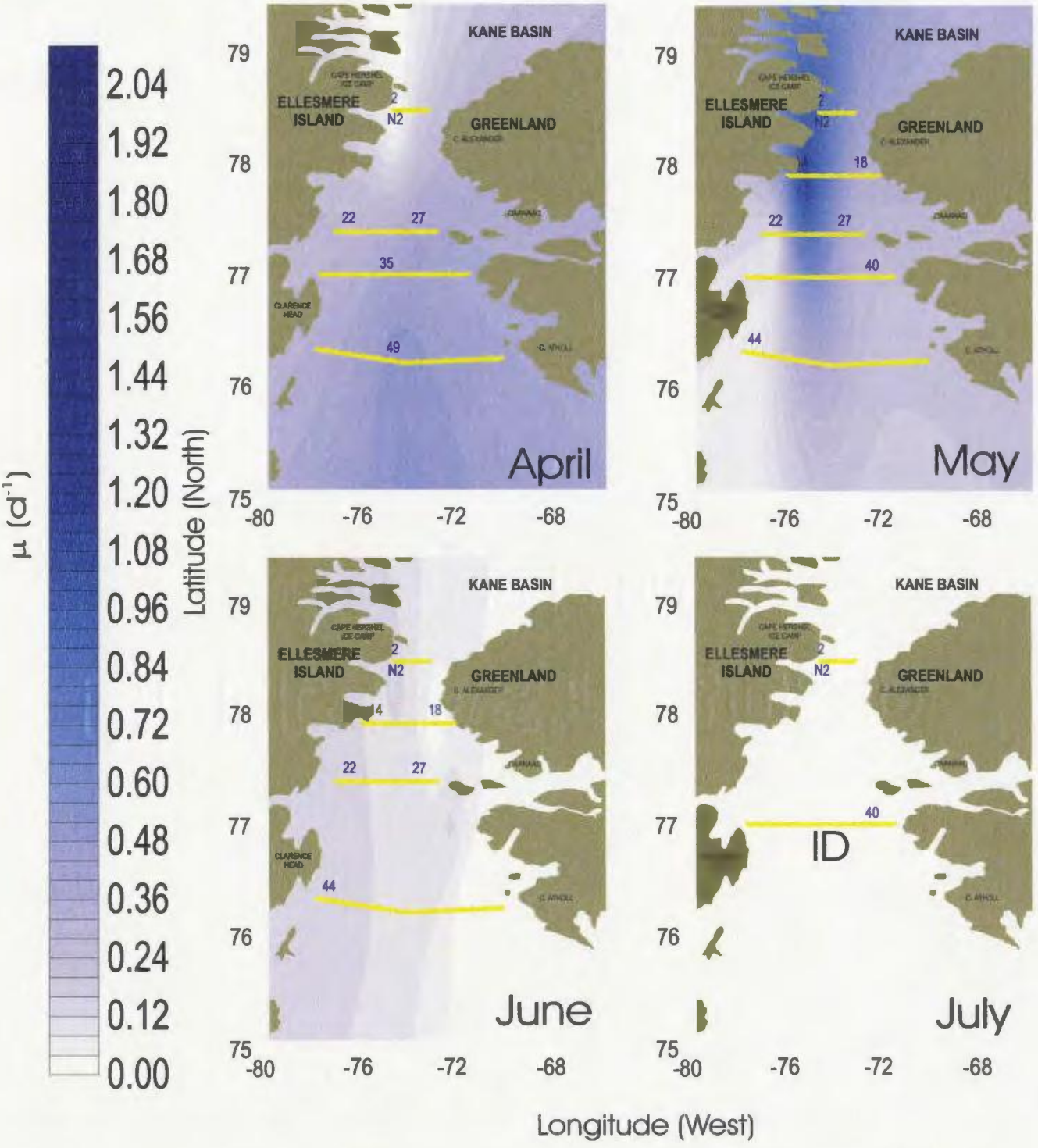

Fig. 2.11 Spatial patterns in growth (μ) rates of large phytoplankton (>5 μm) throughout the North Water Polynya during April, May, June and July, 1998.
Note: ID indicates insufficient data to create contour map

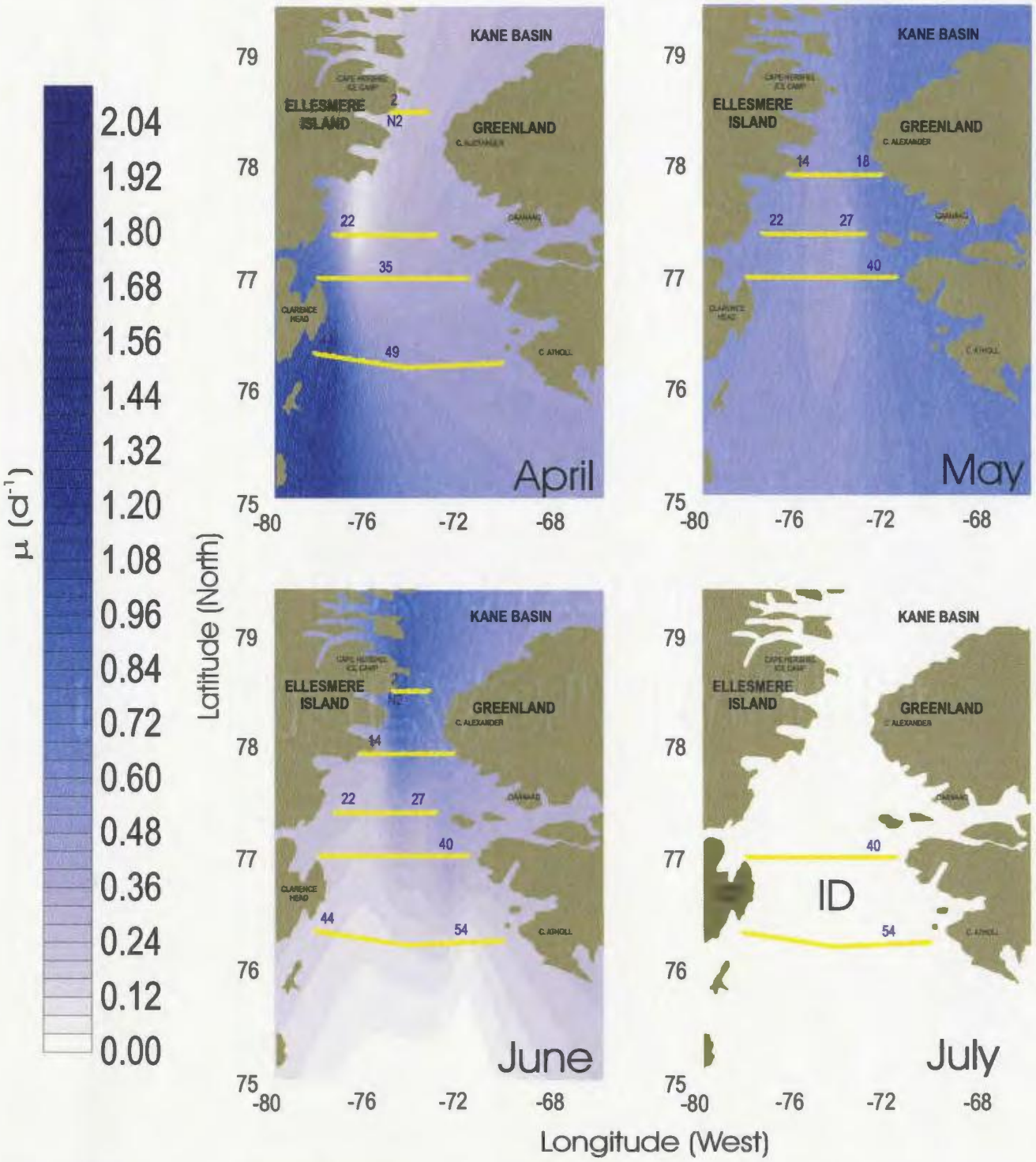

Fig.2.12 Spatial patterns in growth rates of small phytoplankton (<5 μm) throughout the North Water Polynya during April, May, June and July, 1998.

Note: ID indicates insufficient data to create contour map

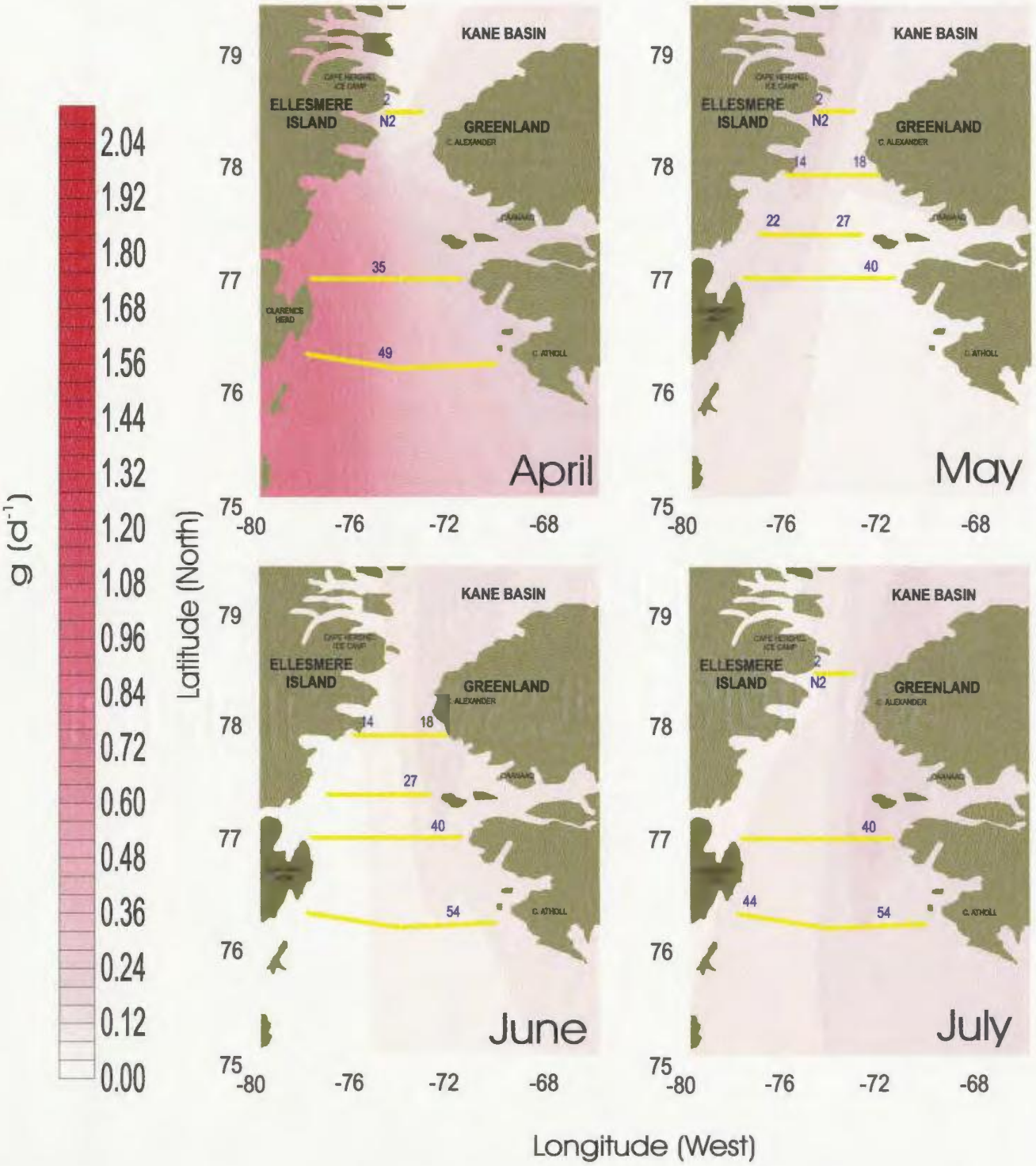

Fig.2.13 Spatial trends in grazing mortality (g) of phytoplankton (>0.7 μm) throughout the North Water Polynya during April, May, June and July, 1998.

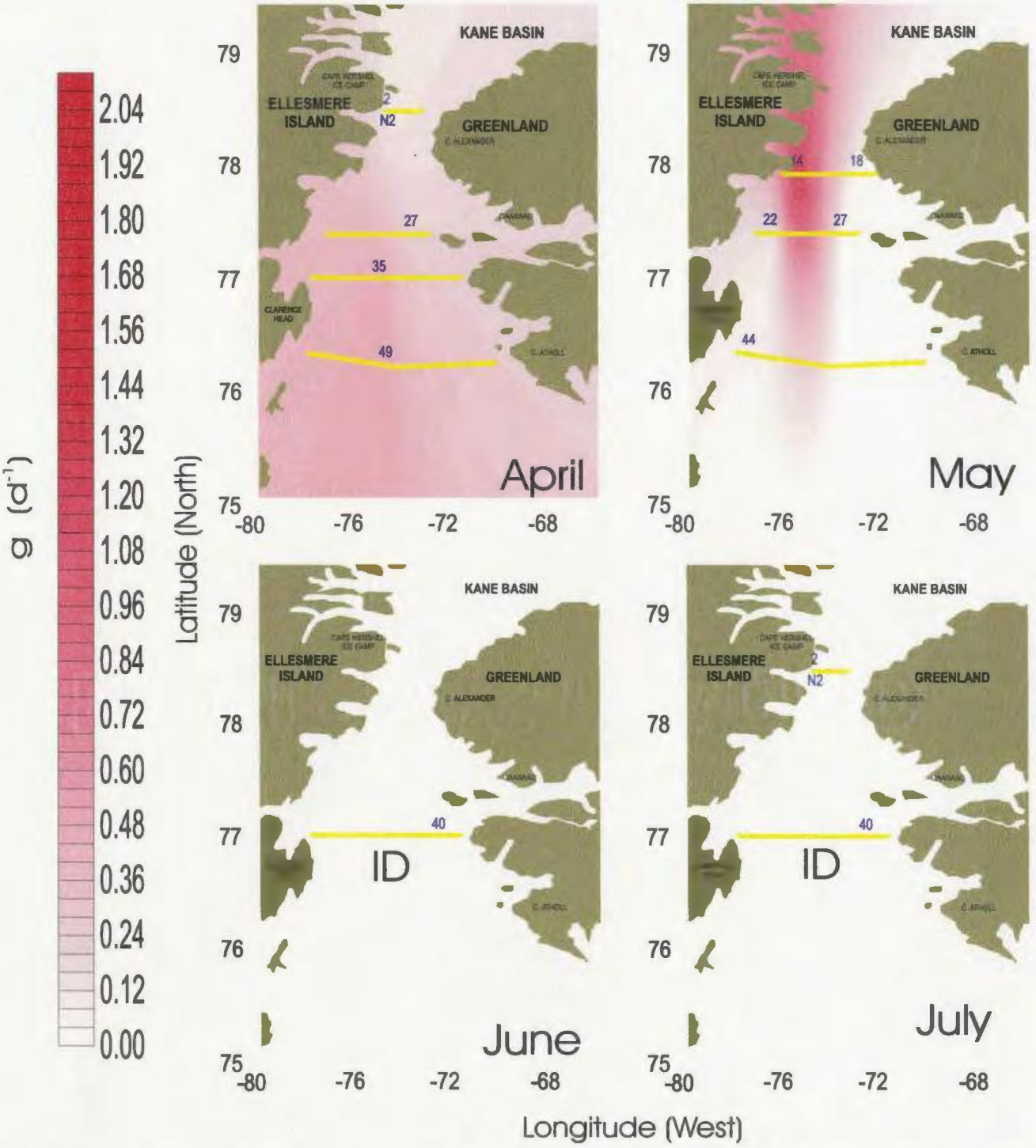

Fig.2.14 Spatial trends in grazing mortality (g) of large phytoplankton (>5 μm) throughout the North Water Polynya during April, May, June and July, 1998.

Note: ID indicates insufficient data to create contour map

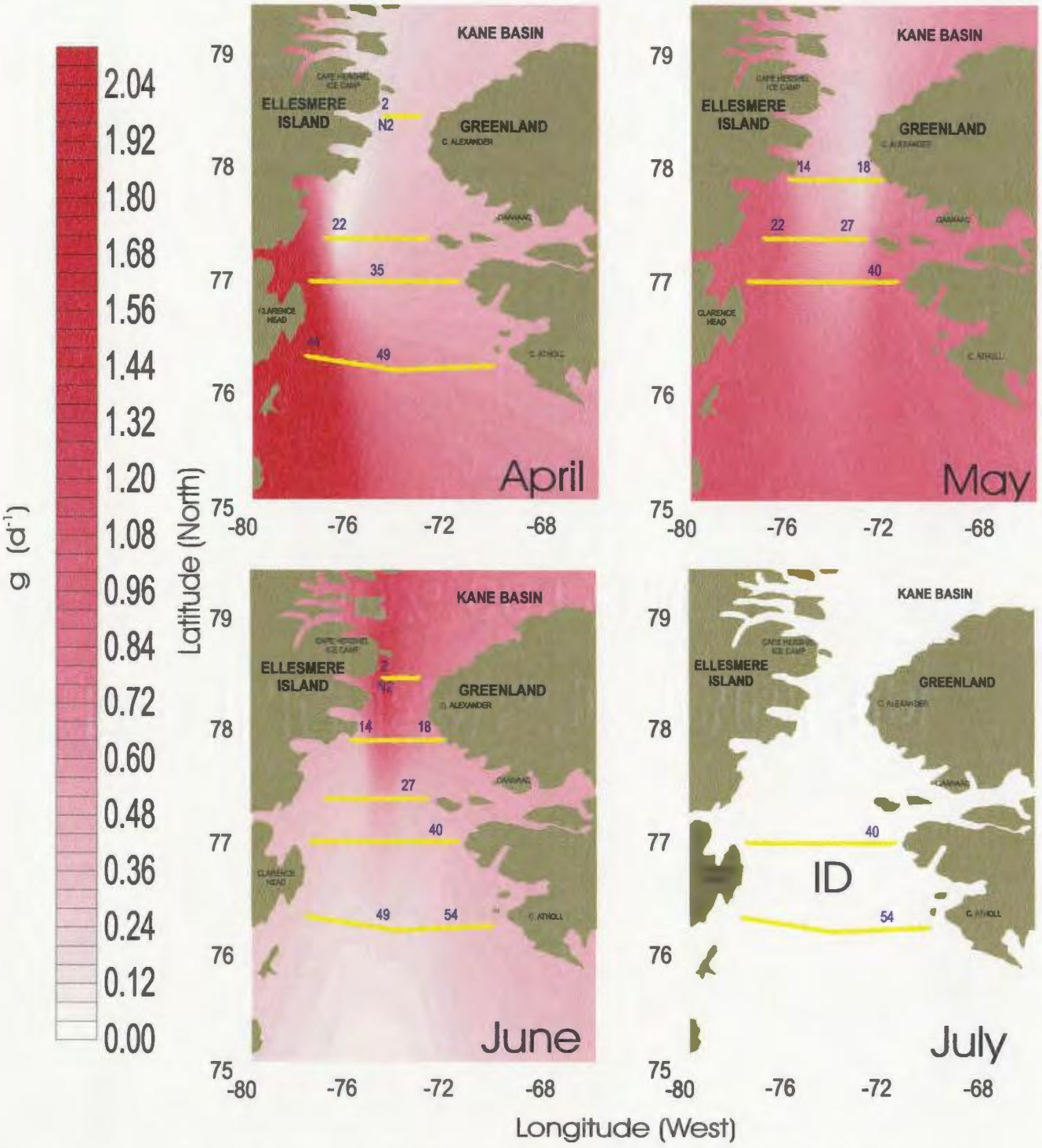

Fig.2.15 Spatial trends in grazing mortality (g) of small phytoplankton (<5 μm) throughout the North Water Polynya during April, May, June and July, 1998.

Note: ID indicates insufficient data to create contour map

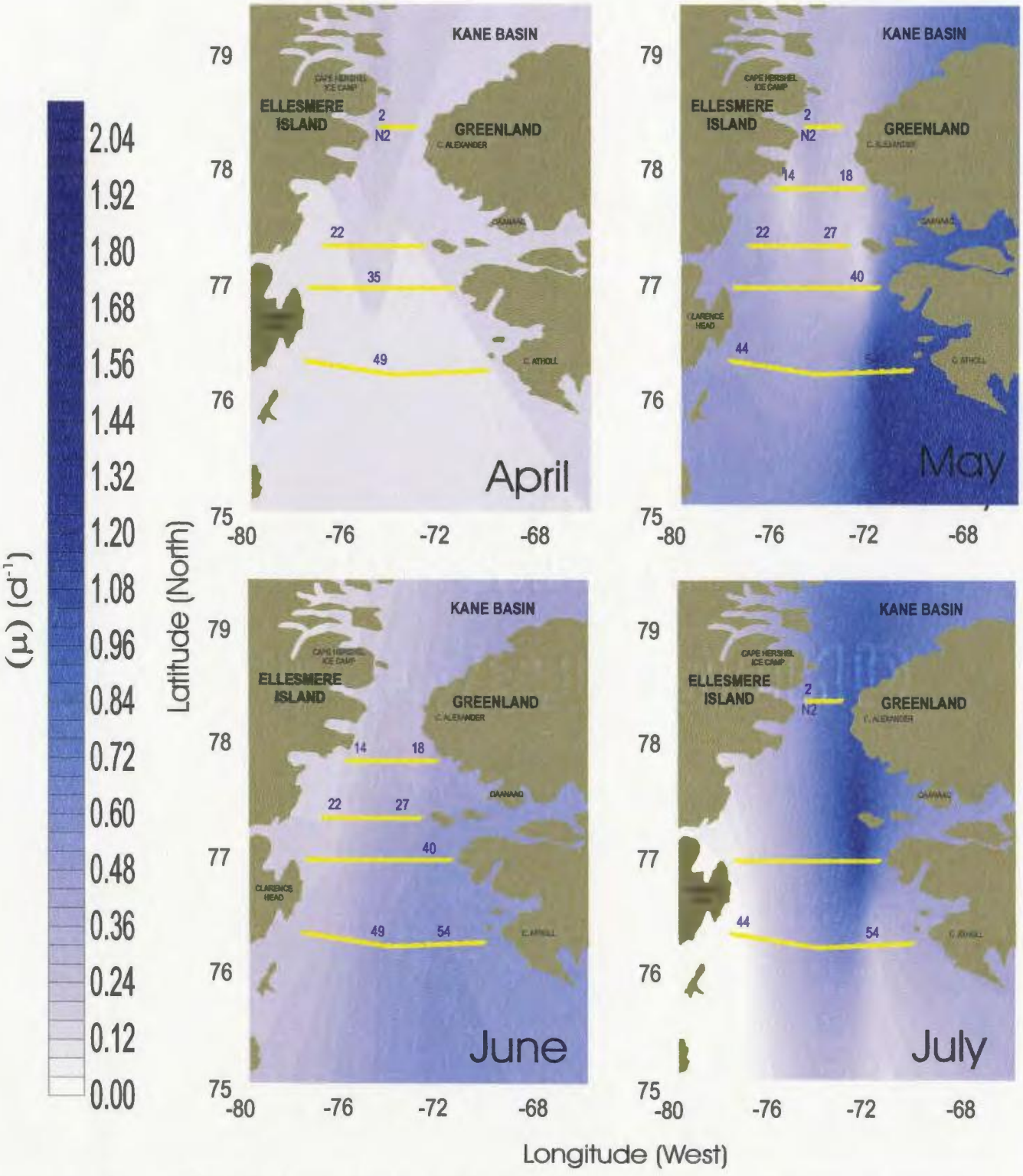

Fig. 2.16 Spatial trends in observed in growth (μ) rates of bacteria measured throughout the North Water Polynya during April, May, June and July, 1998.

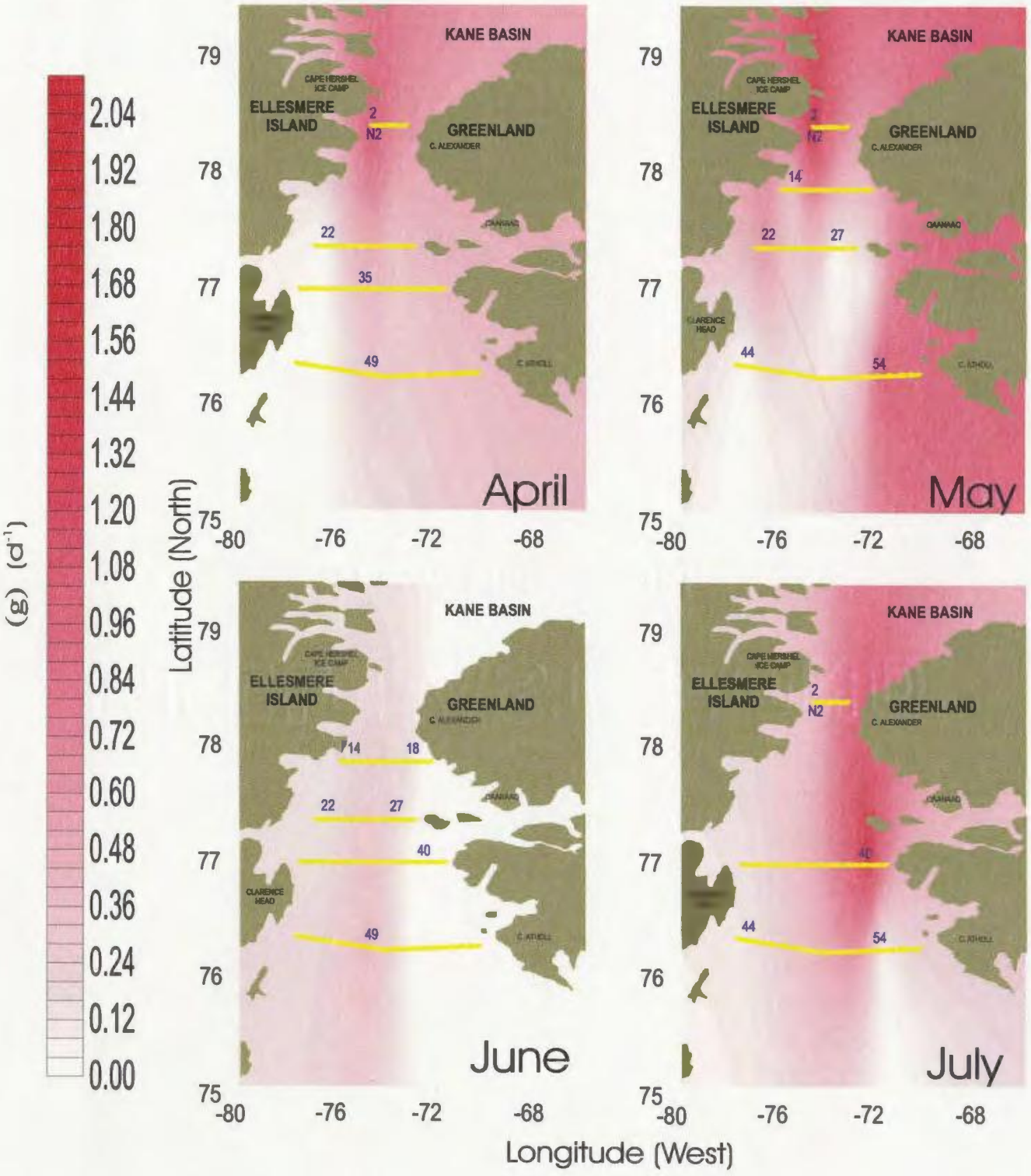

Fig.2.17 Spatial trends in grazing mortality (g) of bacteria throughout the North Water Polynya during April, May, June and July, 1998

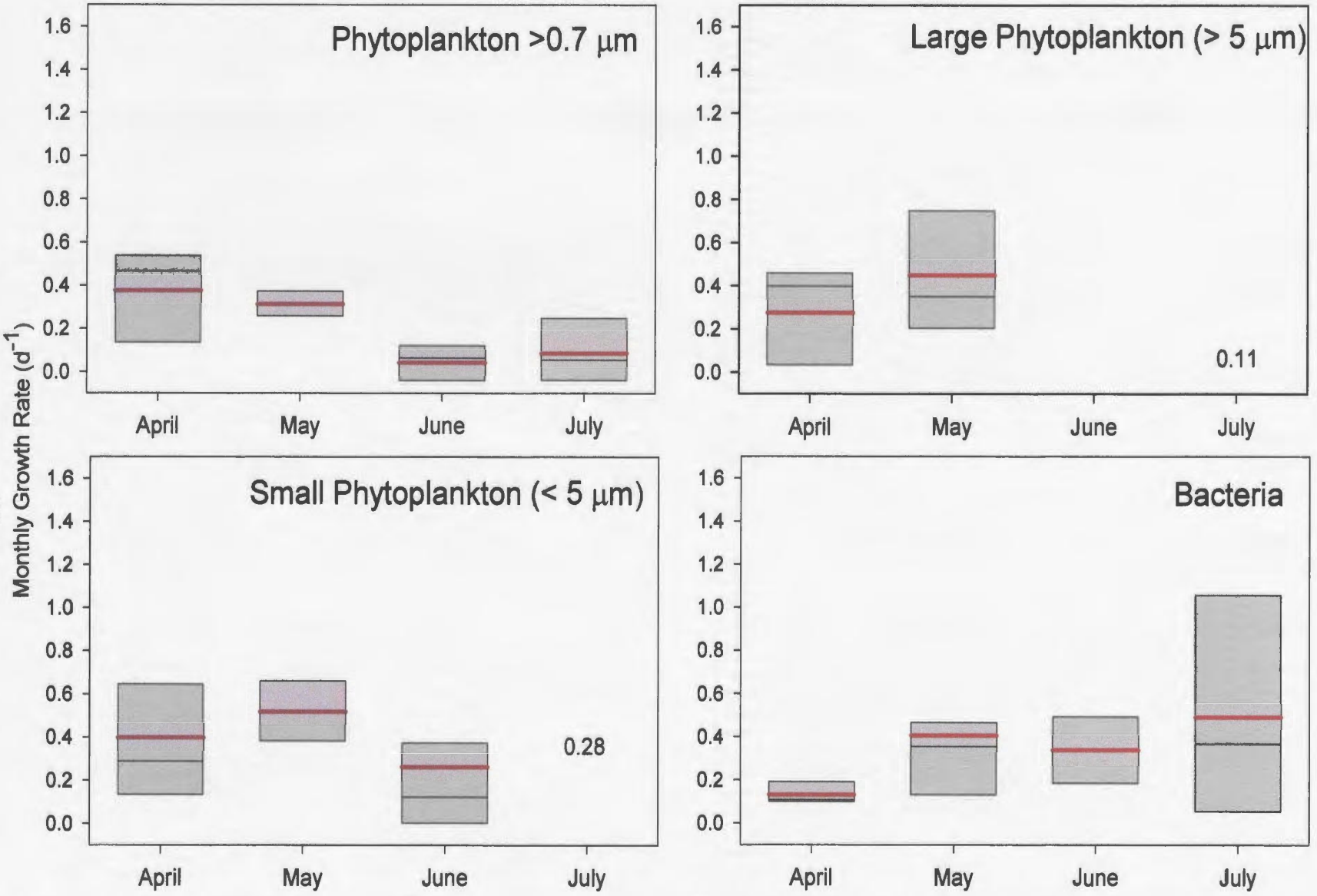

Fig. 2.18 Polynya-wide monthly growth rates for each prey type- phytoplankton (>0.7μm, >5μm, <5μm) and bacteria. The black line within each box represents the median. The box boundary closest to zero represents the 25th percentile and the boundary of the box farthest from zero indicates the 75th percentile. The red line within the boxes represents the calculated mean.

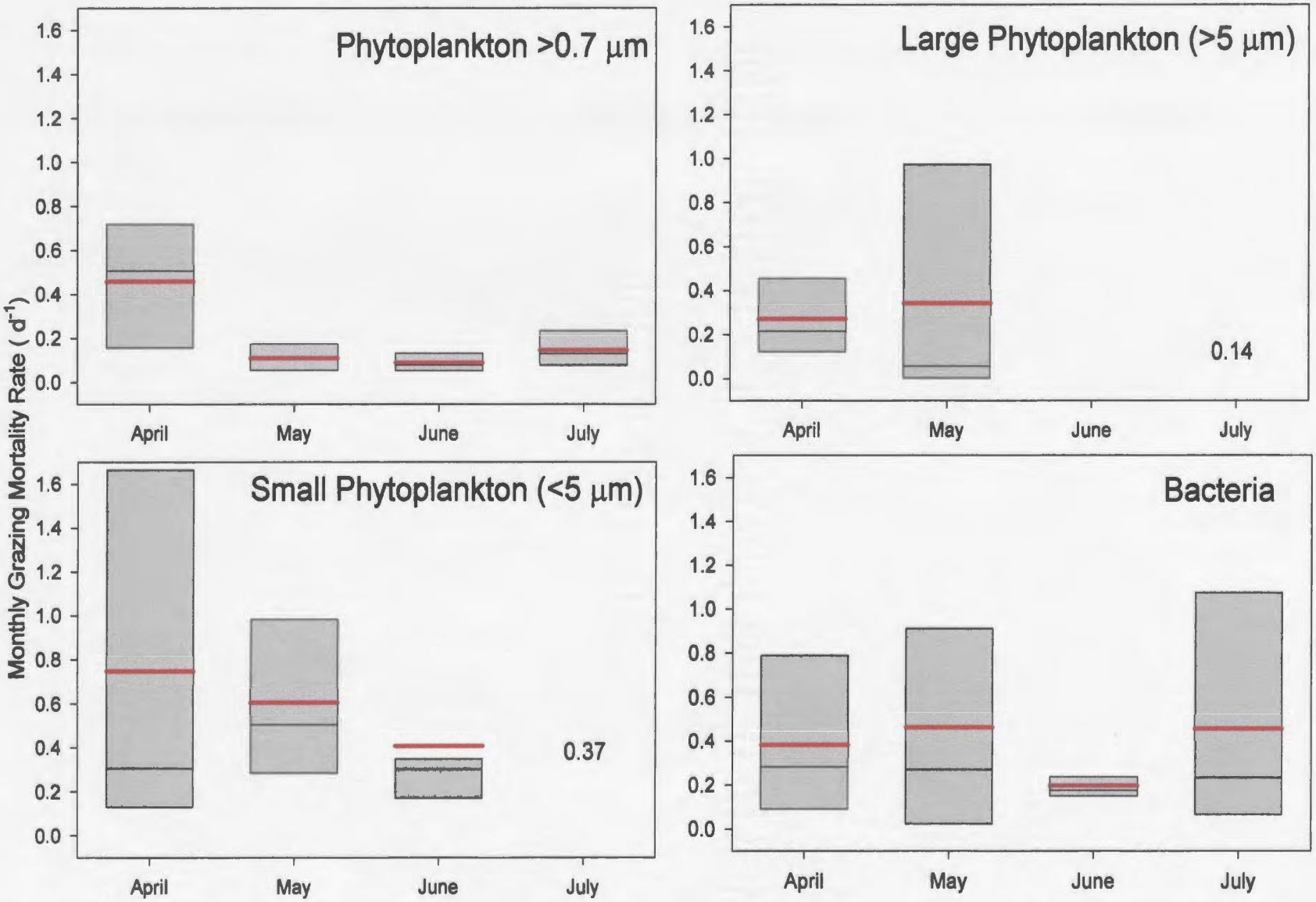

Fig. 2.19 Polynya-wide monthly grazing mortality rates for each prey type- phytoplankton (>0.7μm, >5μm, <5μm) and bacteria. The black line within each box represents the median. The box boundary closest to zero represents the 25th percentile and the boundary of the box farthest from zero indicates the 75th percentile. The red line within the boxes represents the calculated mean.

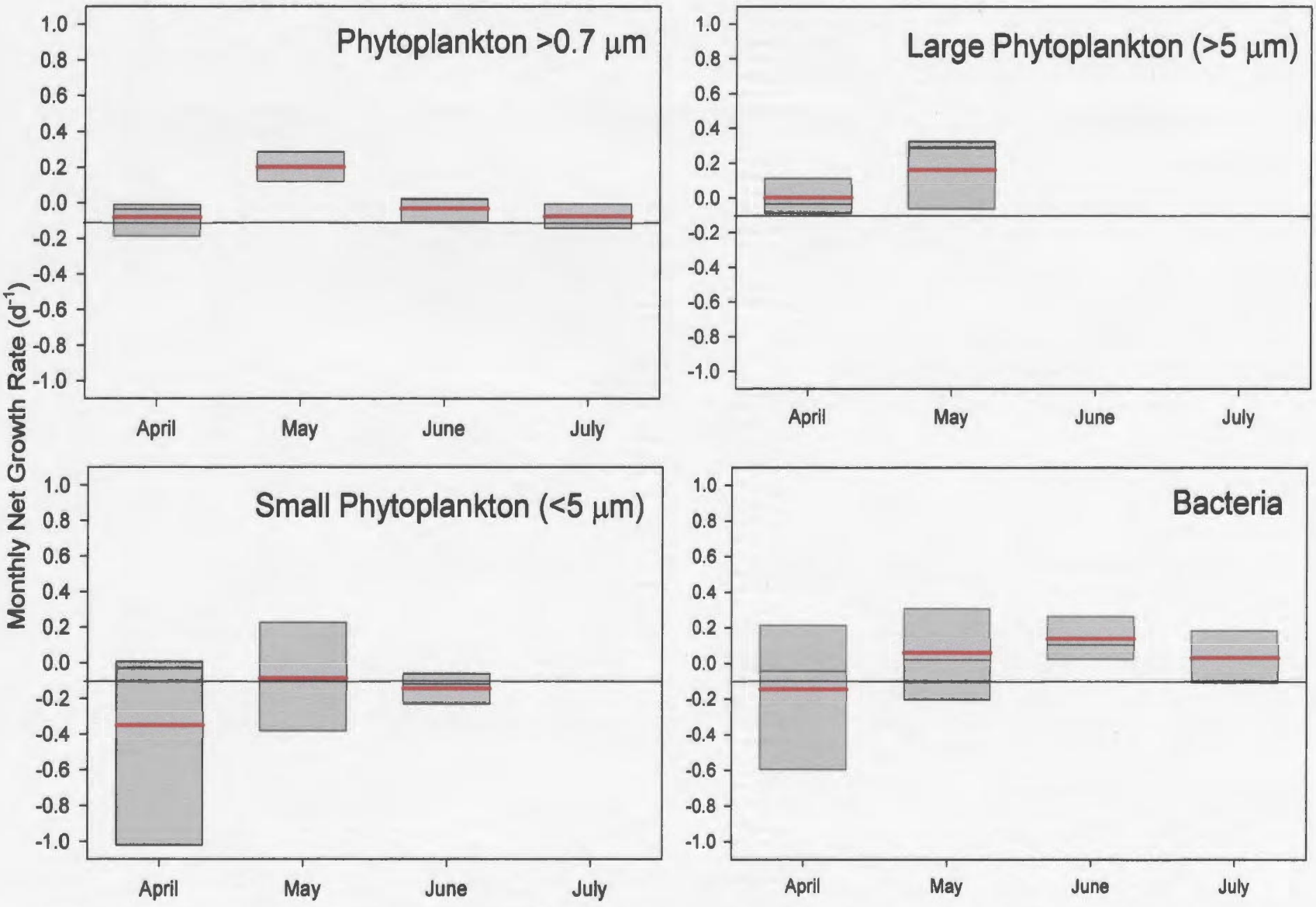

Fig. 2.20 Polynya-wide monthly net growth rates (NGR = μ - g) for each prey type - phytoplankton (>0.7μm, >5μm, <5μm) and bacteria. The black line within each box represents the median. The box boundary closest to zero represents the 25th percentile and the boundary of the box farthest from zero indicates the 75th percentile. The red line within the boxes represents the calculated mean.

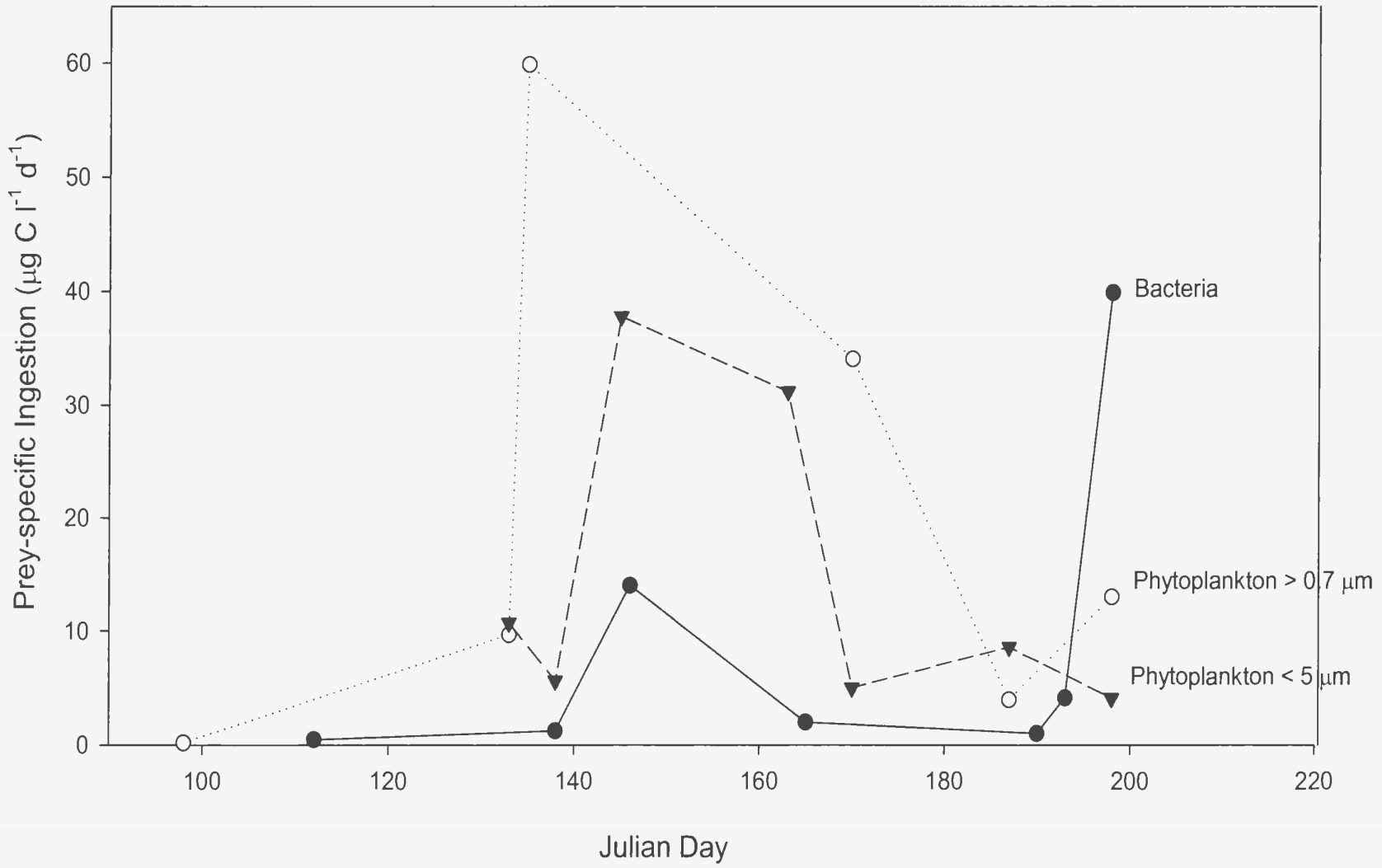

Figure 2.21 Calculated prey-specific rates of ingestion of the various prey types - phytoplankton (>0.7 μm, >5 μm, <5 μm) and bacteria, throughout the North Water Polynya as the study progressed from April to July, 1998.

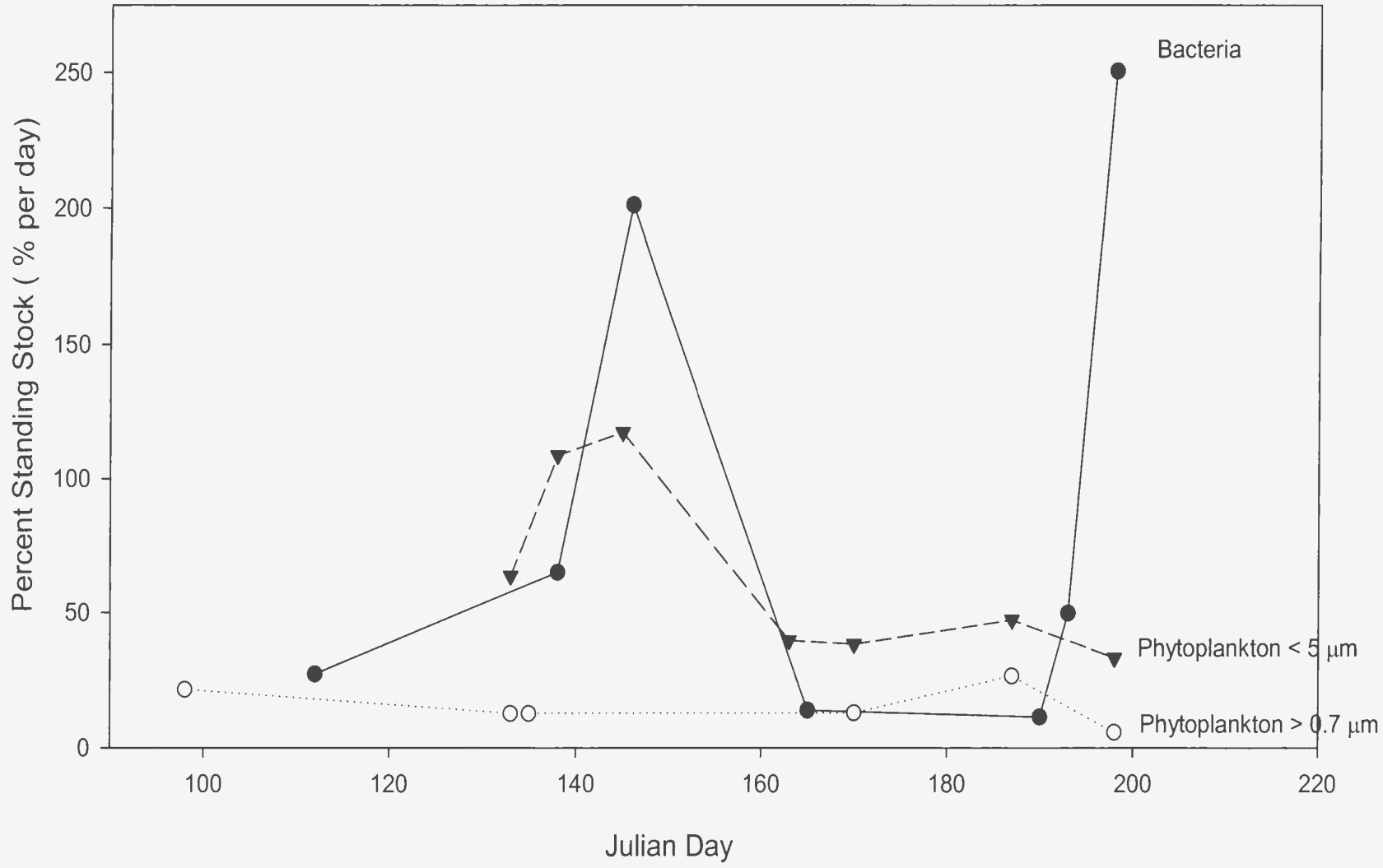

Figure 2.22 Calculated percent standing stock consumed of the various prey types - phytoplankton (>0.7 μm, >5 μm, <5 μm) and bacteria, throughout the North Water Polynya as the study progressed from April to July, 1998.

Chapter Three:

Size Selective Grazing of Microzooplankton in the North Water Polynya

3.1 Introduction

Microzooplankton are a link between phytoplankton and bacteria and metazoan grazers. Since small cells, such as bacteria, are not efficiently utilised by most larger organisms, grazing of these small cells by microzooplankton allows nutrients to be transferred to higher trophic levels or rapidly remineralized. Bacterivory is an important mechanism both for nutrient regeneration (Jumars et al. 1989) and for the transfer of nutrients or energy to higher trophic levels (Azam et al. 1983; Sherr and Sherr 1988). Microzooplankton regulate bacterioplankton and small phytoplankton through top-down control (Verity et al. 1996) oftentimes grazing at high enough rates to terminate the bloom. Grazing processes may influence the flux of nutrients from surface to depth. Grazing by microzooplankton recycles carbon and nutrients within the mixed layer, whereas grazing by larger zooplankton results in carbon losses in the form of fecal pellets that sink rapidly below the euphotic zone (Longhurst and Harrison 1989; James and Hall 1998).

Bacterivory by heterotrophic nanoflagellates, mixotrophic flagellates and small ciliates is one of the main mechanism of bacterial mortality in the upper ocean (Azam et al. 1983; Fenchel 1984; Landry et al. 1984; Sanders and Porter 1988; Kuuppo-Leinikki 1990; Fuhrman 1992; Sherr and Sherr 1994). Furthermore, microzooplankton grazing is thought to impact the size structure, diversity, and apparent morphotype of the bacterial community (Gude 1989; Posch et al. 1999). Changes in the bacterial size distribution to

"inedible" or less vulnerable (e.g. small cells, filaments, aggregates), or less desirable (very large or inactive) cell types have been described both in the field and in the laboratory (Gude 1979; Bird and Kalff 1993; Gonzalez et al. 1993; Jurgens and Gude 1994; Gasol et al. 1995; Simek et al. 1997). Most of these studies have taken place in freshwater systems or using laboratory studies of microbial interactions.

Size Selectivity

Grazing by microzooplankton may influence both the size distribution of bacterial communities, and their taxonomic compositions (Hahn and Hofle 1999; Simek et al. 1999; Hahn and Hofle 2001; references cited within). Planktonic bacterial populations tend to be dominated by small cells suggesting that either large bacteria may be preferably exploited by protozoans, small cells may be preferably avoided, or there are differences in the growth rates of the cells. Also, predators appear to prefer prey which are motile which are also the prey which are more likely to be nutrient replete as these cells are able to locate regions of high substrate concentrations (Burkhill et al. 1987; Monger and Landry 1992; Gonzalez et al. 1993).

Bacterivores can graze selectively, and in particular most protists graze based on size (Chrzanowski and Simek 1990; Peters 1994; Hahn and Hofle 2001). This has important implications when measuring growth and grazing mortality rates of bacteria based on changes in cell abundance. Results may be biased if the bacterial community consists of both fast-growing and slow-growing cells and if the microzooplankton are grazing each size class selectively (Paranjape 1990). Several studies exist which show the

occurrence of different sized cells growing at different rates (Bird and Kalff 1993; Gallegos et al. 1996; Pernthaler et al. 1996).

Other researchers suggest that predators select prey based on nutrient quality of the cells or they select cells which are actively growing and dividing (Anderson et al. 1986; Chrzanowski and Simek 1990; Gonzalez et al. 1990; Sherr et al. 1992; Gonzalez et al. 1993; Sherr and Sherr 1994; Lebaron et al 1999; Lovejoy et al. 2000). This results in grazing of the larger, active size fraction of bacteria. In a study by Kuuppo-Leinikki (1990), heterotrophic nanoflagellates grazed the larger rod-shaped bacteria (also see Andersson et al. (1986) and Krambeck (1988)). Jurgens and DeMott (1995) found that flagellates were more selective when they were grown under food-saturated conditions than food-limited situations. This selectivity has both direct and indirect effects on the microbial community including direct cropping certain prey size classes while indirectly regenerating nutrients (Anderssen et al. 1986).

The primary objectives of the research described within this chapter were (1) to assess size selective bacterivory of microzooplankton at different locations in the North Water Polynya and at different times of the year and (2) to determine patterns of size selective bacterivory in the North Water Polynya. To address these objectives, the rates of growth and grazing mortality three size classes of bacterial prey were measured using the dilution technique (Landry and Hassett 1982) over the four month study period from April to July, 1998.

3.2 Methodology

Size selective grazing by <202 μm microzooplankton in the North Water Polynya was studied by combining the dilution assay approach (Landry and Hassett 1982) with image analysis to study the change in cell size distributions during the time course of the experiment. The dilution approach is generally used to examine simple predator-prey dynamics specifically prey growth and predator grazing on those prey, however the approach can be useful when combined with an image analysis study to determine even more about the grazing dynamics in a system. A brief review of the dilution approach follows, however full descriptions and assumptions of this approach can be found in Chapter 1.

The dilution approach, as introduced by Landry and Hassett (1982) combines particle-free sea water with natural sea water in increasing proportions of natural sea water (RSW) from 10% to 100% RSW. Samples are drawn from each treatment at the start of the experiment and after a 48 hour incubation period. Prey apparent growth rate for individual samples are calculated based on the exponential model of population growth

$$1) \qquad r = NGR = \ln (P_t/P_o)/t$$

Here **r** is the net growth rate (NGR) observed over incubation time interval (**t**), in days. NGR can be calculated as the difference between instantaneous rates of population growth (μ) and grazing mortality (**g**) (Landry 1993). $\mathbf{P_o}$ and $\mathbf{P_t}$ are the initial and final prey abundances, estimated from bacterial cell counts.

The change in bacterial abundance over time within each size class, or NGR, is plotted against dilution factor (percent dilution). The slope of the linear relationship is the grazing mortality rate and the ordinal intercept of the regression is the rate of growth of the prey, or a specific size fraction of the prey, in the absence of grazers. While there are some limitations associated with this technique, the approach is generally accepted as a relatively simple method of measuring prey growth and grazing mortality rates. The assumptions have also been rigorously tested by some researchers and have been found to be robust (Tremaine and Mills 1987).

Modifications To the Dilution Approach

Data from image analysis was grouped into three size classes based on cell diameters; <0.5 μm, 0.5 - 1.0 μm, >1.0 μm. The fraction of total cells within each size fraction was calculated as.

2) $\text{Fraction}_{(\text{size category})} = F_{(\text{size category})} = (\#\ \text{of cells}_{(\text{size category})})/(\text{total cells measured})$

To apply these values to the natural population, the fraction of cells in each size category were multiplied by the number of cells in the raw seawater to give the actual cell number per sample.

3) $T_{(\text{size category})} = F_{(\text{size category})} * T_{(\text{sample})}$

Here, $\mathbf{T}_{(\text{size category})}$ represents the total numbers of cells within a size category, $\mathbf{F}_{(\text{size category})}$ is calculated from formula 2, and $\mathbf{T}_{(\text{sample})}$ is the total number of cells in the sample. From this value (i.e. $\mathbf{T}_{(\text{size category})}$), which was determined for time initial ($\mathbf{T}_{i(\text{size category})}$) and time

final samples ($\mathbf{T_{f\ (size\ category)}}$), a growth rate was calculated using a modification of the exponential model of population growth (Formula 1).

4) $AGR_{(size\ category)} = \ln (T_{f\ (size\ category)}/T_{i\ (size\ category)})/t$

This rate was calculated for each sample in the dilution series and from this, a cell-size dependent grazing mortality rate (slope of the regression line) and growth rate (ordinal of the regression line) was estimated. Comparison between cell sizes in the initial time and the final sample was used to assess changes in the size distribution of the bacteria.

Sampling Site

Samples were collected aboard the Canadian Coast Guard icebreaker *Pierre Radisson* during an expedition from early April 1998 to late July 1998. The research was carried out as a component of the multidisciplinary International North Water Polynya Study). To observe changes in the size distribution of the bacterial prey over time, dilution assays were carried out (Landry and Hassett 1982) at ten stations. Some stations were visited more than once, for a total of 30 experiments (Figure 3.1, Figure 3.2). Eleven of these experiments were selected for detailed image analysis. This subset included eight different stations, ranging from May until July (Table 3.2). The experiments at these stations were chosen because of the slide and image quality. Slides which produced images of low quality or which produced cell images of too low fluorescence for accurate measurement by image analysis were excluded from the analysis.

Sample Analysis

Bacterial cell sizes were determined from water samples preserved in 2% glutaraldehyde. Samples for quantification of bacteria were filtered onto 25mm diameter, 0.2 μm black polycarbonate filters, stained with acridine orange (Hobbie et al. 1977), and examined on a BH2-RFC Olympus epifluorescence microscope at a magnification of 1250x using blue-light excitation (BP440, DM455, AFC+Y475). There were two filters per sample and a minimum of 300 cells per filter were counted manually and sizes were determined with an Image-Pro Plus V4.0 Image Analysis System.

Image analysis systems are semi- automated instruments which are designed for rapid counting and measuring of individual particles in natural populations or in laboratory cultures. These systems are equipped to capture and store images, measurements and size distributions. In this image analysis study the epifluorescence microscope was equipped with a highly sensitive camera linked to a desktop computer. The image analysis system used here was digitally calibrated using a stage micrometer and initial calibration software. Cells which fluoresce on the slide were captured by a Pro-Series, High Performance Monochrome CCD camera and the image diverted to a personal computer. Image analysis software was invoked to retain the image and to measure cell diameters, cell lengths, and cell widths. The images were individually examined, and the cell sizes were recorded. Manual determination of the fluorescent intensity threshold was essential in determination of cell edges. Detrital particles or specific cells (i.e. clumped or aggregated) were screened out from the analysis either

through the direct removal from the working image, or by constraints assigned to acceptable diameters. Slides for individual experiments were made at the same time so that bacterial slide quality and cell sizes within an experiment were comparable. The output measured variables for each sample were diverted to an Excel spreadsheet. Cell volumes were calculated using formulae created for volume determination of spheres or cylinders. Cells with an aspect ratio < 1.5 were calculated as spheres whereas cells with an aspect ratio >1.5 were calculated using the formula for cylinders. Mean cell volume (MCV) was determined after log transforming the data and calculating the mean volume for each size class.

3.3 Results

3.3.1 Station Information

Table 3.2 summarises the physical and biological characteristics of the stations that were sampled. Chlorophyll data were provided by Dr. Bert Klein (Université Laval, Québec, QC). The locations of the stations within the Polynya are presented in Figure 3.2. The polynya was separated into North, East and West regions. These regions were selected to correspond to the water mass distributions, as well as phytoplankton and bacterial distributions, through the polynya in June 1998 (Bacle 2000; Rivkin et al. 2000 unpublished data; Tremblay et al. 2002). Stations used in this study were selected based on quality of the slides produced from samples collected at those stations. Five stations were in the Eastern region of the Polynya, three stations were examined in each of the Northern and Western regions of the Polynya.

3.3.2 Biological Characteristics

Areal chlorophyll *a* concentrations (courtesy of Dr. Bert Klein) ranged from ~5 to > 700 mg m^{-2} and large-sized phytoplankton (> 5 μm) were dominant. Bacterial abundances ranged from 76 to 886 x 10^{11} cells m^{-2}.

Published and generally accepted carbon conversion factors were used to convert prey abundances to carbon. Bacterial carbon was estimated using 20 fg C $cell^{-1}$ (Kirchman et al. 1993; Zubkov et al. 1998) and chlorophyll *a* was converted to carbon assuming a C:Chlorophyll *a* ratio of 55 (Booth et al. 1993). Phytoplankton and bacterial biomass measured from initial experimental samples ranged from 2.9 to 398.0 μgC L^{-1} and 1.61 to 17.71 μgC L^{-1} respectively during this study. Highest phytoplankton biomass was seen from late May until late June whereas bacterial stocks continued to increase from June through July (Figure 3.3 (a) and 3.3 (b))

Mean bacterial cell volume varied throughout the study (Figure 3.4) Mean cell volumes ranged from 0.08 - 0.31 μm^3 in time zero samples and from 0.08 - 0.34 μm^3 in time final samples. Mean cell volume decreased during six, and increased during five incubations. Five of the six experiments which resulted in a decrease in mean cell volume were from samples collected on the eastern side of the Polynya. While the remaining station is classified as a "North" station, it also is located on the eastern side of the Polynya.

3.3.3 Overview of Size Class Changes

The number of cells in each size category was determined at each time interval (Formula 3 in Methods). Figures 3.5 (May 26th, 1998) and 3.6 (June 19th, 1998) illustrate representative plots showing the changes in cell abundance in each size class for each dilution. The difference between the two figures shown is that Figure 3.5 shows a consistent increase in the number of cells in the large size class whereas there is a decrease in the numbers of large cells in Figure 3.6. Both stations are locationed in the eastern region of the polynya.

Cells in the small size class (<0.5 μm) did now show any consistent pattern of increase or decrease. The number of small cells increased in only three of the experiments (May 26th, June 11th, June 19th).

The number of cells in the medium size class (0.5 - 1.0 μm), increased in all dilutions in all experiments, except one dilution (90% RSW) on June 10th. The largest increase occurred on May 26th (Figure 3.5) where the number of cells in this size class increased by more than 3-fold for all dilutions.

The number of cells in the large (> 1.0 μm) size class generally increased at all dilutions and in all experiments. Exceptions to this pattern were noted on May 26th (Figure 3.5), one dilution on June 11th (62 % RSW) and one dilution on July 9th (25% RSW). Greatest increases in large-sized cell numbers were observed in experiments conducted on May 28th (> 2-fold), June 12th (> 3-fold), and July 12th (> 2-fold). An experiment conducted on June 19th (Figure 3.6), showed an increase in the number of

cells in the large size class for the dilutions less than 50% RSW but no apparent change in the cell size distributions in dilutions greater than 50% RSW. On June 21st, cells in the large size class increased in dilutions less than 62 % RSW whereas fewer large size cells were observed at higher dilutions of RSW.

3.3.4 Size Selective Growth and Grazing Mortality

Table 3.3 shows the rates of growth and grazing mortality for each bacterial size class. Figure 3.7 illustrates two sample dilution plots of the three size classes. The plots presented are representative plots showing two contrasting patterns i.e. highest growth and grazing mortality of the small cells on May 26th, and the opposite trend on June 12th.

None of the linear regression parameters calculated to determine μ or g for small cells were significant ($\alpha = 0.05$). Three experiments resulted in significant regressions for medium cells (June 10th, June 19th and June 21st) and two experiments were significant for large cells (June 19th and June 21st). The majority of the cells measured were in the medium size class and showed the clearest changes in distribution through the course of the experiment. For example see Figures 3.5 and 3.6 which both clearly show changes in the number of cells in the medium size class.

Small Bacteria Growth rates of small sized bacteria were positive in four experiments (Table 3.2). The highest growth rate of 1.53 d^{-1} was observed in the eastern region on May 26th. The next highest was on June 11th, which is in the northeastern region of the Polynya with a rate of 0.89 d^{-1}. Grazing mortality rates were also highest in these experiments (0.52 d^{-1} and 0.82 d^{-1} respectively).

Medium Bacteria Growth rates of medium bacteria were positive in 8 of the experiments. Rates were highest early in the season (0.77 d^{-1}), and decreased as the season progressed. Grazing mortality of this size fraction was low and remained < 0.19 d^{-1} throughout the study. Three of the experiments which resulted in significant regressions had positive slopes (which gives a negative grazing mortality rate)

Large Bacteria Growth rates of large size bacteria increased as the season progressed through June and decreased during July. In the beginning of the study, growth was moderate but quickly increased to peak on June 19th at 1.38 d^{-1}. The exception to this trend occurred on June 11th where growth was negative (-1.7 d^{-1}). This station is located in the North eastern region of the Polynya. Grazing mortality rates were similar to trends in growth rates with rates fairly low in May, and steadily increasing through June to peak at 1.47 d^{-1} on June 19th.

3.3.5. Seasonal Patterns

Figure 3.8 (a) and Figure 3.8 (b) show the time-dependent change in rates of growth and grazing mortality of each size class. Seasonal patterns of grazing mortality closely follow the patterns of growth shown but neither show a clear seasonal progression. Upon closer examination, two experiments stand out in Figure 3.8 (a). These experiments carried out on May 26th and June 11th. Interesting patterms in grazing mortality rates are also noted in Figure 3.8(b), for experiments conducted on June 21st and July 9th in addition to those of May 26th and June 11th. In all cases, both growth and grazing mortality of medium sized cells lies between the rates for small and large sized cells and are fairly consistent throughout the season.

3.4 Discussion

Methodological Approach to Study Growth and Grazing Mortality

Analytical methods combining epifluorescence microscopy and image analysis have enabled the quantification of various sizes and shapes of microbial prey and predators (Fenchel 1980; Krambeck et al. 1981; Sieracki et al. 1998; Posch et al. 1999; Shopov et al. 2000). Several studies have examined changing cell volumes as well as size selective grazing (Table 3.1). Because of the differing methodologies in measurement of cell size it is important to clearly specify which cells are classified as small, medium or large as designations tend to be different depending on the methods used.

The dilution assay approach is often used to measure community grazing impact. In this study, the technique is applied to evaluate size selective grazing of microzooplankton on various size classes of bacteria by coupling image analysis with the dilution assay. Simply examining changes in mean cell volumes throughout the course of the experiment may not give an accurate representation of what is occurring within an experimental container (Pernthaler et al. 1996) and the separation into size classes more clearly shows the changes taking place in the bacterial community. While our results are variable and many assumptions are required to interpret our data, some consistent patterns appear, indicating that this approach may be valuable for future studies of size selective grazing.

Due to the effects of storage on acridine orange stained samples, some slides were not suitable for the purposes of image analysis. Because the accuracy of image analysis depends upon the quality of the images, not all samples were included in the analysis due

to high background fluorescence, loss of fluorescence of cells, and general difficulty in obtaining a clear image for image storage. To accurately determine cell sizes using image analysis, bright, clear images with sharp edges are optimal and these were the only images which were utilised. Detrital particles found in the sample image were deselected by the user prior to acquiring size information. Thus complete automation of the approach is not recommended. To ensure high quality of measured variables, slides should be made immediately and analysed as soon as possible to ensure good quality images with high fluorescence.

For the research reported here, most cells that were measured fell within the medium size class (>70%). Small and large sized cells were each generally less than 20% of the total cells measured. While previous researchers suggest that 300 cells is needed to obtain a representative and reproducible sample population, we recommend that a minimum number of cells within each size class must be measured in order to provide the accuracy of the regression equation slope and intercept. Furthermore, the best results for medium sized cells were for samples where more than 250 cells *per slide* were measured. Again, with a larger number of cells measured, more size class ranges may be identified with greater accuracy. This would be a better method of pinpointing specific size classes of bacteria. As a result, we recommend that a *minimum* of 1500 cells per slide must be measured to ensure an accurate representation of each size class. Depending on the number of cells on each filter on a slide, multiple slides per sample should be made to eliminate the likelihood of re-measuring the same cells. Also, a systematic scan of the slides should be undertaken and a consistent pattern of cell measurement carried out

rather than a random approach. Because of the efficiency of image analysis measurements this is a reasonable recommendation.

One assumption inherent in the dilution model is that prey growth is the same in each experimental bottle. Here, growth rates are estimated for different size classes which grow at different rates, and are influenced by nutrients (i.e. recycling). Bacterial abundances are influenced by increasing predator concentration as a function of dilution and grazing pressure. This complicates the analysis of the dilution regression results for the individual size classes.

Biological Characteristics of the North Water Polynya

Klein et al. (2002) reported a regional separation of phytoplankton biomass and primary production. Maximum values differed for each of the four regions and phytoplankton biomass tended to consist of larger size fractions in the North, East and West. Bacteria also exhibited regional trends which correspond to both reducing ice cover and increasing phytoplankton biomass. Biomass of both bacteria and phytoplankton began increasing in the East and then spread North and West until the peak of the bloom.

In Chapter Two, we examined bacterivory and size-specific herbivory of microzooplankton in the North Water Polynya. Growth and grazing mortality of total (>0.7 μm) phytoplankton as well as small (<5 μm) and large (>5 μm) fractions. Small (<5 μm) phytoplankton were growing at a higher rate than the large (>5 μm) phytoplankton and were also more vigorously grazed. It is likely that the microzooplankton are

selectively grazing the smaller, more active phytoplankton cells in the North Water Polynya.

Mean cell volume varied throughout the study, however all experiments in which mean cell volume decreased during the experiment were conducted at stations which were located on the eastern side of the polynya. This suggests that in these experiments microzooplankton are preferentially grazing the larger size fractions of bacteria i.e. they are preferentially grazing the more active, nutrient-replete cells (Anderson et al. 1986; Chrzanowski and Simek 1990; Gonzalez et al. 1990; Gonzalez et al. 1993; Lovejoy et al. 2000). The alternative hypothesis is that the bacteria within the community are responding to grazing pressure through cell inactivation which results in smaller cells having some protection from grazing (Chrzanowski and Simek 1990; del Giorgio et al. 1996). The increased number of smaller cells types in these experiments may result from nutrient limitation resulting in a larger number of small starved bacteria (Krambeck and Krambeck 1984; Palumbo et al. 1984; Psenner and Sommaruga 1992). This concept is further explored using growth and grazing mortality rates.

Growth and Grazing Mortality of specific size classes

Growth rates and grazing mortality rates of the size classes do not appear to have any particular seasonal pattern nor any pattern which is dependent upon dilution factor (see Figure 3.5 and 3.6). For small bacteria, regression slopes were positive in six experiments (resulting in a negative g). This violates the assumptions of the dilution assay and may indicate a positive response of small prey to microzooplankton mediated nutrient recycling. Three experiments were significant for medium sized cells (June 10th, June

19th and June 21st) and two experiments were significant for large sized cells (June 19th and June 21st).

For the medium sized cells class, two experiments resulted in a positive, yet significant regression slope which may indicate enhanced cell growth in the higher dilutions. One experiment showed this response for the large-sized cells. This may be as a result of nutrient recycling from grazing processes. The relatively large scatter in the dilution plots of each size class contributes to the non-significant results obtained.

Seasonal Progression

Initial observation of growth and grazing mortality rates on Figure 3.6 (a) and (b) suggest a variable pattern in the seasonal progression of size specific growth and grazing mortality. Most experiments resulted in highest growth of the large size fraction. There were two exceptions (indicated by asterisks) where the trend is reversed and the smallest size class were growing at the higher rate. These two experiments were conducted at stations located in the eastern region of the Polynya.

Grazing mortality was also highest for the largest size fraction. Four exceptions to this general pattern show the smallest size with the highest grazing mortality rate. The first three exceptions were conducted at stations located in the eastern region of the Polynya. The remaining experiment, conducted on July 9th, is located in the south western region of the Polynya. Here, higher growth of small cells resulted in higher cell numbers in the smaller size classes. This means that previous indications that grazing is higher on the large sized cells, as suggested by a decrease in mean cell volume (Figure 3.4), is incorrect. In fact, the higher growth of small sized cells resulted in greater

numbers of small cells and hence lower mean cell volumes in these experiments. The result is that it is not increased grazing on large cells which contribute to the decrease in mean cell volume but actually the increase in small cells which are being measured. These cells are then more vigorously grazed by the microzooplankton.

Higher growth and grazing mortality on small cells on the eastern side of the polynya may not be simply a result of size selective grazing. While we have not measured predator community composition, changes in the size distribution of the predators themselves may also result in differential grazing. The presence of small size predators would result in grazing on small sized prey. Alternatively, the cells themselves may be responding to changing, or decreasing nutrient availability resulting in smaller, nutrient starved cells. These cells may appear to be preferentially grazed here simply due to the relative abundance of prey which are available to be grazed by the microzooplankton.

Implications for the Microbial Food Web

Relationships can be obscured during the analysis of food web interactions due to feedback effects and cascading interactions of grazing. Remineralization of limiting nutrients during grazing, may positively affect both the protozoans present in the experimental vessels as well as the bacterial prey. In substrate replete conditions, flagellates graze bacterial prey very rapidly exerting control over the prey in bloom conditions, however these prey are not digested completely leading to the release of nutrients (Gonzalez et al. 1993 and references cited within). Gonzalez et al. (1993) also found that flagellates differentially digested large, growing cells versus small starved cells. This results in a lower clearance rate on the smaller cells and may provide some

refuge for these cells from grazing pressure. Here, experiments conducted in the eastern region of the North Water Polynya show the smaller cells that became more abundant and were being grazed more vigorously as the dominant prey type available to the predators. Other experiments conducted in the west and north indicated grazing on the largest size of bacteria. The differences observed between regions of the polynya may simply be due to a change in the prey size which is available or changing predator communities.

Laboratory experiments, such as the dilution approach, examining direct and indirect interactions are a simplification of the complex interactions that occur in a natural system. One such direct effect may result from unusually high predation which occurs when the protozoans themselves are not controlled by their immediate predators. This results in an increase in the number of protozoans present (Jurgens et al. 1994; Vaque et al. 1994). Jurgens et al. (1994) also suggested that the bacterial community may develop more grazing resistant forms when the removal of metazooplankton results in higher numbers of microzooplankton and therefore increased grazing pressure.

Jurgens et al. (1997) conducted another study that further defined the impact of predator and prey. They established that the presence of mesozooplankton not only contributed to the direct removal of microzooplankton predators, but that mesozooplankton were also able to graze the larger size fraction of bacteria. Mesozooplankton may also graze even the more complex growth forms, which were previously 'protected' from grazing when only the microzooplankton grazing was examined (Gude 1989; Jurgens et al. 1994; Jurgens et al. 1997). Because of the interactions involving all trophic levels within the grazing chain, a simple explanation of

size shifts or community morphology shifts may not be adequate to describe community dynamics. Clearly however, such size specific effects must be studied to properly understand the complexities of trophic interactions in the real world.

Predator selectivity of prey may influence carbon flow through the microbial food web. Bacteria are dependent upon substrate supply and availability. Actively growing bacteria are the preferred prey of microzooplankton and thus, with increased predation of these bacteria, there are also increased demands for the nutrients necessary to maintain prey stocks (Chrzanowski and Simek 1990). In addition, grazers selecting actively growing cells are not only cropping prey stocks but are also decreasing net production of the prey thorough the removal of larger, active cells (Gonzalez et al. 1990).

3.5 Summary

The results of this study show that size selection of bacterial prey in the North Water Polynya occurs. However because of the large error associated with the technique, many of the results obtained were statistically non-significant. A picture of size selective grazing in the North Water Polynya can be presented which involves differing selective approaches based on region.

While a decrease in mean cell volume was observed within several experiments suggesting that large cells are being grazed, in actual fact it is the increased growth of small cells which results in the lower mean cell volume. These cells are then being grazed vigorously, particularly in the eastern region of the Polynya. The high grazing on small cells may occur as a result of changing nutrients in the water column, or changing predator communities. This is in contrast to results from other studies which suggest that

microzooplankton prefer the large size prey (Anderson et al. 1986; Chrzanowski and Simek 1990; Gonzalez et al. 1990; Monger and Landry 1992; Gonzalez et al. 1993; Sherr and Sherr 1994; Lovejoy et al. 2000). Large cells are the preferred prey in the North and West regions of the Polynya.

In the North and West, remineralization of nutrients, or release of substrate by predators during intense grazing, may have contributed to positive feedback on the bacterial prey itself. In this case, there were a greater number of large, active cells available for the microzooplankton. A predominance of small cells in the East may occur as a response to low nutrient levels. These cells may then be grazed simply because they were the dominant prey size or there may have been a shift in the microzooplankton community itself. So, either changing nutrient concentrations or the effect of grazing on size distribution both play a role in shaping the size of bacterial cells within a community.

This research presents a method of examining size selectivity of natural bacteria by microzooplankton predators. A dilution approach was combined with the technology of computer-aided image analysis to measure size selection. There are many possible sources of error associated with this technique however, to our knowledge, there have not been any studies which measure size selective grazing on natural marine bacterial populations. Results presented here suggest that previous studies which study size selective feeding using only changes in mean cell volumes may not be representative of what is actually occurring in nature. Changes in mean cell volume (MCV) of the population does not adequately reflect differential changes within different size classes in a bacterial community. Few studies encompass both size selective grazing and the

structure of the bacterial communities and grazer communities. It is believed that defence tactics of bacterial prey are limited to size-dependent strategies. Greater diversity in this field would contribute to our knowledge of the interplay between bacteria and bacterivorous protists. Consequences of grazing pressure, size selective feeding and growth strategies of protozoa can influence carbon fluxes (Jurgens et al. 1997) and examining the carbon flux through the various components of the microbial food web is essential in determining the role of the Arctic in carbon cycling models.

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Table 3.1: Summary of published studies on the size-selective grazing of bacteria by microzooplankton.

References	Results	Notes
Bird and Kalff 1993	More intense grazing on larger cells (i.e. > 0.6μm)	Freshwater study, using beads (0.27μm, 0.57μm, 1.0μm)
Coffin and Sharp 1987	not a size selective study.	Volumes varied seasonally and spatially.
Chrzanowski and Simek 1990	Preferred large cells (0.8-1.2 μm^3) but not the largest size available	small cells were 0.4-0.6 μm^3
Kuuppo-Leinikki 1990	Heterotrophic nano-flagellates grazed the larger rod-shaped bacteria	Cell volume in grazed fraction was kept small.
Epstein and Shiaras 1992	Mid-sized bacteria (0.025 - 0.1 μm^3) were grazed most heavily by all protozoans,	Ciliate showed greater preference for larger bacteria than flagellates.
Jimenex-Gomez et al. 1994	Heterotrophic nanoflagellates preferred larger cells.	In most dilute, MCV increased from 0.07-0.11. In RSW, MCV was smaller than in dilutions.
Gonzalez 1996	Preferred small cells (<0.1 μm^3)	grazing by heterotrophic nanoflagellates.
Pernthaler et al. 1996	preferred grazing of larger cells (0.4 - 1.6 um)	Classified four functional size groups of bacteria.
Jurgens et al. 1997		Shift in size structure to large aggregates and long filaments.
Hahn and Hofle 1999	Preferred larger cells (0.75-1.0 μm)	Flagellate predation resulted in smaller MCV
Hahn et al. 1999		Filament formation by bacteria not a response to grazing pressure but a result of grazing-stimulated growth.
Jurgens et al. 1999	Shift to large cells (3-6 um in length)	Removal of metazooplankton stimulated protozoan grazing and hence bacterial response.
Lebaron et al. 1999	Grazers preferred active cells (1.0 - 2.5 μm in length)	Small and large cells produced as a result of grazing

Note : MCV - Mean Cell Volume; RSW - Raw Sea Water

Table 3.1 continued

References	Results	Notes
Posch et al. 1999	Only one predator grazed the smallest cells (0.3-0.9μm).	Cells divided into five size classes. Three predators used.
Jurgens and Simek 2000	Maximum clearance rate obtained for latex beads 2.76 μm	filter feeding ciliate efficiently fed upon cells sized from 0.5 to 5 μm

Note : MCV - Mean Cell Volume; RSW - Raw Sea Water

Table 3.2 : Characteristics of stations sampled for image analysis of bacterial cell size specific grazing rates during April through July, 1998. Bacteria and chlorophyll *a* values reported for each station are integrated through the upper 100m. Regional designations can be seen in Figure 3.1. Depth reported is the sampling depth. Community growth rates (μ) and grazing mortality rates (g) calculated from dilution analyses are reported.

Date 1998 (Julian Day)	**Station Number**	**Latitude (°N)**	**Longitude (°W)**	**Region**	**Depth (m)**	**Temp (°C)**	**μ (d^{-1})**	**g (d^{-1})**	**Integrated Bacterial Abundance (10^{11}cells/m^2)**	**Integrated Total Chl (mg/m^2)**	**Flagellates cells L^{-1}**
May 26 (146)	54	76.27	71.91	E	15	-0.5	1.21 ***	0.91***	249	590.8	419 000
May 28 (150)	44	76.38	77.41	W	35	-0.4	0.47**	0.02	676.8	440.5	na
June 10 (161)	14	77.83	75.55	N	15	-1.5	0.19	0.20	494.8	331	499 000
June 11 (162)	18	77.83	73.15	N	10	-1.1	0.26	0.17	703.2	723.7	na
June 12 (163)	27	77.35	73.8	E	10	-1.1	0.41 **	0.19	270.6	531.8	524 000
June 14 (165)	22	77.35	76.58	W	16	-1.1	0.16 ***	0.13 **	694	278.1	190 000
June 19 (170)	40	77	72.42	E	16	-0.5	0.54 ***	0.16	778.5	480	447 000
June 21 (172)	54	76.27	71.91	E	35	-0.4	0.20	-0.02	806.4	112.9	64 900
July 9 (190)	44	76.38	77.41	W	21	-1.0	0.01	0.12 *	493.7	145.5	na
July 12 (193)	2	78.36	74.71	N	9	-0.7	0.54 ***	0.35 ***	335.9	180.9	na
July 17 (198)	40	77	72.42	E	14	-0.4	1.23 ***	1.32**	885.6	87.5	na

Note : NA = data not available for these stations.

Table 3.3 : Rates of growth (μ) and grazing mortality (g) for three size classes of bacteria measured by image analysis, from the North Water Polynya during 1998. SE is the standard error of the mean, μ or g. N is the number of observations per experiment.

Date 1998	Julian Day	Station	r^2	μ (d^{-1})	SE	g (d^{-1})	SE	N
Small Cells								
May 26	146	54	0.28	1.53 ***	0.31	0.52	0.41	6
May 28	150	44	0.00	0.16	0.67	0.12	0.84	5
June 10	161	14	0.46	-0.87 *	0.31	-0.65	0.41	5
June 11	162	18	0.28	0.89	0.80	0.82	0.94	4
June 12	163	27	0.40	-0.57	0.36	-0.75	0.46	6
June 14	165	22	0.65	-0.73	0.34	-0.80	0.41	4
June 19	170	40	0.58	-0.32	0.33	-1.04	0.44	6
June 21	172	54	0.00	-0.01	0.29	-0.04	0.37	6
July 9	190	44	0.05	-0.20 *	0.08	0.09	0.18	7
July 12	193	2	0.00	0.04	0.11	0.01	0.16	6
July 17	198	40	0.15	-1.28	0.87	-0.95	1.31	5
Medium Cells								
May 26	146	54	0.29	0.77 ***	0.09	0.16	0.12	6
May 28	150	44	0.56	0.36 ***	0.05	-0.13	0.06	5
June 10	161	14	0.75	-0.33 **	0.09	-0.37 *	0.12	5
June 11	162	18	0.01	0.14	0.17	0.03	0.20	4
June 12	163	27	0.08	0.31 ***	0.03	0.03	0.05	6
June 14	165	22	0.70	0.23 *	0.07	0.19	0.09	4
June 19	170	40	0.62	0.37 ***	0.03	-.13 **	0.04	6
June 21	172	54	0.66	0.04	0.04	-0.16 **	0.06	6
July 9	190	44	0.35	-0.13 ***	0.02	-0.07	0.04	7
July 12	193	2	0.02	0.17 *	0.07	-0.03	0.10	6
July 17	198	40	0.00	-0.08 **	0.02	0.00	0.04	5
Large Cells								
May 26	146	54	0.39	-0.60 **	0.18	-0.39	0.25	6
May 28	150	44	0.16	0.67 **	0.22	0.20	0.27	5
June 10	161	14	0.12	0.62 **	0.18	0.15	0.24	5
June 11	162	18	0.50	-1.70	1.38	-2.26	1.62	4
June 12	163	27	0.14	0.71 **	0.20	0.21	0.26	6
June 14	165	22	0.42	1.18	0.64	0.94	0.77	4
June 19	170	40	0.82	1.28 ***	0.22	1.24 ***	0.29	6
June 21	172	54	0.89	-0.13	0.15	-0.98 **	0.20	6
July 9	190	44	0.28	-0.04	0.14	-0.42	0.30	7
July 12	193	2	0.11	0.42 ***	0.07	-0.08	0.11	6
July 17	198	40	0.02	0.18	0.31	-0.10	0.47	5

Note: Small < 0.5 μm ; Medium 0.5-1.0 μm ; Large > 1.0 μm
Reported significance levels are designated as : * $\alpha < 0.1$, ** $\alpha < 0.05$, *** $\alpha < 0.01$.
g reported in the table is the regression slope multiplied by -1. Statistics reported for g correspond to slope measurements.

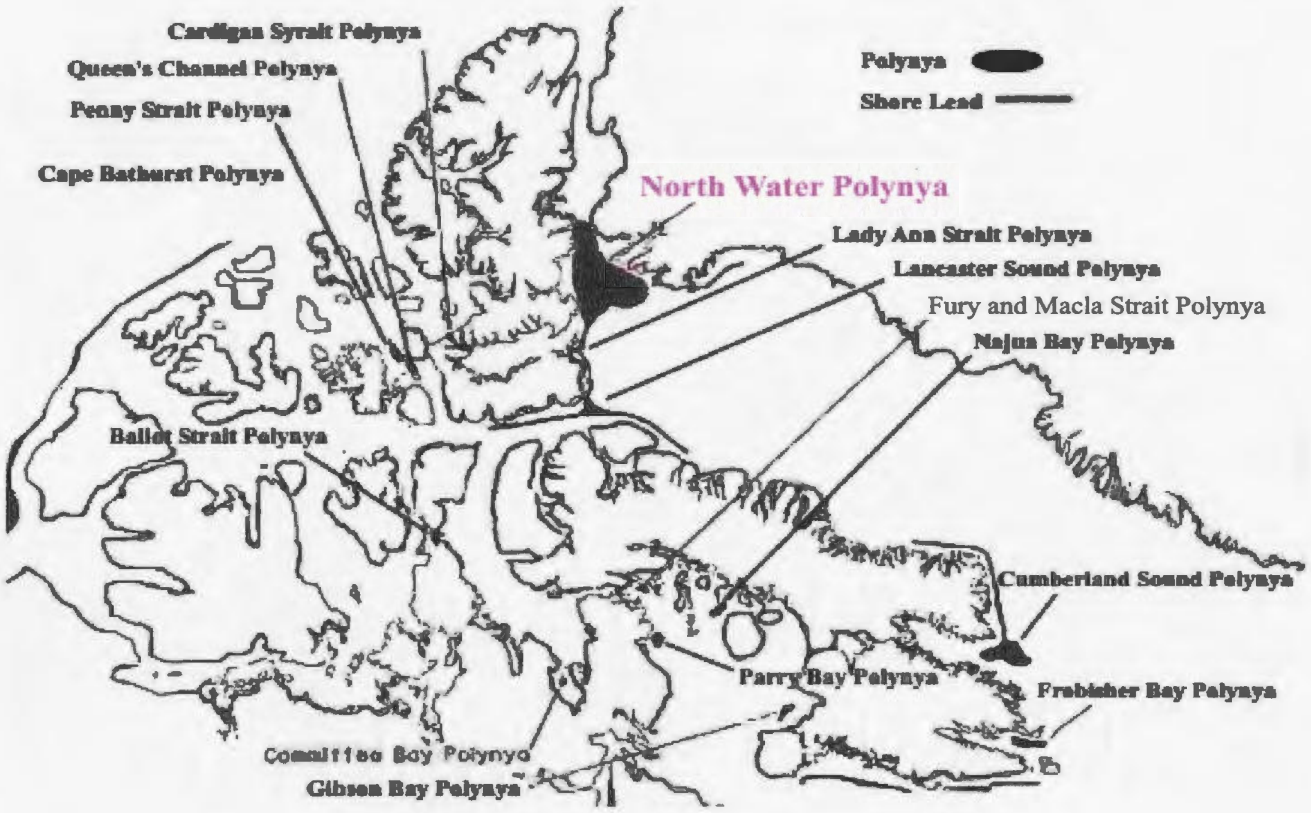

Figure 3.1 Geographical location of the North Water Polynya relative to other polynyas in the Arctic
Map source:http://www.fsg.ulaval.ca/giroq/now/

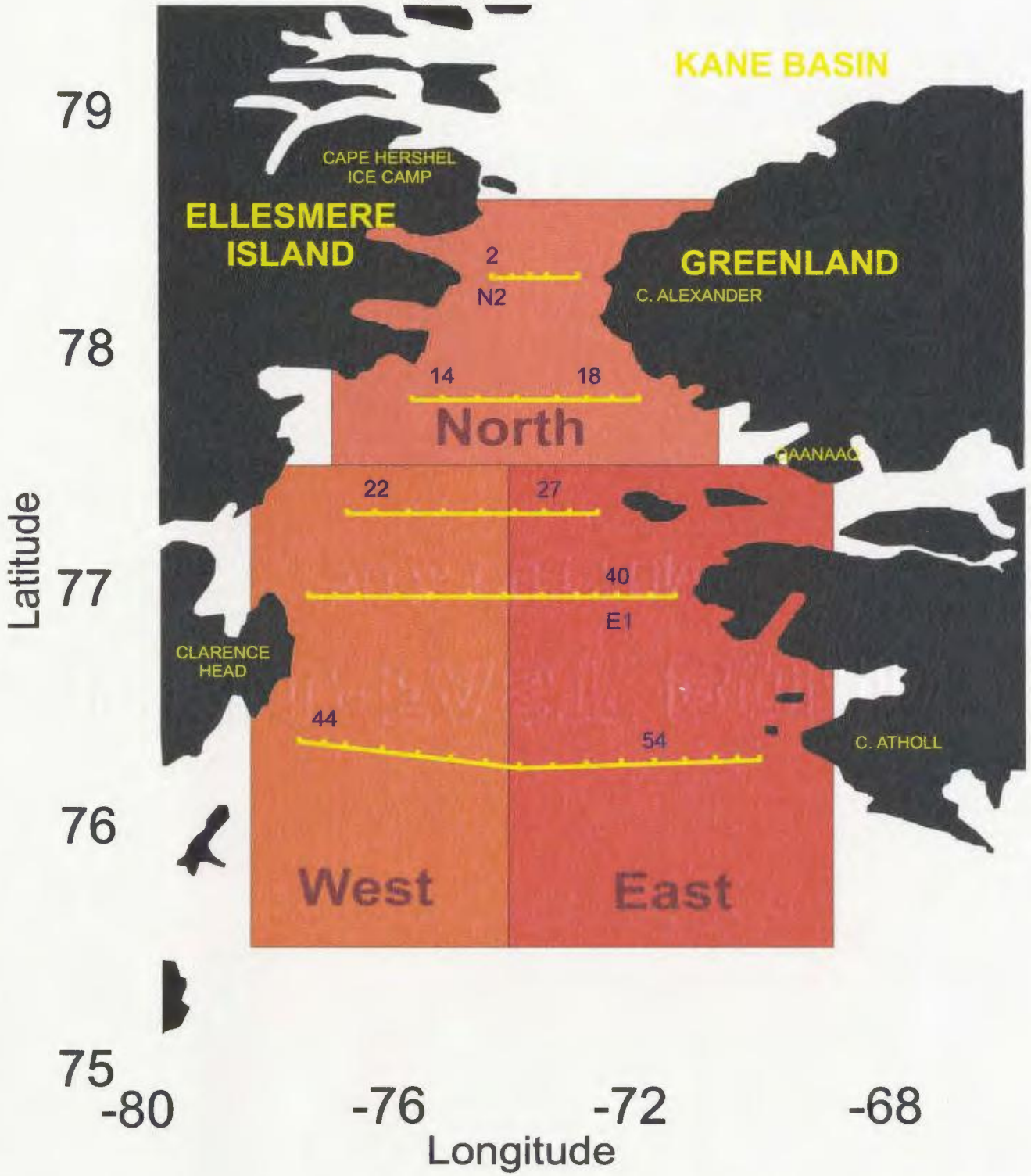

Figure 3.2 Map of the North Water Polynya showing transects with stations sampled for microzooplankton grazing experiments, and analysed with image analysis.

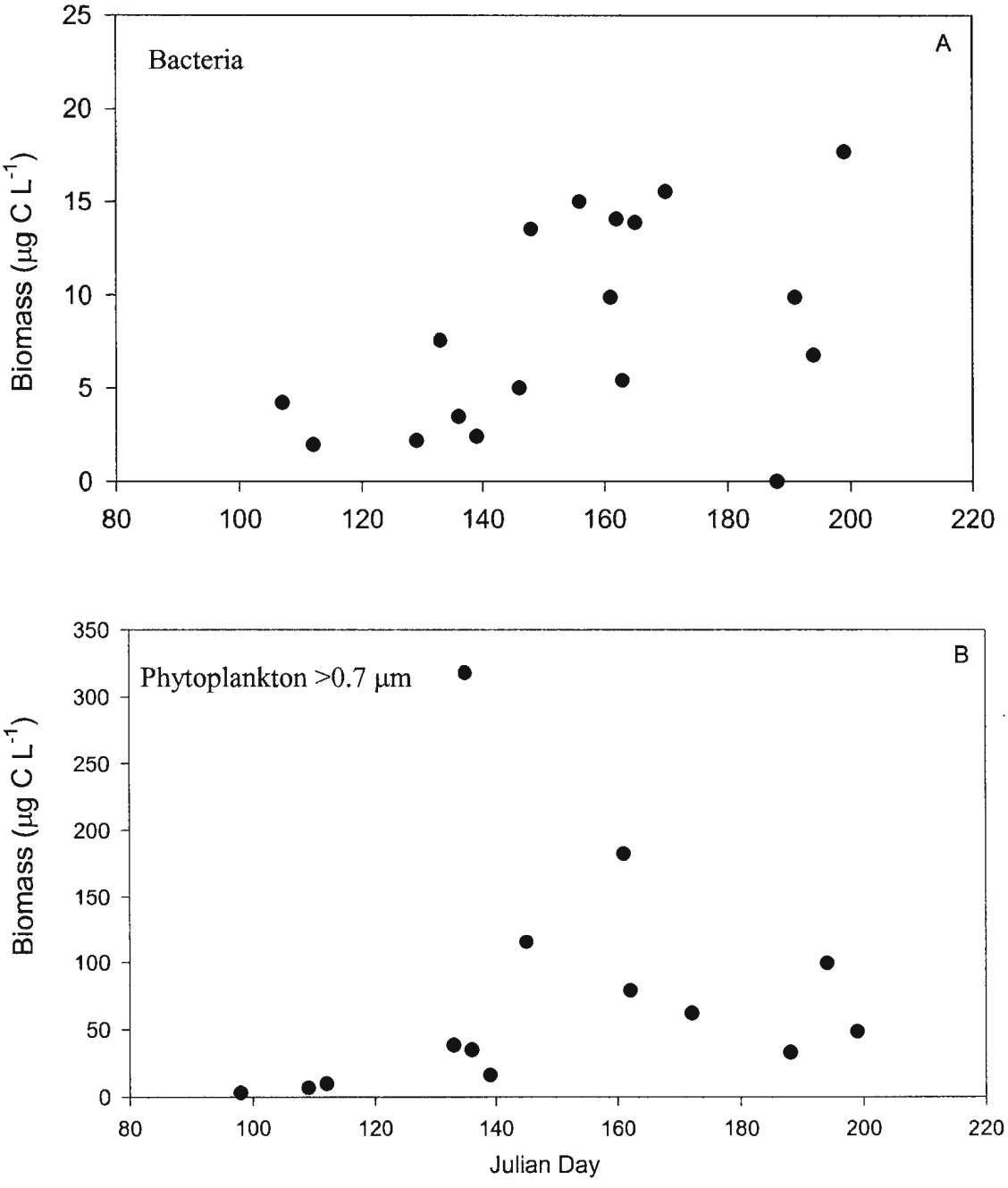

Figure 3.3 Bacteria and total chlorophyll *a* (>0.7µm) biomass, in the North Water Polynya at stations where dilution experiments were conducted from April through July, 1998

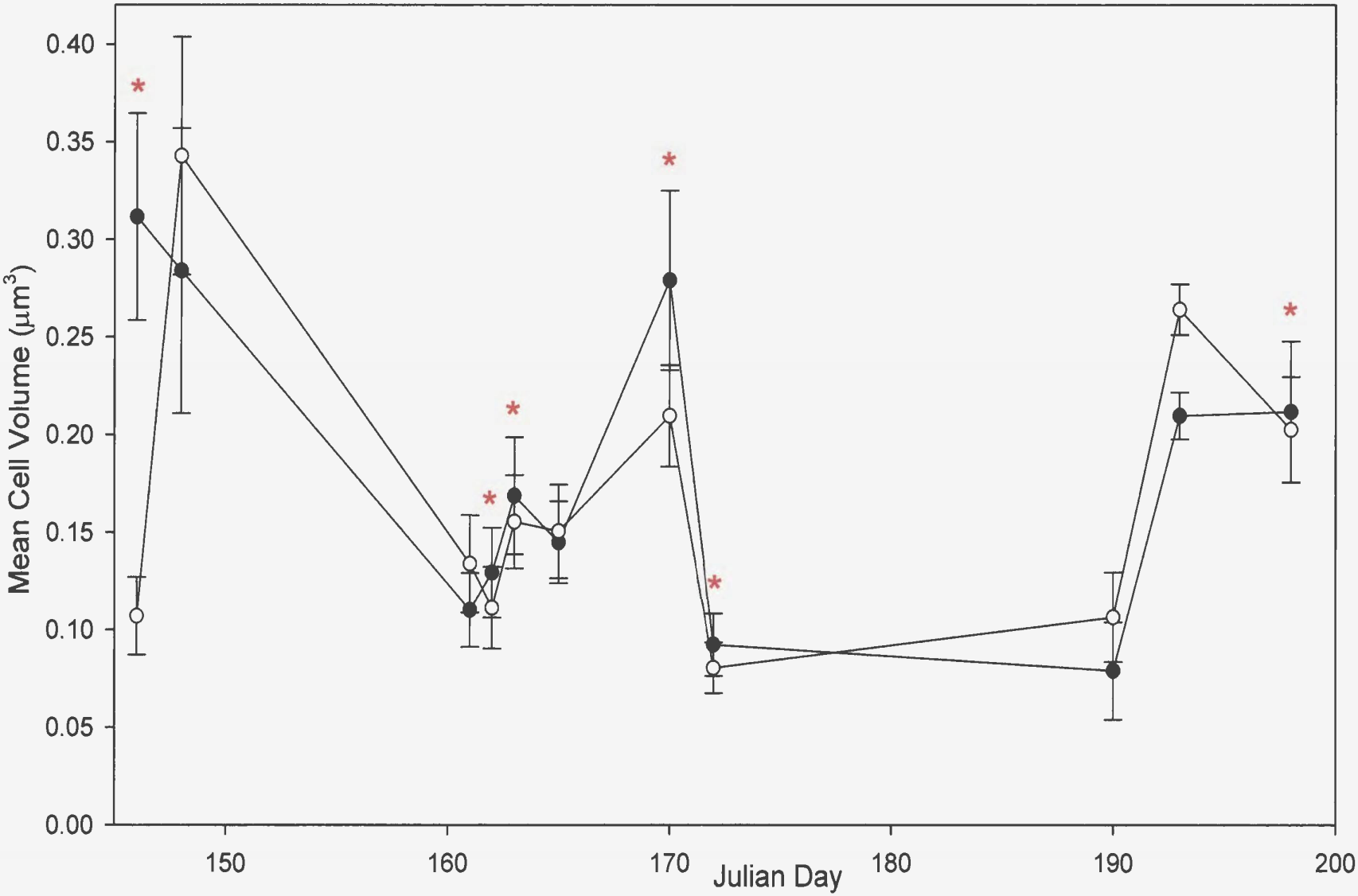

Figure 3.4 Mean cell volumes (MCV) of bacteria sampled throughout the North Water Polynya from May to July, 1998. Closed circles represent Initial MCV, and open circles represent final MCV. Asterisks (*) represent stations where experiments resulted in a decrease in MCV. Errors bars indicate the standard error.

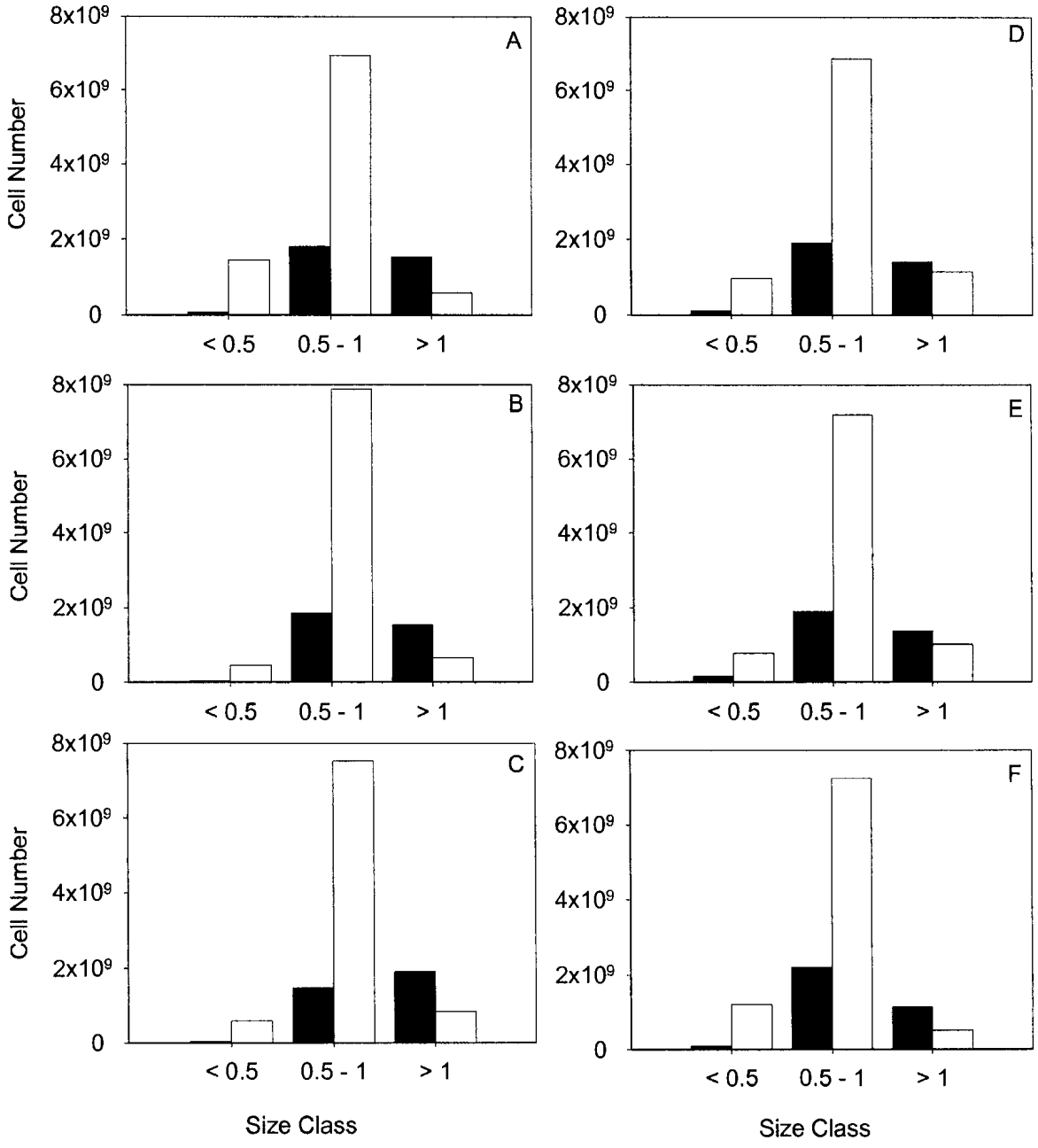

Figure 3.5 : Cell numbers in each size class at time of initial and final sampling on May 26th, 1998 (station 54). Graphs A-F represent various dilutions (25, 37.5, 50, 62, 90, 100% RSW). Filled bars are initial cell abundances and open bars are final cell abundances.

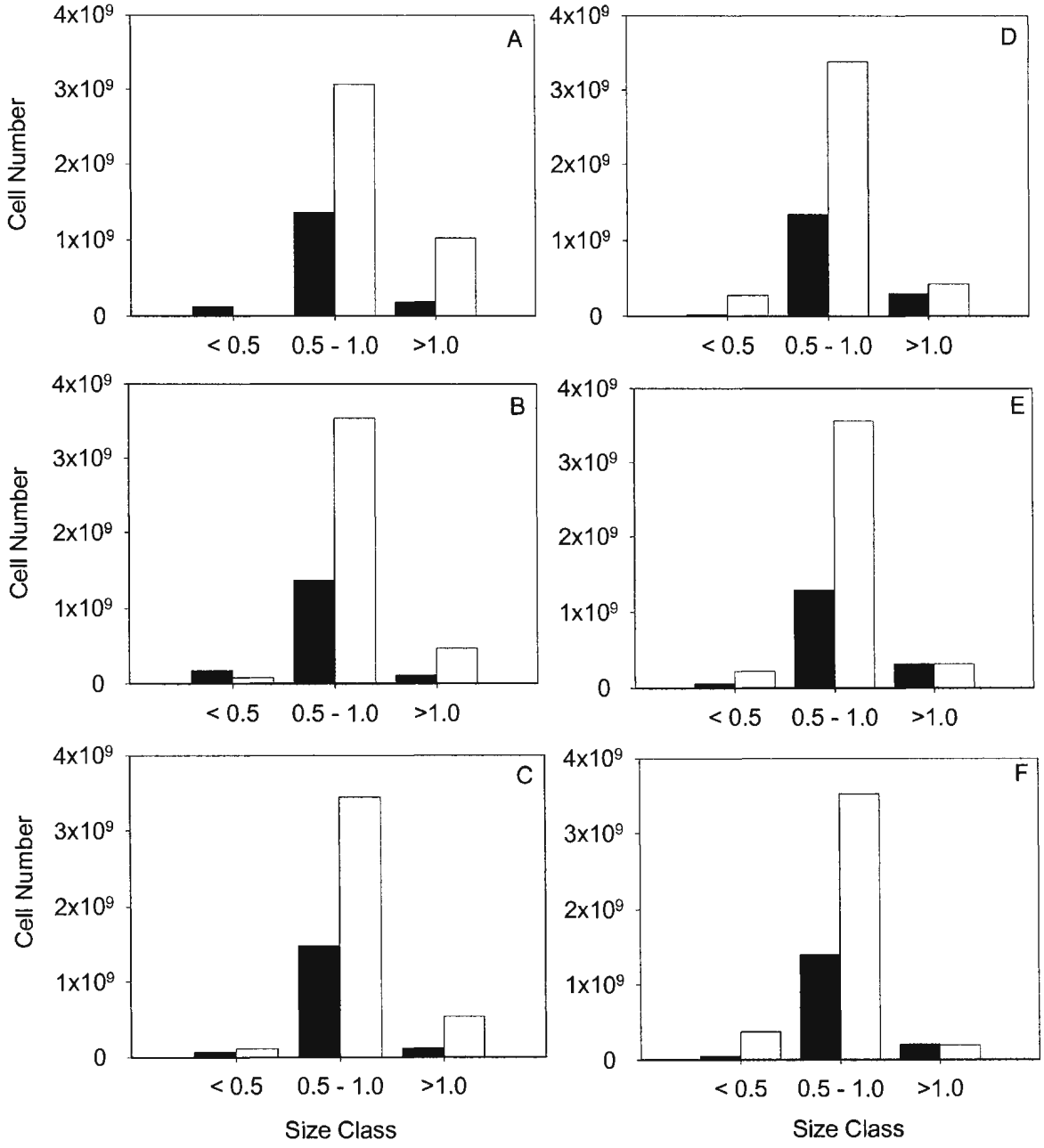

Figure 3.6 : Cell numbers in each size class at time of initial and final sampling on June 19th, 1998 (station 40). Graphs A-F represent various dilutions (25, 37.5, 50, 62, 90, 100% RSW). Filled bars are initial cell abundances and open bars are final cell abundances.

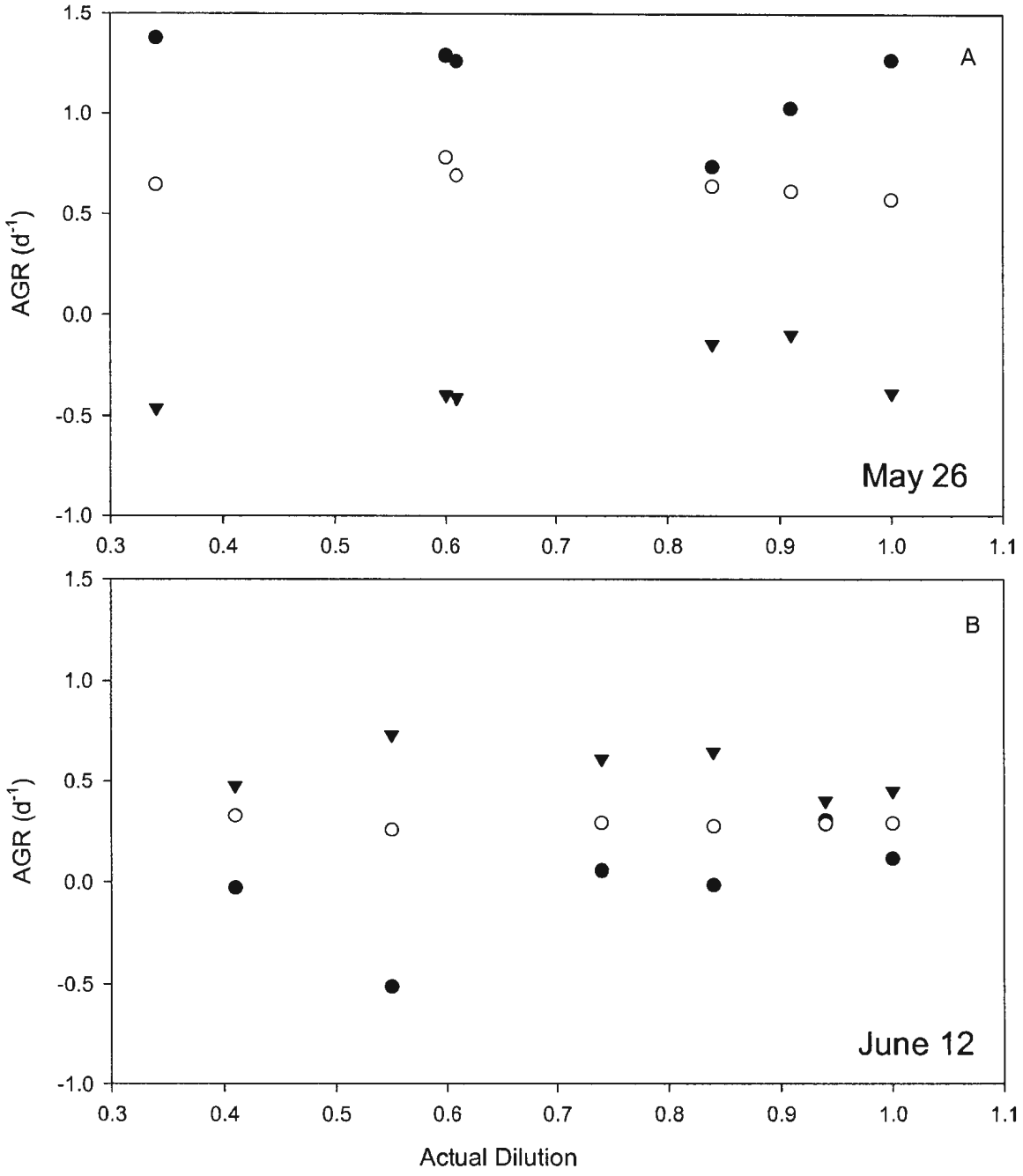

Figure 3.7 Two representative dilution plots of bacteria in the North Water Polynya in 1998. Three size classes are presented in each graph : small (<0.5 μm) closed circles; medium (0.5 - 1.0 μm) open circles; and large (>1.0 μm) closed triangles. Growth and grazing mortality for each size class are calculated from the regression between apparent growth rate (AGR) and actual dilution.

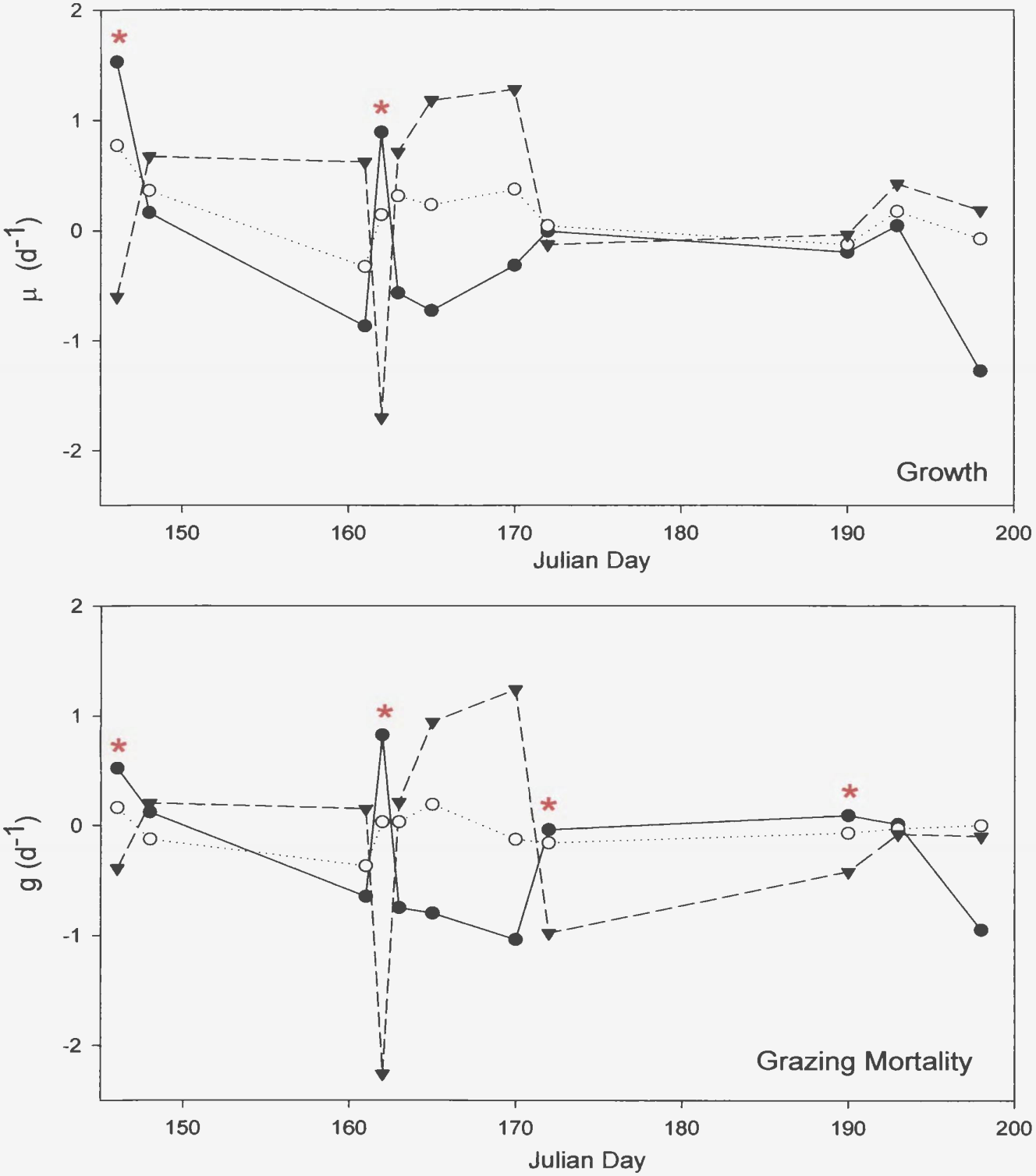

Figure 3.8 Rates of growth (μ) and grazing mortality rates (g) for three size classes of bacteria (Small <5 μm, closed circles; Medium 0.5 - 1.0 μm, open circles; Large > 1.0 μm, closed triangles) measured in the North Water Polynya from May to July , 1998. Asterisks (*) represents experiments of interest which are discussed in the text.

Appendix A

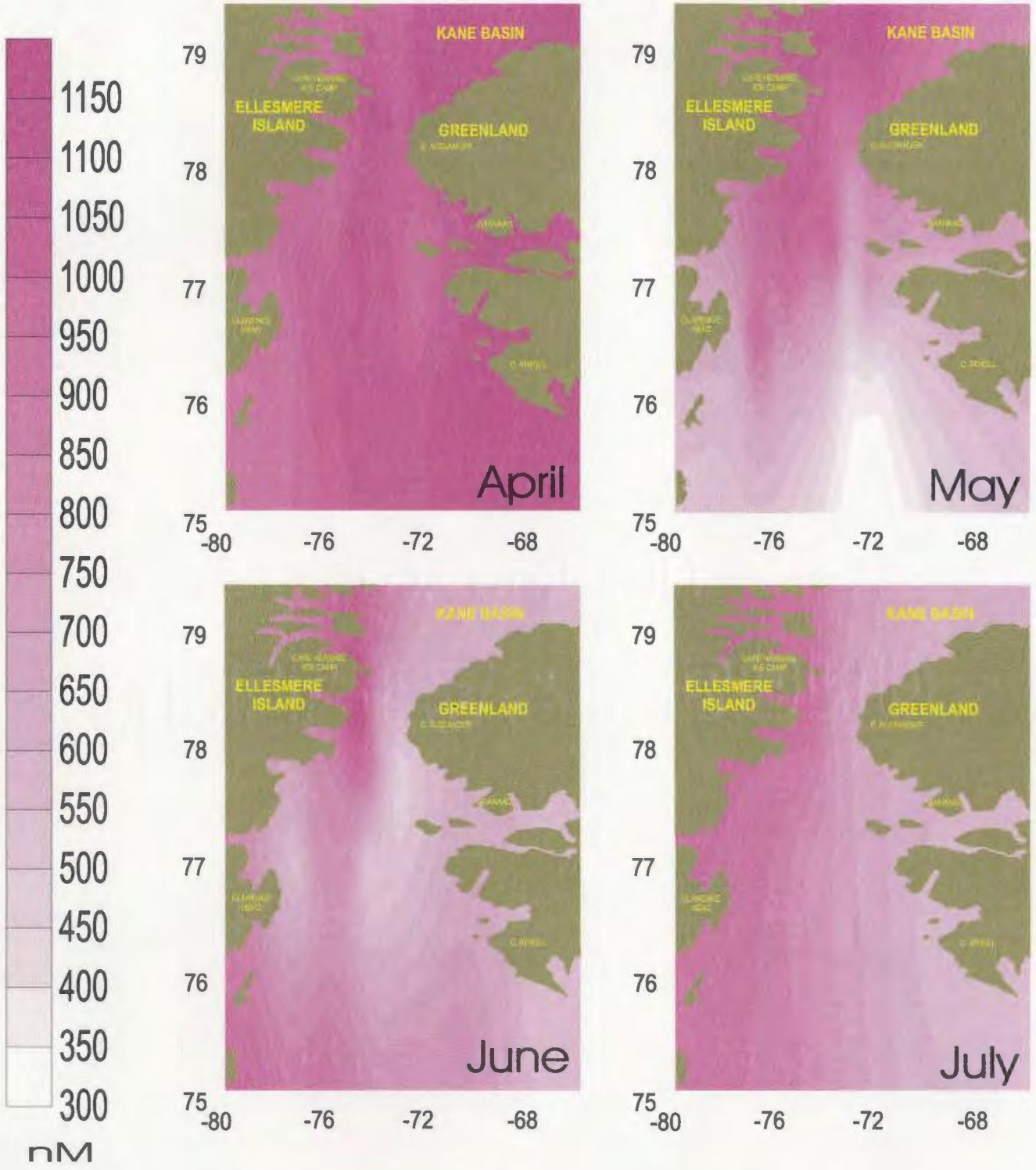

Figure A.1 Spatial patterns of inorganic nitrogen (Nitrate + Nitrite) concentrations measured in the North Water Polynya during April, May, June and July, 1998.

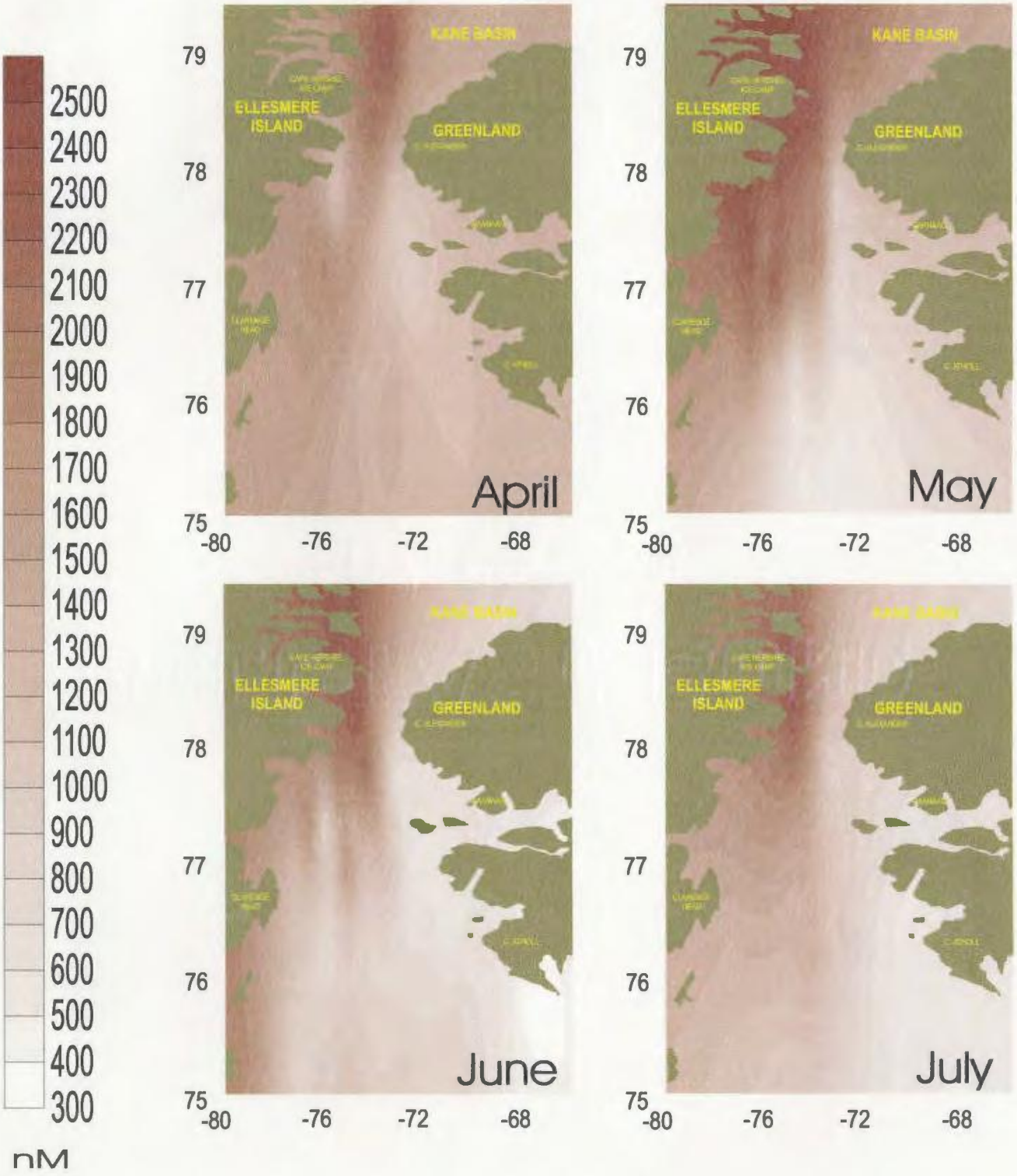

Figure A.2 Spatial patterns of silicate concentrations measured in the North Water Polynya during April, May , June and July,1998.

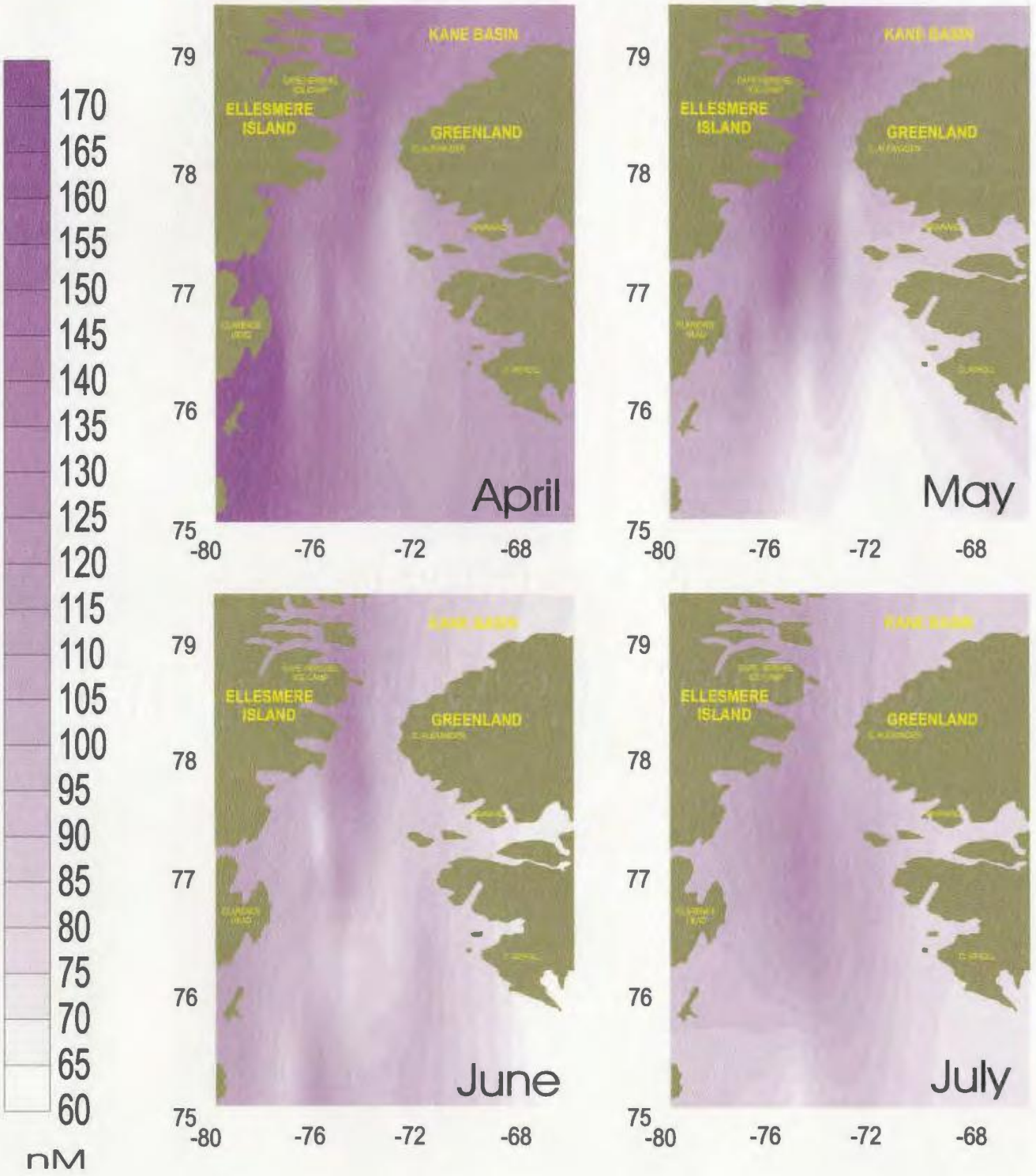

Figure A.3 Spatial patterns of phosphate concentrations measured in the North Water Polynya during April, May, June and July, 1998.

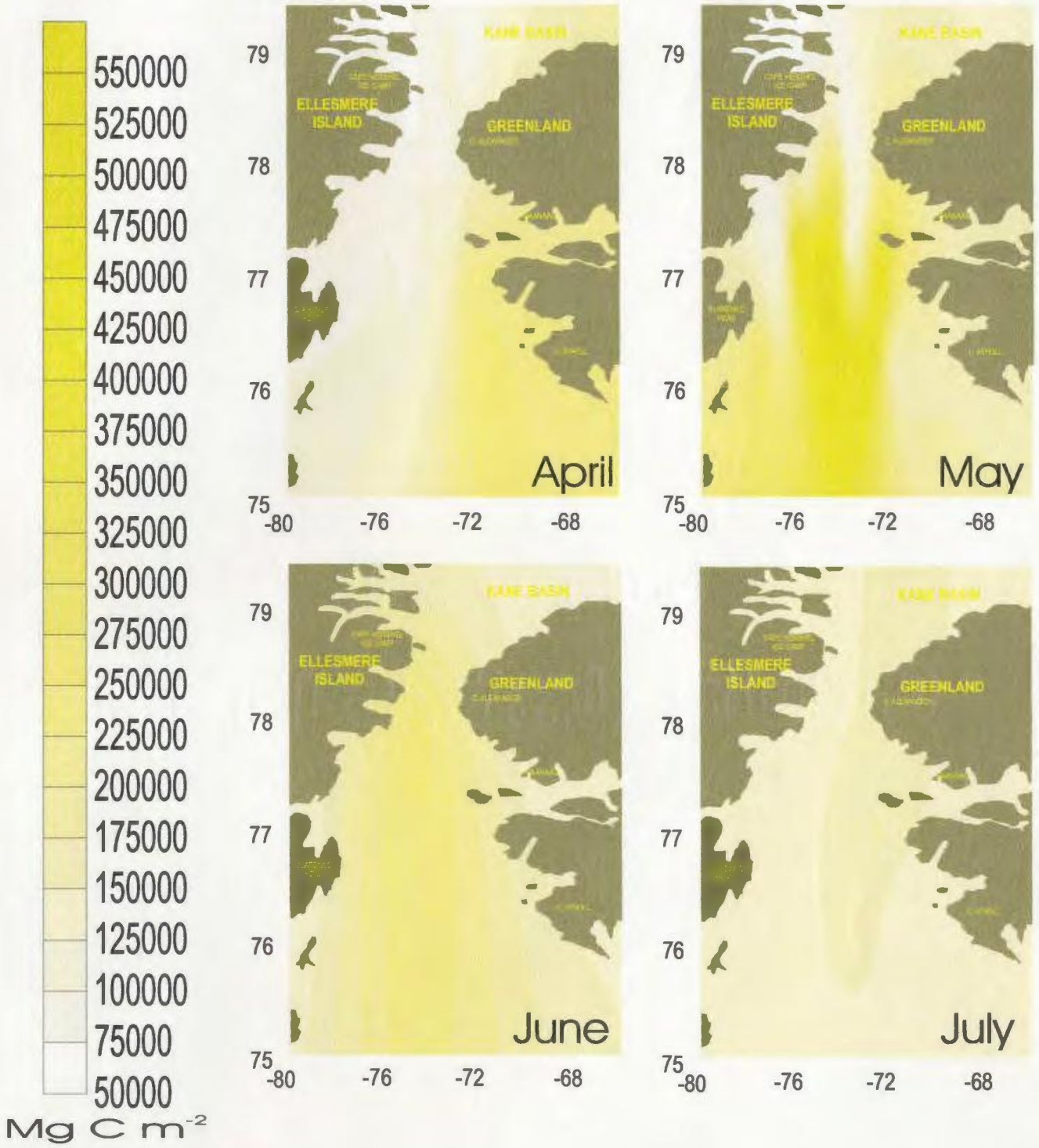

Figure A.4 Spatial patterns of Dissolved Organic Carbon (DOC) concentrations measured in the North Water Polynya during April, May, June and July, 1998.