MICROZOOPLANKTON BACTERIVORY AND HERBIVORY IN OCEANIC AND COASTAL ENVIRONMENTS: COMPARISONS OF THE SUBARCTIC PACIFIC WITH NEWFOUNDLAND COASTAL WATERS

JENNIFER NANCY PUTLAND

MICROZOOPLANKTON BACTERIVORY AND HERBIVORY IN OCEANIC AND COASTAL ENVIRONMENTS: COMPARISONS OF THE SUBARCTIC PACIFIC WITH NEWFOUNDLAND COASTAL WATERS

by

Jennifer Nancy Putland

A thesis submitted to the School of Graduate Studies in partial fulfilment of the requirements for the degree of

Master of Science

Department of Biology, School of Graduate Studies, Faculty of Science

Memorial University of Newfoundland

1997

St. John's Newfoundland

Abstract

A comparative analysis was used to estimate top-down control by microzooplankton on microbial prey and the relative ingestion of various prey by microzooplankton. Using the dilution technique (Landry and Hassett 1982), the rates of ingestion of autotrophic and heterotrophic picoplankton and total (>0.7 μm) phytoplankton by microzooplankton were measured during spring, summer, and winter from 1995 to 1996 in the surface layers of both the subarctic Pacific (SAP) and Newfoundland coastal waters (NCW). In the SAP, size fractionated dilution assays were also conducted to determine the ingestion by small (<35 μm) and large (<202 μm) microzooplankton. The microzooplankton grazing impact (measured as the percentage of prey potential production ingested) in the SAP was primarily by <35 μm protists and was greatest on bacteria, *Synechococcus*, and <35 μm phytoplankton. The mean values of potential production ingested by microzooplankton were ca. 109%, 123%, 65%, and 28% for bacteria, *Synechococcus*, <35 μm and 5-202 μm phytoplankton, respectively. In NCW, the mean values of potential production ingested by microzooplankton were ca. 88%, 167%, and 97% for bacteria, autotrophic picoplankton, and >0.7 μm phytoplankton, respectively. Total ingestion of microbial carbon varied seasonally in the SAP and NCW, with minimum (ca. 2 to 4 μg C· L^{-1} · d^{-1}) and maximum (6 to 13 μg C· L^{-1} · d in the SAP and ca. 20 μg C· L^{-1} · d^{-1} in NCW) total ingestion rates during winter and summer, respectively. In the SAP and NCW, autotrophic and heterotrophic picoplankton generally represented a large portion (>40%) of the

carbon ingested by microzooplankton. This was because microzooplankton generally ingested prey proportional to their availability and autotrophic and heterotrophic picoplankton represented most (>40%) of the microbial biomass. The comparative approach used in this thesis led to two important quantitative generalizations about microbial food web processes in subarctic waters. First, microzooplankton, on average, ingest ca. 80% and 100% of picoplankton (autotrophic and heterotrophic) and >0.7 μm phytoplankton potential production, respectively. Second, autotrophic and heterotrophic picoplankton represent ca. 69% of the carbon ingested by microzooplankton. These quantitative generalizations represent important advances in microbial ecology as they facilitate hypothesis testing and the detection of unusual systems.

Acknowledgments

I extend my deepest thanks to those who assisted me throughout this thesis. I thank the dive team at the Ocean Sciences Centre for collecting water samples in Logy Bay, Dr. Cynthia McKenzie and Cheryl Ledrew for advice and assistance in microscopy, Mike Riehl and Paul Matthews for lab assistance, and Eva Janes, Mark Howell, and Kelly Bennett for chlorophyll analyses. For their assistance, comradery, and sense of humour on cruises to Station Papa I thank Paul Matthews, Dr. Ken Crocker, Mike Lipsen, Hugh McLean, Nelson Sherry, Dr. Philip Boyd, Todd Mudge and the Captain and crew of the J.P. Tully. For allowing me access to the library at the Institute of Ocean Sciences, I thank Dr. Ken Denman. I also thank Drs. Robin Anderson, Don Deibel, and my supervisor Richard Rivkin for financial support, comments and advice. Finally, I am forever grateful to my family for their unwavering support and words of wisdom.

I dedicate this thesis to Charles Douglas Sauer,

for being a wonderful father.

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Chapter 1

General Introduction

1. 1. Marine pelagic food webs - from past to present

Our understanding of marine plankton community structure has evolved over the last twenty years. The flow of energy from producers to consumers was initially described using the herbivorous (or linear) food chain (Figure 1. 1A) (Steele 1974). However, this description of marine plankton community structure was shown to be incomplete when new methods and instruments revealed the quantitative importance of small autotrophic and heterotrophic microbes (Pomeroy 1992). Size fractionation and epifluorescence microscopy were two methods that were integral to the discovery of small microbes. Using size fractionation, pico- and nanophytoplankton were found to account for a large portion of autotrophic production and biomass (Malone 1971, Pomeroy 1974, Li et al. 1983, Platt et al. 1983). With the introduction of direct cell counts by epifluorescence microscopy, bacterioplankton and heterotrophic nanoplankton were recognized to be abundant and cyanobacteria (i.e. *Synechococcus*) were found to numerically dominate autotrophic picoplankton (i.e. picophytoplankton) (Hobbie et al. 1977, Johnson and Seiburth 1979, Waterbury et al. 1979, Davis and Seiburth 1982). The development of methods to estimate bacterial production (e.g. the frequency of dividing cell method and the tritiated thymidine incorporation method) also showed that bacterial production was ca. 20% of primary

production and assuming a growth efficiency of 50%, bacteria were estimated to consume up to 50% of primary production (Hagström et al. 1979, Fuhrman and Azam 1982).

Azam et al. (1983) were the first to conceptualize the quantitative importance of small autotrophic and heterotrophic microbes. They introduced the concept of a *microbial loop* wherein bacteria and cyanobacteria are ingested by flagellates and, in turn, flagellates are grazed by ciliates who are ingested by mesozooplankton (Figure 1. 1B). They suggested that the microbial loop returns energy (dissolved organic matter) released from phytoplankton to the herbivorous food chain. However, due to the number of trophic transfers from bacteria to higher trophic levels, a lively debate over whether the microbial loop is a *link* (i.e. source) or a *sink* (i.e. loss) of food for the herbivorous food chain ensued (Ducklow et al. 1986, Sherr et al. 1987). Sherr and Sherr (1988) later proposed that the microbial loop should not be considered separate from the herbivorous food chain because of the strong trophic link between microzooplankton (i.e. all protists and metazoans <202 μm in size) and phytoplankton (Sherr et al. 1986b). Sherr and Sherr (1988) introduced the concept of a *microbial food web* wherein microzooplankton ingest bacteria, cyanobacteria, as well as nano- and microphytoplankton and, in turn, are ingested by mesozooplankton (Figure 1. 1C). In this food web microzooplankton effectively repackage bacteria and autotrophs into parcels large enough to be ingested by mesozooplankton (Sherr and Sherr 1988, Gifford 1991). Recently, Legendre and Rassoulzadegan (1995) introduced the concept of a *multivorous food web* wherein

mesozooplankton omnivory and herbivory and microzooplankton herbivory and bacterivory co-occur (Figure 1. 1D).

1. 2. Microzooplankton grazing

Microzooplankton play an important role in marine pelagic food webs. Studies show that microzooplankton (1) exert top-down control on population levels of bacterioplankton and phytoplankton (Sherr et al. 1986b, Banse 1992, Sanders et al. 1992, Caron et al. 1991, Verity et al. 1996, Reckerman and Veldhuis 1997), (2) regenerate nutrients (Goldman and Caron 1985, Jumars et al. 1989, Caron 1991, Harrison 1992, Ferrier-Pages and Rassoulzadegan 1994a&b), and (3) transfer energy from microbial prey to higher trophic levels (Johnson et al. 1982, Pace et al. 1990, Stoecker and Capuzzo 1990, Capriulo et al. 1991, Pfannkuche and Lochte 1993). Yet, most of these studies have focused on either bacterivory or herbivory over short (e.g. days) time scales at one location (e.g. Table 3. 7). Such time, space, and prey specific studies hamper the development of generalizations about microbial food web processes (Pace 1991), which are important for ecosystem models (Fasham 1995). In this thesis, a comparative analysis, an approach considered essential for the development of generalizations (Pace 1991), was used to quantify top-down control by microzooplankton on various prey and the relative importance of carbon from various prey to microzooplankton in subarctic waters. Simultaneous field measurements of microzooplankton herbivory and bacterivory were

made over the seasonal cycles in two contrasting environments - Ocean Station Papa, subarctic Pacific and Logy Bay, Newfoundland coastal waters (Figure 1. 2). The potential implications of the results to the vertical export of biogenic carbon are discussed.

1. 3. The subarctic Pacific

The subarctic Pacific (SAP) has a surface layer with relatively low (ca. 33‰) salinity (Miller et al. 1991a). The resulting permanent halocline (at ca. 100 m) prevents rapid vertical mixing between the surface and deep layer (Miller et al. 1991a & refs. cited therein). As surface seawater temperature ranges from ca. 5 to 12°C (Miller et al. 1991a, Boyd et al. 1995a), a seasonal thermocline develops above the permanent halocline. Winter mixing of the surface layer with the zone between the seasonal thermocline and halocline increases surface layer nutrient concentrations (e.g. nitrate increases to ca. 17 μM) (Frost 1991). Despite the seasonal changes in nutrient concentrations (Frost 1991), levels of major nutrients remain high year round. For example, surface layer concentrations of nitrate, phosphate, and silicate are always $\geq$6, $\geq$0.2, and $\geq$14 μM, respectively (Miller et al. 1991b).

Standing stocks of phytoplankton do not show strong seasonal cycles as the annual range is 0.1 to 0.4 μg chlorophyll $a \cdot L^{-1}$. The SAP is therefore classified as a High Nutrient Low Chlorophyll (HNLC) region. The lack of a spring bloom is typical of HNLC regions (Cullen 1991, Banse 1996), but contrasts with our classical understanding of

pelagic production processes where high macronutrient concentrations in the surface layer coupled with strong seasonal stratification should lead to increased primary production (Miller 1993). The HNLC condition in the SAP is attributed to iron limitation and grazer control (Miller et al. 1991a&b, Frost 1991, Banse 1996). Iron limitation is thought to select a flora dominated by small (<5 μm) autotrophs that primarily utilize ammonium as a nitrogen source (Booth 1988, Wheeler and Kokkinakis 1990, Morel et al. 1991, Miller et al. 1991a&b, Miller 1993, Boyd et al. 1996). Top-down control of autotrophs is thought to be by microzooplankton (Strom and Welschmeyer 1991, Miller et al. 1991a&b, Landry et al. 1993, Miller 1993, Boyd et al. 1995b). Although data are scarce, microzooplankton may also be important consumers of bacterioplankton and *Synechococcus* (Strom and Welschmeyer 1991, Landry et al. 1993a, Kirchman et al. 1993, Booth et al. 1993). Microzooplankton may therefore be important bacterivores as well as herbivores in the SAP.

1. 4. Newfoundland coastal waters

Newfoundland coastal waters (NCW) are characterized as having two distinct oceanographic environments (Kendaris 1980). There is an inshore branch of the Labrador current at depth where temperatures range from -2°C to 1°C year round (Kendaris 1980, deYoung and Sanderson 1995) and a surface water mass which is influenced by atmospheric forces (Kendaris 1980). Surface layer seawater temperatures typically range

from -2 to 14°C (deYoung and Sanderson 1995). As in other subarctic locations, the structure of the water column and distribution of major nutrients in the surface layer follow the seasonal temperature cycle. For example, during winter the water column is isothermal (<0°C) and deep vertical mixing increases the concentration of major nutrients, such as silicate and nitrate, in the surface waters. In spring, when the solar energy absorbed by the ocean increases, a thermocline develops and restricts deep vertical mixing. As a result, major nutrients within the surface mixed layer, particularily silicate, are exhausted. Throughout the summer a strong thermocline (ca. 30 m) develops which further prevents replenishment of nutrients to the surface mixed layer from deep water. In the fall, solar energy decreases, surface water cools, winds increase, the thermocline breaks down (deYoung and Sanderson 1995), and nutrients are replenished to the surface waters.

Phytoplankton standing stocks are seasonally variable in NCW. High amplitude (≥3 μg chlorophyll *a* · L^{-1}) diatom blooms occur at the onset of density stratification in the spring (Crocker 1994, Redden 1994, Navarro and Thompson 1995, McKenzie unpubl.). Due to the generally low nutrient levels, North Atlantic waters are classified as Low Nutrient High Chlorophyll (LNHC) (Fasham 1995). After the spring bloom (ca. mid to late May), phytoplankton stocks remain at low (<0.5 μg chlorophyll *a* · L^{-1}) levels for the remainder of the year (June to April) and are dominated by pico- and nanophytoplankton (Crocker 1994). Stocks of bacterioplankton also remain at relatively low (ca. 3. 0 x 10^8 cells · L^{-1}) levels for most of the year, but increase (ca. 1. 0 x 10^9 cells · L^{-1}) during late

summer (Crocker 1994). The predominance of large diatoms during the spring bloom is due to the lack of nutrient limitation and the critical depth (the depth or level above which photosynthetic production for the water column equals the total respiration of the water column per unit surface area, Sverdrup et al. 1942) exceeding the mixed layer depth (also see Kuparinen and Kuosa 1993). In contrast, small autotrophs predominate phytoplankton stocks for the rest of the year because large autotrophs are nutrient limited (e.g. nitrate, silicate) from early summer to fall and light limited during winter (also see Kiørobe 1993).

The standing stocks of bacteria and phytoplankton are ultimately controlled by loss factors (Lehman 1991). Loss factors include advection, sinking, viral lysis and grazing mortality (Banse 1992). Sources of grazing mortality include that from micro- and mesozooplankton (Paranjape 1990, Urban et al. 1992, Urban et al. 1993a&b, McKenzie et al. 1995, Ohman and Runge 1994, Tamigneaux et al. 1997). No comprehensive study of microzooplankton grazing has been conducted in NCW. This may be because of the belief that the phytoplankton population consists of large cells that are not efficiently grazed by microzooplankton (Fasham 1995) and that surface seawater temperatures are too low (e.g. <0°C) for the microbial food web to be active (Pomeroy and Deibel 1986). Yet, studies show that microzooplankton can not only ingest large phytoplankton (Smetacek 1981, Strom and Strom 1996, Archer et al. 1996), but they are also important grazers of bacterioplankton and phytoplankton over a wide range of temperatures (e.g. <0°C to >10°C) (e.g. Wright and Coffin 1984, Sherr et al. 1986a, Campbell and Carpenter 1986,

Wikner and Hagström 1988, Kuosa 1990, Caron et al. 1991, Weisse and Scheffel-Möser 1991, Bernard and Rassoulzadegan 1993, Burkill et al. 1993a&b, Burkill et al. 1995, Landry et al. 1995a). Microzooplankton grazing may therefore be an important loss factor for bacterioplankton and phytoplankton in NCW.

1. 5. Biogenic carbon export

Vertical export of biogenic carbon from the ocean surface layer to depth is important to benthic fisheries and global climate change (Fenchel 1988, Legendre 1990). New production (i.e. production associated with oxidized nutrients such as nitrate) is assumed to be equivalent to organic matter sinking from the euphotic zone (Eppley and Peterson 1979, Eppley 1989, Platt et al. 1992). While a significant portion of new production can sink to depth as cell aggregates or within zooplankton feces (Neilsen and Richardson 1989, Legendre 1990), a portion of the production consumed within the euphotic zone is catabolized thereby releasing metabolic products including reduced nitrogen (Roman et al. 1988, Legendre and Gosselin 1989, Harrison 1992, Landry et al. 1993b, Kivi et al. 1996). This regenerated nitrogen is utilized by bacteria and small autotrophs (Harrison and Wood 1988, Suttle et al. 1990). It is generally assumed that due to their slow sinking rates and small size, regenerated production from these small organisms is recycled within the euphotic zone (Platt et al. 1989&1992). However, this paradigm neglects to consider that these small organisms can be packaged into rapidly

sinking particles. Bacteria and small autotrophs may not only be physically aggregated into fast-sinking marine snow (Goldman 1984, Goldman 1988), but they may also be ingested by mesozooplankton for export in fast-sinking mesozooplankton fecal pellets and body parts (Peinert et al. 1989, Noji 1991, Legendre et al. 1993, Fortier et al. 1994). Mesozooplankton may ingest bacteria and small autotrophs directly (Crocker et al. 1991, Flood et al. 1992, Alldredge and Madin 1992, Turner and Tester 1992, Legendre et al. 1993) or indirectly by ingesting microzooplankton (Stoecker and Capuzzo 1990, Gifford 1991, Pfannkuche and Lochte 1993). The export of regenerated production from bacteria and small autotrophs is not considered in models predicting biogenic carbon export. Clearly, neglecting to consider the export of this regenerated production could not only lead to inaccurate predictions of the amount of carbon available to benthic fisheries, but also the ocean's role in climate change.

1. 6. Thesis objectives

The primary objectives of this thesis were to develop quantitative generalizations about (1) top-down control by microzooplankton on various prey, and (2) the relative ingestion of various prey by microzooplankton in subarctic waters. Toward these objectives, this study measured and compared (1) microzooplankton top-down control on autotrophic and heterotrophic picoplankton and >0.7 μm phytoplankton, and (2) the relative ingestion of autotrophic and heterotrophic picoplankton and >0.7 μm

phytoplankton by microzooplankton from two contrasting environments - the SAP (Chapter 2) and NCW (Chapter 3). Sherr and Sherr (1994) have suggested that protistan herbivory is a more significant pathway of carbon flow in pelagic food webs than is bacterivory. Thus, the null hypothesis, *that the contribution of autotrophic and heterotrophic picoplankton to total carbon ingested by microzooplankton is less than that of >0.7 μm phytoplankton,* was rigorously tested by measuring the relative ingestion of autotrophic and heterotrophic picoplankton as well as >0.7 μm phytoplankton by microzooplankton over the seasonal cycle in the surface layers of Logy Bay, NCW (47° 38' 14"N, 52° 39' 36"W) and Ocean Station Papa, the SAP (50°N, 145°W) (Figure 1. 2).

To determine top-down control by microzooplankton and the relative ingestion of prey carbon by microzooplankton, the rates of growth and grazing mortality of microbial prey were measured using the seawater dilution technique (Landry and Hassett 1982). Similar methods were used in each environment so as to facilitate the comparison of the results. The results from the SAP and NCW were statistically compared (Chapter 4) with the aim of developing generalizations about microbial food web processes in subarctic waters.

Figure 1. 1. Schematics of proposed trophic interactions in marine pelagic food webs. Thick lines represent the perceived importance of a source of dissolved organic matter (DOM).

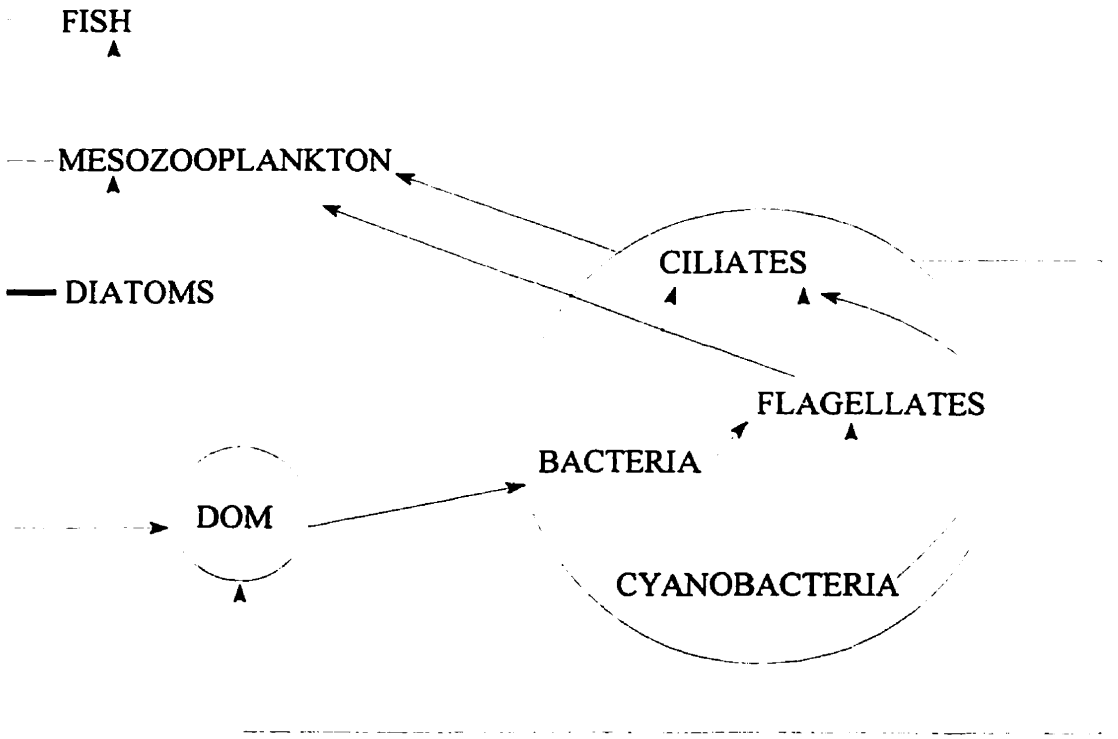
A. HERBIVOROUS FOOD CHAIN

FISH

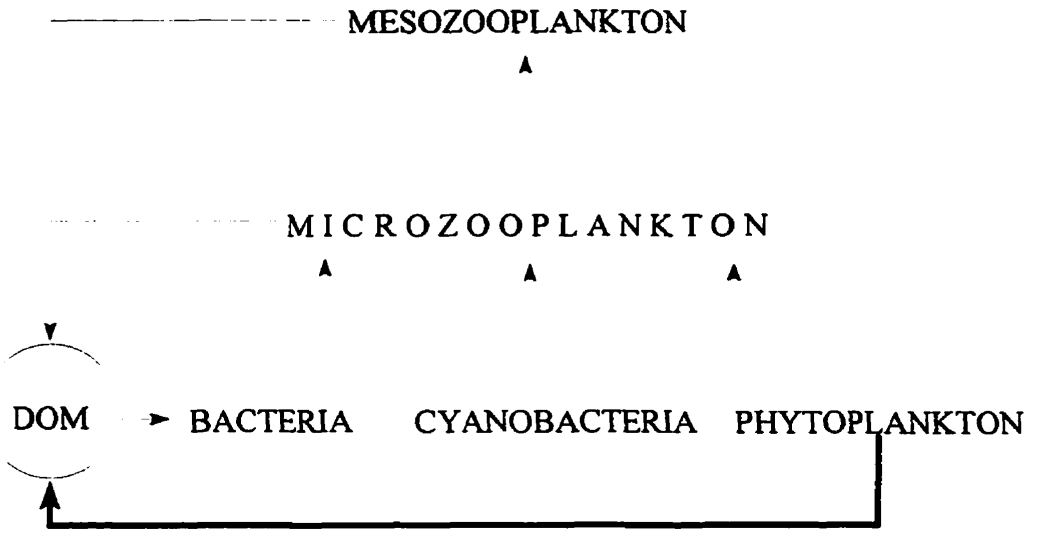
COPEPODS

DIATOMS

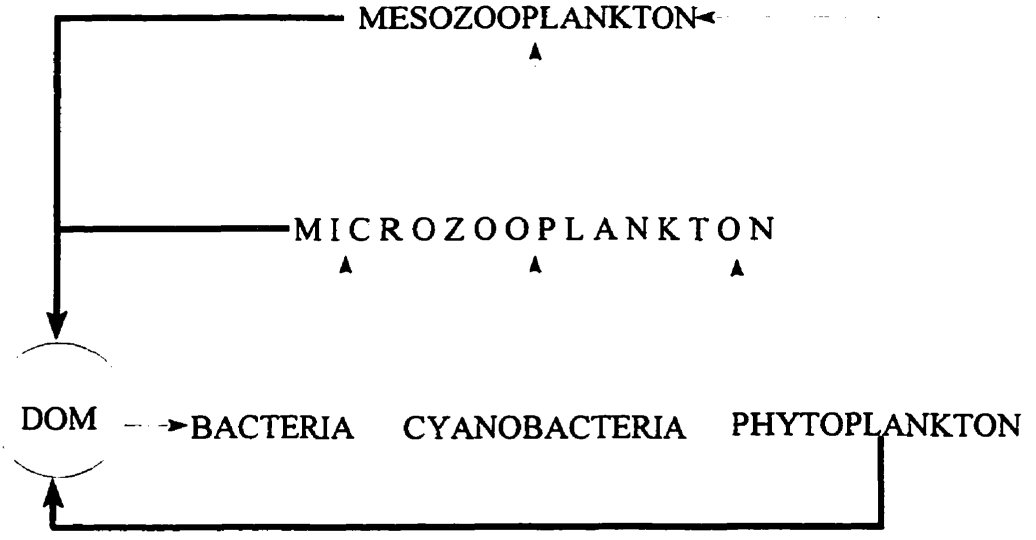
B. HERBIVOROUS FOOD CHAIN AND MICROBIAL LOOP



C. MICROBIAL FOOD WEB



D. MULTIVOROUS FOOD WEB



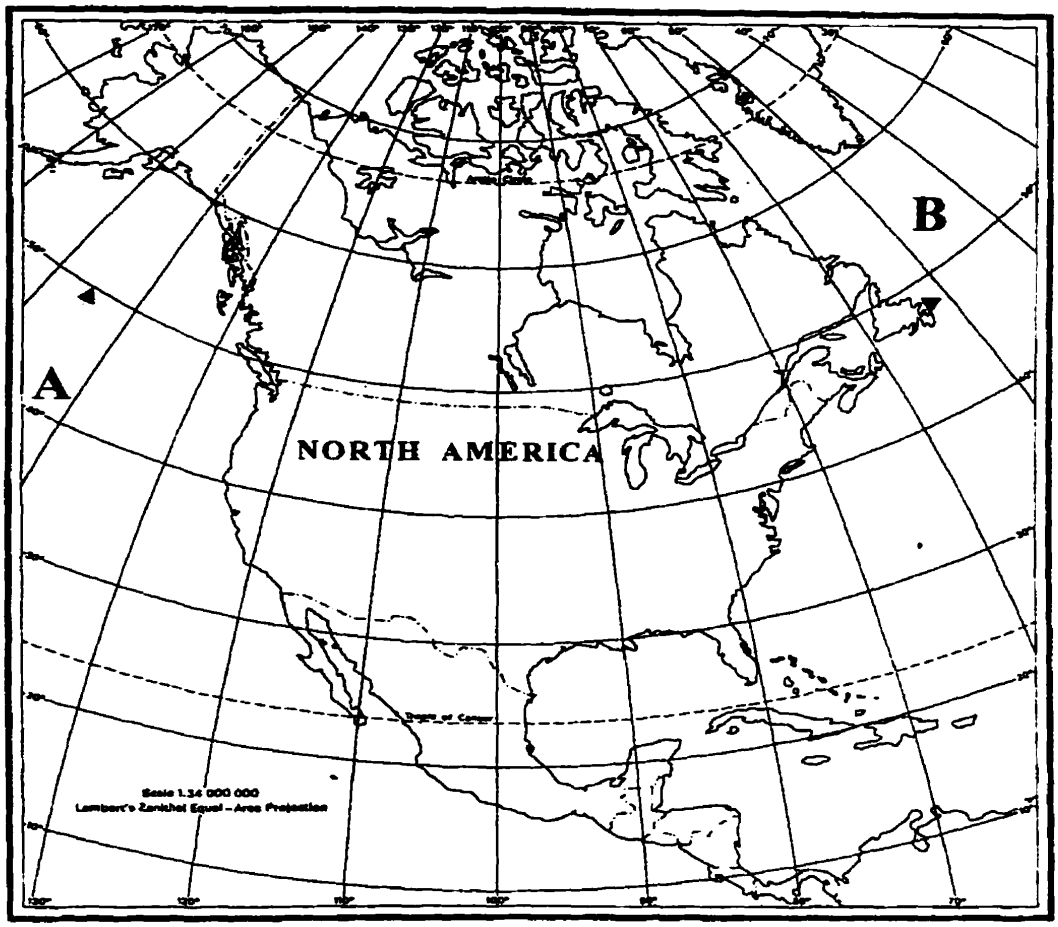


Figure 1. 2. Study sites for microzooplankton grazing studies were Ocean Station Papa (A) (50°N, 145°W) in the subarctic Pacific and Logy Bay (B) (46°38'14"N, 52°39'36"W) in Newfoundland coastal waters.

Chapter 2

Microzooplankton herbivory and bacterivory in the subarctic Pacific during spring, summer, and winter.

2. 1. Abstract

In High Nutrient Low Chlorophyll (HNLC) regions, such as the subarctic Pacific, phytoplankton rate processes and stocks appear to be constrained by nutrient availability and microzooplankton grazing, respectively. However, the role of microzooplankton in controlling other types of prey in HNLC regions has not been quantified. Using dilution assays, the rates of ingestion of autotrophic and heterotrophic picoplankton and both large (>5 μm) and small (<5 μm) phytoplankton by <35 μm and <202 μm microzooplankton were measured in the surface layer during May, September, and March at Ocean Station Papa (50°N, 145°W). Microzooplankton grazing impact (% potential production ingested) was primarily by <35 μm protists and was generally greatest on bacteria, *Synechococcus*, and <35 μm phytoplankton. The mean values of potential production ingested by microzooplankton were ca. 109%, 123%, 65%, and 28% for bacteria, *Synechococcus*, <35 μm and 5 to 202 μm phytoplankton, respectively. Total ingestion rates were greater in spring and summer (6 to 13 $\mu g \cdot L^{-1} \cdot d^{-1}$), than during winter (2 to 4 $\mu g\ C \cdot L^{-1} \cdot d^{-1}$). Most (53 to 100%) of the carbon ingested was derived from bacteria and *Synechococcus* and this is likely because microzooplankton generally ingested prey proportional to their

availability and bacteria and *Synechococcus* carbon predominated microbial stocks. These results, showing strong top-down control on both prokaryotic and eukaryotic prey year-round, support the idea that microzooplankton are the dominant grazers in the subarctic Pacific.

2. 2. Introduction

Early observations from Canadian Coast Guard weatherships patrolling Ocean Weather Station Papa (50°N, 145°W) have shown that phytoplankton standing stocks remain at low levels (0.1 to 0.4 chlorophyll $a \cdot L^{-1}$) all year. Due to the continuously high levels of macronutrients (e.g. silicate, nitrate, and phosphate) in the surface layers, the subarctic Pacific is one of the world's three HNLC (High Nutrient Low Chlorophyll) ocean regions. The lack of phytoplankton blooms in the subarctic Pacific is contrary to the classical understanding of pelagic production processes where the continuous availability of macronutrients in the surface layers, coupled with strong seasonal stratification, should allow phytoplankton stocks to bloom (Miller 1993). The historical explanation for the absence of phytoplankton blooms in the subarctic Pacific is the *major grazer hypothesis* (Miller et al. 1991a&b). This hypothesis states that large filter feeding copepods endemic to the region (*Neocalanus, Eucalanus,* and *Metridia*) are the principal grazers responsible for maintaining phytoplankton stocks at a low and constant level. In particular, Heinrich (1957) proposed that copepodites spawned from *Neocalanus* during late winter prevented the accumulation of phytoplankton biomass during spring. However, results from the Subarctic Pacific Ecosystem Research (SuPER) program do not support this hypothesis. According to Dagg's (1993) direct estimates and Frost's (1993) ecosystem model, the grazing capacity of the copepod community is insufficient during spring to control phytoplankton standing stocks.

Two hypotheses were put forth by the SuPER group to explain the HNLC condition in the subarctic Pacific. First, they proposed that iron limitation results in low production rates of large phytoplankton cells and a phytoplankton community dominated by small (<5 μm) cells that primarily utilize ammonium as a nitrogen source. Second, they proposed *the mixing and micrograzer hypothesis* wherein high rates of daily primary production are balanced by microzooplankton grazing pressure (Miller et al. 1991a&b, Frost 1991). The close coupling between phytoplankton production and microzooplankton grazing is thought to be maintained year-round due to the presence of the relatively shallow permanent halocline which permits phytoplankton growth and thereby a microzooplankton population (Evans and Parslow 1985, Miller et al. 1991a&b). Results from the SuPER project (Wheeler and Kokkinakis 1990, Strom and Welschmeyer 1991, Landry et al. 1993a) and other studies (Martin et al. 1989, Morel et al. 1991, Boyd et al. 1995b, Boyd et al. 1996) suggest that these two hypotheses are not mutually exclusive, but instead compliment each other.

Despite the significant contributions made by the SuPER project to our understanding of plankton dynamics in the subarctic Pacific, there is still a great deal to be learned about the rates and pathways of carbon flow in the region. For example, at what rate are small (<5 μm) and large (>5 μm) phytoplankton ingested by small (<35 μm) and large (<202 μm) microzooplankton? Also, are the large stocks of autotrophic and heterotrophic picoplankton (Booth et al. 1993, Kirchman et al. 1993) ingested by

microzooplankton in the surface layer? Certainly, in other marine environments microzooplankton are vigorous grazers of bacterioplankton and *Synechococcus* (e.g. Wright and Coffin 1984, Burkill et al. 1993a). If picoplankton are ingested, at what rate are they ingested by small and large microzooplankton and are phytoplankton ingested at a faster rate than picoplankton? Neglecting to consider the ingestion of picoplankton by microzooplankton may confound our interpretation of the rates and pathways of carbon transfer in the surface layers of the subarctic Pacific.

To improve the understanding of carbon flow in this system, I measured the ingestion of bacterioplankton, *Synechococcus*, <5 μm, >5 μm, and total (i.e. >0.7 μm) phytoplankton (as measured by chlorophyll *a*) by <202 and <35 μm microzooplankton at Ocean Weather Station Papa during spring, summer, and winter. The results show that grazing activity was primarily by <35 μm microzooplankton and was generally greatest on bacteria, *Synechococcus*, and <35 μm phytoplankton. The results also show that bacteria and *Synechococcus* represented most of the carbon ingested. The implication of these results to food web structure and vertical carbon export are discussed.

2. 3. Materials and Methods

2. 3. 1. Study site

Sampling was carried out in the subarctic Pacific. The subarctic Pacific has a surface layer with relatively low (ca. 33 ‰) salinity (Miller et al. 1991a). The resulting permanent halocline (at ca. 100 m) prevents vertical mixing between surface and deep layers (Miller et al. 1991a & refs. cited therein). Surface seawater temperatures range from ca. 5 to 12°C and the surface mixed layer depth ranges from 15 to 100 m (Parsons and Lalli 1988, Miller et al. 1991a&b).

2. 3. 2. Seawater collection

Before equipment contacted seawater it was soaked overnight in 5% HCL and then copiously rinsed with Nanopure water. Tubing (Fisherbrand clear plastic) was soaked for another night in seawater (Price et al. 1986). Gelman and Nitex filters were sequentially rinsed with Nanopure water and seawater immediately before use. Vinyl gloves were worn whenever water was handled.

Seawater for dilution assays was collected at Ocean Station Papa (OSP 50°N, 145°W) (Figure 2. 1) aboard the *J.P. Tully*. Prior (8-12 h) to initiating dilution assays, water for preparing the diluent was collected from 40 m using 10-L Go-Flo bottles (attached to Kevlar line) and transferred into polycarbonate carboys. This seawater was serially gravity filtered through a 10 μm Nitex screen and 0.2 μm Gelman capsule filter

and collected into a polycarbonate carboy. Approximately 1 h prior to starting the dilution assays, water was collected from the surface mixed layer (ca. 10 m) using a 10-L Go-Flo (General Oceanics) CTD/rosette system. As phytoplankton growth is maximal at this depth (Booth et al. 1988), this water was used to prepare the size fractionated (<35 μm or <202 μm) microbial populations (see details below). The Niskin bottles were drained from large-bore valves through tubing into polyethylene buckets and the water gently transferred into a 230-L Nalgene tank. The concentration of chlorophyll *a* and densities of bacterioplankton, *Synechococcus*, and protists in the 230-L tank were determined as described below.

2. 3. 3. Set-up for dilution assays

Once the particle free water (PFW) was prepared, appropriate volumes were added to 4 L polycarbonate cubitainers to dilute the <35 μm or <202 μm size fractionated water to eight target dilutions of 90, 80, 70, 60, 50, 25, 10, and 0% (PFW: <35 μm or <202 μm size fractionated water). The <35 μm and <202 μm size fractionationed water was prepared by dispensing the freshly collected seawater from the 230-L tank through tubing that was equipped with the appropriate size Nitex screening. To reduce damaging microzooplankton during the filling process, the tubing was submerged below the waterline in the 4-L polycarbonate cubitainers. After filling, the cubitainers were incubated on deck for ca. 48 h in a flowing surface seawater incubator with incident irradiances

attenuated to ca. 33% of ambient using neutral density screening.

2. 3. 4. Sampling dilution assays

The concentration of chlorophyll *a* and abundances of bacteria, *Synechococcus*, and protists in all cubitainers were determined after an incubation of ca. 4 h (hereafter referred to as time zero) and 48 h. The 4 h acclimation period was incorporated into the sample design because large and disproportionate changes in prey abundances have been observed to occur within the first few hours of preparing dilution assays (Anderson and Rivkin 1998, Rivkin unpubl.). Samples (500 mL) were preserved in alkaline Lugol's (final concentration 1% by volume) and stored at room temperature in the dark; whereas 250 mL samples were preserved in glutaraldehyde (1.5% final concentration) and stored in darkness at 4°C (Sherr and Sherr 1993). Particulate material was collected onto 25 mm GF/F and 5 μm Poretics filters, respectively at <127 mm Hg vacuum and stored in darkness at -20°C until extracted for chlorophyll *a*. During August 1995, duplicate (250 mL) seawater samples were filtered for estimating chlorophyll *a*. Since the coefficient of variation between the replicate filters was less than 5% (n=100), single 500 mL samples were filtered in 1996. In addition, during 1996 cruises 500 mL samples were filtered onto 5 μm Poretics filters to determine the concentration of >5 μm chlorophyll *a*. The concentration of <5 μm chlorophyll *a* was then calculated as the difference between total (>0.7 μm) and >5 μm chlorophyll *a*.

2. 3. 5. Sample analysis

Within 3 months of sample collection, chlorophyll *a* from filters was extracted in 90% acetone for ca. 18 h at -20°C. Chlorophyll *a* concentration was measured fluorometrically (Parsons et al. 1984) using the acid ratio method with a Sequoia-Turner fluorometer that was calibrated with pure chlorophyll *a* (Sigma Chemical Co., St. Louis, MO, USA).

Abundances of bacteria, *Synechococcus*, and nanoflagellates were determined from the glutaraldehyde preserved samples using a BH2-RFC Olympus epifluorescence microscope. Within 3 months of sample collection, water was filtered onto 0.2 μm black polycarbonate (Poretics) filters and stained with acridine orange for bacterial counts (Hobbie et al. 1977). Bacteria were counted at a magnification of 1000x using blue excitation (BP440, DM455, AFC+Y475). Nanoflagellates were stained with Primulin (Caron 1983) and counted on the same 0.4 μm black polycarbonate filters as were used to count *Synechococcus* (Sherr et al. 1993). Nanoflagellates and *Synechococcus* were counted at a magnification of 600x. Cells were visualized using UV (UG1, DM400, L420) and green excitation (BP545, DM570, O590) for nanoflagellates and *Synechococcus*, respectively (MacIsaac and Stockner 1993, Sherr et al. 1993). *Synechococcus* were identified as fluorescing orange coccoid cells that had a diameter of ca. 0.5 μm. Only heterotrophic nanoflagellates (i.e. cells without chlorophyll *a* fluorescence under blue excitation) were counted (Caron 1983). For the August-September 1995 cruise, slides for

nanoflagellates and *Synechococcus* were prepared and counted within 3 months of collection. During the February-March and May cruises, slides were prepared at sea (within 48 h of sample collection) and stored at -20°C until counted (ca. 1 mo). For bacteria and *Synechococcus*, a minimum of 200 cells (ca.10 random fields counted; Coefficient of Variation=20%) were counted per filter (Kirchman 1993). Reported cell abundances (Tables 2. 1 and 2. 2) are the mean of abundances estimated from duplicate filters. A total of about 100 to 200 nanoflagellate cells (i.e. flagellates <20 μm in size) were counted in random fields on one filter and this generally represented ca. 1% of the filter area.

Abundances of ciliates and dinoflagellates were determined from the Lugol's preserved samples by the Utermöhl method using phase contrast on a Zeiss Axiovert 35 inverted light microscope. Each 500 mL sample was first settled for 8 d and then concentrated to 50 mL by gently aspirating the supernatant. The concentrated samples were settled in 50 mL chambers for 48 h (Hasle 1978). Ciliates and dinoflagellates were counted in random fields at a magnification of 400x. A total of 200 cells (ciliates plus dinoflagellates) was enumerated for each sample (Venrick 1978a). Dinoflagellates made up most (ca. 58-100%) of the cells counted. On average, 10% of the chamber area was counted per sample.

2. 3. 6. The dilution method

The dilution method (Landry and Hassett 1982) simultaneously estimates the rates of growth and grazing mortality of a microbial prey population in the presence of grazers. In principle, a seawater sample is diluted with particle-free seawater in varying rations of seawater to particle-free diluent. It is assumed that prey growth is density independent, whereas grazing mortality is density dependant. Each incubation vessel in the dilution series yields an independent estimate of the prey apparent growth rate (AGR) calculated using equation 1,

$$AGR\ (d^{-1}) = 1/t\ [ln\ (P_t/P_o)] \qquad (1)$$

where t is the duration of the incubation in days and P_o and P_t are the sizes of initial and final prey stocks per litre (estimated from chlorophyll *a* or cell counts), respectively. The rates of prey growth and grazing mortality are estimated by the linear regression of AGR versus dilution factor (DF) (Figure 2. 2A). The *y*-intercept of the regression is the prey growth (μ, divisions $\cdot$ d^{-1}) in the absence of grazing, whereas the slope of the regression estimates mortality (g, d^{-1}) due to microzooplankton grazing.

2. 3. 7. Statistical analysis

For each dilution assay, the rates of μ and g were determined using the method of Landry and Hassett (1982). Model I linear regressions were conducted for each prey type

(i.e. bacterioplankton, *Synechococcus*, total and <5 μm and >5 μm chlorophyll *a*) in each <35 μm and <202 μm size fractionated assay. However, prey AGR was regressed against the actual dilution factor (ADF) rather than the target dilution factor (TDF). The ADF was calculated using equation 2,

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

where Chl a_o (X_i) is the time zero chlorophyll *a* concentration at target dilution factor X_i and Chl a_o (X_o) is the time zero chlorophyll *a* concentration of the unmodified (i.e. 0% PFW) treatment. Chlorophyll *a* was used to determine the ADF due to the greater precision in estimating chlorophyll *a* (CV ~ 5%) as opposed to cell counts (CV ~ 20% for bacteria or *Synechococcus*). Since the ADF is a direct estimate of the dilution factor, it is likely to be a better proxy for grazing intensity than the TDF - especially if grazer clearance rates and densities do not change significantly during the course of the dilution assay (Landry et al. 1995b).

In cases where the relationship between AGR and ADF was non-linear, piecewise linear regression was used to estimate the rates of growth and grazing mortality. Piecewise linear regression was used for non-linear plots as non-linear funtional responses of microzooplankton to varying food concentration can compromise simple linear regression analysis (Landry 1994). For example, the dilution gradient may reduce prey densities

below the threshold level and elicit reduced clearance rates. If simple linear regression procedures are used, then prey growth and grazing mortality will be overestimated (Gifford 1988, Landry 1994). Piecewise linear regression was performed by decomposing the dilution plot into two regions, a region with a significant negative slope and a region where the slope was not significantly different from zero, around an inflection point (Figure 2. 2B). The point of inflection was determined as the dilution factor where the coefficient of determination (r^2) changed by more than 40%. Prey growth was estimated using the relationship between AGR and ADF for the region with the negative slope. The *y*-intercept of this regression was assumed to be the rate of prey growth. Prey grazing mortality was estimated using equation 3,

$$g = \mu\text{-}AGR_{mean} \qquad (3)$$

where AGR_{mean} is the mean AGR of the region with no slope.

For each prey type, Analysis of Covariance (ANCOVA) was used to test whether there were significant differences for either μ or g among <35 μm and <202 μm size fractionated dilution assays (Sokal and Rohlf 1995). If there were significant differences for either μ or g among the size fractions, then size fractions were analyzed separately. However, if there were no significant differences for μ and g among the size fractions, then the data for the different size fractions was combined and μ and g determined from

the regression analysis of the pooled data set. A significance level of $P<0.10$ was used for conservative ANCOVA tests (Sokal and Rohlf 1995).

During the February-March and May 1996 cruises, μ and g of <5 μm and >5 μm chlorophyll *a* were estimated in both the <35 μm and <202 μm dilution assays. Prior to testing whether μ or g for the different size fractions of chlorophyll *a* were significantly different among <35 μm and <202 μm dilution assays (as described above), ANCOVA was used to test whether μ or g were significantly different within each size fractionated dilution assay. For the August- September 1995 and May1996 cruise results, ANCOVA was also used to test whether there were significant differences in either μ or g among among days and depths, respectively for each prey type.

2. 3. 8. Microzooplankton grazing impact

The grazing impact on microbial prey by the microzooplankton community was estimated by calculating microbial prey net growth rates per day (NGR, d^{-1}), percentage of potential production ingested per day (% P_p, d^{-1}), percentage of standing stock ingested per day (%P_o, d^{-1}), and daily ingestion rate of microbial carbon (I_c, μg Carbon $\cdot L^{-1} \cdot d^{-1}$) where,

$$NGR = \mu - g \qquad (4)$$

$$\%P_p = \left(((P_o e^{\mu} - P_o) - (P_o e^{(\mu - g)} - P_o))/(P_o e^{\mu} - P_o)\right) \times 100 \qquad (5)$$

$$\%P_o = \left(((P_oe^{\mu} - P_o) - (P_oe^{(\mu-g)} - P_o))/P_o\right) \times 100 \quad (6)$$

$$I_c = C_oe^{\mu} - C_oe^{(\mu-g)} \quad (7)$$

where $(P_oe^{\mu} - P_o)$ is potential production, $(P_oe^{(\mu-g)} - P_o)$ is realized production, C_o is prey carbon (μg Carbon· L^{-1}) at time zero in the unmodified dilution treatment.

For regressions where the slopes were positive, mortality due to microzooplankton grazing was assigned a value of 'zero'. Negative growth rates were also assigned a value of 'zero' to indicate that there was no growth.

2. 3. 9. Conversion factors

Prey carbon at time zero in the unmodified dilution treatment (i.e. 0% PFW) was estimated by converting the prey density estimate to carbon using the appropriate carbon conversion factor. Bacterioplankton and *Synechococcus* carbon was estimated by assuming 20 and 250 fg Carbon ·$cell^{-1}$, respectively (Lee and Furhman 1987, Li et al. 1992). Chlorophyll *a* was converted to carbon assuming a C:Chlorophyll *a* ratio of 55 (Booth et al. 1993).

2. 4. Results

2. 4. 1. Microbial prey standing stocks

The concentration of chlorophyll *a* was similar to that reported previously at OSP. Phytoplankton stocks were ca. 0.1 to 0.4 μg chlorophyll *a* $\cdot$ L^{-1} with most (87-90%) of the stock in the <5 μm size fraction (Booth 1988, Miller et al. 1991a&b). Abundances of bacteria and *Synechococcus* (Tables 2. 1 and 2. 2) during summer and spring ranged from 1.7 to 6.1 x 10^8 cells $\cdot$ L^{-1} and 1.2 to 121.0 x 10^6 cells $\cdot$ L^{-1} , respectively and were similar to those reported previously (Booth 1988, Miller et al. 1991a&b, Booth et al. 1993). However, abundance estimates of bacteria and *Synechococcus* during winter ranged from 1.2 to 2.9 x 10^8 cells $\cdot$ L^{-1} and 1.7 to 4.4 x 10^6 cells $\cdot$ L^{-1} , respectively and therefore were considerably lower (2-8 times) than those reported by Boyd et al. (1995a). Most (38-86%) of the microbial carbon was composed of bacteria and *Synechococcus* in all of the dilution assays (Table 2. 2).

2. 4. 2. Protist abundances

Protist abundances at OSP (Tables 2. 1 and 2. 3) in spring and summer were similar to those reported by Booth et al. (1993). For example, heterotrophic flagellates <5 μm, 5-10 μm, and >10 μm in size ranged from 0.3 to 2.5 x 10^5 cells $\cdot$ L^{-1}, 0.1 to 4.2 x 10^4 cells $\cdot L^{-1}$, and undetectable to 0.7 x 10^4 cells $\cdot$ L^{-1}, respectively. Ciliates ranged from undetectable to 3.3 x 10^3 cells $\cdot$ L^{-1}. Assuming that heterotrophic dinoflagellates

represented 72% of the total dinoflagellate count (Boyd et al. 1995a), heterotrophic dinoflagellates ranged from 1.0 to 77.0 x 10^3 cells · L^{-1}. However, winter time protist abundances were generally lower than those reported by Boyd et al. (1995a). For example, heterotrophic flagellates <5 μm, 5-10 μm, and >10 μm in size ranged from 0.4 to 1.0 x 10^5 cells · L^{-1} , 0.3 to 0.8 x 10^4 cells ·L^{-1}, and undetectable to 0.5 x 10^4 cells ·L^{-1} , respectively. Ciliates ranged from undetectable to 0.3 x 10^3 cells · L^{-1} and heterotrophic dinoflagellates ranged from 0.8 to 3.8 x 10^3 cells · L^{-1}. Thus, winter protist abundances were up to 34 times lower than those reported by Boyd et al. (1995a).

Mean protist abundances were greater in the samples taken from the 230-L tank (Table 2. 1) than they were in the time zero <202 μm unmodified dilution treatments (Table 2. 3); however, the differences were not significant (paired ANOVA, $P>0.05$). Within the dilution assays, most (58-100%) protists occurred in the <35 μm size fraction during spring and summer (Table 2. 4). During winter, however, a large portion (73-100%) of ciliates and dinoflagellates occurred in the 35-202 μm size fraction (Table 2. 4).

2. 4. 3. Statistical analysis of dilution plots

A summary of the results of Analysis of Covariance (ANCOVA) tests for size fractionated assays is shown in Table 2. 5. For bacteria (except on 3 Sep), *Synechococcus*, <5 μm chlorophyll *a*, and total chlorophyll *a*, there were no significant differences for μ and g among the <35 μm and <202 μm size fractions indicating that rates of growth

were the same in the <35 μm and <202 μm size fractions and that microzooplankton grazing was primarily by <35 μm protists. Therefore, data from the size fractions was combined to estimate the respective rates of μ and g. On 5 September, however, both μ and g of chlorophyll a were significantly lower in the <202 μm than the <35 μm size fraction. Similarily, in May both μ and g of >5 μm chlorophyll a were significantly lower in the <202 μm than in the <35 μm size fraction. In contrast, in March both μ and g of >5 μm chlorophyll a were significantly greater in the <202 μm than in the <35 μm size fraction. In the cases where there were significant differences for μ and g among the <202 μm and <35 μm size fractions, the chlorophyll a data was not combined.

Table 2. 6 summarizes the results of ANCOVA tests among days in September. For bacteria and *Synechococcus* there were no significant differences for either μ or g among days and so the data from 3, 4, and 6 September was combined to estimate the respective rates of μ and g. As there were significant differences for both μ and g of chlorophyll a among days, the chlorophyll a data from 3, 4, and 6 September was not combined.

Table 2. 7 summarizes the results of ANCOVA tests for the different depths sampled in May. For bacteria and chlorophyll a, there were significant differences for both μ and g among depths and thus the data was not combined. In contrast, for *Synechococcus* there were no significant differences for either μ or g among depths and so *Synechococcus* data from 19 and 22 May was combined to estimate the rates of μ and g.

2. 4. 4. Microzooplankton grazing

Microzooplankton ingested bacterioplankton, *Synechococcus*, and chlorophyll *a*. In most (79%) cases, the relationship between AGR and ADF was linear and had a significant negative slope (Table 2. 8, Figure 2. 3) with r^2 (coefficient of determination) values of 0.47-0.81, 0.18-0.71, 0.47-0.78 for bacterioplankton, *Synechococcus*, and total chlorophyll *a*, respectively (Table 2. 8). Microzooplankton ingested 70-185%, 92-153%, and 50-105% of bacterial, *Synechococcus*, and total chlorophyll *a* potential production, respectively and 21-56%, 20-99%, 16-45% of bacterial, *Synechococcus*, and total chlorophyll *a* standing stocks, respectively (Table 2. 8).

On average, microzooplankton ingested more *Synechococcus* (123%) and bacterial (109%) potential production, than total chlorophyll *a* (62%) potential production. For phytoplankton, the grazing impact (e.g. $\%P_p$ grazed) was greatest on <35 μm chlorophyll *a* during spring and summer and on 5-202 μm chlorophyll *a* during winter (Table 2. 8). On 3 September, all of the phytoplankton was <35 μm (Table 2. 2) and the grazing impact on total chlorophyll *a* was the same (104% P_p) for <35 μm and <202 μm size fractions. However, on 5 September, 35-202 μm phytoplankton were present (ca. 1.7 $\mu g\ C \cdot L^{-1}$) (Table 2. 2) and the grazing impact on <35 μm chlorophyll *a* was greater (105% P_p) than on <202 μm chlorophyll *a* (69% P_p). On 19 May, all phytoplankton was <35 μm (Table 2. 2) and the grazing impact on total chlorophyll *a* was the same (24% P_p) for <35 μm and <202 μm size fractions. However, on 19 May the grazing impact on size

fractionated (<5 μm and >5 μm) chlorophyll *a* was measured. The grazing impact on <35 μm chlorophyll *a* was greater (24% P_p) than on 5-202 μm chlorophyll *a* (0% P_p). In contrast to September and May, the grazing impact on 5-202 μm phytoplankton in March was greater (83% P_p) than on <35 μm chlorophyll *a* (0% P_p).

Relative Preference Indices (RPI) were calculated for each prey to assess prey preference by microzooplankton grazers by adapting equations from McCarthy et al. (1977). The RPI's were determined using the equation,

$$RPI = (I_{(p1)} / I_{(p1)} + I_{(p2)} + I_{(p3)}) \quad x \quad (C_{(p1)} / C_{(p1)} + C_{(p2)} + C_{(p3)})^{-1}$$

The RPI is the ratio of the fraction of prey type 1, 2 or 3 ingested (I) to the fraction of prey type 1, 2 or 3 occurring *in situ* (C) (i.e. at time zero in the unmodified dilution treatment). A value less than 1 indicates 'avoidance' of the prey, a value greater than 1 indicates 'preference' of the prey, and a value of unity indicates that the prey are ingested in proportion to their availability *in situ*. In this study, the RPI's for bacterioplankton, *Synechococcus*, and total chlorophyll *a* were not significantly different among size fractionated assays (paired ANOVA, $P>0.05$) (Figure 2. 4A, B) and although RPI's were variable, the mean RPI's for all prey examined were ca. 1 (Figure 2. 4C).

Mortality due to microzooplankton grazing did not always balance the growth rates of bacteria, *Synechococcus*, or chlorophyll *a* (Figure 2. 5). For bacteria, grazing mortality

in September, March, and May was similar (ca. 0.31 d^{-1}). However, bacterial growth rates were ca. 2-4 times greater in September than in March and May. As a result, the net growth rates of bacteria were positive in September. *Synechococcus* net growth rates were positive only in March when growth was ca. 4-6 times greater and grazing mortality was ca. 2-3 greater than in May and September. There were no clear seasonal patterns for growth, grazing mortality, or net growth rates for chlorophyll *a* . Net growth rates for chlorophyll *a* were positive in September and May. The only time that the net growth of chlorophyll *a* was negative or zero was for <35 μm chlorophyll *a* in September. The zero net growth in March was not due to vigorous grazing activity, as both growth and grazing were zero (Table 2. 8).

The total microbial carbon ingested was not significantly different among <35 μm and <202 μm assays (paired ANOVA, $P>0.10$) (Figure 2. 6). In May and September, the total ingestion rates (ca. 6 to 13 μg C$\cdot$ $L^{-1} \cdot d^{-1}$) were not different and were greater than in March (ca. 2 to 4 μg C$\cdot$ $L^{-1} \cdot d^{-1}$). There were no significant differences in the percentage of bacteria, *Synechococcus*, chlorophyll *a* ingested among <35 μm and <202 μm assays (paired ANOVA, $P>0.10$) (Figure 2. 7). Bacteria plus *Synechococcus* represented the majority (53-100%) of the carbon ingested by microzooplankton during all study periods (Table 2. 8, Figure 2. 7). The contribution of bacteria and *Synechococcus* to the total microbial carbon ingested was significantly greater than that of total chlorophyll *a* (Table 2. 9).

2. 5. Discussion

2. 5. 1. Methodological considerations

Methodological artifacts may influence the interpretation of the results of grazing studies by affecting the rates of prey growth and grazing mortality. For example, prey growth rates can be affected by differential nutrient availability across the dilution series (Landry 1993) and changes in irradiance fields (McManus 1995) and rates of grazing mortality can be affected if delicate protists are damaged during sample collection and handling or are food limited (Landry 1993&1994).

In this study, the rates of prey growth were likely not affected by differential nutrient availability or shifting light levels. First, nutrient concentrations within the diluent were likely high as concentrations of inorganic nitrogen are persistently high in the subarctic Pacific (Miller et al. 1991b) and diluent water was collected from 40 m which is always below the thermocline and thus enriched with nutrients (Frost 1991). It is therefore unlikely that prey growth was nutrient limited, except perhaps at the ADF=1. However, since nutrient supply rate would be directly proportional to protist abundance (Goldman and Caron 1985), or ADF, nutrient limited growth at the ADF=1 would be unlikely. A compensatory relationship between nutrients supplied from diluent and those from protist nutrient regeneration likely does not result in differential nutrient availability along the dilution gradient. Second, previous studies (Landry et al. 1995b and references cited therein) suggest that rates of prey growth during 24 and 48 h incubations are not

affected by shifts in light levels or differential nutrient concentrations. Moreover, many phytoplankton have the ability to continue growing at light saturated rates for an equivalent of ca. 2 generation time when irradiances are reduced (Rivkin et al. 1982). Third, the growth rates are not significantly different from concurrent estimates made using different techniques (Tables 2. 10 and 2. 11).

Factors that may have affected grazing mortality estimates include damage of protists during handling and non-linear functional responses (Landry 1993&1994). However, there were no significant differences for protist abundances among initial and time zero samples to indicate that grazing mortality was underestimated due to damage of protists. Further, since there were more dilution factors (n=8) per assay than most dilution studies (n=4) (e.g. Landry and Hassett 1982, Landry et al. 1984, Campbell and Carpenter 1986, Burkill et al. 1987, Strom and Welschmeyer 1991, McManus and Ederington-Cantrell 1992, Burkill et al. 1993a&b, Burkill et al. 1995, Boyd et al. 1995b, Landry et al. 1995a, Boyd et al. 1996, Fronemann and Perissinotto 1996), non-linear dilution plots were easily resolved. Piecewise linear regression (PLR) was used to analyze these plots and thus it is unlikely that estimates of grazing mortality were affected by satiated feeding. Although PLR estimates of growth and grazing mortality are not significantly different from 3-point estimates (Tables 2. 12 and 2. 13), I recommend the use of PLR rather than the 3-point method. Unlike the 3-point method, which estimates grazing mortality from 1 data point and growth by extrapolating from 2 data points (Gallegos 1989, Evans and

Paranjape 1992), PLR estimates rates from the relation between AGR and ADF for each section (usually $\geq$ 3 data points per section) and therefore is a statistically more precise method to estimate growth and grazing mortality.

Another factor which may have affected the estimates of growth and grazing mortality is environmental heterogeneity (Venrick 1978b). However, since there were no significant differences for both growth and grazing mortality for bacterioplankton and *Synechococcus* among days in September (Table 2. 6), it is probable that the samples were representative of the stations sampled.

2. 5. 2. Top-down control

Microzooplankton actively ingested bacteria, *Synechococcus*, and phytoplankton in September, March, and May at OSP. The present estimates of microzooplankton grazing impact (i.e. percentage of potential production ingested) on phytoplankton (Table 2. 8) are comparable to the spring (22-76%), summer (2-77%), and winter (76-100%) estimates previously reported at OSP (Strom and Welschmeyer 1991, Landry et al. 1993a, Boyd et al. 1995b, Boyd et al. 1996). In addition, the grazing impact on bacterioplankton and *Synechococcus* (Table 2. 8) was just as vigorous as observed in other marine environments (Chapter 3, Table 3. 7). As the producer-micrograzer linkage remains functional throughout the year (Table 2. 8), the results support the mixing and micrograzer hypothesis (Miller et al. 1991a&b) that the permanent halocline permits active prey growth

all year and thus maintains an active micrograzer population.

The microzooplankton grazing impact was generally greatest on small prey such as bacteria, *Synechococcus*, and <35 μm phytoplankton (Table 2. 8). These results are coincident with those of Strom and Welschmeyer (1991) which showed that microzooplankton grazing is coupled closest to the growth of small phytoplankton cells. This is likely because microzooplankton fit the 10:1 predator: prey size ratio 'rule' (Fenchel 1988). Not only does the distribution of protists (Table 2. 4) indicate that protists <35 μm in size predominated the microzooplankton assemblage, but the size fractionation results (Table 2. 5) also suggest that the primary micrograzers were <35 μm in size. The predominance of microzooplankton <35 μm in size may be attributed to top-down control by mesozooplankton (Gifford 1993, Crocker et al. 1997). In contrast to the spring and summer results, the results from winter are the first to indicate that microzooplankton actively ingest large (i.e. 5 to 202 μm) phytoplankton at OSP. The greater impact on 5 to 202 μm phytoplankton during winter was probably due to the co-occurrence of large (i.e. 35 to 202 μm) ciliates and dinoflagellates (Table 2. 4) and large (i.e. 35 to 202 μm) phytoplankton (Table 2. 2). Presumably, large phytoplankton were abundant during winter due to increased levels of ambient iron (Boyd et al. 1996), whereas the presence of 35 to 202 μm ciliates and dinoflagellates during winter may have been due to a reduction in top-down control (Boyd et al. 1995a) brought about by low winter surface layer mesozooplankton abundances (Cooney 1988).

Mortality due to microzooplankton grazing did not consistently balance phytoplankton growth (Figure 2. 5). Net growth (i.e. NGR>0) of phytoplankton in the presence of microzooplankton is thought to be an incubation artifact (Welschmeyer et al. 1991, Landry et al. 1993a) due to alleviation of Fe-limitation (through contamination) causing 'uncontrolled' fast-diatom growth. However, it is unlikely that the NGR of phytoplankton was positive because of fast-growing large phytoplankton. First, Boyd et al. (1996) showed that it takes at least 2 days for Fe-limited phytoplankton to respond to Fe-enrichment and subsequently increase stocks. Second, the size fractionation results suggest that large phytoplankton were slow-growing in September and May. For example, if large (i.e. 35 to 202 μm) phytoplankton were fast growing on 5 September, then phytoplankton growth in the <202 μm assay would have been similar to, or greater than, phytoplankton growth in the <35 μm assay. However, phytoplankton growth in the <202 μm assay was less than that in the <35 μm assay (Table 2. 8). During May, large (i.e. 5 to 202 μm) phytoplankton were also a slow-growing component of the phytoplankton (Table 2. 8). Thus, the positive NGR of phytoplankton during May and September was due to low grazing mortality, rather than fast diatom growth. The only time grazing mortality balanced phytoplankton growth was in September for <35 μm phytoplankton. The overall lack of microzooplankton control of phytoplankton growth (i.e. NGR>0) coupled with the virtually constant stocks of phytoplankton suggests that other herbivores may be important. Yet, studies show that the dominant mesozooplankters do not exert

substantial direct top-down control on phytoplankton (Dagg 1993, Tsuda and Sugisaki 1994, Crocker et al. 1997). Thus, while microzooplankton grazing is clearly a significant loss for the phytoplankton community, other loss processes, such as aggregation (Goldman 1988) and viral lysis (Fuhrman and Noble 1995), may be important to preventing phytoplankton blooms at OSP.

Similar to phytoplankton, top-down control on bacterioplankton and *Synechococcus* may be primarily by microzooplankton. Based on the 10:1 predator to prey size ratio "rule" in plankton food webs (Fenchel 1988), microzooplankton likely are the primary bacterivores. However, there are exceptions to the 10:1 rule. Tunicates (i.e. appendicularians, salps, doliolids) may also ingest bacterioplankton and *Synechococcus*. Unlike other mesozooplankton (e.g. copepods) (Nival and Nival 1976), tunicates can efficiently graze bacterial- sized particles (Alldredge and Madin 1982, Crocker et al. 1991, Flood et al. 1992, Deibel and Lee 1992). However, their grazing impact is likely to be intermittent due to their variable spatial and temporal distribution (Alldredge and Madin 1982, Michaels and Silver 1988, Peinert et al. 1989 & refs. cited therein). If microzooplankton are the primary bacterivores at OSP, then stocks of bacterioplankton and *Synechococcus* should increase during September and March, respectively in response to their positive net growth rates (Figure 2. 5) (also see Sanders et al. 1992). Bacterial abundance data does show that abundances are greater in summer (4 to 6.1 x 10^8 cells $\cdot$ L^{-1}) than in winter (1 to 3 x 10^8 cells $\cdot$ L^{-1}) and spring (1 to 4 x 10^8 cells $\cdot$ L^{-1}). However,

Synechococcus abundance data shows that abundances are greatest in May (65 to 121 x 10^6 cells · L^{-1}) rather than in March (2 to 4 x 10^6 cells · L^{-1}) or September (1 to 2 x 10^6 cells · L^{-1}). Long time series data of bacterioplankton and *Synechococcus* abundance, similar to that of phytoplankton stocks, would be valuable in assessing whether microzooplankton are the primary bacterivores at OSP.

2. 5. 3. Ingestion of microbial carbon

The amount of microbial carbon ingested by microzooplankton was seasonal (Figure 2. 6). While the carbon ingestion rates during summer are similar to those predicted by Boyd et al. (1995a), the ingestion rates during winter were ca. 5 to 18 times lower than those they predicted. The similarity between the present direct estimates of ingestion during summer and those predicted by Boyd et al. (1995a) may be because Boyd et al. used appropriate gross growth efficiencies and protist abundances that were similar to those in this study. In contrast, the difference between the direct estimates of ingestion during winter and those they predicted may be because the winter protist abundances were lower (Table 2. 3) than those used by Boyd et al. to estimate carbon requirements. Further, the gross growth efficiencies (GGE) used by Boyd et al. may have been too low, as GGE may increase with a decrease in temperature (Choi and Peters 1992). The difference between the winter abundance data on protists and microbial prey and those reported by Boyd et al. (1995a) suggests that there are interannual variations in the winter

abundances of plankton components. Further studies should be conducted during winter to gain a better understanding of winter time microzooplankton grazing.

Bacterioplankton and *Synechococcus* represented most of the carbon ingested by microzooplankton (Figure 2. 7, Table 2. 8). This was likely because microzooplankton generally ingested prey in proportion to their availability (Figures 2. 4C) and a large portion of microbial biomass was comprised of bacterioplankton and *Synechococcus* (Table 2. 2). That protist abundances and both bacteria and *Synechococcus* abundances were low during winter (Tables 2. 2 and 2. 3) suggests that bacteria and *Synechococcus* were important prey. Results of Strom (1991), showing that the herbivorous dinoflagellate *Gymnodinium* (isolated from OSP) increases its ingestion of *Synechococcus* when *Synechococcus* stocks increase, also suggest that *Synechococcus* are important prey. Eukaryotic autotrophic picoplankton may also be important prey of microzooplankton. These autotrophs are similar in size to bacteria and *Synechococcus* and comprise a large portion of the microbial biomass in the subarctic Pacific (Booth et al. 1988a&b, Booth et al. 1993). If microzooplankton actively ingest eukaryotic autotrophic picoplankton (Shapiro and Guillard 1986, Kuosa 1990, Kuosa 1991), then picoplankton (i.e. bacteria, *Synechococcus*, eukaryotic autotrophic picoplankton) may represent an even larger portion of the carbon ingested at OSP.

2. 5. 4. Ecological implications to food web structure and biogenic carbon export

The results of this study have implications to food web structure and biogenic carbon export at OSP. Legendre and Rassoulzadegan (1995) proposed that a multivorous food web (Chapter 1, Figure 1.1D) characterizes the pelagic food web in the subarctic Pacific. However, data on microzooplankton bacterivory (and mesozooplankton omnivory) was lacking to support their hypothesis. The present results showing that microzooplankton bacterivory and herbivory are active during all seasons (Table 2. 8) combined with the results of Dagg (1993), Gifford (1993), and Crocker et al. (1997) which show that mesozooplankton are herbivorous and omnivorous, support the proposed dominance of a multivorous food web in the surface layers of the subarctic Pacific. Given that mesozooplankton acquire most of their dietary carbon from microzooplankton (Crocker et al. 1997), it is likely that the food web at OSP is ultimately picoplankton-based because bacteria and *Synechococcus* dominate the carbon ingested by microzooplankton (Figure 2. 7). Thus, commercially important salmon species that spend a large portion of their life cycle feeding in pelagic subarctic Pacific waters (Parsons and Lalli 1988) may ultimately depend upon picoplankton.

In the subarctic Pacific, new production (i.e. nitrate-based production) is low which, by classical definition, suggests that the vertical export of biogenic carbon is low (Eppley and Peterson 1979, Wheeler 1993). This paradigm neglects to consider that bacteria and small autotrophs, which utilize regenerated nitrogen (Harrison and Wood

1988, Suttle et al. 1990), can be ingested and repackaged into an exportable form. If a multivorous food web characterizes the pelagic food web at OSP, then the microbial prey ingested by microzooplankton (primarily bacteria and *Synechococcus*, Figure 2. 7) can be transferred to mesozooplankton (e.g. copepods). Since mesozooplankton can produce sinking body parts and fecal pellets and vertically migrate (Matsueda et al. 1986, Noji 1991), there is a potential for regenerated production to be exported out of the euphotic zone. Neglecting to consider this repackaging and export pathway could lead to underestimates of the vertical export of biogenic carbon in the subarctic Pacific.

Table 2. 1. Dates, depths, and times at which water samples were collected for dilution assays conducted at Ocean Station Papa (50°N, 145°W). Temperature (Temp) from CTD profile taken during hydrocast. Chlorophyll *a* (Chl *a*) concentration and bacteria (Bact), *Synechococcus* (Syn), and protist abundances correspond to initial samples drawn from 230-L tank.

Date	Depth (m)	Time	Temp (°C)	Chl *a* (>0.7 µm) (µg·L^{-1})	Bact (10^8 cells·L^{-1})	Syn (10^6 cells·L^{-1})	Flagellates (cells·L^{-1})			Ciliates (cells·L^{-1})	Dinoflagellates (cells·L^{-1})
							<5 µm	5-10 µm	>10 µm		
3 Sep 95	10	0900	13.1	0.2	4.0	ne	130 000	8 500	4 000	700	51 000
5 Sep 95	8	1030	13.1	0.4	6.5	1.4	250 000	42 000	7 000	500	16 000
6 Sep 95	10	0830	13.1	0.4	5.7	1.8	150 000	5 000	3 200	2 700	107 000
1 Mar 96	10	0900	5.6	0.2	1.2	1.7	39 000	3 400	4 500	300	5 300
19 May 96	15	0830	7.7	0.1	2.4	65.0	110 000	9 000	nd	1 900	2 600
22 May 96	45	0700	7.7	0.2	1.3	85.0	45 000	8 400	nd	3 300	4 300

ne - not estimated.
nd - not detected.

Table 2. 2. Distribution of microbial carbon in time zero samples collected from unmodified dilution treatments at Ocean Station Papa. Concentration (Concn.) is the abundance of bacteria (Bact, x 10^8 cells $\cdot L^{-1}$) and *Synechococcus* (Syn, x 10^6 cells $\cdot L^{-1}$) and concentration of chlorophyll *a* (Chl *a*, μg Chl *a* $\cdot L^{-1}$). Concentrations of Bact, Syn, and Chl *a* were converted to carbon (C_o, μg C $\cdot L^{-1}$) by assuming 20 fg C·cell^{-1}, 250 fg C·cell $^{-1}$, and a C:Chl *a* ratio of 55, respectively. Total Chl *a* is >0.7 μm and <5 μm Chl *a* is 0.7 to 5 μm. The contribution of bacteria and *Synechococcus* carbon to total microbial carbon is % Pico.

Time	Size fraction (µm)	Prey	Concn.	C_o	Total C_o [1]	% of Total C_o	% Pico[2]
3 Sep 95	<202	Bact	4.4	8.8	17.1	51	51
		Syn	ne	ne		ne	
		Total Chl *a*	0.15	8.3		49	
		<5µm Chl *a*	ne	ne		ne	
		>5µm Chl *a*	ne	ne		ne	
3 Sep 95	<35	Bact	3.5	7.0	15.3	46	46
		Syn	ne	ne		ne	
		Total Chl *a*	0.15	8.3		54	
		<5µm Chl *a*	ne	ne		ne	
		>5µm Chl *a*	ne	ne		ne	
5 Sep 95	<202	Bact	5.3	10.6	28.5	37	38
		Syn	1.2	0.3		1	
		Total Chl *a*	0.32	17.6		62	
		<5µm Chl *a*	ne	ne		ne	
		>5µm Chl *a*	ne	ne		ne	
5 Sep 95	<35	Bact	6.1	12.2	28.5	43	44
		Syn	1.4	0.4		1	
		Total Chl *a*	0.29	15.9		56	
		<5µm Chl *a*	ne	ne		ne	
		>5µm Chl *a*	ne	ne		ne	
6 Sep 95	<202	Bact	5.9	11.8	31.5	37	38
		Syn	1.7	0.4		1	
		Total Chl *a*	0.35	19.3		61	
		<5µm Chl *a*	ne	ne		ne	
		>5µm Chl *a*	ne	ne		ne	
1 Mar 96	<202	Bact	2.9	5.8	15.7	37	44
		Syn	4.4	1.1		7	
		Total Chl *a*	0.16	8.8		56	
		<5µm Chl *a*	0.14	7.7		49	
		>5µm Chl *a*	0.02	1.1		7	

Table 2. 2. *Continued.*

Time	Size fraction (µm)	Prey	Concn.	C_o	Total C_o [1]	% of Total C_o	% Pico[2]
1 Mar 96	<35	Bact	2.9	5.8	12.8	45	52
		Syn	3.7	0.9		7	
		Total Chl *a*	0.11	6.1		48	
		<5µm Chl *a*	0.10	5.5		43	
		>5µm Chl *a*	0.01	0.6		5	
19 May 96	<202	Bact	3.6	7.2	38.3	19	86
		Syn	102.0	25.5		67	
		Total Chl *a*	0.10	5.6		15	
		<5µm Chl *a*	0.09	5.0		13	
		>5µm Chl *a*	0.01	0.6		2	
19 May 96	<35	Bact	3.8	7.6	39.7	19	86
		Syn	106.0	26.5		67	
		Total Chl *a*	0.10	5.6		14	
		<5µm Chl *a*	0.09	5.0		12	
		>5µm Chl *a*	0.01	0.6		2	
22 May 96	<202	Bact	1.7	3.4	42.0	8	80
		Syn	121.0	30.3		72	
		Total Chl *a*	0.15	8.3		20	
		<5µm Chl *a*	0.13	7.2		17	
		>5µm Chl *a*	0.02	1.1		3	

ne - not estimated.

[1] Total C_o = Bact (C_o) + Syn (C_o) + Total Chl *a* (C_o)

[2] % Pico = ((Bact (C_o) + Syn (C_o)) ÷ Total C_o) x 100

Table 2. 3. Protist abundances (cells · L^{-1}) in time zero samples collected from unmodified dilution treatments at Ocean Station Papa.

Time	Size fraction (µm)	Flagellates			Ciliates	Dinoflagellates
		<5 µm	5-10 µm	>10 µm		
3 Sep 95	<202	110 000	13 000	5 000	nd	65 000
	<35	90 000	10 000	5 000	300	38 000
5 Sep 95	<202	140 000	4 000	1 500	600	27 000
	<35	148 000	20 000	3 000	2 300	37 000
6 Sep 95	<202	50 000	2 000	2 000	nd	62 000
1 Mar 96	<202	100 000	8 000	nd	300	4 500
	<35	80 000	5 200	nd	nd	1 200
19 May 96	<202	100 000	5 000	nd	1 000	2 800
	<35	90 000	4 000	nd	700	2 100
22 May 96	<202	30 000	800	nd	1 100	1 500

nd - not detected.

Table 2. 4. Number [1] (cells · L^{-1}) and percent distribution[2] of protists in <35 μm and 35-202 μm size fractions in time zero samples from unmodified dilution treatments at Ocean Station Papa.

Time	Size (μm)	<5 μm Flagellates		5-10 μm Flagellates		>10 μm Flagellates		Ciliates		Dinoflagellates	
		No.	%	No.	%	No.	%	No.	%	No.	%
3 Sep 95	35-202	20 000	18	3 000	23	0	-	nd	-	27 000	42
	<35	90 000	82	10 000	77	5 000	100	300	100	38 000	58
5 Sep 95	35-202	<0	-	<0	-	<0	-	<0	-	<0	-
	<35	148 000	100	20 000	100	3 000	100	2 300	100	3 000	100
1 Mar 96	35-202	20 000	20	2 800	25	nd	-	300	100	3 300	73
	<35	80 000	80	5 200	65	nd	-	nd	-	1 200	27
19 May 96	35-202	10 000	10	1 000	20	nd	-	300	30	700	25
	<35	90 000	90	4 000	80	nd	-	700	70	2 100	75

[1] The number of protists in 35-202 μm size fraction = Number of protists in <202 μm assay - Number of protists in <35 μm assay (from Table 2. 3).

[2] The percent distribution = Number of protists ÷ Number of protists in <202 μm assay.

nd - not detected.

0 - zero is the difference between the number of protists in <202 μm and <35 μm assays.

<0 - a negative value is the difference between the number of protists in <202 μm and <35 μm assays.

Table 2. 5. Results from Analysis of Covariance testing for significant differences for either growth (μ) or grazing mortality (g) among <35 μm and <202 μm assays for bacteria (Bact), *Synechococcus* (Syn), and chlorophyll *a* (Chl *a*) at Ocean Station Papa. Total Chl *a* is >0.7 μm and <5 μm Chl *a* is 0.7 to 5 μm. Significance was $P<0.10$. NS denotes No Significant difference and S denotes a Significant difference.

Date	Prey	μ (d^{-1})	g (d^{-1})
3 Sep 95	Bact	S	NS
	Syn	ne	ne
	Total Chl *a*	NS	NS
	<5 μm Chl *a*	ne	ne
	>5 μm Chl *a*	ne	ne
5 Sep 95	Bact	NS	NS
	Syn	NS	NS
	Total Chl *a*	S	S
	<5 μm Chl *a*	ne	ne
	>5 μm Chl *a*	ne	ne
1 Mar 96	Bact	NS	NS
	Syn	NS	NS
	Total Chl *a*	NS	NS
	<5 μm Chl *a*	NS	NS
	>5 μm Chl *a*	S	S
19 May 96	Bact	NS	NS
	Syn	NS	NS
	Total Chl *a*	NS	NS
	<5 μm Chl *a*	NS	NS
	>5 μm Chl *a*	S	S

ne - not estimated.

Table 2. 6. Results from Analysis of Covariance testing for significant differences for either growth (μ) or grazing mortality (g) among days in September for Bacteria (Bact), *Synechococcus* (Syn), and total (>0.7 μm) chlorophyll *a* (Chl *a*) at Ocean Station Papa. Significance was $P<0.10$. NS and S as in Table 2. 5.

Date	Prey	μ (d^{-1})	g (d^{-1})
3, 4, 6 Sep 95	Bact	NS	NS
	Syn	NS	NS
	Total Chl *a*	S	S

Table 2. 7. Results from Analysis of Covariance testing for significant differences for either growth (μ) or grazing mortality (g) among depths (15 and 45 m) in May for Bacteria (Bact), *Synechococcus* (Syn), total (>0.7 μm) chlorophyll *a* (Chl *a*), <5 μm (0.7 to 5 μm) Chl *a*, and >5 μm (5 to 202 μm) Chl *a* at Ocean Station Papa. Significance was $P<0.10$. NS and S as in Table 2. 5.

Date	Prey	μ (d^{-1})	g (d^{-1})
19, 22 May 96	Bact	S	S
	Syn	NS	NS
	Total Chl *a*	S	S
	<5 µm Chl *a*	S	S
	>5 µm Chl *a*	S	S

Table 2. 8. Rates of growth (μ, divisions·d^{-1}) and grazing mortality (g,d^{-1}) for bacteria (Bact), *Synechococcus* (Syn), and chlorophyll *a* (Chl *a*) in the surface layer at Ocean Station Papa (and at 45 m on 22 May). Microzooplankton grazing impact is expressed as prey net growth rate (NGR, d^{-1}), % of prey stock ingested (% C_o, d^{-1}), % of prey potential production ingested (% Pp, d^{-1}), and prey carbon ingested (I_c , μg C· L^{-1} d^{-1}). The percentage of total carbon ingested derived from bacteria and *Synechococcus* is % Pico. Where n>8, data was pooled due to ns differences between sites/times for μ and g. Due to loss/damage of samples, some sample sizes are not multiples of 8.

Time	Size (μm) fraction	Prey	n	r^2	μ (±SE)	g (±SE)	NGR	%C_o	%P_p	I_c	%Pico
3 Sep 95	<202	Bact	31	0.47***	0.57 (0.04)	0.38 (0.07)	0.19	56	73	5.0	72
		Total Chl *a*	16	0.54***	0.20 (0.03)	0.21 (0.05)	-0.01	23	104	1.9	
3 Sep 95	<35	Bact	8	0.62**	0.47 (0.07)	0.43 (0.12)	0.04	56	93	3.9	67
		Total Chl *a*	16	0.54 ***	0.20 (0.03)	0.21 (0.05)	-0.01	23	104	1.9	
5 Sep 95	<202	Bact	31	0.47***	0.57 (0.04)	0.38 (0.07)	0.19	56	73	5.9	68
		Syn	24	0.18**	0.12 (0.05)	0.19 (0.08)	-0.07	20	153	0.1	
		Total Chl *a*	8	0.47**	0.21 (0.03)	0.14 (0.05)	0.07	16	69	2.8	
5 Sep 95	<35	Bact	31	0.47***	0.57 (0.04)	0.38 (0.07)	0.19	56	73	6.8	53
		Syn	24	0.18**	0.12 (0.05)	0.19 (0.08)	-0.07	20	153	0.1	
		Total Chl *a*	8	0.78**	0.31 (0.04)	0.33 (0.07)	-0.02	38	105	6.1	

Table 2. 8. *Continued.*

Time	Size (µm) fraction	Prey	n	r^2	μ (±SE)	g (±SE)	NGR	$\%C_o$	$\%P_p$	I_c	%Pico
6 Sep 95	<202	Bact	31	0.47***	0.57 (0.04)	0.38 (0.07)	0.19	56	73	6.6	75
		Syn	24	0.18**	0.12 (0.05)	0.19 (0.08)	-0.07	20	153	0.1	
		Total Chl *a*	8	0.25 ns	-0.37 (0.04)	0.12 (0.07)	-0.12	11	ng	2.2	
1 Mar 96	<202	Bact	14	0.81***	0.16 (0.03)	0.32 (0.04)	-0.16	32	185	1.9	77
		Syn (PLR)	6	0.59**	0.73 (0.15)		0.08	99	92	1.1	
			8			0.65 (0.03)					
		Total Chl *a*	14	0.00 ns	-0.19 (0.06)	-0.10 (0.11)	0.00	0	ng	0.0	
		<5 µm Chl *a*	20	0.00 ns	-0.22 (0.12)	-0.12 (0.19)	0.00	0	ng	0.0	
		>5 µm Chl *a*	8	0.39*	0.69 (0.12)	0.53 (0.23)	0.16	82	83	0.9	
1 Mar 96	<35	Bact	14	0.81***	0.16 (0.03)	0.32 (0.04)	-0.16	32	185	1.9	100
		Syn (PLR)	6	0.59**	0.73 (0.15)		0.08	99	92	1.0	
			8			0.65 (0.03)					
		Total Chl *a*	14	0.00 ns	-0.19 (0.06)	-0.10 (0.11)	0.00	0	ng	0.0	
		<5 µm Chl *a*	20	0.00 ns	-0.22 (0.12)	-0.12 (0.19)	0.00	0	ng	0.0	
		>5 µm Chl *a*	20	0.00 ns	-0.22 (0.12)	-0.12 (0.19)	0.00	0	ng	0.0	

Table 2. 8. *Continued.*

Time	Size (µm) fraction	Prey	n	r^2	μ (±SE)	g (±SE)	NGR	%C_o	%P_p	I_c	%Pico
19 May 96	<202	Bact (PLR)	8	0.64***	0.28 (0.07)		-0.08	40	124	2.9	91
			8			0.36 (0.01)					
		Syn	24	0.71***	0.21 (0.02)	0.27 (0.03)	-0.06	29	125	7.4	
		Total Chl *a*	16	0.00 ns	0.50 (0.04)	0.10 (0.07)	0.40	16	24	0.9	
		<5 µm Chl *a*	21	0.11*	0.53 (0.04)	0.12 (0.07)	0.41	19	27	1.0	
		>5 µm Chl *a*	7	0.60**	0.23 (0.08)	-0.47 (0.15)	0.23	0	0	0.0	
19 May 96	<35	Bact (PLR)	8	0.64***	0.28 (0.07)		-0.08	40	124	3.0	91
			8			0.36 (0.01)					
		Syn	24	0.71***	0.21 (0.02)	0.27 (0.03)	-0.06	29	125	7.7	
		Total Chl *a*	16	0.00 ns	0.50 (0.04)	0.10 (0.07)	0.40	16	24	1.0	
		<5 µm Chl *a*	21	0.11*	0.53 (0.04)	0.12 (0.07)	0.41	19	27	1.0	
		>5 µm Chl *a*	21	0.11*	0.53 (0.04)	0.12 (0.07)	0.41	19	27	0.1	
22 May 96	<202	Bact (PLR)	4	0.91**	0.25 (0.03)		0.08	21	70	0.7	65
			4			0.17 (0.02)					
		Syn	24	0.71***	0.21 (0.02)	0.27 (0.03)	-0.06	29	125	8.8	
		Total Chl *a*	8	0.60**	0.64 (0.05)	0.27 (0.08)	0.37	45	50	3.7	
		<5 µm Chl *a*	8	0.68***	0.71 (0.06)	0.43 (0.11)	0.28	71	69	5.1	
		>5 µm Chl *a*	8	0.43**	0.39 (0.08)	-0.37 (0.15)	0.39	0	0	0.0	

n: Number of data points in regression

significance level of regression analysis denoted by stars: *** = $P<0.01$, ** = $P<0.05$, * = $P<0.10$, ns = $P>0.10$.

NGR $=\mu-g$ (negative estimates of μ or g were assigned values of zero)

% $C_o = (((C_o e^{\mu} - C_o) - (C_o e^{(\mu-g)} - C_o))/C_o) \times 100$, where C_o is prey carbon

% $P_p = (((P_o e^{\mu} - P_o) - (P_o e^{(\mu-g)} - P_o))/(P_o e^{\mu} - P_o)) \times 100$, where P_o is prey density

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

% Pico during March and May = (Bact (I_c) + Syn (I_c)) ÷ (Bact (I_c) + Syn (I_c) + <5 μm Chl a (I_c) + >5 μm Chl a (I_c)) x100

and during Sep % Pico = (Bact (I_c) + Syn (I_c)) ÷ (Bact (I_c) + Syn (I_c) + Total Chl a (I_c)) x100

PLR: indicates that piecewise linear regression was used to estimate growth and grazing mortality

ng: no growth

Table 2. 9. Analysis of Variance test to determine if the contribution of bacteria and *Synechococcus* to the total carbon ingested by microzooplankton at Ocean Station Papa was significantly different from that of total (>0.7 μm) chlorophyll *a*.

SOURCE	DF	SS	MS	F	p
FACTOR	1	10325	10325	50.75	<0.001
ERROR	10	2035	203		
TOTAL	11	12360			

Table 2. 10. Growth rates (μ, d^{-1}) of bacteria (Bact) and chlorophyll *a* (Chl *a*) at Ocean Station Papa estimated from dilution assays and other independent techniques.

Date	Prey	$\mu_{Dilution}$	μ_{Other}
3, 5, 6 Sept 95	Bact	0.57	0.58[1]
19 May 96	Bact	0.28	0.12[1]
3, 5, 6 Sept 95	Total Chl *a*	0.14[2]	0.63[3]
1 Mar 96	Total Chl *a*	0.00	0.12[3]
19 May 96	Total Chl *a*	0.50	0.53[3]

[1] Growth determined in bacterivore-free seawater cultures (from Rivkin et al. 1997).

[2] Mean growth rate of <202 μm chlorophyll *a* in September.

[3] Growth determined using the equation: ln (C^{14} + C)/ C, where C^{14} and C are water column integrated daily productivity and phytoplankton carbon, respectively. Phytoplankton carbon was converted from chlorophyll *a* assuming a C: Chl *a* of 55 (Booth et al. 1993) (Boyd and Harrison unpubl.).

Table 2. 11. Results of paired Analysis of Variance testing for significant differences among growth rates estimated from dilution assays and from "other" independent techniques (see Table 2. 10). "Method" refers to technique used to estimate growth (i.e. dilution and "other") and "Time" refers to the times when growth rates were estimated.

Source	DF	SS	MS	F	P
Method	1	0.02401	0.02401	0.82	0.415
Time	4	0.37126	0.09281	3.19	0.144
Error	4	0.11654	0.02913		
Total	9	0.51181			

Table 2. 12. Piecewise linear regression (PLR) and 3-point method (3-pt.) estimates of *Synechococcus* (Syn) and bacterial (Bact) growth (μ, d^{-1}) and grazing mortality (g, d^{-1}) when dilution plots were non-linear at Ocean Station Papa.

		μ (d^{-1})		g (d^{-1})	
Time	Prey	PLR	3-pt.[1]	PLR	3-pt.[2]
1 Mar 96	Syn	0.73	0.79	0.65	0.73
19 May 96	Bact	0.28	0.27	0.36	0.32
22 May 96	Bact	0.25	0.21	0.17	0.17

[1] $\mu = (DF_2 (AGR_1) - DF_1 (AGR_2)) \div (DF_2 - DF_1)$, where DF_2 is the second lowest dilution factor and DF_1 is the lowest dilution factor. The AGR_1 and AGR_2 are prey apparent growth rates at the lowest and second lowest dilution factor, respectively (Gallegos 1989).

[2] $g = \mu$ - AGR, where μ is prey growth (as defined above) and AGR is the apparent growth rate for the unmodified dilution treatment (Gallegos 1989).

Table 2. 13. Results from paired Analysis of Variance testing for significant differences between 3-point and piecewise linear regression estimates of growth and grazing mortality at Ocean Station Papa. "Tech" refers to the technique used to estimate the rate (i.e. PLR or 3-point) and "Time" refers to the times when rates were estimated.

Source	DF	SS	MS	F	P
Tech	1	0.00021	0.00021	0.16	0.704
Time	5	0.62804	0.12561	97.50	0.000
Error	5	0.00644	0.00129		
Total	11	0.63469			

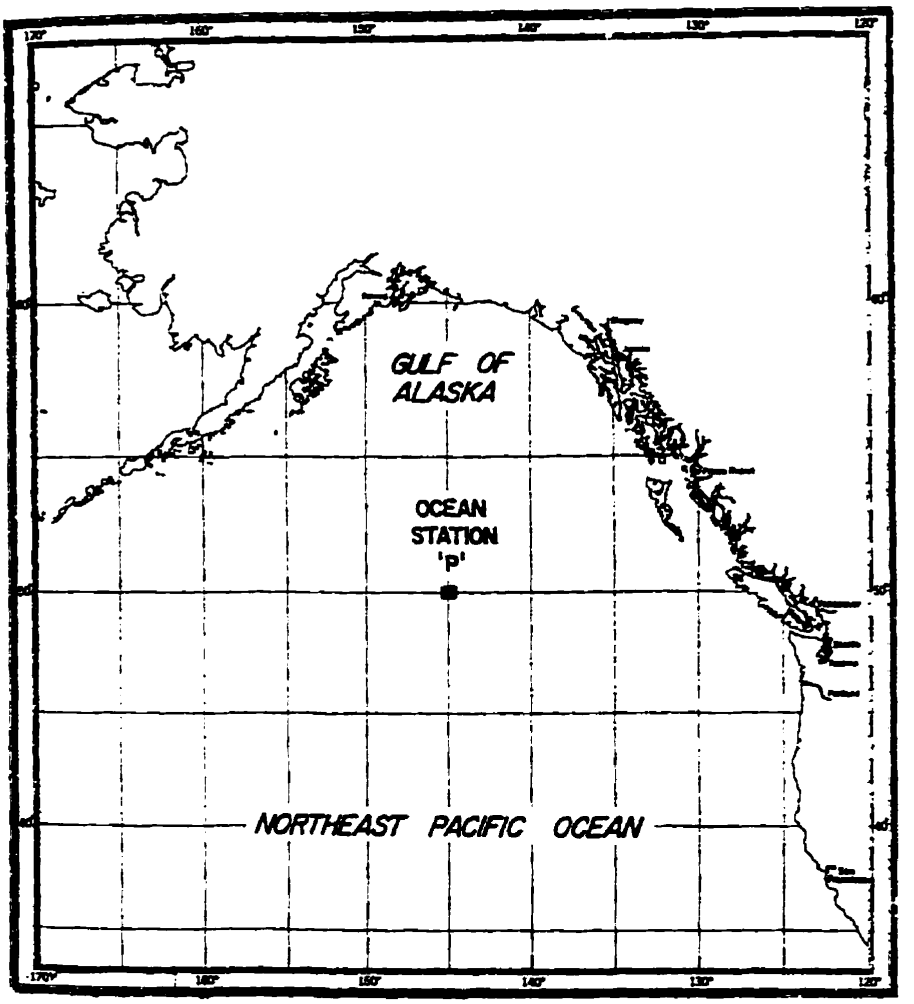


Figure 2. 1. Study site in the subarctic Pacific was Ocean Station Papa (50°N, 145°W).

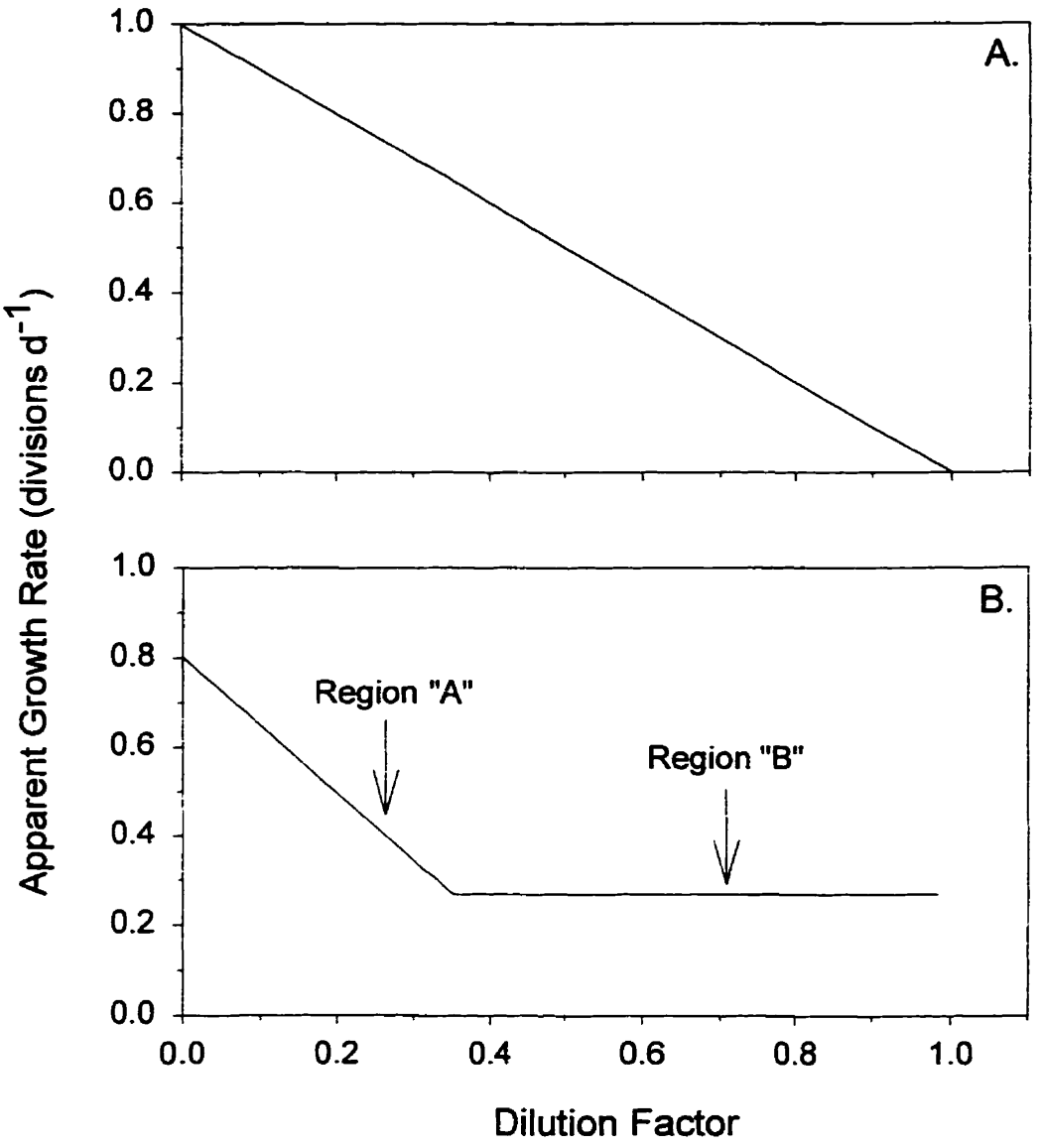


Figure 2. 2. Idealized dilution plots. Rates of prey growth and grazing mortality estimated using Model I linear regression when dilution plot was linear (A). However, when dilution plot was non-linear (B), piecewise linear regression was used to estimate prey and grazing mortality. Prey growth was estimated from the *y*-intercept of the regression of "Region A". Grazing mortality was estimated by subtracting the mean Apparent Growth Rate in "Region B" from prey growth estimated in "Region A".

Figure 2. 3. Representative dilution plots of Apparent Growth Rate versus Actual Dilution Factor for bacterioplankton, *Synechococcus*, and total chlorophyll *a* on 5 September 1995 in the <202 μm size fractionated assay conducted at Ocean Station Papa. Dashed lines are 95% confidence intervals.

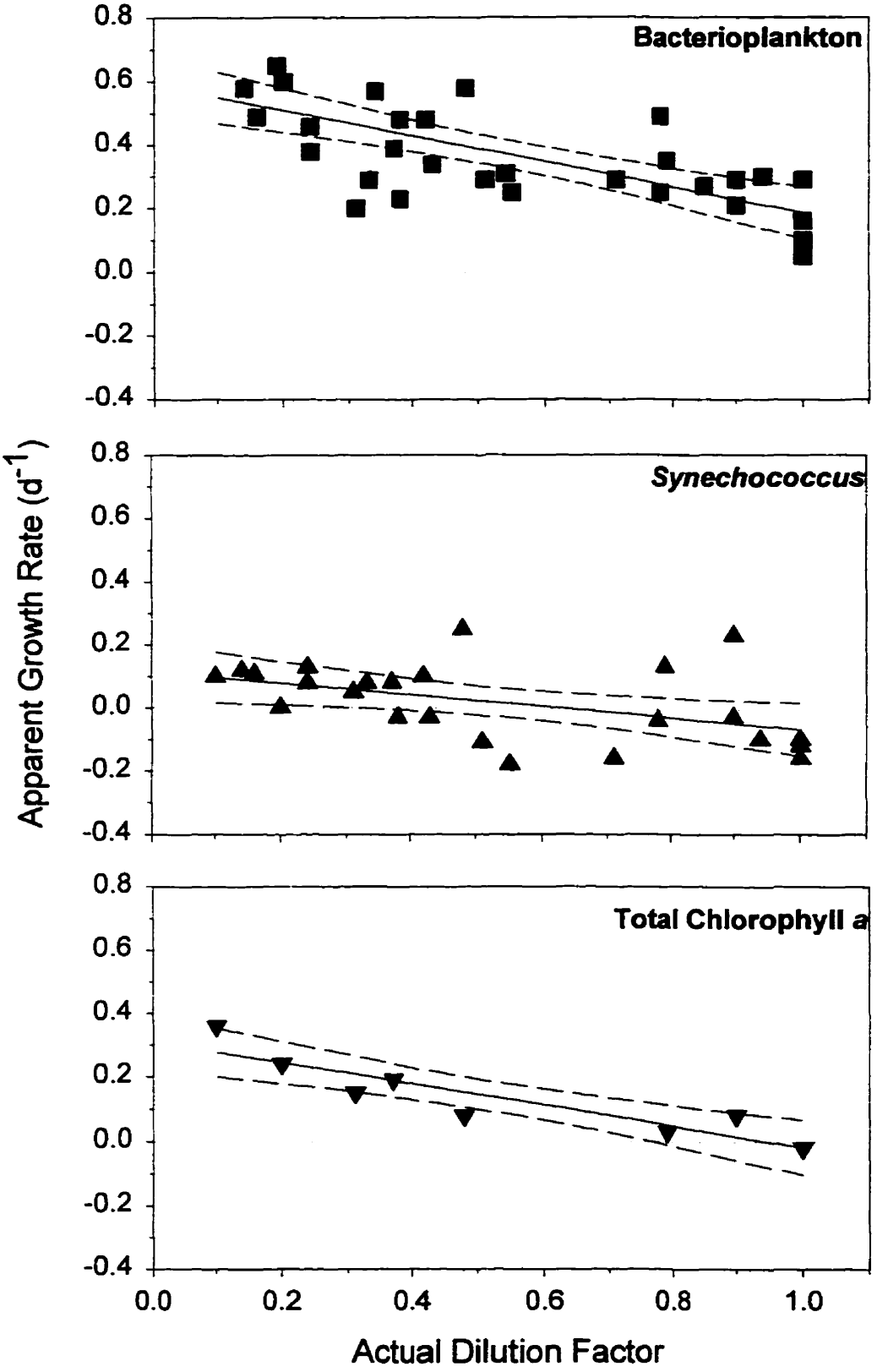
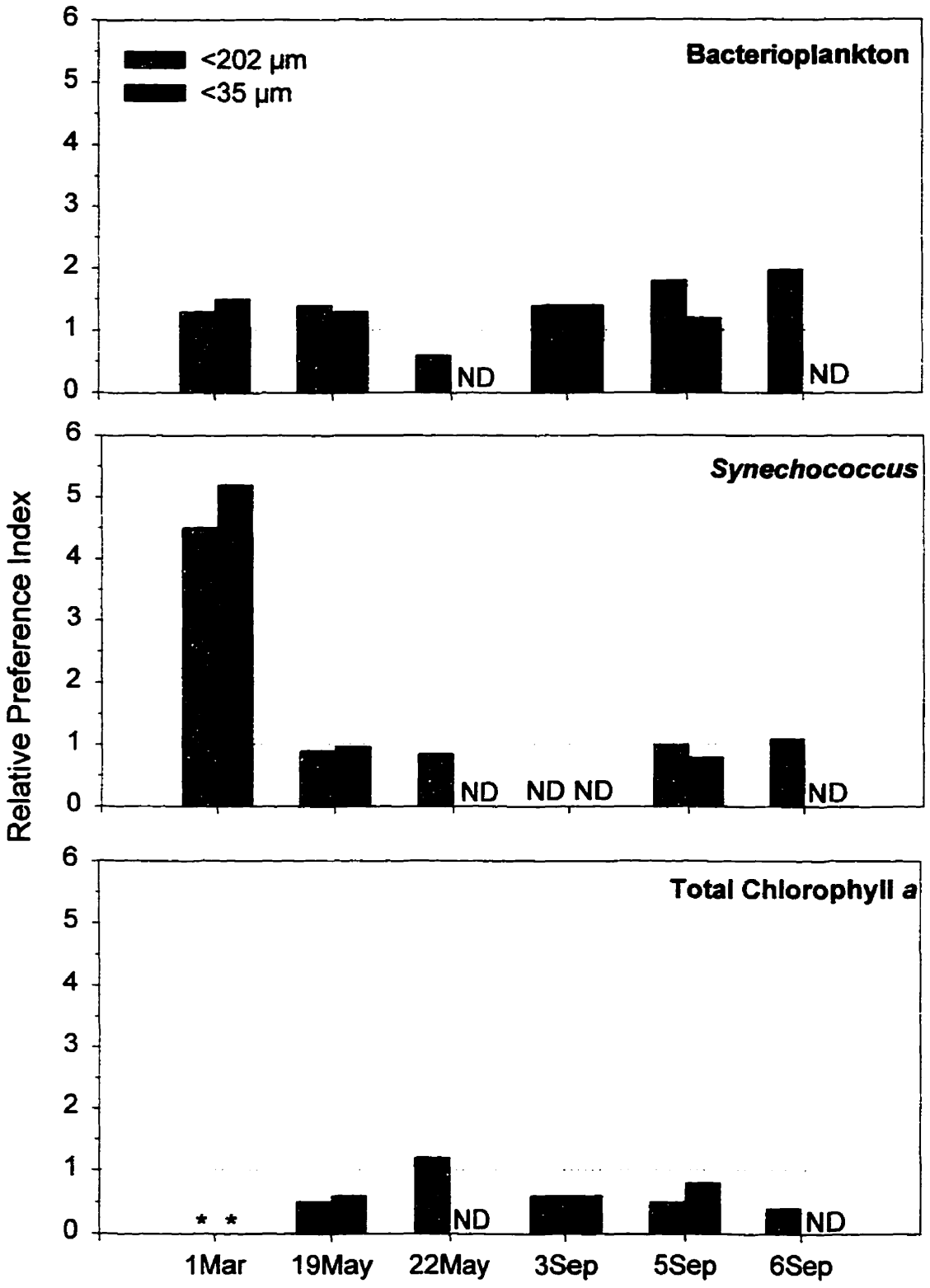

Bacterioplankton
Synechococcus
Total Chlorophyll a
Apparent Growth Rate (d-1)
Actual Dilution Factor
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
0.0
0.2
0.4
0.6
0.8
1.0

Figure 2. 4A. Relative Preference Indices (RPI) of <35 μm and <202 μm microzooplankton for bacterioplankton, *Synechococcus*, and total (>0.7 μm) chlorophyll *a* at Ocean Station Papa. The RPI's were calculated by adapting equations from McCarthy et al. (1977). Asterisks indicate that the RPI is zero because ingestion was zero. ND indicates cases where ingestion was Not Determined.


Relative Preference Index
<202 µm
<35 µm
Bacterioplankton
Synechococcus
Total Chlorophyll a
ND
ND ND ND
* *
0
1
2
3
4
5
6
1Mar
19May
22May
3Sep
5Sep
6Sep

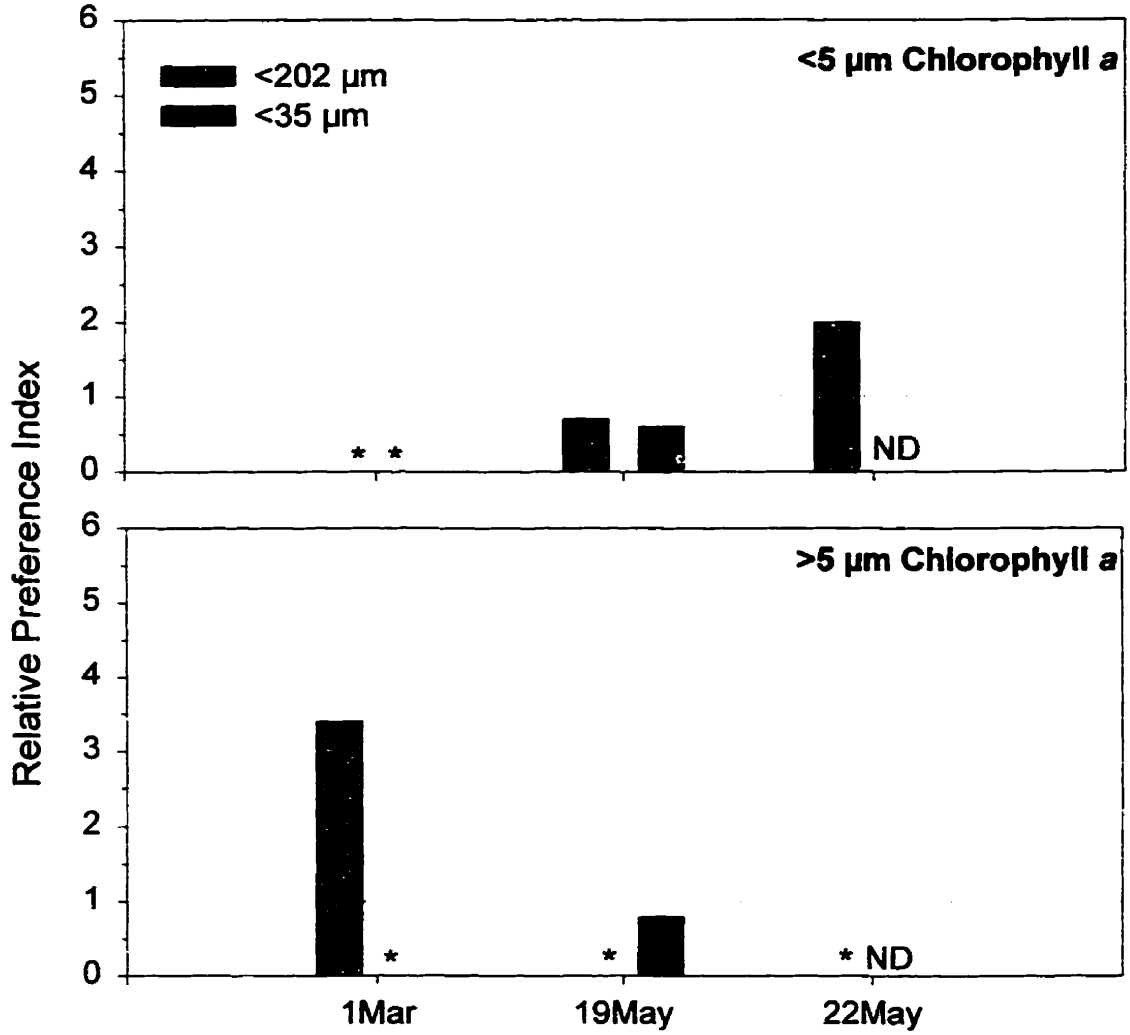


Figure 2. 4B. Relative Preference Indices (RPI) of <35 µm and <202 µm microzooplankton for size fractionated chlorophyll *a* at Ocean Station Papa. The RPI's were calculated by adapting equations from McCarthy et al. (1977). Asterisks indicate that the RPI was zero because ingestion was zero. ND indicates cases where ingestion was Not Determined.

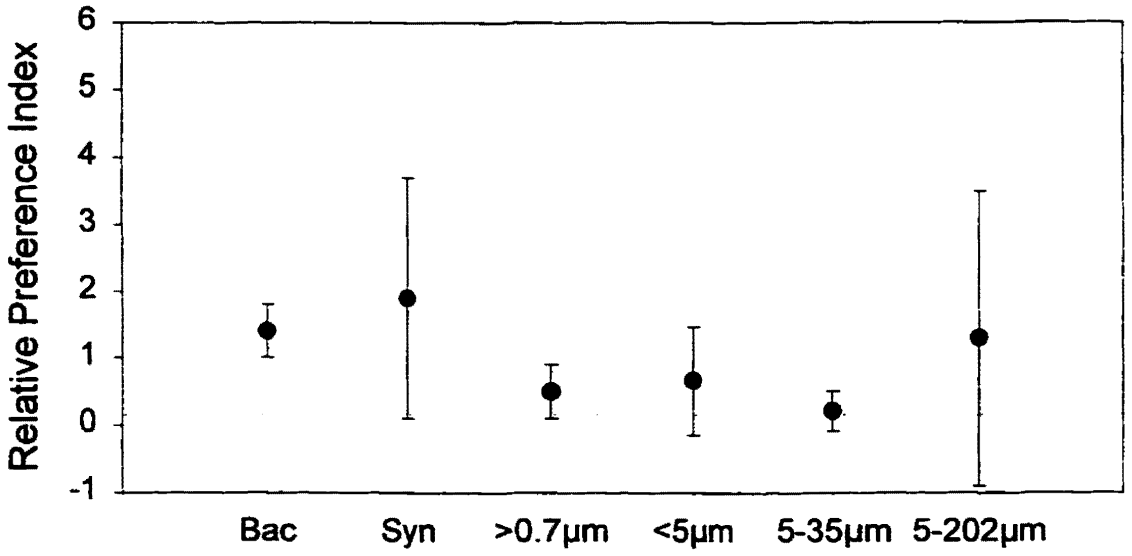
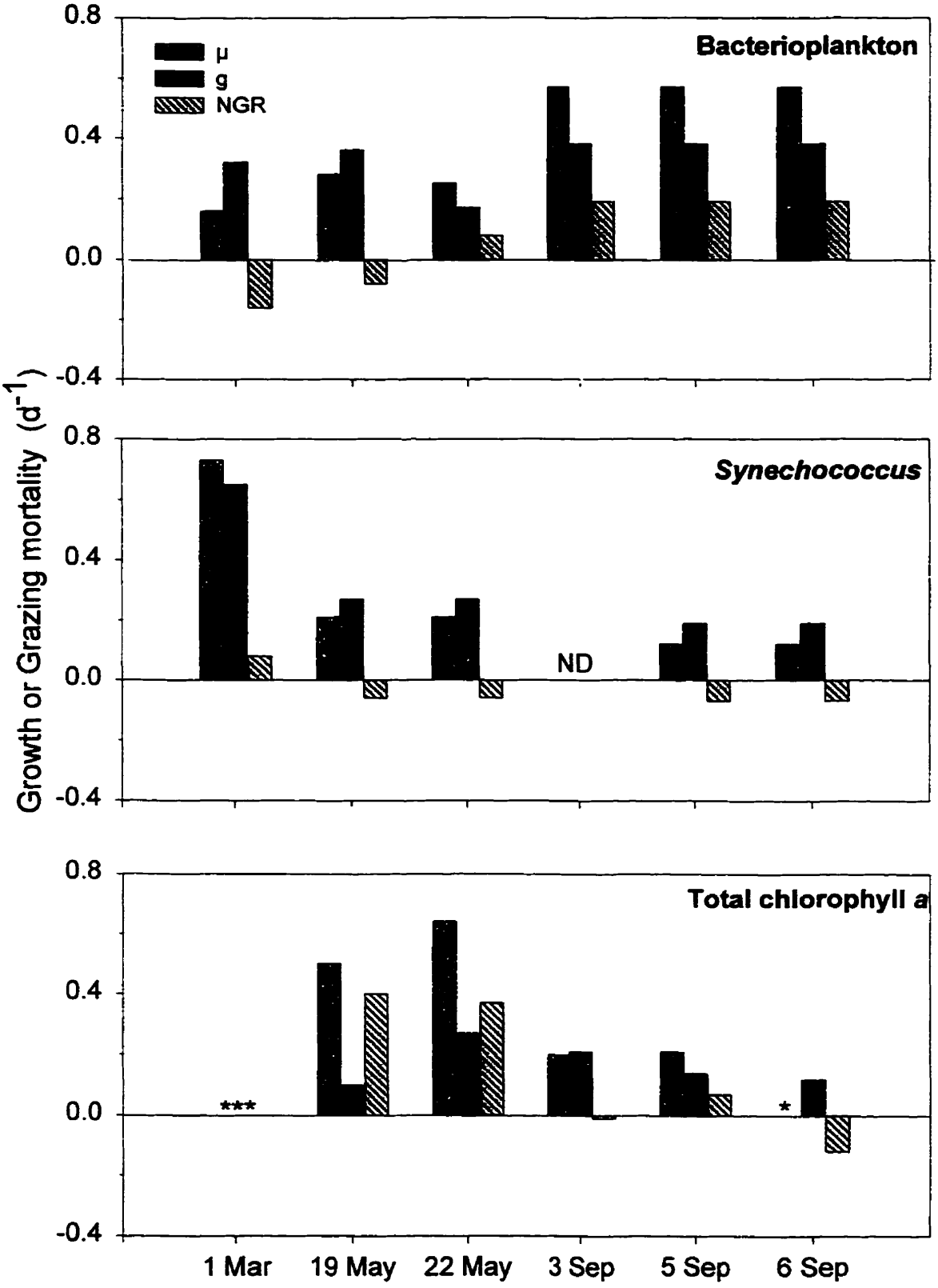


Figure 2. 4C. Mean Relative Preference Indices (± SD) of microzooplankton for bacterioplankton, *Synechococcus*, and size fractionated chlorophyll *a* at Ocean Station Papa.

Figure 2. 5. Rates of growth (μ, d^{-1}), grazing mortality (g, d^{-1}), and net growth for bacterioplankton, *Synechococcus*, and total (>0.7 μm) chlorophyll *a* in <202 μm dilution assays at Ocean Station Papa. Net growth rate is the difference between growth and grazing mortality. Asterisks denote a value of zero. ND indicates cases where rates were Not Determined.


Bacterioplankton
μ
g
NGR
Synechococcus
ND
Total chlorophyll a
***
*
0.8
0.4
0.0
-0.4
Growth or Grazing mortality (d-1)
1 Mar
19 May
22 May
3 Sep
5 Sep
6 Sep

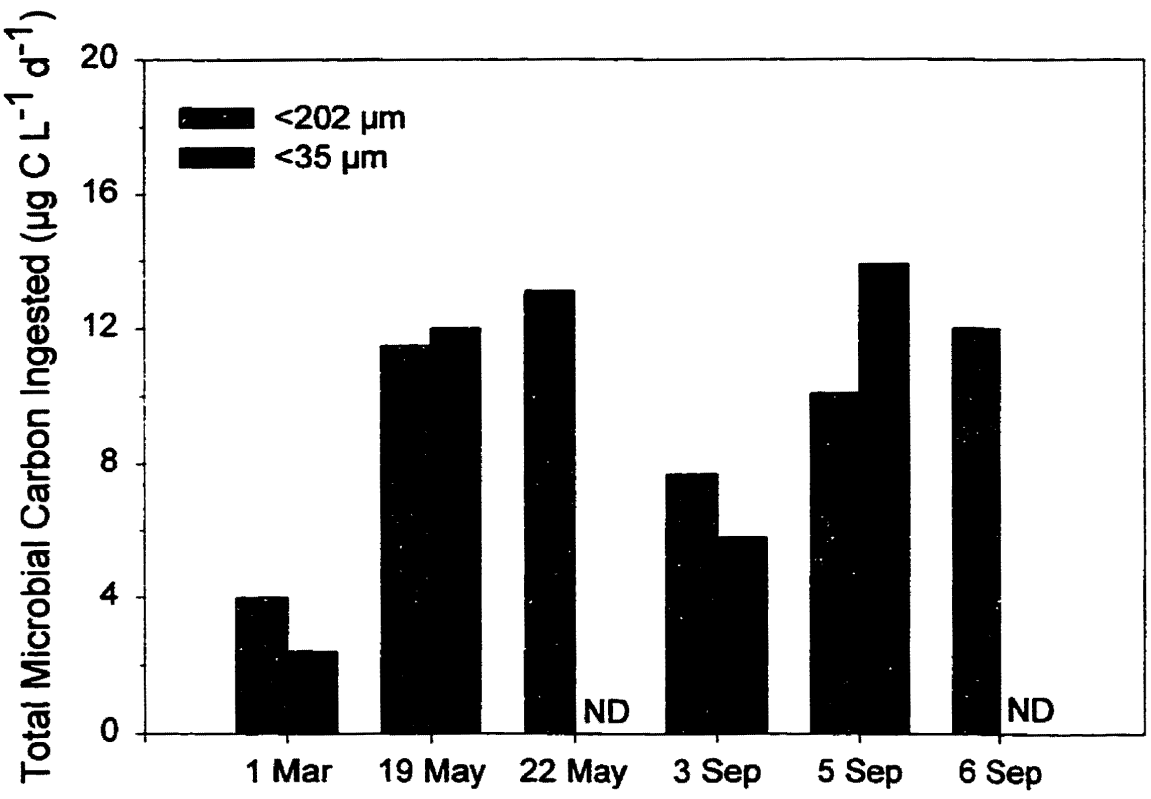
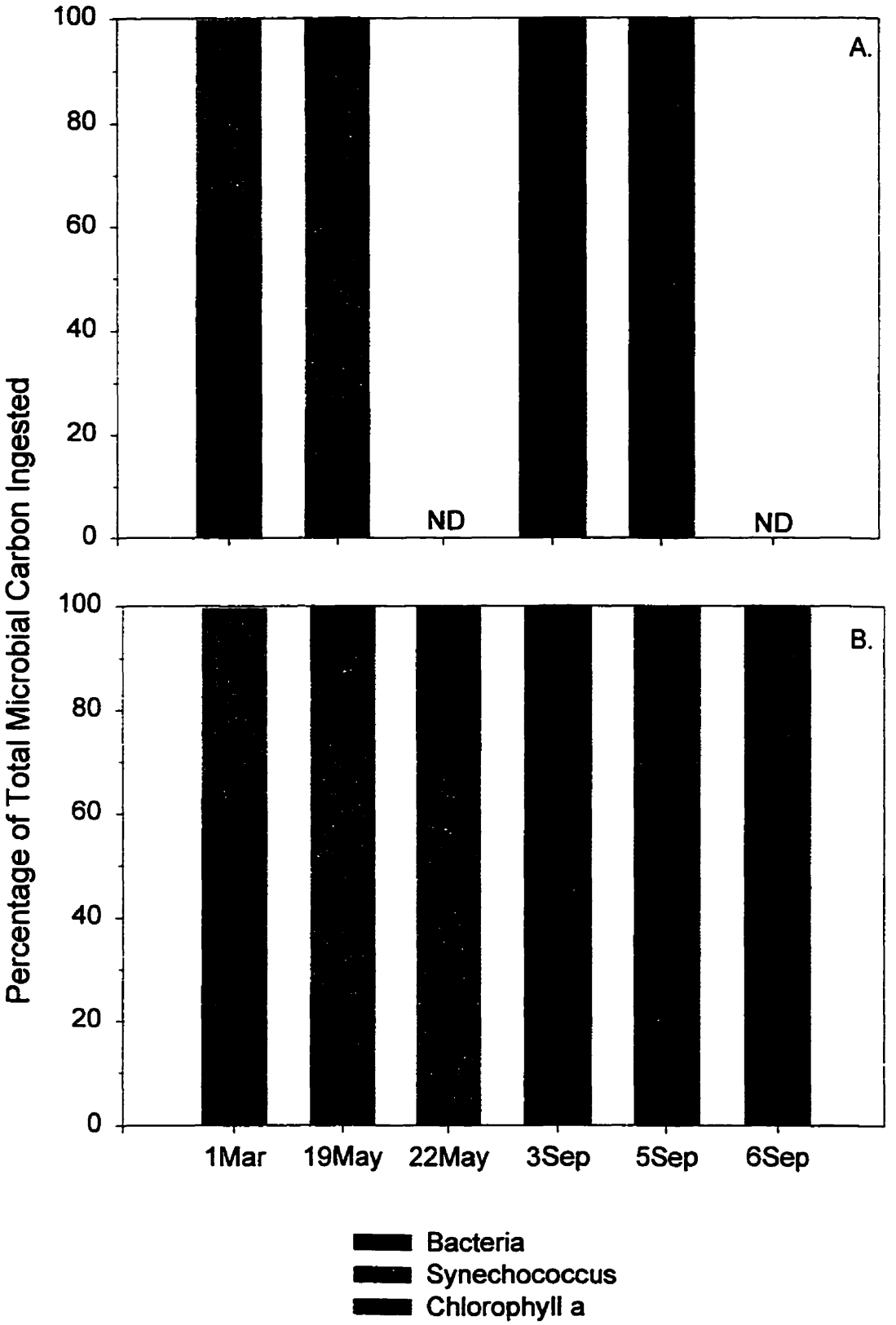


Figure 2. 6. Total ingestion of microbial prey carbon by <35 µm and <202 µm microzooplankton at Ocean Station Papa. Total carbon ingested is the sum of the carbon ingested from bacteria, *Synechococcus*, and total (>0.7 µm) chlorophyll *a*. ND indicates that ingestion was Not Determined.

Figure 2. 7. Percentage of total microbial carbon ingested by <35 μm (A) and <202 μm (B) microzooplankton that was derived from bacteria, *Synechococcus*, and total (>0.7 μm) chlorophyll *a* at Ocean Station Papa. ND indicates cases where ingestion was Not Determined.


Percentage of Total Microbial Carbon Ingested
100
80
60
40
20
0
A.
ND
ND
B.
1Mar
19May
22May
3Sep
5Sep
6Sep
Bacteria
Synechococcus
Chlorophyll a

Chapter 3

Microzooplankton herbivory and bacterivory in Newfoundland coastal waters during spring, summer, and winter

3. 1. Abstract

Grazing by microzooplankton on autotrophic and heterotrophic picoplankton as well as >0.7 μm phytoplankton (as measured by chlorophyll *a*) was studied in July, August, October, January, and April in the surface layer of Logy Bay, Newfoundland (47°38'14"N, 52°39'36"W). Rates of growth and grazing mortality of bacteria, *Synechococcus*, and >0.7 μm phytoplankton were measured using the seawater dilution technique. Microzooplankton ingested 83-184%, 96-367%, and 64-118% of bacterial, *Synechococcus*, and >0.7 μm phytoplankton daily potential production, respectively. The trends in prey net growth rates (i.e. growth-grazing mortality) followed the seasonal cycles of prey biomass, thereby suggesting that microzooplankton are important grazers in Newfoundland coastal waters. Ingestion was lowest during January and October (ca. 2.1 μg C· L^{-1} · d^{-1}) and highest in August (20.4 μg C· L^{-1} · d^{-1}). Aside from April when >0.7 μm phytoplankton represented the majority (81%) of carbon ingested, bacterioplankton and <1 μm phytoplankton represented most of the carbon ingested (ca. 40-100%). Although microzooplankton have here-to-fore been unrecognized as an important grazer population in Newfoundland coastal waters, these results suggest that they play an important role to carbon flow within the pelagic food web.

3. 2. Introduction

In middle to high latitude waters there are seasonal cycles of bacteria and phytoplankton biomass. During spring, microplankton, such as diatoms and dinoflagellates, dominate phytoplankton biomass during short high amplitude blooms (Andersson et al. 1994, Mousseau et al. 1996, Tamigneaux et al. 1997, McKenzie unpubl.). These blooms are replaced by pico- and nanophytoplankton during summer, fall, and winter (Joint et al. 1986, Andersson et al. 1994). While phytoplankton stocks remain low and relatively constant before and after the spring bloom (Kuosa 1991, Hansen 1991, Kiørobe 1993), stocks of *Synechococcus* and bacterioplankton peak during late summer/early fall and remain relatively stable for the remainder of the year (Waterbury et al. 1986, Pick and Caron 1987, Kuparinen and Kuosa 1993, Mousseau et al. 1996). Microbial biomass cycles are the result of changes in net growth rate, or the balance between growth and loss processes (Banse 1992). While factors such as light, nutrients, and temperature influence growth and set the upper limit for biomass production, ultimately loss factors regulate the size of microbial standing stocks (Lehman 1991, Banse 1992).

Potential fates of bacterioplankton and phytoplankton include advection, vertical mixing, sinking, and mortality due to viral lysis and grazing (Banse 1994). While the relative importance of each of these loss factors is poorly understood, mortality due to grazing is generally considered to be one of the most important (e.g. Fuhrman 1992). In

Newfoundland coastal waters (NCW), grazing studies have focussed on *Calanus finmarchicus* and *Oikopleura vanoeffeni* (Knoechel and Steel-Flynn 1989, Deibel and Lee 1992). Urban et al. (1992) have shown that *C. finmarchicus* and *O. vanoeffeni* ingest pico, nano- and microplankton. While grazing, or top-down control, by *C. finmarchicus* and *O. vanoeffeni* is likely important to controlling microbial stocks, so may top-down control by microzooplankton. To date, no comprehensive study of microzooplankton grazing has been conducted in NCW. This may be due to the presumptions that the phytoplankton population consists of large cells that are not efficiently grazed by microzooplankton (Fasham 1995) and surface seawater temperature too low (e.g. <0°C) for the microbial food web to be active (Pomeroy and Deibel 1986, Pomeroy and Weibe 1988). Yet, data is lacking to support these ideas. Studies in other environments not only show that microzooplankton can ingest large phytoplankton (Smetacek 1981, Strom and Strom 1996, Archer et al. 1996), but also show that microzooplankton are active grazers over a wide range of temperatures (e.g. <0°C to >10°C) (Paranjape 1987, Choi and Peters 1992, Burkill et al. 1995, Fronemann and Perrissinotto 1996, Archer et al. 1996, Landry et al. 1984, Campbell and Carpenter 1986, Burkill et al. 1993a, Harrison et al. 1993).

In this study, microzooplankton grazing studies were conducted during periods representative of the seasonal cycle of temperature and microbial stocks to determine if top-down control by microzooplankton is important in the surface layers of NCW. Towards this objective, the rates of growth and grazing mortality of bacterioplankton,

Synechococcus, and total (>0.7 μm) phytoplankton (as measured by chlorophyll *a*) were estimated using dilution assays (Landry and Hassett 1982). The results suggest that microzooplankton are important grazers in NCW and that bacterioplankton and <1 μm phytoplankton represent most of the carbon ingested. The implications of these results to carbon flow in the pelagic food web are discussed.

3. 3. Material and Methods

3. 3. 1. Study sites

Water samples were collected in Conception Bay and Logy Bay on the east coast of Newfoundland (Figure 3. 1). The two bays are exposed to the North Atlantic Ocean and have an inshore branch of the Labrador current at depth, and a seasonal warmer surface layer (Kendaris 1980). The temperature of the Labrador current ranges from -2°C to -1°C, whereas the warmer surface layer experiences temperatures from -2°C to 14°C (Kendaris 1980, Crocker 1994, deYoung and Sanderson 1995). In Conception Bay and Logy Bay, the mixed layer depth ranges from ca. 5 to 30 m from spring to summer. During winter, the water column is isothermal with mixing extending to ca. 200 m in Conception Bay and ca. 65 m in Logy Bay.

3. 3. 2. Seasonal cycles of microbial prey in Conception Bay

Microzooplankton grazing experiments were conducted five times during the year and these times were selected based on the seasonal cycles of temperature and the abundances of microbial prey. The seasonal cycles of temperature and microbial prey (i.e. bacterioplankton, *Synechococcus*, and phytoplankton as measured by chlorophyll *a*) were characterized using surface mixed layer data collected in Conception Bay during 1992 to 1994. This data set was used because it is comprehensive and near to our study site, Logy Bay. Field sampling protocols for Conception Bay are described elsewhere (Rivkin et al. in prep.).

3. 3. 3. Sample collection

Microzooplankton grazing was examined in Logy Bay (47°38'14"N, 52°39'36"W) using the dilution technique (Landry and Hassett 1982). Logy Bay has open ocean access to the North Atlantic Ocean and was chosen as the study site for the grazing studies because of its proximity the Ocean Sciences Centre, Memorial University of Newfoundland. Prior to conducting dilution assays, all equipment that would contact seawater was soaked overnight in 5% HCL and thoroughly rinsed with distilled water. Tubing (Fisherbrand clear plastic) was soaked for another night in seawater (Price et al. 1986). Gelman and Nitex filters were rinsed with distilled water exclusively. Vinyl gloves were worn during all water handling procedures.

Seawater for dilution assays was collected from a zodiac with 5 L PVC bottles. Seawater (20 L) was collected from 5 m and transferred into a darkened polycarbonate carboy. This water was used to prepare size fractionated predator and prey populations (see details below). Water (30 L) for preparing the particle-free diluent was collected from 30 m and transferred into separate polycarbonate carboys. The carboys were delivered to the Ocean Sciences Centre, Memorial University of Newfoundland within 1 h of seawater collection and the initial concentration of chlorophyll *a* and densities of bacterioplankton, *Synechococcus*, and protists in the 5 m collected seawater were estimated using the same procedures that were used for dilution assay samples (see details below).

3. 3. 4. Set-up for dilution assays

Particle-free water (PFW) was prepared by serially gravity filtering the 30 m water through a 10 μm Nitex mesh and 0.2 μm Gelman capsule into a polycarbonate carboy. Several hours were required to prepare the PFW by this gentle method, thus the carboy containing the 5 m seawater was placed in an outdoor incubator cooled with flowing seawater pumped from 5 m in Logy Bay. Once the PFW was prepared, the appropriate volumes were added to 4 L polycarbonate cubitainers. The PFW was used to dilute size fractionated seawater to eight target dilutions of 90, 80, 70, 60, 50, 25, 10, and 0% (PFW: $<$202 μm size fractionated seawater). All dilutions examined grazing by $<$202 μm microzooplankton. However, to examine grazing by small microzooplankton, an additional dilution assay examining grazing by $<$35 μm microzooplankton was conducted in October. The $<$35 μm and $<$202 μm size fractionated seawater was prepared by dispensing the 5 m seawater through tubing that was equipped with the appropriate size Nitex screening. Tubing was submerged below the waterline in the cubitainers so as to reduce damaging the microzooplankton during the filling process. After filling, the cubitainers were incubated for ca. 48 h in the outdoor incubator with incident irradiances attenuated to ca. 33% of ambient using neutral density screening.

3. 3. 5. Sampling dilution assays

The concentration of chlorophyll *a* and abundances of bacteria, *Synechococcus*, and

protists were determined in all cubitainers at the beginning of the incubation (hereafter referred to as time zero) and again after ca. 48 h. The first samples were withdrawn ca. 4 h after preparing the dilution assays because non-linear changes in prey abundances can occur immediately after setting up the dilution assay (Anderson and Rivkin 1998, Rivkin unpubl.). For the enumeration of bacteria, *Synechococcus*, and nanoflagellates, 250 mL samples were collected and preserved in glutaraldehyde (1.5% final concentration) and stored in darkness at 4°C (Sherr and Sherr 1993). For the enumeration of ciliates and dinoflagellates, 500 mL samples were preserved in alkaline Lugol's (final concentration 1% by volume) and stored at room temperature in the dark (Sherr and Sherr 1993). For analysis of total (>0.7 μm) chlorophyll *a*, replicate 250 mL samples were filtered onto 25 mm GF/F filters at <127 mm Hg vacuum and stored in darkness at -20°C. In 1996, the sampling procedure for chlorophyll *a* was modified. Since the coefficient of variation between the replicate filters was less than 5% (n=100), single 500 mL samples were collected. In addition, 500 mL samples were filtered for <1 μm chlorophyll *a* onto 1 μm Poretics filters. The <1 μm chlorophyll *a* concentration was calculated as the difference between total and >1 μm chlorophyll *a* concentration.

3. 3. 6. Sample analysis

Within three months of sample collection, chlorophyll *a* was extracted from filters in 90% acetone for ca. 18 h at -20°C. The concentration of chlorophyll *a* was measured

fluorometrically (Parsons et al. 1984) using the acid ratio method with a Sequoia-Turner fluorometer that was calibrated with commercially prepared pure chlorophyll *a* (Sigma Chemical Co., St. Louis, MO, USA).

Abundances of bacteria, *Synechococcus*, and nanoflagellates were determined using a BH2-RFC Olympus epifluorescence microscope. Within three months of sample collection, seawater was filtered onto 0.2 μm black polycarbonate (Poretics) filters and stained with acridine orange for bacterial counts (Hobbie et al. 1977). Bacteria were visualized using blue excitation (BP440, DM455, AFC+Y475) and counted at a magnification of 1000x. Slides for nanoflagellates and *Synechococcus* were prepared and counted within one month of sample collection. Nanoflagellates were stained with Primulin (Caron 1983) and counted on the same 0.4 μm black polycarbonate filters as were used to count *Synechococcus* (Sherr et al. 1993). Nanoflagellates and *Synechococcus* were counted at a magnification of 600x. Cells were visualized using UV (UG1, DM400, L420) and green excitation (BP545, DM570, O590) for nanoflagellates and *Synechococcus*, respectively (MacIsaac and Stockner 1993, Sherr et al. 1993). *Synechococcus* were identified as yellow-orange fluorescing coccoid cells that had a diameter of ca. 1 μm. Only heterotrophic (i.e. cells without chlorophyll *a* autofluorescence under blue excitation) nanoflagellates were counted (Caron 1983). For bacteria and *Synechococcus*, at least 200 cells were counted per filter (in a minimum of 10 random fields; Coefficient of Variation ≈ 20%). Bacteria and *Synechococcus* abundances were calculated as the mean of cell

abundances estimated from duplicate filters. Nanoflagellates were counted in random fields. A minimum of 100 nanoflagellate cells (i.e. flagellates <20 μm in size) were counted on a single filter. In general, the total area enumerated for nanoflagellates was ca. 1% of the filter.

Abundances of ciliates and dinoflagellates were determined by the Utermöhl method using phase contrast on a Zeiss Axiovert 35 inverted light microscope. Each 500 mL sample was first settled for 8 d and then concentrated to 50 mL by gently aspirating the supernatant. The concentrated samples were settled in 50 mL chambers for 48 h (Hasle 1978). Ciliates and dinoflagellates were counted in random fields at a magnification of 400x. For each sample, a total of 200 cells (ciliates plus dinoflagellates) was enumerated (Venrick 1978a) and dinoflagellates represented most (ca. 76-100%) of the cells counted. The total area enumerated per sample was about 5% of the chamber area.

3. 3. 7. The dilution method

The dilution method (Landry and Hassett 1982) simultaneously estimates the rates of growth and grazing mortality of a microbial prey population in the presence of microzooplankton grazing. In principle, a seawater sample is diluted with particle-free seawater in varying ratios of seawater to particle-free diluent. It is assumed that prey growth is density independent and grazing mortality is density dependent. Each incubation vessel in the dilution series yields an independent estimate of the apparent growth rate

(AGR) of the prey (equation 1),

$$AGR\ (d^{-1}) = 1/t\ [ln\ (P_t/P_o)] \quad (1)$$

where t is the duration of the incubation in days and P_o and P_t are the initial and final prey densities per litre (estimated from chlorophyll *a* or cell counts), respectively. The rates of prey growth and grazing mortality are estimated by linear regression of AGR versus dilution factor (Figure 3. 2). The *y*-intercept of the regression estimates prey growth, μ (divisions $\cdot$ d^{-1}), in the absence of grazing, whereas the slope of the regression estimates grazing mortality, g (d^{-1}), due to microzooplankton.

3. 3. 8. Statistical analyses

For each dilution assay, the rates of prey growth and grazing mortality were determined by the method of Landry and Hassett (1982). Model I linear regressions were conducted for each prey type (i.e. bacterioplankton, *Synechococcus*, and chlorophyll *a*) in each size fractionated (i.e. <35 μm and <202 μm) assay. However, prey AGR's were regressed against the actual dilution factor (ADF) rather than the target dilution factor (TDF). The ADF was calculated using the equation,

$$ADF = Chl\ a_o\ (X_i) / Chl\ a_o\ (X_o) \quad (2)$$

where Chl a_o (X_i) is the time zero chlorophyll *a* concentration at target dilution factor X_i and Chl a_o (X_o) is the time zero chlorophyll *a* concentration of the unmodified (i.e. 0% PFW) treatment. Chlorophyll *a* was used to determine the ADF in all dilution assays due to the precision in estimating chlorophyll *a* (CV≈5%) as opposed to bacterial or *Synechococcus* cell counts (CV≈20%). Since the ADF is a direct estimate of the dilution factor, it is likely to be a better proxy for grazing intensity than the TDF; especially if grazer clearance rates and densities do not change significantly during the course of the dilution assay (Landry et al. 1995b).

For the size fractionated assays (<35 μm and <202 μm) conducted in October, Analysis of Covariance (ANCOVA) was used to test whether either μ or g for each prey type were significantly different among size fractionated assays. If there were significant differences for either μ or g, then the data was analyzed separately. However, if there were no significant differences for μ and g among the size fractions, then the data from the different size fractions was pooled and μ and g estimated from the regression of the pooled data. Analysis of Covariance was also used to test whether either μ or g were significantly different among size fractionated phytoplankton (i.e. <1 μm chlorophyll *a*, 1-202 μm, and >0.7 μm) in January as well as in August. For conservative ANCOVA tests, a significance level of $P<0.10$ was used (Sokal and Rohlf 1995).

3. 3. 9. Microzooplankton grazing impact

The grazing impact on microbial prey by microzooplankton was determined by

calculating microbial prey net growth rates (NGR, d^{-1}), percentage of standing stock ingested (% P_o, d^{-1}), percentage of potential production ingested (% P_p, d^{-1}), and ingestion rate of microbial prey carbon (I_c, μg Carbon $\cdot L^{-1} \cdot d^{-1}$) by microzooplankton using the following formula,

$$NGR = \mu\text{-}g \quad (3)$$

$$\% P_o = \left(((P_o e^{\mu} - P_o) - (P_o e^{(\mu-g)} - P_o))/P_o\right) \times 100 \quad (4)$$

$$\% P_p = \left(((P_o e^{\mu} - P_o) - (P_o e^{(\mu-g)} - P_o))/(P_o e^{\mu} - P_o)\right) \times 100 \quad (5)$$

$$I_c = C_o e^{\mu} - C_o e^{(\mu-g)} \quad (6)$$

where $(P_o e^{\mu} - P_o)$ is potential production, $(P_o e^{(\mu-g)} - P_o)$ is realized production, and C_o is prey carbon (μg Carbon $\cdot L^{-1}$) at time zero in unmodified dilution treatment.

In cases where μ or g where negative, a value of zero was assigned to the corresponding rate estimate to indicate that there was no growth or grazing mortality.

3. 3. 10. Conversion factors

Prey carbon at time zero in unmodified dilution treatment (i.e. 0% PFW) was estimated by converting the prey density estimate to carbon using the appropriate carbon conversion factor. Bacterioplankton and *Synechococcus* abundance estimates were converted to carbon assuming 20 and 250 fg Carbon $\cdot$ $cell^{-1}$, respectively (Lee and

Fuhrman 1987, Li et al. 1992). Chlorophyll *a* estimates were converted to carbon assuming a C:Chlorophyll *a* ratio of 55 (Booth et al. 1993).

3. 4. Results

3. 4. 1. Seasonal cycles of microbial prey in Conception Bay

The Conception Bay data was organized by depth strata and station. Based on the CTD profiles of temperature, depth strata were defined as surface mixed layer, thermocline, and deep mixed layer. Kruskal-Wallis Analysis of Variance tests indicated that there were no significant differences for surface mixed layer temperature ($H=1.76$, $P=0.42$), total chlorophyll *a* concentration ($H=0.27$, $P=0.87$), *Synechococcus* abundance ($H=0.55$, $P=0.76$), or bacterial abundance ($H=3.43$, $P=0.18$) among the stations sampled. Thus, the surface mixed layer data was combined from all stations (Figure 3. 3 A-D) and for comparison are presented with available surface mixed layer from Logy Bay (Figure 3. 3 E-H).

The cycles of temperature, bacteria, and chlorophyll *a* in Conception Bay are comparable to those in Logy Bay (there were insufficient data on the distribution of *Synechococcus* in Logy Bay to compare to Conception Bay data). For example, in both bays the annual temperature minima (ca. -2°C) and maxima (ca. 14°C) occur around March and September, respectively (Figure 3. 3A;E). For most of the year (i.e. December to June), bacteria and *Synechococcus* abundance are ca. 3.0×10^8 cells $\cdot$ L^{-1} and 1.3×10^6 cells $\cdot$ L^{-1}, respectively (Figure 3. 3B;F;C). However, bacterial abundance increases to ca. 1.0×10^9 cells $\cdot$ L^{-1} from ca. July to October and *Synechococcus* abundance increases to ca. 7.5×10^6 cells $\cdot$ L^{-1} from ca. July to November (Figure 3. 3B;F;C). Chlorophyll *a*

concentrations are relatively stable and low (<0.5 μg chlorophyll *a* · L^{-1}) for most of the year except from April to May when chlorophyll *a* increases to 4 μg chlorophyll *a* · L^{-1} (Figure 3. 3D;H). Thus, the cycles of temperature and microbial prey in Conception Bay data were a good proxy for those in Logy Bay. To examine microzooplankton grazing during biologically important times (e.g. spring bloom, non-spring bloom period, bacterial bloom, temperature minimum and maximum), the rates of growth and grazing mortality of bacterioplankton, *Synechococcus*, and chlorophyll *a* were measured during spring (April), summer (July and August), fall (October), and winter (January).

3. 4. 2. Distribution of microbial carbon

In most of the dilution assays, a large portion (up to 79%) of the microbial carbon consisted of picoplankton (i.e. bacteria and <1 μm chlorophyll *a*) (Table 3. 2). Although the concentration of <1 μm chlorophyll *a* was not measured in July or October, Crocker (1994) reported that <1 μm chlorophyll *a* represent ca. 40% of total chlorophyll *a* from mid June to February in Logy Bay. Thus, it's likely that picoplankton represented ca. 79% (65% bacteria and 14% <1 μm chlorophyll *a*) of the total microbial carbon in July and ca. 54% (23% bacteria and 31% <1 μm chlorophyll *a*) in October. In January and August, picoplankton also represented a large portion (69-76%) of the microbial carbon. However, during the spring bloom (April) picoplankton only represented 26% of total carbon which was totally derived from bacteria as both *Synechococcus* and <1 μm

chlorophyll *a* were not detected. Thus, for most of the year, picoplankton represented the majority (54-79%) of the total microbial carbon in the surface layer.

Synechococcus only represented a small portion of <1 μm chlorophyll *a* carbon (Table 3. 2). Using the above estimates of <1 μm chlorophyll *a* carbon, *Synechococcus* comprised $<17\%$ of <1 μm chlorophyll *a* carbon. The minimum contribution of *Synechococcus* carbon to <1 μm chlorophyll *a* carbon was in July and April and the maximum was in October.

3. 4. 3. Protist abundances

Protists were abundant in Logy Bay (Tables 3. 1 and 3. 3). As also observed by Sleigh et al. (1996), micrometazoans (e.g. copepod nauplii) were rarely observed and therefore were not enumerated. Flagellates were the most numerous protists followed by dinoflagellates and then ciliates. Peak abundances of flagellates, ciliates, and dinoflagellates occurred in August. Minimum abundances of flagellates and ciliates occurred during April, whereas the minimum dinoflagellate abundance occurred during October. Mean protist abundances in initial samples (Table 3. 1) were greater than those in time zero unmodified dilution treatments (Table 3. 3); however, the differences were generally not significant (paired ANOVA, $P>0.05$).

3. 4. 4. Microzooplankton grazing

Tables 3. 4 and 3. 5 summarize the results from ANCOVA tests. As Table 3. 4 indicates, there were no significant differences for either μ and g among <35 μm and <202 μm size fractions for *Synechococcus* and thus *Synechococcus* data from the size fractions was pooled to estimate the rates of μ and g. In contrast, the growth rates for both bacteria and chlorophyll *a* were significantly different among sizes fractions and thus bacteria and chlorophyll *a* data in the different size fractions was analyzed separately. The ANCOVA results for the size fractionated chlorophyll *a* (Table 3. 5) indicate that there were significant differences among the growth rates of <1 μm, 1-202 μm, and >0.7 μm chlorophyll *a* in January and thus the chlorophyll *a* data was analyzed separately. In contrast, in August there were no significant differences for either μ or g for <1 μm, 1-202 μm, and >0.7 μm chlorophyll *a* and therefore the data was combined to estimate μ and g.

Although some slopes of AGR vs. ADF were not significantly different from zero, in most (60%) cases, the relationship between AGR and ADF was linear and had a significant negative slope (Table 3. 6 and Figure 3. 4). Significant slopes had r^2 (coefficient of determination) values that ranged from 0.65-0.75, 0.54-0.55, and 0.32-0.68 for bacterioplankton, *Synechococcus*, and chlorophyll *a*, respectively (Table 3. 6). Microzooplankton ingested 83-184%, 96-367%, and 64-118% of bacterial, *Synechococcus* and chlorophyll *a* production, respectively and 34-111%, 25-30%, and 16-131% of

bacterial, *Synechococcus* and chlorophyll *a* standing stocks, respectively (Table 3. 6).

The seasonal patterns of μ, g, and NGR for bacteria, *Synechococcus*, chlorophyll *a* differed (Figure 3. 5). For bacteria, both growth and grazing mortality generally increased from January to August and then decreased. Bacterial NGR increased from January to October. For *Synechococcus*, growth increased from a minimum value in January to a maximum value in October, whereas grazing mortality decreased during the same period. *Synechococcus* NGR increased from January to October. For chlorophyll *a*, growth and grazing mortality increased from January to July and then decreased. The net growth rate of chlorophyll *a* was zero or less for most of year prior to the spring phytoplankton bloom in April (Figure 3. 3D;H).

Daily ingestion of microbial carbon increased from January (2.1 μg C$\cdot$ L^{-1}) to August (20.4 μg C$\cdot$ L^{-1}) and then decreased in October (2.1 μg C$\cdot$ L^{-1}) (Figure 3. 6). During January and August the contribution of picoplankton (i.e. bacterioplankton and <1 μm chlorphyll *a*) to total carbon ingested was large (Table 3. 6). In July and October, the ingestion of <1 μm chlorophyll *a* was not measured and thus the contribution of picoplankton to total carbon ingested could have been large during these periods as well. During the spring bloom (i.e. 24 April), *Synechococcus* and <1 μm chlorophyll *a* were not detected and bacterioplankton represented only a small (19%) portion of the carbon ingested.

To assess the prey preference of microzooplankton, Relative Preference Indices

(RPI) were calculated for each prey by adapting equations from McCarthy et al. (1977). The RPI's were determined using the equation:

$$RPI = (I_{(p1)} / I_{(p1)} + I_{(p2)} + I_{(p3)}) \quad x \quad (C_{(p1)} / C_{(p1)} + C_{(p2)} + C_{(p3)})^{-1}$$

The RPI is the ratio of the fraction of prey type 1, 2 or 3 ingested (I) to the fraction of prey type 1, 2 or 3 occurring *in situ* (i.e. at time zero in the unmodified dilution treatment) (C). A value < 1 indicates 'avoidance' of the prey, a value > 1 indicates 'preference' for the prey, and a value of unity indicates that the prey are ingested in proportion to their availability *in situ*. In this study, the RPI's were variable (Figure 3. 7A). However, the mean RPI's of microzooplankton for bacteria, *Synechococcus* and total chlorophyll *a* were ca. 1 (Figure 3. 7B).

3. 5. Discussion

3. 5. 1. Methodological considerations

The details of methodological considerations are discussed in Chapter 2. The rates of prey growth were likely not affected by differential nutrient availability or shifting light levels. Nutrient concentrations in Logy Bay are high from mid-September through late May and prey growth would be potentially nutrient limited only during late spring through summer. Only two (i.e. July and August) of the five experiments were carried out during the period of potential nutrient limitation. The water used as the diluent was collected from 30 m, which is below the summer mixed layer depth and had elevated inorganic nutrient concentrations (Rivkin, unpubl.) even during the July and August experiments. As a result, it is unlikely that prey growth was nutrient limited, except perhaps at the ADF=1. However, nutrient limited prey growth at the ADF=1 would be unlikely as nutrient supply rate, which is directly proportional to protist abundance (Goldman and Caron 1985), would be maximal at the ADF=1. In addition, estimates of prey growth (and grazing mortality) were computed from regressions with an average of 10 independent observations (range = 5 to 24) with normally distributed residuals which strongly suggests that none of the observed AGR were disproportionally influenced by nutrients. Furthermore, results from previous studies suggest that the rates of prey growth are not affected by shifting light levels or differential nutrient availability (Rivkin et al. 1982, Landry et al. 1995b & refs. cited therein, Chapter 2).

Rates of mortality due to microzooplankton grazing were likely not affected by grazer satiation or under-representation of microzooplankton caused by damage during handling. Non-linear dilution plots, which indicate grazer satiation (Gifford 1988, Gallegos 1989), were not observed. In addition, there were no significant differences between protist abundances in time zero unmodified samples and initial seawater samples to suggest that protists were under-represented.

3. 5. 2. Top-down control

Microzooplankton exerted top-down control on bacterioplankton, *Synechococcus*, and phytoplankton in Logy Bay. As indicated by the percentage of potential production ingested (Table 3. 6), microzooplankton top-down control on bacterioplankton, *Synechococcus*, and phytoplankton in Logy Bay was substantial. In fact, together the trends in NGR (Figure 3. 5) and seasonal cycles of microbial prey (Figure 3. 3) suggest that microzooplankton are important grazers of microbial prey in NCW. Seasonal cycles of microbial prey are the reflection of changing net growth rate, which is the balance between growth and loss processes (Banse 1992). In this study, the NGR (i.e. μ-g) of bacteria and *Synechococcus* (Figure 3. 5) increased during the same time periods when bacteria and *Synechococcus* stocks increase (Figure 3. 3B, F, C). Phytoplankton NGR and stocks also followed similar trends. For example, the net growth of phytoplankton was only positive during the spring bloom and was ca. zero for most of the year when

phytoplankton stocks are relatively constant (Figure 3. 3D, H). While there are other potential fates of microbial biomass, such as viral lysis (Proctor and Fuhrman 1990, Fuhrman and Noble 1995) and ingestion by mesozooplankton (e.g. *Calanus finmarchicus*, *Oikopleura vanoeffeni*) (Deibel and Lee 1992, Urban et al. 1992), the tracking of NGR estimated in this study with the changes in stock sizes for bacteria, *Synechococcus*, and phytoplankton suggests that microzooplankton bacterivory and herbivory are important in NCW. The size fractionated results in October show that most of the grazing activity on microbial prey was by <35 μm protists (Table 3. 4). Studies in other environments also suggest that microzooplankton are important grazers of bacteria, *Synechococcus*, and phytoplankton (Sherr et al. 1986a&b, Weisse 1989, Kudoh et al. 1990, Capriulo et al. 1991, Sanders et al. 1992, Landry et al. 1993a, Vaqué et al. 1994, Šolić and Krstulović 1994, Landry et al. 1996) and that a large portion of the grazing activity is by grazers <20 μm in size (Weisse 1989, Caron et al. 1991, Verity et al. 1996, Reckermann and Veldhuis 1997). As microbial biomass in pelagic systems is generally <5 μm in size (Sherr et al. 1986b), it is possible that microzooplankton are important grazers because they conform to the 10: 1 predator to prey size ratio "rule" (Fenchel 1988).

The top-down control by microzooplankton estimated in this study is similar to that reported in other environments (Table 3. 7). The results also show that during January and April, when seawater temperatures were low (i.e. $\leq$ 0°C), bacterial growth was active (doubling time ca. 4-9 d), albeit at a seasonal minimum (Figure 3. 5). These results

indicate that despite seasonally cold temperatures in NCW (Figure 3. 3A, E), the microbial food web remains active all year. Thus, the results do not support the view that the microbial food web is inactive at low seawater temperatures during the spring bloom (Pomeroy and Deibel 1986, Pomeroy and Weibe 1988).

Active microzooplankton herbivory during the spring bloom may have been due to the predominance of *Gymnodinium* spp.. As observed by others (Shapiro et al. 1988, Harrison et al. 1993, Burkill et al. 1993b, Verity et al. 1993a, Sleigh et al. 1996), *Gymnodinium* spp. predominated the dinoflagellate assemblage (ca. 80% of total dinoflagellates counted in our samples) during the spring bloom (personal obs., Figure 3. 8). These dinoflagellates can engulf large diatoms (Lessard 1991, Hansen 1991, Jacobson and Anderson 1993, Hansen et al. 1994, Neuer and Cowles 1995, Strom and Strom 1996) even at low (i.e. $<0°C$) temperatures (Archer et al. 1996). Assuming these *Gymnodinium* spp. had ingestion rates similar to those reported for two gyrodinium species in the Antarctic (i.e. 33 and 53 μg C $cell^{-1}$ h^{-1} at temperatures $<0°C$) (Archer et al. 1996), then *Gymnodinium* spp. in Logy Bay may have ingested up to 8.7 μg C L^{-1} d^{-1}, or 87% of the total phytoplankton carbon ingested by the microzooplankton assemblage.

Active bacterial growth at low temperatures during the spring bloom may have been due to high (i.e. micromolar) ambient substrate levels. Recent studies suggest that temperature suppression of bacterial growth is alleviated by increased substrate levels (Pomeroy et al. 1991, Weibe et al. 1992, Pomeroy and Weibe 1993, Weibe et al. 1993).

Substrates can be supplied from phytoplankton exudates (Bird and Kalff 1984, Cole et al. 1988, Ducklow and Carlson 1992), viral lysis (Proctor and Fuhrman 1990, Fuhrman and Noble 1995), as well as from the excretion, defecation, and sloppy feeding of micro- and mesozooplankton (Roman et al. 1988, Jumars et al. 1989, Harrison 1991, Ferrier-Pagès and Rassoulzadegan 1994a&b). However, the production of bacterial substrates from mesozooplankton is likely low as mesozooplankton grazing is minimal during the spring bloom (Redden 1994). Since dissolved substrates from phytoplankton are insufficient to support active bacterial growth (Smetacek and Pollehne 1986), substrates from microzooplankton are probably essential to supporting active bacterial growth during the spring bloom. It is conceivable that during the spring bloom the presence of gymnodinium dinoflagellates is not only important for active microzooplankton herbivory, but also for active bacterial growth.

3. 5. 3. Ingestion of microbial carbon

The total microbial carbon ingested by microzooplankton followed the seasonal temperature cycle (Figures 3. 3A, E and 3. 6). This may, in part, occur because protist growth, clearance, and respiration rates increase with temperature, while gross growth efficiency decreases with temperature (Caron et al. 1986, Caron et al. 1991, Choi and Peters 1992). For example, the lower ingestion rates during winter, spring, and fall may be due to the lower protist abundances (Tables 3. 1 and 3. 3) caused by lower

temperatures decreasing protist growth. Lower respiration rates and higher GGE at lower temperatures may further decrease the carbon requirements of the microzooplankton community. The lower ingestion during October may also be due to microzooplankton avoiding bacteria and preferring to ingest *Synechococcus* (Figure 3. 7A). In contrast, the higher ingestion rates during summer are likely due to higher protist abundances caused by higher temperatures increasing protist growth (exceeding losses e.g. ingestion by mesozooplankton). The higher respiration rates and lower GGE at higher temperatures may also increase the carbon requirements of protists during summer.

From June to March picoplankton represented a large portion of the carbon ingested by microzooplankton (Table 3. 6). This was shown in August and January (Table 3. 6), but not in July and October because the ingestion of <1 μm phytoplankton was not estimated. However, the ingestion of <1 μm phytoplankton in July and October can be indirectly estimated. The present results (Figure 3. 7) as well as those of Reckermann and Veldhuis (1997) show that microzooplankton, on average, ingest prey in proportion to their availability. Data from Crocker (1994) also show that <1 μm phytoplankton represent ca. 40% of total phytoplankton in July and October (Table 3. 2). Thus, 40% of the phytoplankton ingested in July and October was likely derived from <1 μm phytoplankton. This means that about 64% of the total carbon ingested in July was derived from picoplankton (40% from bacteria and 24% from <1 μm phytoplankton). Similarily, in October ca. 40% of the total carbon ingested was derived from picoplankton (100%

from <1 μm phytoplankton). Using these indirect estimates (as well as direct estimates from August and January), the proportional contribution of picoplankton to total carbon ingested from June to March was significantly greater than that of >0.7 μm phytoplankton (Table 3. 8). As microzooplankton are important grazers in NCW (Table. 3. 6), this suggests that for most of the year the food web in the surface layer may be picoplankton-based. Lessard and Rivkin (1986) also presented results which suggest that the food chain in McMurdo Sound is detrital-based. We are not aware of other studies that have simultaneously examined microzooplankton herbivory and bacterivory with which to compare the present results. Given the importance of determining the rates and pathways of carbon flow in marine pelagic food webs, it is evident that additional studies simultaneously measuring microzooplankton herbivory and bacterivory are needed.

Synechococcous generally represented a small portion ($<1\%$) of the <1 μm phytoplankton ingested (Table 3. 6). Only in October did *Synechococcous* represent a substantial (42%) portion of the <1 μm phytoplankton ingested (based on above indirect estimate of <1 μm phytoplankton ingested). This was likely due to the peak in *Synechococcous* biomass during the temperature maximum (Figure 3. 3A, C, E, G) as well as the preference by microzooplankton (Figure 3. 7A). *Synechococcus* biomass peaks during the temperature maximum in many environments and thus, *Synechococcous* are thought to be temperature dependant (Glover 1985, Caron et al. 1985, Joint 1986, Waterbury et al. 1986, Pick and Caron 1987, Kuosa 1991, Miyazono et al. 1992,

Kuparinea and Kuosa 1993, Booth et al. 1993, Fogg 1995). In contrast, eukaryotic autotrophs are thought to be an increasingly important biomass component of autotrophic picoplankton in higher latitudes or colder waters (Murphy and Haugen 1985, Li 1995). It follows that most of the < 1 μm phytoplankton ingested by microzooplankton was likely derived from eukaryotic autotrophs.

3. 5. 4. Ecological implications to the vertical export of biogenic carbon

In middle to high latitude coastal waters, large benthic fisheries depend upon biogenic carbon from the overlying water column. The vertical export of the spring bloom (i.e. phytodetritus) to depth is considered to be a major source of nutrition for the benthic community (Cushing 1989, Nielsen and Richardson 1989, Legendre 1990, Gage and Tyler 1991, Beinfang and Zeimann 1992, Navarro and Thompson 1995). Models predicting the vertical export of biogenic carbon generally equate spring diatom production to export (Kiørobe 1993). The role of microzooplankton in biogenic export is generally perceived to be minimal. Yet, the present results as well as those of Urban et al. (1993a&b) suggest that microzooplankton may be more important to particle flux from the surface layer than previously thought. First, microzooplankton grazing may increase the potential for small microbes, such as bacteria and < 1 μm phytoplankton, to be exported to the benthos (also see Burkill et al. 1993a) because microzooplankton are ingested by mesozooplankton for most of the year (Urban et al 1992., Ohman and Runge 1994). The microbial carbon

ingested by microzooplankton (primarily picoplankton; see Table 3. 6) may thus be transferred to mesozooplankton. Indeed, studies by Urban et al. (1992) show that picoplankton are transferred to higher trophic levels, as bacteria and cyanobacteria occur in mesozooplankton fecal pellets. Through vertical migration and the production of actively sinking carcasses, hard body parts, aggregates, and fecal pellets (Noji 1991, Urban et al. 1993a&b), mesozooplankton may facilitate the export of small microbes to the benthos. Second, active microzooplankton herbivory (and bacterial growth) may decrease the flux of the spring bloom to the benthos. Our results during the spring bloom (April) indicate that bacteria consume ca. 40% of phytoplankton production (assuming a 30% gross growth efficiency, Pomeroy and Weibe 1988) and that microzooplankton can ingest a significant portion of phytoplankton production (Table 3. 6). As mesozooplankton are primarily herbivorous during the spring bloom (Urban et al. 1992, Ohman and Runge 1994) and microzooplankton and bacteria generally don't sink or produce sinking body parts/fecal pellets (Stoecker 1984, Small et al. 1987), the spring phytoplankton production consumed by microzooplankton and bacteria will likely not be exported to depth (Verity et al. 1993b, Legendre and LeFèvre 1995). Clearly, models predicting the vertical export of biogenic carbon should consider the impact of vigorous microzooplankton grazing on particle flux.

Table 3. 1. Dates and times when water samples were collected for dilution assays conducted in Logy Bay (47°38'14"N, 52°39'36"W). Temperature (Temp), chlorophyll *a* (Chl *a*) concentration, and bacteria (Bact), *Synechecoccus* (Syn), and protist abundances correspond to samples drawn from freshly collected 5 m seawater.

Date	Time	Temp (°C)	Chl *a* (>0.7 µm) (µg ·L^{-1})	Bact (10^8 cells·L^{-1})	Syn (10^6 cells·L^{-1})	Flagellates (cells·L^{-1})			Ciliates (cells· L^{-1})	Dinoflagellates (cells· L^{-1})
						<5 µm	5-10 µm	>10 µm		
11 Jul 95	1100	9.5	0.13	5.2	nd	460 000	37 000	8 600	600	4 000
04 Oct 95	1100	10.0	0.45	2.8	5.6	200 000	33 000	12 000	600	7 000
31 Jan 96	1000	0.0	0.09	0.6	0.4	370 000	38 000	9 000	1 000	9 700
24 Apr 96	1030	-1.0	1.0	6.8	nd	10 000	4 000	1 000	300	8 000
06 Aug 96	1000	12.5	0.25	5.7	0.6	850 000	87 000	4 600	3 000	17 000

nd - not detected.

Table 3. 2. Distribution of microbial carbon in time zero samples collected from unmodified dilution treatments in Logy Bay. Concentrations (Concn.) of bacteria (Bact, x 10^8 cells·L^{-1}), *Synechococcus* (Syn, x 10^6 cells·L^{-1}), and Chlorophyll *a* (Chl *a*, μg Chl *a*·L^{-1}) were converted to carbon (C_o, μg C·L^{-1}) assuming 20 fg C·$cell^{-1}$ and 250 fg C·$cell^{-1}$ for bacteria and *Synechococcus*, respectively and a C: Chl *a* ratio of 55. The % Pico is the percent contribution of picoplankton to total carbon. The % Syn is the percent contribution of Syn to <1 μm Chl *a*. Total Chl *a* is >0.7 μm and <1 μm Chl *a* is 0.7 to 1 μm.

Time	Size fraction (μm)	Prey	Concn.	C_o	Total C_o[2]	% Total C_o	% Pico[3]	% Syn[4]
11 Jul 95	202	Bact	7.3	14.6	22.3	65	79	0
		Total Chl *a*	0.14	7.7		35		
		< 1μm Chl *a*	0.06[1]	3.1		14		
		> 1μm Chl *a*	0.08	4.6		21		
		Syn	nd	na		na		
04 Oct 95	202	Bact	3.8	7.6	32.9	23	54	10
		Total Chl *a*	0.46	25.3		77		
		< 1μm Chl *a*	0.18[1]	10.1		31		
		> 1μm Chl *a*	0.28	15.2		46		
		Syn	4.1	1.0		3		
04 Oct 95	35	Bact	3.4	6.8	27.1	25	55	17
		Total Chl *a*	0.37	20.3		75		
		< 1μm Chl *a*	0.15[1]	8.1		30		
		> 1μm Chl *a*	0.22	12.2		45		
		Syn	5.6	1.4		5		
31 Jan 96	202	Bact	1.8	3.6	9.2	39	69	1
		Total Chl a	0.10	5.6		61		
		< 1μm Chl *a*	0.05	2.8		30		
		> 1μm Chl *a*	0.05	2.8		30		
		Syn	0.1	0.03		0.3		
24 Apr 96	202	Bact	9.7	19.4	73.9	26	26	na
		Total Chl *a*	0.99	54.5		74		
		< 1μm Chl *a*	nd	na		na		
		> 1μm Chl *a*	0.99	54.5		74		
		Syn	nd	na		na		

Table 3. 2. *Continued.*

Time	Size fraction (μm)	Prey	Concn.	C_o	Total C_o[2]	% Total C_o	% Pico[3]	% Syn[4]
06 Aug 96	202	Bact	5.8	11.6	23.2	50	76	3
		Total Chl *a*	0.21	11.6		50		
		< 1μm Chl *a*	0.11	6.1		26		
		> 1μm Chl *a*	0.10	5.5		24		
		Syn	0.8	0.2		0.9		

nd - not detected.

na - not applicable

[1] From June to February the mean contribution of < 1 μm Chl *a* to total Chl *a* is 40% (Crocker 1994).

[2] Total C_o = Bact (C_o) + Total Chl *a* (C_o)

[3] % Pico = ((Bact (C_o) + < 1 μm Chl *a* (C_o)) ÷ Total C_o) x 100

[4] % Syn = (Syn (C_o)) ÷ (< 1 μm Chl *a* (C_o)) x 100

Table 3. 3. Protist abundances (cells·L^{-1}) in time zero samples collected from unmodified dilution treatments in Logy Bay.

Date	Flagellates			Ciliates	Dinoflagellates
	<5 µm	5-10 µm	>10 µm		
11 Jul 95	130 000	5 000	1 500	300	3 600
04 Oct 95, <202 µm	56 000	21 000	3 800	700	3 300
04 Oct 95, <35 µm	35 000	4 400	5 600	1 000	5 800
31 Jan 96	400 000	20 000	9 000	200	4 000
24 Apr 96	10 000	2 000	nd	nd	7 600
06 Aug 96	800 000	50 000	4 000	1 400	11 000

nd - not detected.

Table 3. 4. Results from Analysis of Covariance testing for significant differences for either growth (μ) or grazing mortality (g) among <35 μm and <202 μm size fractions for Bacteria (Bact), *Synechococcus* (Syn), and chlorophyll *a* (Chl *a*) in October in Logy Bay. Significance was $P<0.10$. NS indicates No Significant difference and S indicates a Significant difference.

Time	Prey	μ (d^{-1})	g (d^{-1})
04 Oct 95	Bact	S	NS
	Chl *a*	S	NS
	Syn	NS	NS

Table 3. 5. Results from Analysis of Covariance testing for significant differences for either growth (μ) or grazing mortality (g) among size fractionated (<1 μm, 1-202 μm, and >0.7 μm) chlorophyll a in January as well as in August in Logy Bay. Significance was $P<0.10$. NS and S as in Table 3. 4.

Time	μ (d^{-1})	g (d^{-1})
31 Jan 96	S	NS
06 Aug 96	NS	NS

Table 3. 6. Rates of growth (μ, divisions·d^{-1}) and grazing mortality (g, d^{-1}) for bacteria (Bact), *Synechococcus* (Syn), and chlorophyll *a* (Chl *a*) in the surface layer of Logy Bay, Newfoundland. Microzooplankton grazing impact is expressed as prey net growth rate (NGR, d^{-1}), % of prey stock ingested (%C_0, d^{-1}), % of prey potential production ingested (% P_p, d^{-1}), and prey carbon ingested (I_c, μg C·L^{-1}·d^{-1}). The contribution of carbon ingested from bacteria and < 1 μm Chl *a* to total microbial carbon ingested is % Pico. Where n>8, data was pooled due to ns differences between sites/times for μ and g. Due to loss/damage of samples, some sample sizes are not multiples of 8.

Time	Size (μm) fraction	Prey	n	r^2	μ (±SE)	g (±SE)	NGR	% C_0	% P_p	I_c	% Pico
11 Jul 95	<202	Bact	9	0.65**	0.41 (0.04)	0.36 (0.09)	0.05	45	90	6.7	(+) 40
		Total Chl *a*	9	0.68**	0.75 (0.13)	0.98 (0.23)	-0.23	131	118	10.2	
04 Oct 95	<202	Bact	8	0.00 ns	0.34 (0.15)	-0.01 (0.24)	0.34	0	0	0	(+) 14
		Syn	15	0.54**	0.23 (0.03)	0.22 (0.05)	0.01	25	96	0.3	
		Total Chl *a*	8	0.11 ns	0.03 (0.03)	0.07 (0.05)	-0.04	7	229	1.8	
04 Oct 95	<35	Bact	8	0.00 ns	0.18 (0.09)	0.04 (0.17)	0.14	5	24	0.3	(+) 15
		Syn	15	0.54**	0.23 (0.03)	0.22 (0.05)	0.01	25	96	0.3	
		Total Chl *a*	8	0.57**	0.23 (0.03)	0.14 (0.04)	0.09	16	64	3.4	

Table 3. 6. *Continued.*

Time	Size fraction (μm)	Prey	n	r^2	μ (±SE)	g (±SE)	NGR	% C_o	% P_p	I_c	% Pico
31 Jan 96	<202	Bact	8	0.75**	0.17 (0.04)	0.34 (0.07)	-0.17	34	184	1.2	100
		Syn	5	0.55*	0.08 (0.05)	0.33 (0.13)	-0.25	30	367	0.01	
		Total Chl *a*	8	0.00 ns	-0.52 (0.19)	-0.27 (0.32)	0.00	0	0	0	
		<1 μm Chl *a*	7	0.00 ns	-0.56 (0.45)	0.43 (0.66)	-0.43	35	ng	0.9	
		>1 μm Chl *a*	8	0.00 ns	-0.07 (0.08)	-0.05 (0.15)	0.00	0	0	0	
24 Apr 96	<202	Bact	8	0.07 ns	0.08 (0.05)	0.12 (0.10)	-0.04	12	147	2.4	19
		Total Chl *a*	6	0.55*	0.24 (0.04)	0.16 (0.06)	0.08	19	69	10.2	
06 Aug 96	<202	Bact	8	0.71**	0.85 (0.09)	0.64 (0.15)	0.21	111	83	12.8	82
		Syn	8	0.11 ns	0.20 (0.09)	0.20 (0.15)	0.00	22	100	0.04	
		Total Chl *a*	24	0.32**	0.49 (0.09)	0.51 (0.15)	-0.02	67	103	7.6	
		<1 μm Chl *a*	24	0.32**	0.49 (0.09)	0.51 (0.15)	-0.02	65	103	4.0	
		>1 μm Chl *a*	24	0.32**	0.49 (0.09)	0.51 (0.15)	-0.02	65	103	3.6	

n: number of data points in regression

significance level of the regression: **$P<0.05$, *$P<0.10$, ns = $P>0.10$.

NGR = μ-g (Negative rates of μ and g were assigned values of zero)

Table 3. 6. *Continued.*

% C_o = (((($C_o e^{\mu}$-C_o)-($C_o e^{(\mu-g)}$-C_o))/C_o) x 100, where C_o is prey carbon

% P_p = (((($P_o e^{\mu}$-P_o)-($P_o e^{(\mu-g)}$-P_o))/($P_o e^{\mu}$-P_o)) x 100, where P_o is prey density

ng: no growth

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

% Pico = (I_c (Bact) + I_c (<1 μm Chl *a*)) ÷ (I_c (Bact) + I_c (Total Chl *a*)) x 100

(+): ingestion of <1 μm Chl *a* not determined, therefore % Pico may be greater than reported

Table 3. 7. Grazing impact (% of potential production ingested, P_p) on phytoplankton, *Synechococcus* and bacterioplankton by microzooplankton (i.e. <202 μm micrograzers) in various marine environments.

Author	Region	% P_p (d^{-1})	Temp. (°C)
Landry & Hassett (1982)	Washington coast	17-52	DNR
Paranjape (1987)	Jones Sound, NWT	40-114	-1 to 1
Paranjape (1987)	Baffin Bay, NWT	37-88	-1 to 1
Gifford (1988)	Halifax Harbour, NS	40-100	2 to 20
McManus & Cantrell (1992)	Chesapeake Bay, Md.	35-243	9 to 27
Burkill et al. (1993b)	NE Atantic	39-115	9 to 17
Verity et al. (1993a)	NW Atantic	81-100	13 to 14
Verity et al. (1993b)	NE Atlantic	37-100	DNR
Harrison et al. (1993)	NE Atantic	50-88	12 to 22
Landry et al. (1995a)	Central Equatorial Pacific	55-83	21 to 29
Burkill et al. (1995)	Bellingshausen Sea	21-271	-2 to -1
Froneman & Perissinotto (1996)	South Atlantic	0-60	0 to 22
Verity et al. (1996)	Equatorial Pacific	70-133	25 to 29
Strom & Strom (1996)	Gulf of Mexico	30	21 to 25
Reckermann & Veldhuis (1997)	Arabian Sea	67	25 to 27
Landry et al. (1984)	Kaneohe Bay, HA.	15	DNR
Campbell & Carpenter (1986)	NW Atlantic	36-99	25
Strom & Welschmeyer (1991)	NE Pacific	45-65	8 to 12
McManus &Cantrell (1992)	Chesapeake Bay, Md.	83-164	9 to 27
Burkill et al. (1993a)	NW Indian Ocean	76-111	32
Landry et al. (1995a)	Central Equatorial Pacific	85-228	21 to 25
Reckermann & Veldhuis (1997)	Arabian Sea	102	25 to 27

Table 3. 7. *Continued.*

Author	Region	% P_p (d^{-1})	Temp (°C)
Landry et al. (1984)	Kaneohe Bay, HA.	78	DNR
Wright & Coffin (1984)	MA. Coastal waters	100	DNR
Fuhrman & McManus (1984)	Long Island Sound	>50	23
Ducklow & Hill (1985)	Gulf stream	100	1 to 12
Wikner & Hagström (1988)	Bothnian & Med. Seas	100	DNR
Weisse (1989)	Red Sea & Gulf of Aden	100-138	DNR

DNR: Did Not Report

[1] grazing was measured using water that was collect and mixed from depths between the surface and 100 m

Table 3. 8. Results of Analysis of Variance showing a significant difference between the contributions of picoplankton (bacteria and <1 μm phytoplankton) and >0.7 μm phytoplankton to the total carbon ingested by microzooplankton in Logy Bay.

SOURCE	DF	SS	MS	F	p
FACTOR	1	4418	4418	8.75	0.025
ERROR	6	3030	505		
TOTAL	7	7448			

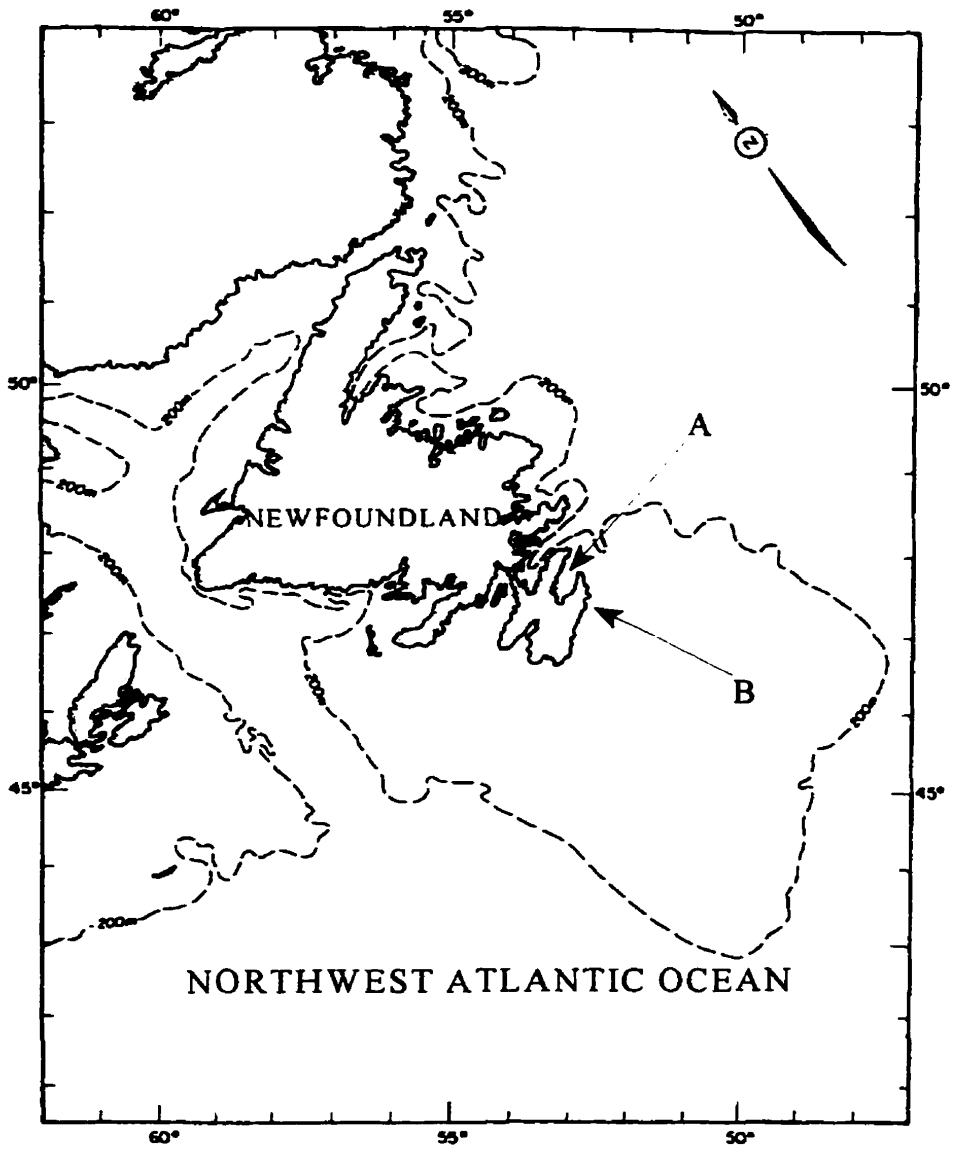


Figure 3. 1. Study sites (A, Conception Bay; B, Logy Bay) in Newfoundland coastal waters.

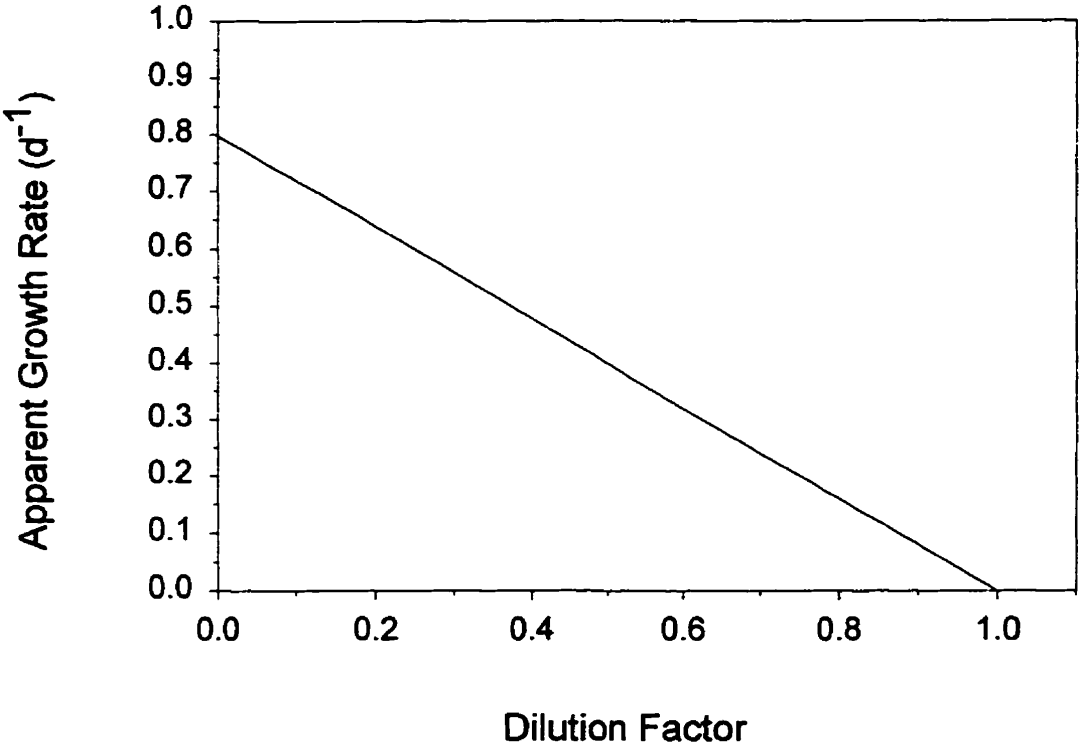


Figure 3. 2. Idealized dilution plot. Rates of prey growth and grazing mortality were estimated using Model I linear regression. The *y*-intercept is prey growth and the slope is mortality due to microzooplankton grazing.

Figure 3. 3. Surface mixed layer (ca. 0-30 m) temperature, abundances of bacterioplankton and *Synechococcus* and concentration of total (>0.7 μm) chlorophyll *a* in Conception Bay (A-D) and Logy Bay (E-H). The Conception Bay data was collected from 1992-1994 by Rivkin et al. (in prep.) and was combined from three stations. The Logy Bay data represented by black symbols was collected by Crocker (1994) from 1992-1994. The white symbols are data collected during this study.

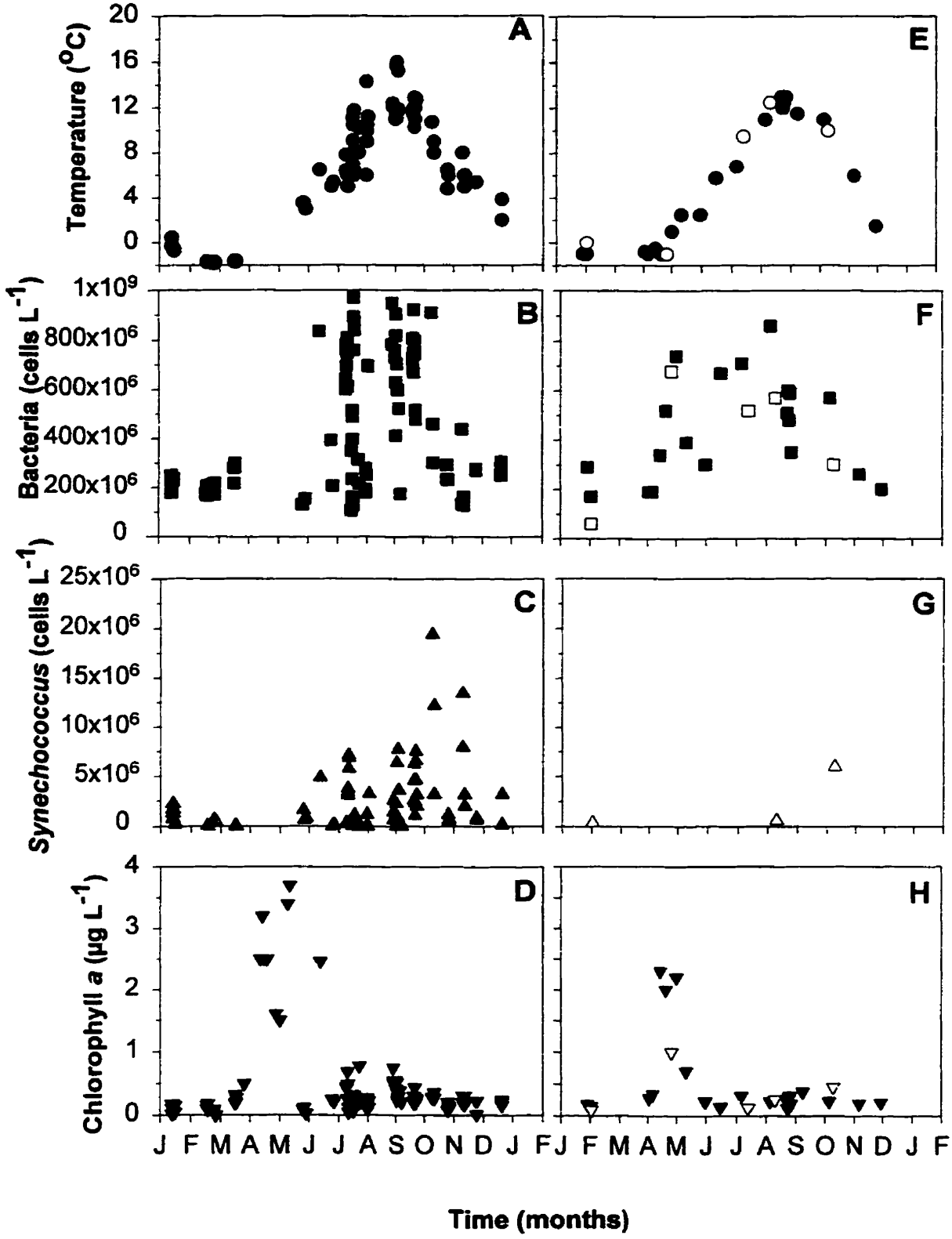

A
E
B
F
C
G
D
H
Temperature (°C)
20
16
12
8
4
0
Bacteria (cells L-1)
1x10⁹
800x10⁶
600x10⁶
400x10⁶
200x10⁶
0
Synechococcus (cells L-1)
25x10⁶
20x10⁶
15x10⁶
10x10⁶
5x10⁶
0
Chlorophyll a (µg L-1)
4
3
2
1
0
J F M A M J J A S O N D J F J F M A M J J A S O N D J F
Time (months)

Figure 3. 4. Representative dilution plots of Apparent Growth Rate versus Actual Dilution Factor for bacterioplankton, *Synechococcus*, and total chlorophyll *a* on 6 August 1996 in Logy Bay. Dashed lines are 95% confidence intervals.

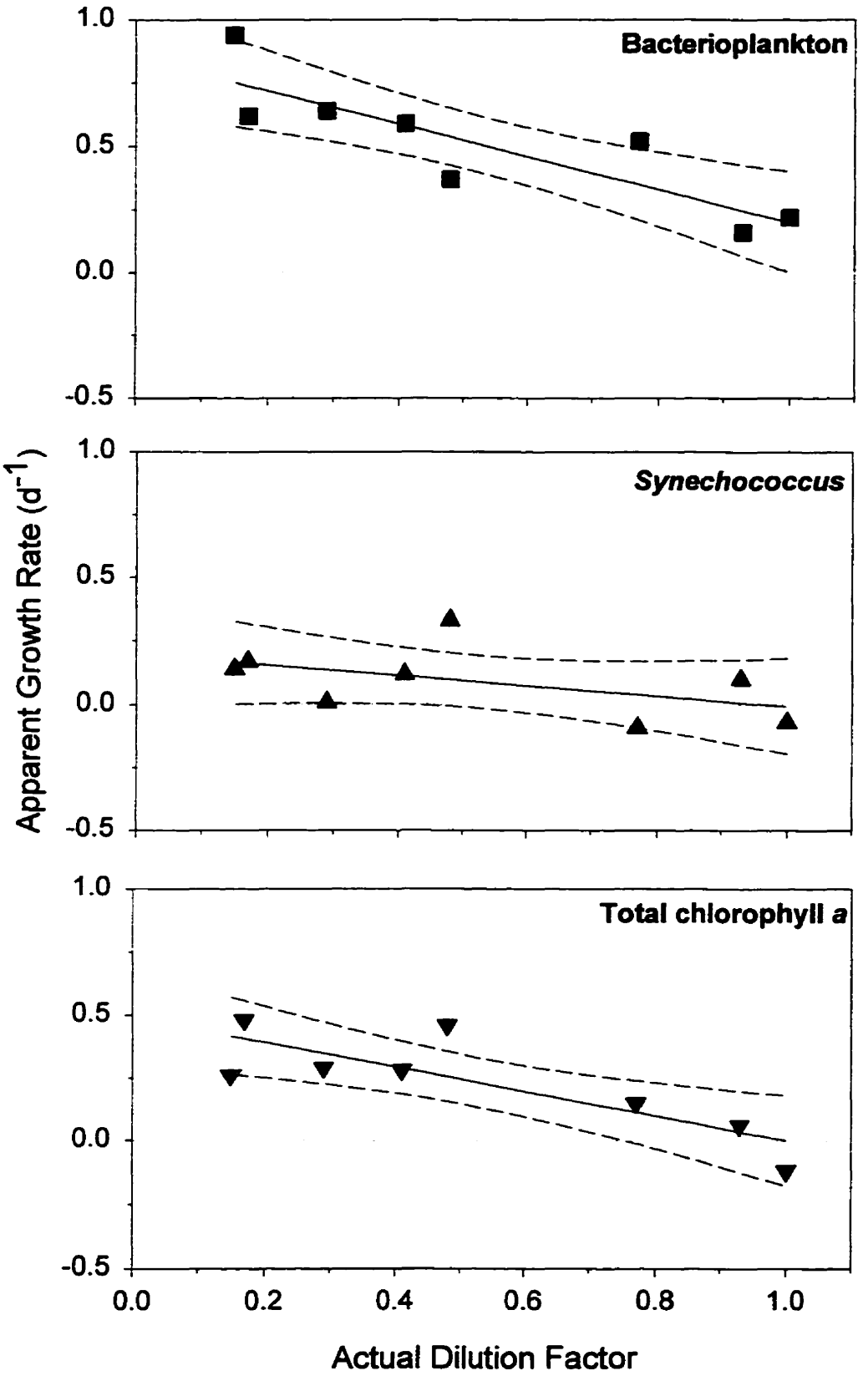
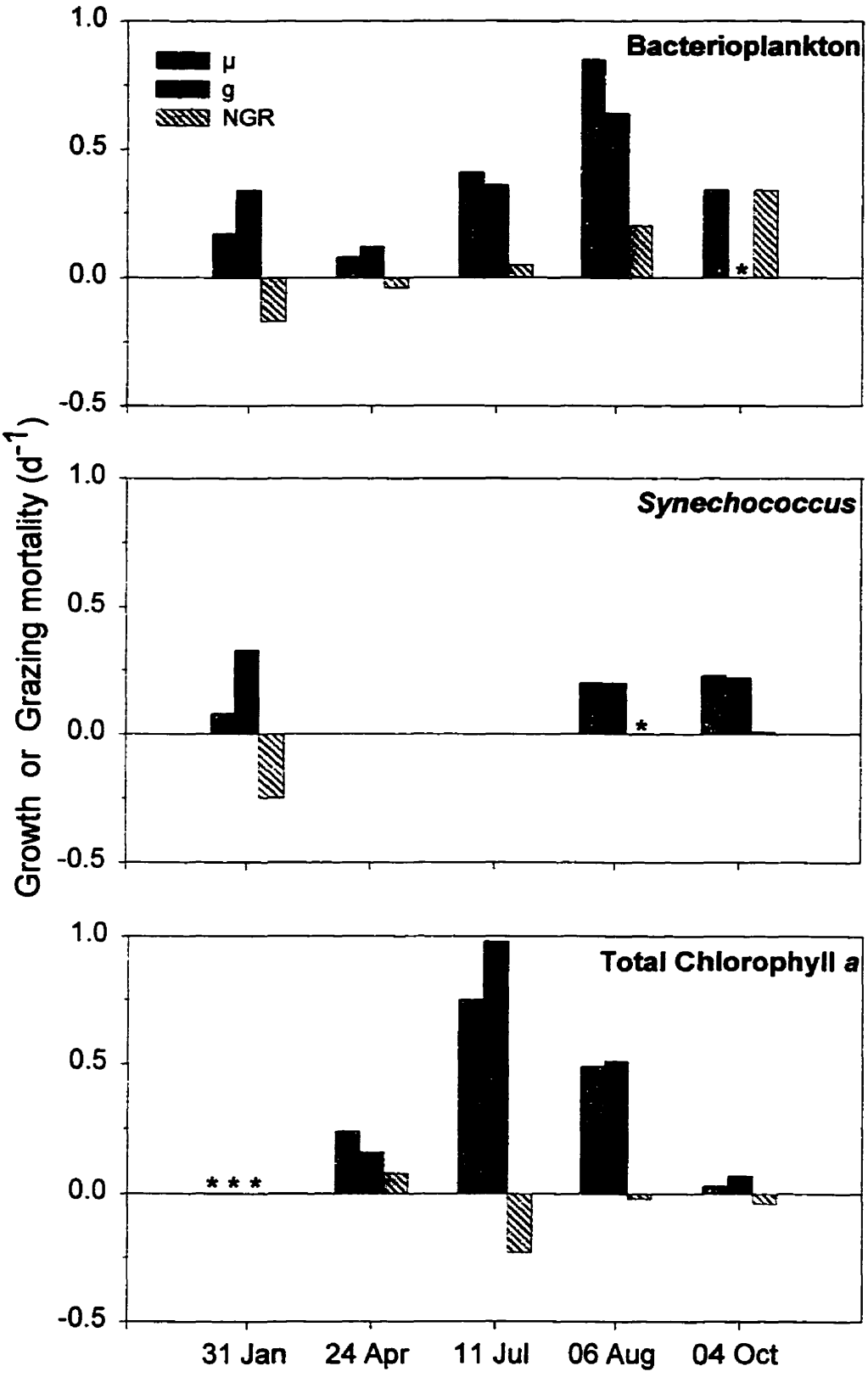

Bacterioplankton
Synechococcus
Total chlorophyll a
Apparent Growth Rate (d-1)
Actual Dilution Factor
1.0
0.5
0.0
-0.5
0.0
0.2
0.4
0.6
0.8
1.0

Figure 3. 5. Rates of growth (μ, d^{-1}), grazing mortality (g, d^{-1}), and net growth rate (NGR, d^{-1}) of bacterioplankton, *Synechococcus*, and total (>0.7 μm) chlorophyll *a* in Logy Bay. Net growth rate is the difference between growth and grazing mortality. Asterisks denote a value of zero due to a negative value for rate estimate or zero NGR.


Bacterioplankton
μ
g
NGR
Synechococcus
Total Chlorophyll a
Growth or Grazing mortality (d-1)
1.0
0.5
0.0
-0.5
31 Jan
24 Apr
11 Jul
06 Aug
04 Oct

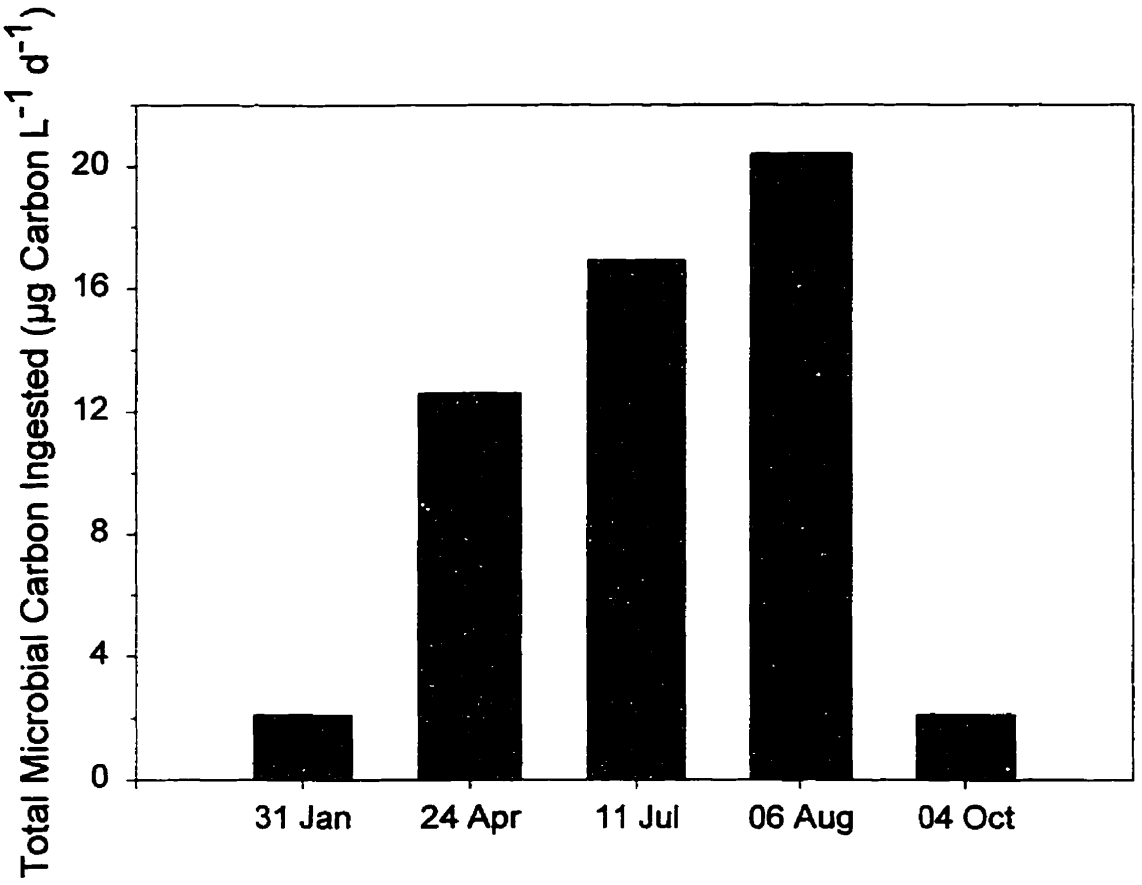


Figure 3. 6. Total ingestion of microbial prey carbon by microzooplankton in Logy Bay. Total carbon ingested is the sum of carbon from bacteria and total (>0.7 µm) chlorophyll *a* ingested.

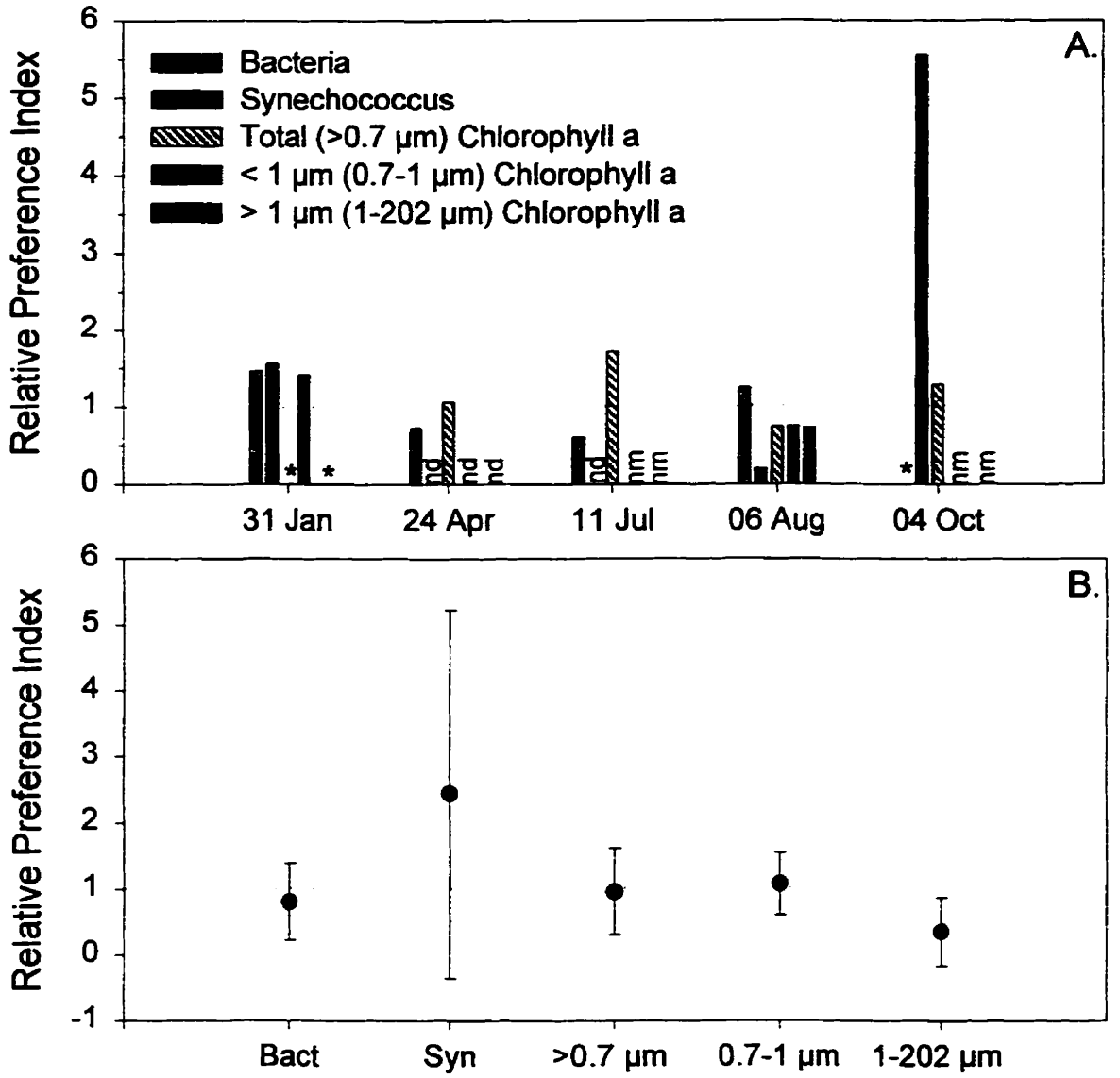
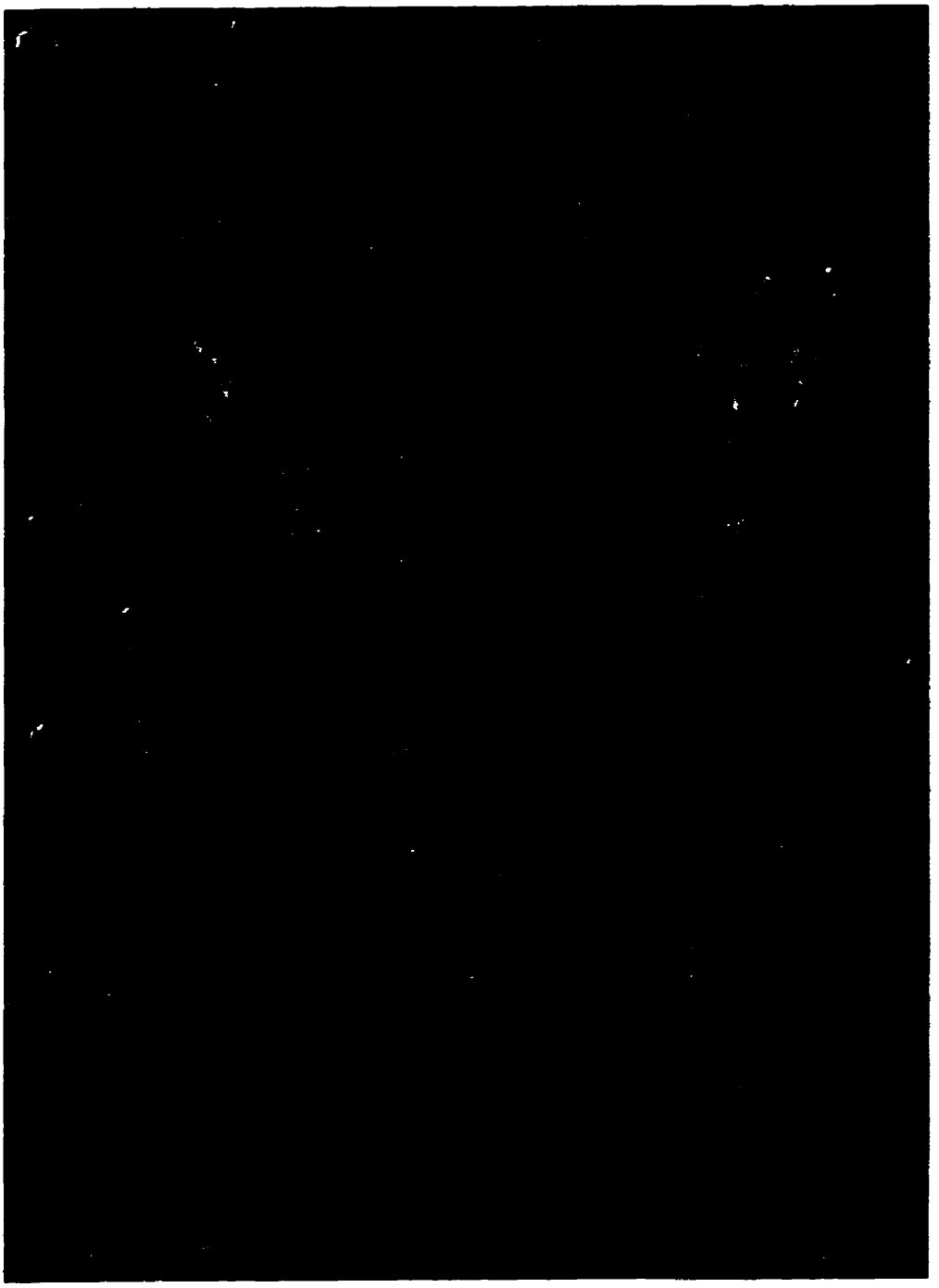


Figure 3. 7. (A) Relative Preference Indices (RPI) of microzooplankton for microbial prey in Logy Bay. Asterisks denote that RPI was zero because ingestion was zero, "nd" denotes that <1 µm chlorophyll *a* was not detected and "nm" indicates that <1 µm chlorophyll *a* was not measured. (B) Mean RPI's for bacteria (Bact), *Synechococcus* (Syn), and size fractionated chlorophyll *a* for all experiments conducted. Standard deviation denoted by error bars.

Figure 3. 8. *Gymnodinium* spp. (ca. 50 μm in length) that numerically predominated the dinoflagellate assemblage on 24 April at 5 m in Logy Bay.



Chapter 4

General Conclusions

4. 1. Synthesis

For each prey type, the relationship between growth and grazing mortality was not significantly different between the two systems (ANCOVA, $P>0.05$). For bacteria and autotrophic picoplankton, the relationships between growth and grazing mortality were also not significantly different (ANCOVA, $P>0.05$). The bacteria and autotrophic picoplankton data were therefore pooled and a regression performed on the pooled data. The regression slopes indicate that, on average, microzooplankton ingest ca. 80% and 100% of picoplankton (heterotrophic and autotrophic) and >0.7 μm phytoplankton potential production, respectively (Figure 4. 1). The relationships between growth and grazing mortality are complex and it is beyond the scope of the data collected to explain them. However, these results suggest that the processes regulating the coupling between growth and grazing mortality in the SAP and NCW were similar. Moreover, the similar relationships between growth and grazing mortality for each prey type, despite the differences between systems (Chapter 1), suggests that the relationships may represent quantitative generalizations about microbial food web dynamics in subarctic waters.

The contribution of picoplankton to total carbon ingested by microzooplankton was not significantly different between the two environments (ANOVA, $P>0.05$). The mean

contribution of picoplankton to total carbon ingested by microzooplankton in the two environments was 69%. Thus, the null hypothesis, *that the contribution of autotrophic and heterotrophic picoplankton to total carbon ingested by microzooplankton is less than that of >0.7 μm phytoplankton*, is rejected. This leads to the alternate hypothesis, *that the contribution of autotrophic and heterotrophic picoplankton to total carbon ingested by microzooplankton is greater than that of >0.7 μm phytoplankton*. Results from Lessard and Rivkin (1986) also showed the predominance of microzooplankton bacterivory, rather than herbivory. To my knowledge, there are no other studies that have examined the relative ingestion of various microbial prey by microzooplankton with which to compare the results. From the results, autotrophic and heterotrophic picoplankton likely formed the majority of carbon ingested because, on average, microzooplankton ingested prey in proportion to their availability (Figures 2. 4 and 3. 7) and picoplankton dominated microbial biomass (Tables 2. 2 and 3. 2)

4. 2. Implications to the vertical export of biogenic carbon

Results from this thesis show that (1) microzooplankton ingest a large portion of microbial production and (2) heterotrophic and autotrophic picoplankton represent most of the total carbon ingested by microzooplankton. If these results are typical of marine microbial food webs worldwide, then picoplankton carbon may represent an important source of carbon exported from the surface layers to the benthos. For instance, in open

oceans autotrophic and heterotrophic picoplankton dominate microbial biomass (Herbland et al. 1985, Dortch and Packard 1989, Cho and Azam 1990, Krupatkina 1990, Berman 1991, Maguzzù and Decembrini 1995). From the results of this thesis, microzooplankton ingest ca. 80% picoplankton production and ca. 69% of the total carbon ingested is derived from picoplankton. In systems dominated by small autotrophs, microzooplankton represent a large portion of the diet of mesozooplankton (Stoecker and Capuzzo 1990, Fessenden and Cowles 1994, Atkinson 1996) because mesozooplankton are generally not effective at ingesting small prey (Stoecker and Capuzzo 1990, Gifford and Dagg 1991, Ohman and Runge 1994, Atkinson 1996, Dubischar and Bathmann 1997). Thus, in open oceans mesozooplankton may indirectly ingest picoplankton by ingesting microzooplankton. As mesozooplankton can vertically migrate and produce rapidly sinking fecal pellets (Matsueda et al. 1986, Noji 1991), there is a potential for picoplankton to be exported from the surface layer to depth. Models of the vertical export of biogenic carbon do not consider the ingestion and repackaging pathways that facilitate the export of carbon from picoplankton. It is generally assumed that picoplankton are recycled within the mixed layer (Platt et al. 1989&1992). However, because open ocean regions represent a large (ca. 75%) area of the world's oceans (Thurman 1985) the vertical export of picoplankton may be globally important. Clearly, to better predict the vertical export of biogenic carbon, models should consider the pathways leading to the export of picoplankton carbon.

4. 3. Summary

The comparative approach used in this thesis has led to two important generalizations about microbial food web processes in subarctic waters. First, microzooplankton, on average, ingest ca. 80%, and 100% of picoplankton (autotrophic and heterotrophic) and >0.7 μm phytoplankton potential production, respectively. Second, autotrophic and heterotrophic picoplankton represent ca. 69% of the carbon ingested by microzooplankton. These quantitative generalizations can be used to test hypotheses and detect outliers in other systems (Pace 1991). Furthermore, these generalizations are important for the development of ecosystem models (Fasham 1995) that examine the flow of carbon between trophic compartments.

Future microbial food web research should focus on refining our understanding of microzooplankton grazing. Specifically, studies should be conducted to determine the ingestion of other autotrophic picoplankton such as *Prochlorococcus* and eukaryotes that can dominate microbial biomass (Olson et al. 1990, Li 1995, Liu et al. 1995, Landry et al. 1995b, Landry et al. 1996). Also, to determine the biogeochemical fate of prey ingested by microzooplankton, that is whether prey ingested are primarily remineralized or transferred to higher trophic levels, the fate of the primary bacterivores and herbivores should be determined. This has been done in freshwater systems and results show that the transfer of picoplankton to higher trophic levels depends upon the prey preference of mesozooplankton (Pace et al. 1990, Carrick et al. 1991, Nagata et al. 1996). Studies

should also examine microzooplankton grazing throughout the water column to acquire areal estimates of microzooplankton grazing. As many systems have a subsurface chlorophyll maxima, it is possible that surface layer estimates of microzooplankton grazing underestimate total carbon flow through microzooplankton. Finally, future studies should utilize field manipulation and comparative analyses to develop generalizations about microzooplankton grazing (Pace 1991). In this way, our understanding of carbon flow within marine systems will continue to improve.

Figure 4. 1. Growth versus grazing mortality for microbial prey from the surface layers of Logy Bay (LB), Newfoundland and Ocean Station Papa (OSP), subarctic Pacific from 1995 to 1996. The 1:1 line represents steady state when growth (μ) = grazing mortality (g). Model II regression equations are,

g = 0.16 ($\pm$0.05) + 0.78 ($\pm$0.14) μ, r^2=0.43, $p<0.01$ for bacteria and autotrophic picoplankton

g = 0.01 ($\pm$0.74) + 1.05 ($\pm$0.20) μ, r^2=0.60, $p<0.01$ for >0.7 μm phytoplankton

For bacteria n=11 (n=6 from LB and n=5 from OSP) and autotrophic picoplankton n=8 (n=5 from LB and n=3 OSP). For >0.7 μm phytoplankton, n=6 from LB and n=7 from OSP. Autotrophic picoplankton include *Synechococcus* and <1 μm phytoplankton. Values in parentheses denote standard error.

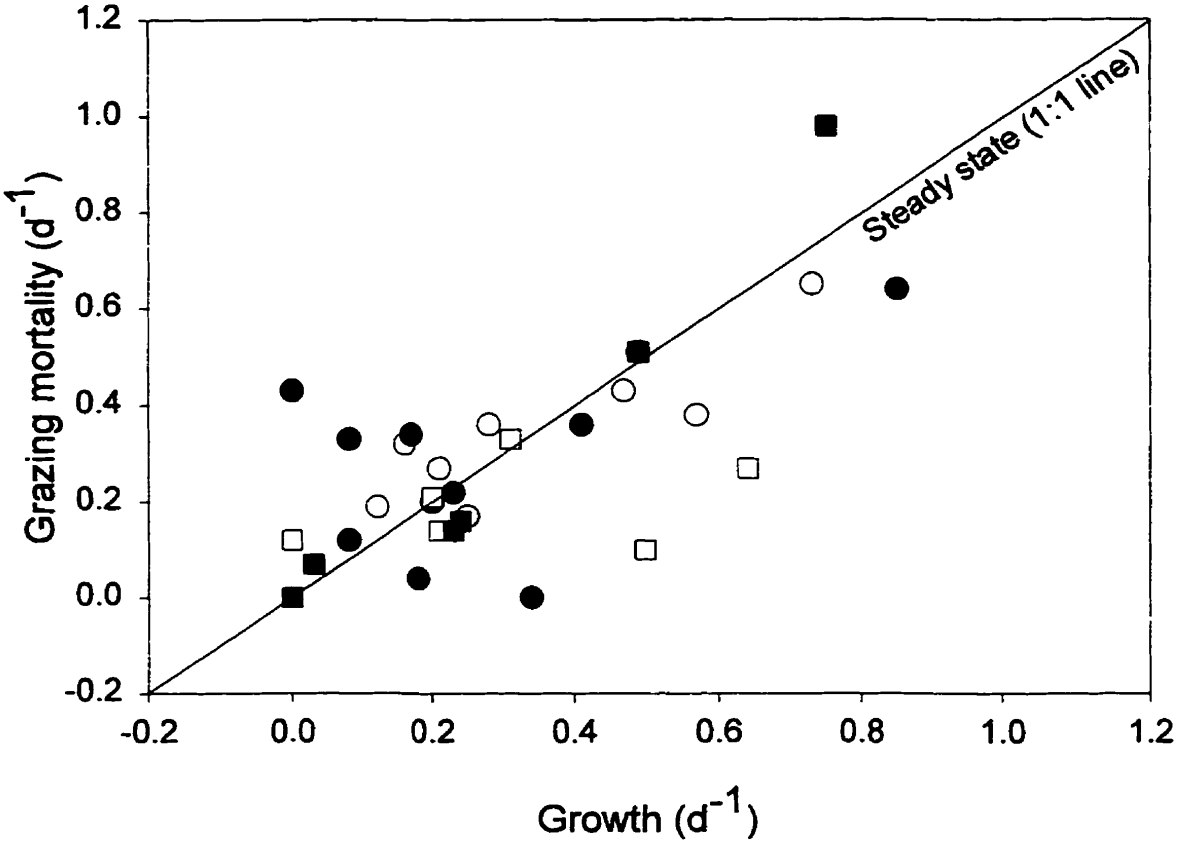

1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
Grazing mortality (d-1)
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Growth (d-1)
Steady state (1:1 line)
Autotrophic and heterotrophic picoplankton:
OSP
LB
Total (>0.7 µm) phytoplankton:
OSP
LB

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IMAGE EVALUATION
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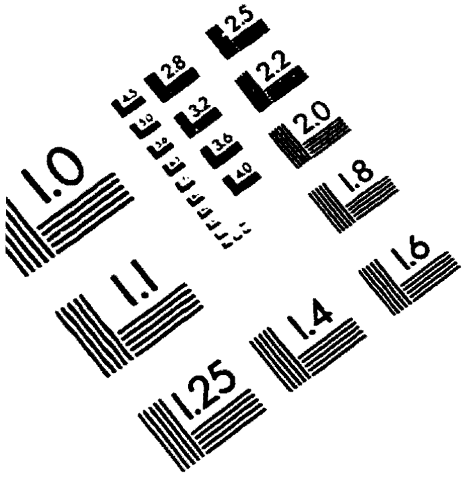

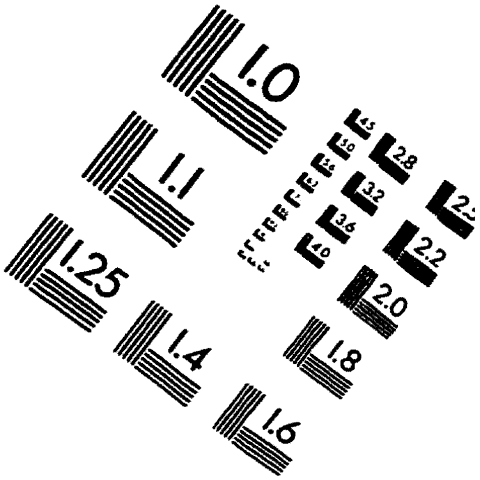

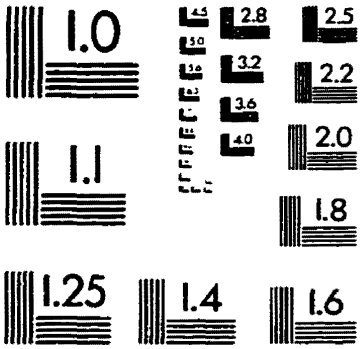

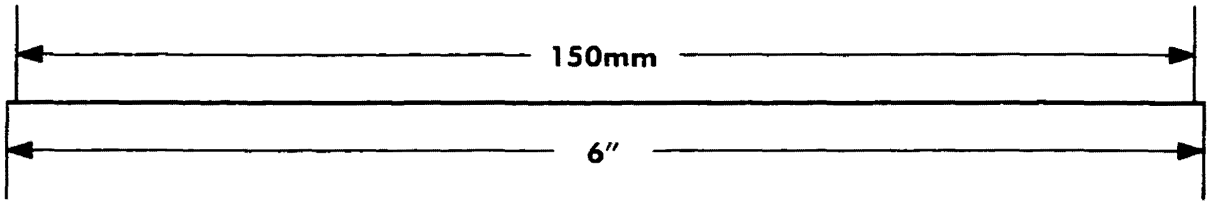

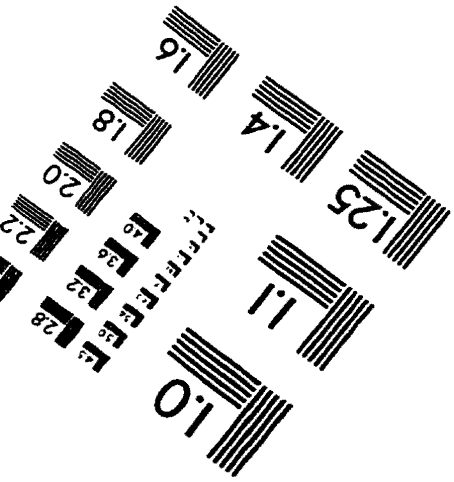

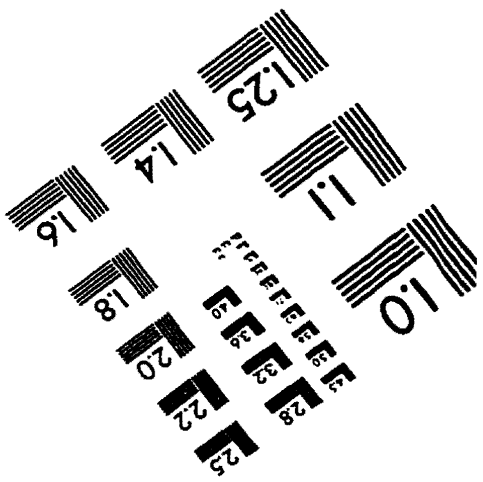

APPLIED IMAGE . Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989