# Microzooplankton grazing impact in the Bering Sea during spring sea ice conditions

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**Abstract**

Microzooplankton grazing impact on phytoplankton in the Bering Sea during spring was assessed in 2008, 2009 and 2010 using two-point dilution assays. Forty-nine experiments were completed in a region encompassing shelf to slope waters, including the 70 m line along the edge of the shelf. A variety of conditions were encountered, with a concomitant range of trophic states, from pre-bloom low chlorophyll-a (Chl-a) < 3 μg $l^{-1}$ during heavy ice cover to late spring open water diatom blooms with Chl-a up to 40 μg $l^{-1}$. Microzooplankton biomass was dominated by large heterotrophic dinoflagellates and ciliates. Both athecate and thecate dinoflagellates, as well as some species of ciliates, fed on diatom cells and chains. Other types of protists, notably thecate amoebae and parasitoid flagellates, were also observed preying on diatoms. Total microzooplankton biomass ranged from 0.1 to 109 μg C $l^{-1}$ and was positively related to Chl-a concentration. Significant rates of microzooplankton herbivory were found in 55% of dilution experiments. Maximum grazing rate was 0.49 $d^{-1}$, and average grazing rate, including experiments with no significant grazing, was 0.09 ± 0.10 $d^{-1}$. Phytoplankton intrinsic growth rates varied from slightly negative growth to > 0.4 $d^{-1}$. Microzooplankton grazing was significant in both non-bloom and bloom conditions, averaging 46 ± 75% of phytoplankton daily growth. Based on the amount of phytoplankton carbon consumed, we estimated potential microzooplankton community growth rates of up to 1.3 $d^{-1}$. Our results confirm the importance of protist grazers in planktonic food webs of high latitude ecosystems. We also conclude that our finding of significant grazing by microzooplankton on spring blooms in the Bering Sea does not support theories about phytoplankton bloom formation based on escape from grazing, due either to predation resistance or to slow growth of herbivorous protists at cold temperature.

**Key-words:** microzooplankton, herbivory, dilution assay, phytoplankton growth, Bering Sea

## 1. Introduction

Microzooplankton, which include ciliates and heterotrophic dinoflagellates from ~ 12 μm to 200 μm in size, are dominant herbivores in planktonic food webs (Sherr and Sherr, 2002, 2007; Calbet and Landry, 2004; Calbet, 2008; Buitenhuis et al., 2010). Protists in this size class are also a significant food resource for mesozooplankton (Levinsen and Nielsen, 2002; Calbet and Saiz, 2005; Olsen et al., 2006; Campbell et al., 2009; Löder et al., 2011) and for fish larvae (Howell-Kübler et al. 1996; Lessard et al., 1996; Montagnes et al. 2010). Phagotrophic ciliates and dinoflagellates are known to be abundant in arctic and sub-arctic marine systems (Howell-Kübler et al. 1996, Levinsen et al., 1999; Levinsen and Nielsen, 2002; Olson and Strom, 2002; Strom and Frederickson, 2008; Sherr et al., 2009). However, the quantitative roles of microzooplankton in the food webs of high latitude regions are not well constrained.

The Bering Sea is highly productive, supporting major commercial and subsidence fisheries, and is also highly sensitive to climate variability (Hunt et al., 2008, 2010, 2011). Extent of winter sea ice, and timing of sea ice retreat during the spring bloom season, have crucial impacts on the magnitude and fate of primary production in this region (Hunt et al., 2011; Lomas et al., 2012, Stabeno et al., 2012). The partitioning of production between plankton and benthos is thought to be directly related to presence or absence of ice during spring, with impacts on water temperature, stratification, and light available to phytoplankton. Late sea ice retreat results in early season, ice-associated diatom blooms that sink to the benthos, while early sea ice retreat promotes late season planktonic diatom blooms that are more efficiently grazed by crustacean zooplankton (Hunt et al., 2002, 2011).

Prior to our study, herbivory by microzooplankton in the Bering Sea had not been evaluated during the critical spring bloom season. Previous research on microzooplankton

grazing in this region has been confined to summer, after sea ice melt (Liu et al., 2002; Olson and Strom, 2002; Strom and Frederickson, 2008). The goals of our project were to estimate the flux of spring bloom production through the microzooplankton in this productive subarctic region, and to compare the importance of microzooplankton and mesozooplankton as herbivores (Campbell et al., ms in prep.). During the three years of this study, the Bering Sea experienced a cold climate regime, with extensive sea ice, cold water temperatures, and ice-edge blooms during spring (Stabeno et al., 2012). Our results thus quantify microzooplankton grazing in spring under cold regime conditions in the Bering Sea.

The results of this study are relevant to a more general issue: the extent to which marine phytoplankton blooms, and especially diatom blooms, result from temporary escape from microzooplankton grazing mortality. Two such theories have been suggested. Irigoein et al. (2005) proposed that bloom-forming phytoplankton are species that chemically or mechanically inhibit microzooplankton predation: the 'loophole' hypothesis. Rose and Caron (2007) surveyed literature on growth rates for monospecific cultures of marine phytoplankton and phagotrophic protists over a range of temperatures, and concluded that at $< \sim 10\ ^{o}C$, maximum growth rates of herbivorous protists were less than those of phytoplankton, while at higher temperatures herbivorous protist growth rates were as high, or higher, than those of phytoplankton. Rose and Caron suggested that temperature constraint on growth rates, and thus potential grazing rates, of microzooplankton is a factor in the initiation and development of mass phytoplankton blooms in high latitude, cold water regions of the ocean. We observed high microzooplankton grazing impact on phytoplankton at low seawater temperatures in the Bering Sea. These observations suggest that our data do not support the ideas that the diatom blooms were initiated either due to predation escape by cell defenses, or to cold temperatures differentially inhibiting

microzooplankton growth. Rather, the blooms occurred because light and nutrient availability in spring allowed diatoms to initially grow faster than co-occurring microzooplankton, which were food limited until the blooms attained higher biomass (Banse,1982; Sherr and Sherr, 2009)

## 2. Methods

### 2.1 Sampling

Microzooplankton herbivory was assessed as part of the Bering Sea Ecosystem Study (BEST) during April/May cruises in 2008 and 2009, and a May/June cruise in 2010. Grazing experiments were carried out at a subset of stations occupied during these cruises along established transects from shelf to slope, including along the 70 m isobath at the edge of the shelf (Fig. 1, Table 1). Water for the dilution assays was collected using a CTD in 30-liter Niskin bottles at a pre-determined depth, either the Chl-a maximum or a depth in the upper mixed layer at the 15%, 25% or 50% light level, corresponding to one of the depths sampled for phytoplankton production just prior to our cast (Lomas et al., 2012). Sampling for dilution experiments was coordinated with sampling for rates of primary production (Lomas et al., 2012) and for mesozooplankton grazing experiments (Campbell et al., ms in prep). In addition, water samples were taken from 6 depths from primary production profile casts for analysis of microzooplankton community composition and biomass. We also acquired samples for microzooplankton analysis from an early spring cruise (mid-March to mid-April, 2010) in the BEST study area. These samples were collected from bottle casts at 15 or 20 m depth and preserved using the same protocol as in our spring cruises. Data on bottom depth, seawater temperature, and nitrate concentration at the depths sampled were provided courtesy of the BEST service team. Percent of sea surface covered by sea ice was visually estimated and recorded by the CTD operator at the time of sampling.

## 2.2 Dilution assays

A two-point dilution assay, consisting of 10% and 100% whole seawater treatments, were carried out following the general protocol of Landry et al. (2008). In this modification of the dilution assay, two equations are solved for the unknowns: phytoplankton intrinsic growth rate, μ, and microzooplankton grazing mortality, m:

$$1)\ m = (kd - k)/(1-x)$$

$$2)\ \mu = k + m$$

where kd is Chl-a based growth rate in the diluted treatment, k is Chl-a based growth rate in the whole water treatment, and x is the fractional dilution used in the diluted treatment, in this case x = 0.1. Strom and Frederickson (2008) compared results using the traditional multi-point dilution series and the two-point protocol in experiments in the southeastern Bering Sea, and found no significant between-method difference in estimates of phytoplankton growth or grazing mortality.

Considerations regarding the dilution technique have been discussed by Gifford (1988), Gallegos (1989), Landry (1993), Neuer and Cowles (1994), Dolan et al. (2000), and Olson and Strom (2002). Two common manipulations in the method are to pre-screen whole seawater to exclude grazers > 200 μm, and to add nutrients to the dilution series to minimize potential nutrient limitation of phytoplankton growth (Landry, 1993). For these experiments, we elected not to pre-screen whole water, since during blooms large diatom cells and chains could have been retained on the screen. We did add nutrients to initial water for experiments in which on-board nutrient analysis indicated that in situ nitrate and phosphate concentrations might be limiting. We were not able to include both nutrient-addition and control non-nutrient addition whole water treatments in our assays.

All carboys, bottles, and tubing used in setting up dilution assays were pre-soaked in 5% HCl and thoroughly rinsed with deionized water. Nitex gloves were worn during experimental set-up. Seawater was gently transferred from Niskin bottles into 50 liter carboys through silicon tubing; care was taken to avoid bubbles in the tubing as the carboys were filled. After collection of seawater, all other preparation steps were carried out in a temperature-controlled environmental chamber set at -1 to 0 $^{o}$C under dim light (approximately 0.1% of incident light). For dilutions, particle-free seawater was prepared by gravity filtration through a Pall 0.2 μm filter presoaked in 5% HCl and thoroughly rinsed with deionized water. Five liters of seawater were passed through the 0.2 μm filter before beginning collection of particle-free water for the dilutions.

Experimental bottles were filled within two to three hours of sample collection. Particle-free water was added to 2-liter polycarbonate bottles to yield 10% whole seawater. As needed to ensure non-nutrient limited growth of phytoplankton, ammonium nitrate and sodium phosphate were added to experimental bottles to yield concentrations of 5 μM N and 0.25 μm P. A carboy filled with whole seawater was gently mixed for several minutes using a plexiglass rod with a small plexiglass disc attached to the end. Then, while the carboy continued to be gently mixed, whole seawater was siphoned out of the carboy to fill triplicate 10% and 100% whole water experimental bottles and an additional 2-liter bottle for initial samples. Parafilm was placed on top of each bottle prior to securing the cap, in order to minimize air bubbles in the bottles, as protist cells can lyse on contact with air (Gifford, 1988).

The experimental bottles were wrapped with combinations of neutral density Scrim and blue plastic film to mimic the approximate in situ light intensity and quality of the water depths sampled (Table 1) and mounted onto a plankton wheel on-deck incubator cooled with flowing

seawater. Temperature in the on-deck incubator was continually monitored using a Hobo temperature recorder immersed in the plankton wheel incubator. Average temperatures during the 24-hour incubations varied from -1.6 to 3.6 $^{o}$C (Table 1).

Initial samples were taken from whole seawater for determination of Chl-a concentration, and for microscopic enumeration of microzooplankton abundance, biomass, and general taxonomic composition. Depending on the phytoplankton concentration, from 25 to 300 ml quadruplicate volumes were settled via vacuum filtration onto GFF filters in dim light. The filters were extracted in 6 ml of 90% acetone in 13 x 100 mm glass culture tubes at -20 $^{o}$C for 18 to 24 hours. At the end of the extraction period, the filter was carefully removed from each tube, and the Chl-a concentration determined using a calibrated Turner Designs fluorometer outfitted with filter sets for the non-acidificaton protocol of Welschmeyer (1994). A solid chlorophyll standard was used to check for fluorometer drift at the beginning of each reading of Chl-a samples. Additional Chl-a measurements from primary production profile samples were provided by M. Lomas using the acidification protocol of Parsons et al. (1984) (Lomas et al., 2012). A cross-comparison of samples using these two methods carried out during the spring cruises showed good replication of Chl-a values.

For determination of microzooplankton biomass and abundance, 200 ml subsamples were preserved with 5% final concentration acid Lugol solution for inverted microscopy. Separate subsamples were preserved for inspection via epifluorescence microscopy with a three-step alkaline Lugol-sodium thiosulfate-2% final concentration formalin fixation protocol (Sherr and Sherr, 1993). Formalin-preserved samples were held at 2 $^{o}$C for 12 to 24 hours, and then settled onto 0.8 μm or 3.0 μm black membrane filters, stained with DAPI (5 μg ml$^{-1}$ final concentration), and mounted onto glass slides that were stored at temperatures of -20 $^{o}$C or lower

until analysis. At the end of the dilution incubations, final samples were taken from each bottle for Chl-a concentration. Depending on the initial phytoplankton concentration and dilution, from 25 to 500 ml triplicate subsamples were filtered for chlorophyll-a determination.

2.2 Calculation of phytoplankton growth and grazing rates

Phytoplankton growth rates in 10% and 100% whole water treatments were calculated by change in Chl-a. Initial Chl-a concentrations in the 10% dilutions were calculated from whole seawater Chl-a concentrations. Phytoplankton growth rates (kd and k) were determined for each experimental bottle using an exponential growth equation based on initial and final Chl-a concentrations in the 10% dilution and WW treatments:

$$kd \text{ or } k = (\ln \text{final Chl-a} - \ln \text{initial Chl-a})\ d^{-1}$$

These growth rates were then used in the two-step dilution equations to calculate values for $\mu$ and m (Eqns. 1 and 2).

In order to estimate daily phytoplankton growth and grazing loss in terms of carbon biomass, we first calculated the daily phytoplankton intrinsic biomass production, and estimated the amount of daily production consumed by microzooplankton, in terms of Chl-a $l^{-1}d^{-1}$: ln WW Chl-a daily intrinsic production = [ln initial WW Chl-a + $\mu$] – ln initial WW Chl-a; Chl-a grazed per day = [initial Chl-a + calculated Chl-a intrinsic production] – final WW Chl-a. We then converted the Chl-a values to daily increase or consumption of phytoplankton carbon biomass (mg C $m^{-3}$ $d^{-1}$) using an average C:Chl-a ratio of 50 empirically determined during the 2008–2009 Bering Sea cruises (Lomas et al., 2012).

Significance of relationships between intrinsic growth rates and grazing rates estimated in the dilution experiments was assessed by two-sample t-test assuming unequal variances.

2.3 Post-cruise sample analysis

Microzooplankton abundance and biomass were determined in initial whole seawater samples for 36 of the experiments and at 6 depths from 100% to 1% light levels for selected primary production casts during the three spring cruises (Lomas et al., 2012), for a total of 125 single-depth samples. In addition, in order to evaluate early spring microzooplankton stocks, we also inspected 10 samples collected at depths of 15 or 20 m in the eastern Bering Sea from 13 March to 3 April 2010 by L. Cooper. From 15 to 50 ml of Lugol-preserved samples were settled for a minimum of 24 hours and then the whole slide inspected by inverted light microscopy. A Nikon inverted microscope mated to a computer digitizing system via a drawing tube was used to identify and measure microzooplankton cells and to convert linear dimensions to cell volumes using equations appropriate for individual cell shapes (Roff and Hopcroft, 1986). All ciliate and dinoflagellate cells in each sample were counted, sized, and categorized into the general taxonomic groups of choreotrichous ciliates, oligotrichous ciliates, didinid ciliates, tintinnids, athecate dinoflagellates, and thecate dinoflagellates. Ciliate and dinoflagellate cells ranged in size from ~ 12–15 μm to 200 μm in size. From 60 to 400 protist cells were counted and sized in each sample inspected. Samples on slides preserved for epifluorescence microscopy were inspected using an Olympus epifluorescence microscope equipped with a multi-wavelength filter set to determine whether dinoflagellates counted in Lugol-preserved samples were heterotrophic or autotrophic; only heterotrophic dinoflagellate morphotypes were included in the microzooplankton data. Cell biomass for dinoflagellates was estimated using an algorithm of Menden-Deuer and Lessard (2000) and for ciliates was estimated using the 0.19 pgC $\mu m^{-3}$ value of Putt and Stoecker (1989). Ratios of heterotrophic dinoflagellate biomass, and of > 40 μm sized microzooplankton biomass, as a fraction of total microzooplankton biomass were also calculated. For primary production profiles, integrated microzooplankton biomass (mgC $m^{-2}$)

was determined over the depth interval sampled, from 0–17 to 0–40 m, and compared to integrated phytoplankton biomass assuming a C:Chl-a ratio of 50 (Lomas et al., 2012).

### 2.4 Microzooplankton biomass-specific grazing rates and potential microzooplankton growth rates

Biomass-specific grazing rates ($d^{-1}$) of the microzooplankton community were calculated as the amount of phytoplankton carbon grazed by the microzooplankton community during the dilution assays ($\mu gC\ l^{-1}d^{-1}$, see section 2.2), divided by the initial standing stock of microzooplankton ($\mu gC\ l^{-1}$). Potential microzooplankton growth rates were estimated using the exponential growth equation:

$$\mu = (\ln Bf - \ln Bo)\ d^{-1}$$

where Bo = initial microzooplankton biomass ($\mu gC\ l^{-1}$) and Bf = Bo + (phytoplankton C grazed) * 0.3, assuming an average gross growth efficiency for the protist community of 30% (Straile, 1997; Landry and Calbet, 2004; Chen and Liu, 2011). Doubling times (days) for the microzooplankton community were calculated from the growth rates: doubling time = ln 2 / $\mu$.

Statistical procedures were done using the NCSS-2001 software package.

## 3. Results

### 3.1 General conditions

The BEST spring process cruises focused on the ice-covered continental shelf and ice-edge outer shelf and shelf break. Stations on the 70 m isobath along the outer shelf, which has been the focus of time series and mooring sampling efforts (Stabeno et al., 2002, 2012), were occupied during all three cruises. A variety of conditions were encountered, from heavy sea ice cover over the shelf during early to mid April, to ice melt and open water in late April to early June (Table 1). All phases of the Bering Sea spring bloom were encountered: pre-bloom and

post-bloom conditions in which Chl-a was < 3 μg $l^{-1}$, growth of sea ice diatoms in March and April, and ice-edge planktonic diatom blooms with Chl-a of > 3 and up to 40 μg $l^{-1}$ during April-June (Table 2). Qualitative assessment of phytoplankton communities by microscopic inspection of samples indicated that pennate diatom species characteristic of sea ice, notably *Fragilariopsis* spp., *Navicula* spp., and *Nitzschia* spp., were often an important component of algae in the water column. However, ice edge and open water blooms were characterized by pelagic centric diatoms, dominated by species of *Chaetocerous*, *Thalassiosira*, and *Cylindrotheca*

3.2 Dilution assay results

A total of 49 dilution assays were completed at 47 stations (Tables 1 and 2). Initial Chl-a concentrations in the experiments varied from ~ 0.1 μg $l^{-1}$ in early April 2008 to 38 μg $l^{-1}$ in May 2009 (Table 2). There was a significant microzooplankton grazing rate in over half (27 out of 49) of the dilution assays (Table 2). Phytoplankton intrinsic growth rates varied from highest values of 0.30 to 0.47 $d^{-1}$ to lowest values of < 0.1 $d^{-1}$ (Table 2). We were not able to compare phytoplankton growth in treatments with and without added nutrients, so growth rates for stations with low initial nutrients may be higher than in situ rates. Grazing mortality as a fraction of phytoplankton growth ranged from zero to a grazing mortality two- to three-fold greater than phytoplankton growth rate (Table 2). Microzooplankton grazing rate was not significantly correlated to phytoplankton growth rate or to Chl-a concentration. Phytoplankton production and microzooplankton grazing impact were converted to units of mg C $m^{-3}$ $d^{-1}$ to facilitate comparison of microzooplankton and mesoplankton herbiviory (Table 3).

Because of the wide variability in phytoplankton stocks encountered during spring, we separated our data into 'non-bloom' versus 'bloom' conditions, using 3.0 μg Chl-a $l^{-1}$ as the cut-off value. About half of our experiments (24) had initial Chl-a concentrations less than this

value, and the rest had Chl-a concentrations of 3.5 to 38 µg Chl-a $l^{-1}$. All data, including results of experiments with non-significant grazing, were included in this analysis. During the three cruises, under non-bloom conditions (Chl-a < 3 µg C $l^{-1}$) microzooplankton grazing averaged 26% to 86% of phytoplankton production, and under bloom conditions, with average Chl-a concentrations of 11 to 22 µg C $l^{-1}$, 31% to 59% of production (Table 3). The daily amount of Chl-a standing stock consumed by microzooplankton averaged from 4% to 11% over the three years (Table 3).

3.3 Microzooplankton composition and biomass

Microzooplankton biomass and general taxonomic composition were analyzed for initial water samples from the dilution experiments for which significant grazing was found, and also for selected primary production profiles. The protist community was in general similar to that found in the Bering Sea during summer (Strom and Frederickson, 2008; Stoecker et al., this issue) and in the Western Arctic Ocean (Sherr et al., 2009). Ciliates were dominated by naked spirotrichs, including species in the genera *Strombidium, Strobilidium, Leegardiella*, and *Laboea*. A few tintinnid species were observed, the most common of which was a *Ptychocylis* sp. Heterotrophic dinoflagellates, including thecate and athecate forms (examples in Fig. 2A–C), were abundant and were frequently found with ingested diatoms, including very large cells and chains. We also observed several other types of protists feeding on diatom cells. These included spirotrich ciliates with ingested diatom chains (Fig. 2D) or large single pennate diatom cells (not shown), parasitoid flagellates feeding on pennate diatom chains (Fig. 2E), and what we identified as a species of testate amoeba that exclusively fed on single centric diatom cells (Fig. 2F).

For all initial water samples collected for dilution assays, total microzooplankton protist biomass varied from 2.0 µg C $l^{-1}$ to 109 µg C $l^{-1}$, averaging 8.4 ± 6.6 µg C $l^{-1}$ under non-bloom

conditions and 45 ± 27 μg C $l^{-1}$ under bloom conditions. For all of the the primary production profiles analysed, microzooplankton protist biomass varied from 0.2 μg C $l^{-1}$ to 100 μg C $l^{-1}$, averaging 11.2 ± 17.2 μg C $l^{-1}$ under non-bloom conditions and 23 ± 23 μg C $l^{-1}$ under bloom conditions. Average values of these parameters under non-bloom and bloom conditions for individual years are presented in Table 4. Heterotrophic dinoflagellates composed, on average, from 65% to 75%, and cells > 40 μm in size 49% to 66%, of total microzooplankton biomass. Epifluorescence microscopic inspection of samples confirmed that the dinoflagellates enumerated did not have chloroplasts, and thus were not autotrophic. Using the Chl-a concentrations we measured in initial dilution assay samples, and Chl-a values determined by Lomas et al. (2012) for the primary production profiles and by Cooper et al. (this issue) for the early spring samples, we found a positive log-log relation between protist biomass and Chl-a concentration, although there was high variability between the two parameters at Chl-a concentrations < 3 (log 0.5) μg $l^{-1}$ (Fig. 3). Integrated microzooplankton biomass for the production profiles was also variable, ranging from 0.11 to 2.17 gC $m^{-2}$. There was a significant positive relation between integrated microzooplankton and phytoplankton biomass (Fig. 4), with integrated microzooplankton C biomass averaging from 1 to 15% (average 4.3%) of integrated phytoplankton C biomass.

3.3 Microzooplankton specific grazing rates, potential growth rates, and doubling times

These rates were averaged for non-bloom and bloom conditions (Table 5), with Chl-a concentrations the same as in Table 4. There were no significant differences (Student's T-test) between these rate values for bloom versus non-bloom Chl-a conditions. Specific grazing rates varied from 0 in dilution assays with no herbivory, to 10.9 $d^{-1}$, averaging about 2 $d^{-1}$ during bloom and 1 $d^{-1}$ during non-bloom conditions. Potential growth rates also showed a wide range,

from 0 to 1.45 $d^{-1}$, with average μ of 0.3 to 0.4 (Table 5). Doubling times calculated for positive growth rates varied from 0.5 to 8.5 days. On average the microzooplankton community had a doubling time of 2–3 days.

## 4.Discussion

### 4.1 Phytoplankton growth rates

Algal biomass and primary production in the Bering Sea during spring is dominated by sea ice and planktonic diatoms > 5 μm in size (Sukhanova et al., 1999; Moran et al., 2012; Lomas et al., 2012). The variety of stages of diatom bloom formation sampled during the three years in this study resulted in high variability in measured phytoplankton intrinsic growth rates (μ). Extensive sea ice cover in April and early May, at the beginning of the bloom season (Table 1) resulted in low phytoplankton biomass due to light limitation: 1.1 ± 1.9 μg Chl-a- $l^{-1}$ for ice cover from 30% to 100%, compared to Chl-a concentrations of 11.6 ± 1.9 μg $l^{-1}$ for ice-free conditions in May and June. Even so, high phytoplankton growth rates from 0.2 to 0.4 $d^{-1}$ were observed at some stations during April/May with significant sea ice cover. The presence of diatom species common in sea ice communities in samples collected at these stations suggested that ice algae were capable of active growth in the water column.

Intrinsic phytoplankton growth rate for all stations at which Chl-a was < 3 μg $l^{-1}$ was, on average, 0.18 ± 0.14 $d^{-1}$. Ice edge and open water diatom blooms encountered in May and June had an equally wide range of growth rates, from 0.045 $d^{-1}$ at the station with highest phytoplankton biomass, 38 μg Chl-a $l^{-1}$, to 0.47 $d^{-1}$ at a station with a developed bloom of 20 μg Chl-a $l^{-1}$. For all dilution assays in which Chl-a was > 3 μg $l^{-1}$, growth rate averaged 0.22 ± 0.12 $d^{-1}$. These values are similar to the average phytoplankton growth rate, 0.21 ± 0.15 $d^{-1}$, found in the Western Arctic Ocean during spring (Sherr et al., 2009), under similar conditions of low

temperatures and extensive ice cover. Phytoplankton growth rates in the Bering Sea and in the Barents Sea during summer, when temperatures are higher and light is less limiting, average from 0.3 to 0.5 $d^{-1}$ (Table 6).

4.2 Microzooplankton grazing impact in the eastern Bering Sea during spring

The main fates of bloom production in the Bering Sea are export to the benthos or consumption in the water column (Moran et al., 2012). A central issue addressed by this study, coupled with the estimates of grazing on phytoplankton by mesozooplankton (Campbell et al., ms in prep.), was the extent to which planktonic grazers consume algal production in the Bering Sea during spring sea ice conditions.

Microzooplankton exert a significant grazing impact on phytoplankton biomass and primary production in all regions of the world ocean, including eutrophic ecosystems (Calbet and Landry, 2004). A prevailing idea about plankton grazers is that microzooplankton mainly consume phytoplankton < 5 μm in size (pico- to small nano-sized cells), while mesozooplankton are dominant herbivores of phytoplankton > 5 μm in size, especially of bloom-forming diatoms. However, it is now apparent that protistan herbivores, and in particular heterotrophic dinoflagellates, are voracious predators of bloom-forming diatoms and are as, or more, significant as mesozooplankton in consuming diatom production in the sea (Jeong et al., 2004; Sherr and Sherr, 2007; Aberle et al., 2007; Campbell et al., 2009; Löder et al., 2011). Our results underscore this new understanding.

Microzooplankton grazing rates, like phytoplankton growth rates, were highly variable during spring in the Bering Sea. Protist herbivores consumed, on average, from 26% to 86% of phytoplankton growth at stations with lowest algal biomass (~ 1 μg Chl-a $l^{-1}$) and from 31% to 50% of growth at stations with significant blooms (~ 10-20 μg Chl-a $l^{-1}$) (Table 3). These grazing

rates are higher than the average microzooplankton grazing impact of about 17% to 22% of daily phytoplankton growth previously reported in the Western Arctic Ocean, but in the range of average grazing impacts on phytoplankton growth in the Barents Sea and in the Bering Sea during summer (Table 6). However, in these prior studies, the average Chl-a concentrations were lower than that of the spring bloom conditions observed in our study, and water temperatures were warmer.

4.3 Microzooplankton biomass and composition

At present, more is known about the biomass, species composition, and distribution of mesozooplankton compared to microzooplankton in marine systems, even though the latter is Irigoien et al. (2004) summarized data on the distribution of phytoplankton and zooplankton, including microzooplankton, in the sea. They found that the maximum biomass of marine microzooplankton, when both ciliates and phagotrophic dinoflagellates were included, was about 100 μg C $l^{-1}$, and that the log-log relation between microzooplankton and phytoplankton biomass was saturated, i.e., leveled off, at phytoplankton biomass greater than 100 μg C $l^{-1}$, equivalent to ~ 2 μg Chl-a $l^{-1}$ assuming a C:Chl-a ratio of 50.

Microzooplankton biomass in the Bering Sea often reaches the global maximum value reported by Irigoien et al. (2004). Strom and Frederickson (2008) reported microzooplankton biomass of up to 118 μg C $l^{-1}$, averaging 38 μg C $l^{-1}$, in the Bering Sea around the Pribilof Islands during summer 2004. Olson and Strom (2002) found an even greater range in microzooplankton biomass, 18 to 164 μg C $l^{-1}$, in the southeast Bering Sea in 1999 when coccolithophorids dominated the phytoplankton community. Our data match these earlier observations, with spring microzooplankton biomass as high as 109 μg C $l^{-1}$ and averaging 42 μg C $l^{-1}$ in initial water samples for dilution assays in which Chl-a was > 3 μg $l^{-1}$ (Table 4).

Strom and Frederickson (2008) reported a generally positive relation between microzooplankton biomass and Chl-a concentrations from 0.2 to 5 μg $l^{-1}$ during the summer of 1999. In this study, we found a positive log-log relation between these two parameters, over a broader range of Chl-a values from 0.1 to 38 μg $l^{-1}$ (Fig. 3). There was a degree of leveling off, or saturation, in the log-log relation at the highest Chl-a concentrations, but not as apparent as that found by Irigoien et al. (2004) for a larger combined data set. Comparison of the depth-integrated microzooplankton and phytoplankton biomass resulted in a linear relationship (Figure 4), although phytoplankton biomass was one to two orders of magnitude greater.

We also confirmed the results of the earlier studies in the Bering Sea that the biomass of herbivorous protists was dominated by heterotrophic dinoflagellates (Table 4). Heterotrophic dinoflagellates ranged from two-thirds to three-quarters of total microzooplankton biomass. The importance of phagotrophic dinoflagellates in marine pelagic systems cannot be overemphasized (Sherr and Sherr, 2007; Jeong et al., 2010). Heterotrophic dinoflagellates often compose > 60% of total microzooplankton biomass in both oligotrophic and eutrophic conditions (Sherr and Sherr, 2009). In this study, we observed athecate, gymnodinoid dinoflagellates with ingested diatom chains and single diatom cells, which usually greatly distended the dinoflagellate cell (e.g., Fig. 2A and B). Heterotrophic gymnodinoid dinoflagellates are frequently observed during diatom blooms, and have been implicated as important consumers of phytoplankton production, in arctic and subarctic marine systems (Putland, 2000; Levinsen and Nielsen, 2002; Hansen et al., 2003; Strom and Frederickson, 2008; Suffrian et al., 2008; Sherr et al., 2009; Ardyna et al., 2011). Thecate heterotrophic dinoflagellates were also common and occasionally seen attached to a diatom cell or chain with an extruded pseudopodial pallium (Fig. 2C).

A surprising observation in our study was that of spirotrichous ciliates with ingested diatom chains (Fig. 2D), or single pennate diatom cells, so large that they distorted the cell. Although benthic ciliates are known to feed on diatoms, pelagic spirotrichous ciliates, e.g., in the genera *Strombidium* and *Strombidinopsis*, are generally considered to consume prey cells much smaller than themselves, mainly nanoflagellates. Smetacek (1981) was the first to report marine pelagic ciliates with ingested large-sized diatoms, in the Kiel Bight, Germany. Subsequently Aberle et al. (2007) found that > 50 µm sized *Strombidium* and *Strombidinopsis* spp. ciliates, rather than heterotrophic dinoflagellates, were the main protist herbivores during mesocosm diatom blooms using water from the Kiel Bight. In their study, the ciliates ingested both diatom chains and single diatom cells equal to, or greater than, the length of the ciliate cell. Johansson et al. (2004) also suggested that ciliates could be significant predators of spring bloom diatoms in the Baltic Sea. Spirotrichous ciliates have additionally been observed with ingested diatom chains in a Brazilian lagoon (Abreu et al., 1997). Thus the phenomenon of pelagic ciliates preying on large-sized diatoms may be widespread in the sea.

Other types of protists in our samples were found feeding on diatoms. A variety of heterotrophic flagellates parasitize marine diatoms (Raven and Waite, 2004) and have been suggested to cause significant mortality in diatom blooms in European coastal waters (Tillmann et al., 1999) and in the Bering Sea in summer (Sukhanova et al., 1999). We observed putative parasitoid flagellates feeding on pennate diatom chains during spring (Fig. 2E). We also found thecate amoebae attached to, and apparently sucking out the contents of, centric diatoms in some samples (Fig. 2F). Similar thecate amoebae were reported preying on centric diatoms, mainly *Chaetocerous* sp., during a mesocosm study in the North Sea (Löder et al. 2011).

We also separately assessed the biomass of heterotrophic nanoflagellates via epifluorescence inspection of preserved DAPI-stained samples collected on 0.8 μm membrane filters (Sherr et al. 1993) during the 2009 and 2010 cruises (Sherr unpublished). The average cell size of these flagellates was 2–3 μm, too small to feed on bloom-forming diatoms unless they were parasitoid species. The average biomass of heterotrophic nanoflagellates was 2–4 μg C $l^{-1}$, about 10% of the average biomass of the microzooplankton. These nano-sized protists would be mainly consuming bacteria and other pico-sized prey, and would not be expected to contribute significantly to herbivory in the Bering Sea during spring.

4.4 Specific microzooplankton grazing and growth rates

In situ growth rates of microzooplankton protists are not well constrained, as it is difficult to assess this parameter at natural food abundances and at low in situ temperatures (Sherr and Sherr, 2009). Determining growth rates by change in in situ protist cell abundance is challenging because microzooplankton abundance is typically too low for statistically accurate counts, and because different protist species may be growing at different rates. While we did carry out several long-term (6–10 day) protist growth experiments in the ship's environmental chamber during our cruises, we were able to document positive growth for only a few morphological types of protists, including gymnodinoid dinoflagellates, a *Ptychocylis* sp. tintinnid ciliate, and the testate amoeba.

An alternate method of estimating growth rates for the overall microzooplankton community is to scale carbon-based phytoplankton consumption to microzooplankton biomass (Strom and Fredrickson, 2008). Our specific grazing rates (μg phytoplankton C per μg MZP C per day) averaged 1.0 $d^{-1}$ for stations with Chl-a < 3 μg $l^{-1}$, and 2.0 $d^{-1}$ for stations with Chl-a > 3 μg $l^{-1}$ (Table 5). These specific grazing rates are greater than those reported by Strom and

Frederickson (2008) for microzooplankton in the Bering Sea in summer 2004, with average Chl-a of 1.4 ± 1.0 μg $l^{-1}$. When a C:Chl-a ratio of 50 was assumed, the same ratio used in our calculation, they found average specific rates of about 0.2 to 0.6 $d^{-1}$. The high rates estimated for bloom stations are due, in part, to higher phytoplankton biomass, which allowed for higher protist specific ingestion rates.

Based on biomass-specific consumption of phytoplankton carbon, and assuming a gross growth efficiency of 30 %, we determined microzooplankton community growth rates of 0.33 ± 0.50 $d^{-1}$ for dilution experiments for stations with Chl-a < 3 μg $l^{-1}$, and 0.43 ± 0.37 $d^{-1}$ for stations with Chl-a > 3 μg $l^{-1}$ (Table 5). The mean estimated growth rate for microzooplankton at non-bloom stations was not significantly different from growth rates at bloom stations due to the limited amount of data and high variability in estimated growth rates. Growth rates of over 1 $d^{-1}$ were found at some stations. These estimated microzooplankton growth rates are in the range of phytoplankton growth rates determined from dilution assays in our study (Table 2).

4.5 Role of microzooplankton in controlling phytoplankton blooms at cold water temperatures

The fact that microzooplankton graze a significant fraction of diatom production in the Bering Sea during spring (Table 3) argues against the 'loophole' hypothesis of Irigoien et al. (2005). Heterotrophic dinoflagellates, as well as other protists, were able to feed on the dominate diatom species composing the spring blooms (examples shown in Fig. 2).

The hypothesis of Rose and Caron (2007) of lower protist growth rates at cold temperature is hampered by lack of relevant data. Their comparison of the maximum growth rates ($\mu_{Max}$) of phytoplankton (mainly diatoms) and of herbivorous protists at cold water temperature was limited to data on growth rates of a laboratory-cultured filter-feeding ciliate and a nanoflagellate grown on algae < 20 μm in size. These protists are not representative of

microzooplankton grazers, predominately heterotrophic dinoflagellates, which prey on large-sized and chain-forming diatoms. In addition, phagotrophic protists living in cold water habitats may be physiologically adapted to low temperature.

Our study showed that growth rates of the microzooplankton community were potentially equivalent to phytoplankton growth rates at the cold temperatures (< 4 $^{o}$C) characteristic of the Bering Sea in spring (Table 5). During blooms, while average phytoplankton growth rate was only 0.22 $d^{-1}$, microzooplankton growth rates were higher, averaging 0.43 $d^{-1}$. The rates of microzooplankton growth we estimated are similar to the rate, 0.3 $d^{-1}$, empirically determined by Bjornsen and Kuparinin (1991) for herbivorous dinoflagellates, *Gymnodinium* spp., in the Southern Ocean at water temperatures of < 0 $^{o}$C. Levinsen and Nielsen (2002) also found that heterotrophic dinoflagellates could grow rapidly during spring diatom blooms in Disko Bay, Greenland, with water temperatures of -1.8 to 6 $^{o}$C. These findings do not support the hypothesis of Rose and Caron (2007) of lower protist growth rates compared to phytoplankton growth rates at temperatures < 10 $^{o}$C in high-latitude marine systems.

We have previously argued that hypotheses about the initiation of diatom blooms as a result of escape from microzooplankton grazing have largely ignored the well-known relationship between protist grazing and growth rates and prey abundance (Sherr and Sherr, 2009). A main reason that microzooplankton are not likely to prevent the initiation of a diatom bloom is due to the disparity in growth rates of diatoms and herbivorous protists in the early stages of a bloom. At the beginning of a bloom, when phytoplankton biomass is low, diatom cells grow at the maximum rate at which nutrient supply, light, and temperature allow. The growth rate of herbivorous protists, however, is related to prey biomass by a functional response curve in which growth rates are much less than $\mu_{Max}$ at low food abundance, and only approach

$\mu_{Max}$ when prey biomass is high. While protist $\mu_{Max}$ may vary by two- to four-fold over a range of environmental temperatures, as shown by Rose and Caron (2007), at any one temperature the specific growth rate can vary over more than an order of magnitude depending on how much prey food is available (Sherr and Sherr 2009). The result of this functional relationship is very low growth rates, and thus potential grazing rates, of herbivorous protists at the beginning of a bloom when phytoplankton biomass is low. Phytoplankton blooms, and in particular diatom blooms, occur because autotrophic cells have intrinsically higher growth rates compared to protist predators in the early stages of bloom development. Microzooplankton grazers can, however, limit biomass accumulation by cropping a portion of daily production as the bloom matures.

Growth rates of microzooplankton grazers do respond positively to higher water temperature in both arctic and temperate habitats (Levinson and Nielsen, 2002; Aberle et al., 2007; Hunt et al., 2010). However, bottom-up (prey abundance) and top-down (predation mortality) factors are likely to supersede temperature effect on growth rates of protistan herbivores in cold temperature marine ecosystems. Modeling the grazing impact of microzooplankton in the Bering Sea as climate change affects sea ice extent and water temperature will not be straightforward.

## 4.5 Conclusions

During spring sea ice conditions in the Bering Sea, both phytoplankton growth rate and microzooplankton grazing impact was highly variable. Microzooplankton grazing averaged about 40–50% of daily phytoplankton production, higher than that previously reported for the Western Arctic Ocean (Sherr et al., 2009), but lower than microzooplankton herbivory in the Bering Sea during summer (Table 6). An unexpected variety of protists were observed feeding

on bloom-forming diatom chains and cells, including athecate and thecate dinoflagellates, species of spirotrichous ciliate, parasitoid flagellates, and a thecate amoeba. Microzooplankton biomass was high and was positively related to phytoplankton stocks. Growth rates estimated for the microzooplankton community, based on amount of phytoplankton carbon consumed, were in the same range as phytoplankton growth rates. Microzooplanktonic protists have a central role in pelagic food webs during spring diatom blooms in the Bering Sea, and should be incorporated into ecosystem models of this region.

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## References


Aberle, N., Lengfellner, K., Sommer, U., 2007. Spring bloom succession, grazing impact and herbivore selectivity of ciliate communities in response to winter warming Oecologia 150, 668–681.

Abreu, P.C., Odebrecht, C., 1997. Bacteria and Protozooplankton. In U.Seeliger, C. Odebrecht, J.P. Castello (Eds.) Subtropical Convergence Environments, the Coast and Sea in the Southwestern Atlantic. Springer, Berlin, pp. 37–39.

Ardyna, M., Gosselin, M., Michel, C., Poulin, M., Tremblay, J.É., 2011. Environmental forcing of phytoplankton community structure and function in the Canadian High Arctic: contrasting oligotrophic and eutrophic regions. Mar. Ecol. Prog. Ser. 442, 37–57.

Banse, K., 1982. Cell volume, maximal growth rates of unicellular algae and ciliates, and the role of ciliates in the marine pelagial. Limnol. Oceanogr. 27, 1059-1071.

Bjørnsen, P.K., Kuparinen, J., 1991. Growth and herbivory by heterotrophic dinoflagellates in the Southern Ocean, studied by microcosm experiments. Mar. Biol. 109, 397–405.

Buitenhuis, E.T., Rivkin, R.B., Sailley, S., Le Quéré, C., 2010. Biogeochemical fluxes through microzooplankton, Global Biogeochem. Cycles, 24, GB4015, doi:10.1029/2009GB003601.

Calbet, A., 2008. The trophic roles of microzooplankton in marine systems. ICES J. Mar. Sci. 65, 325–331.

Calbet, A., Landry, M.R., 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. Limnol. Oceanogr. 40, 51–57.

Calbet, A., Saiz, E., 2005. The ciliate–copepod link in marine ecosystems. Aquat. Microb. Ecol. 38, 157–167.

Campbell, R.G., Sherr E.B., Ashjian, C.J., Plourde, S., Sherr, B.F., Hill, V., Stockwell, D.A., 2009. Mesozooplankton prey preference and grazing impact in the Western Arctic Ocean. Deep-Sea Res. II 56, 1274–1289.

Chen, M., Liu, H., 2011. Experimental simulation of trophic interactions among omnivorous copepods, heterotrophic dinoflagellates and diatoms. J. Exp. Mar. Biol. Ecol. 403, 65–74.

Cooper, L., et al. New insights on the northern Bering Sea ecosystem from early seasonal sampling in March 2008, 2009, and 2010. This issue.

Dolan, J.R., Gallegos, C.L., Moigis, A., 2000. Dilution effects on microzooplankton in dilution grazing experiments. Mar. Ecol. Prog. Ser. 200, 127–139.

Gallegos, C.L., 1989. Microzooplankton grazing on phytoplankton in the Rhode River, Maryland: nonlinear feeding kinetics. Mar. Ecol. Prog. Ser. 57, 23–33.

Gifford, D.J., 1988. Impact of grazing by microzooplankton in the Northwest Arm of Halifax Harbour, Nova Scotia. Marine Ecological Progress Series 47, 249–258.

Hansen, A.S., Nielsen, T.G., Levinsen, H., Madsen, S.D., Thingstad, T.F., Hansen, B.W., 2003. Impact of changing ice cover on pelagic productivity and food web structure in Disko Bay, West Greenland: a dynamic model approach. Deep-Sea Res. I 50, 171−187.

Howell-Kübler, A.N., Lessard, E.J., Napp, J.M., 1996. Springtime microprotozoan abundance and biomass in the southeastern Bering Sea and Shelikof Straight, Alaska. J. Plank. Res. 18, 731−745.

Hunt, G.L., Stabeno, P.,Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M., Bond, N.A., 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Res. II 49, 5821–5853.

Hunt, G.J., Stabeno, P., Strom, S., Napp, J.M., 2008. Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain. Deep-Sea Res. II 55, 1919–1944.

Hunt, G.L., Allen, B.M., Angliss, R.P., Baker, T., Bond, N., Buck, G., Byrd, G.V., Coyle, K.O., Devol, A., Eggers, D.M., Eisner, L., Feely, R., Fitzgerald, S., Fritz, L.W. Gritsay, E.V., Ladd, C., Lewis, W., Mathis, J., Mordy, C.W., Mueter, F., Napp, J., Sherr, E., Shull, D., Stabeno, P., Stepanenko, M.A., Strom, S., Whitledge, T.E., 2010. Status and trends of the Bering Sea region, 2003-2008. In: McKinnell, S.M, Dagg, M.J. (Eds.), The Marine ecosystems of the North Pacific Ocean; status and trends, 2003-2008. PICES, pp. 196–267.

Hunt, G.L., Jr., Coyle, K.O., Eisner, L., Farley, E.V., Heintz, R., Mueter, F., Napp, J.M., Overland, J.E., Ressler, P.H., Salo, S., Stabeno, P.J., 2011. Climate impacts on eastern Bering Sea food webs: A synthesis of new data and an assessment of the Oscillating Control Hypothesis. Ices J. Mar. Sci. doi: 10.1093/icesjms/fsr036.

Irigoien, X., Huisman, J., Harris, R.P., 2004. Global biodiversity patterns of marine phytoplankton and zooplankton. Nature 429, 863–867.

Irigoien, X., Flynn. K.J., Harris, R.P., 2005. Phytoplankton blooms: a 'loophole' in microzooplankton grazing impact? J. Plankton Res. 27, 313–321.

Jeong, H.J., Yoo, Y.D., Kim, S.T., Kang, N.S., 2004. Feeding by the heterotrophic dinoflagellate *Protoperidinium bipes* on the diatom *Skeletonema costatum*. Aquat. Microb. Ecol. 36, 171–179.

Jeong, H.J., Yoo, Y.D., Kim, J.S., Seong, K., Ah Kang, N.S., Kim, T.H., 2010. Growth, feeding and ecological roles of the mixotrophic and heterotrophic dinoflagellates in marine planktonic food webs. Ocean Sci. J. 45, 65–91.

Johansson, M., Gorokhova, E., Larsson, U., 2004. Annual variability in ciliate community structure, potential prey and predators in the open northern Baltic Sea proper. J. Plankton Res. 26, 67–80.

Landry, M.R., 1993. Estimating rates of growth and grazing mortality of phytoplankton by the dilution method. In: Kemp, P.F., Sherr, B.F., Sherr, E.B. and Cole J.J. (eds.), Handbook of Methods in Aquatic Microbial Ecology. Lewis Publ., Boca Raton, FL, pp. 715–722.

Landry, M.R., Calbet, A., 2004. Microzooplankton production in the oceans. ICES J. Marine Sci., 61, 501–507.

Landry, M.R., Brown, S.L., Rii, Y.M., Selph, K.E., Bidigare, R.R., Yang, E.J., Simmons, M.P., 2008. Depth-stratified phytoplankton dynamics in Cyclone Opal, a subtropical mesoscale eddy. Deep-Sea Res. II 55, 1348–1359.

Lessard, E.J., Martin, M.P., Montagnes, D.J.S., 1996. A new method for live-staining protists with DAPI and its application as a tracer of ingestion by walleye pollock (*Theragra chalcogramma*) larvae. J Exp Mar Biol Ecol 204, 43–57.

Levinsen, H., Nielsen, T.G., 2002. The trophic role of marine pelagic ciliates and heterotrophic dinoflagellates in arctic and temperate coastal ecosystems: A cross-latitude comparison. Limnol. Oceanogr. 47, 427–439.

Levinsen, H., Nielsen, T.G., Hansen, B.W., 1999. Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. II. Heterotrophic dinoflagellates and ciliates. Aquatic Microb. Ecol. 16, 217–232.

Liu, H., Suzuki, K., Saino, T., 2002. Phytoplankton growth and microzooplankton grazing in the subarctic Pacific Ocean and the Bering Sea during summer 1999. Deep-Sea Research I 49, 363–375.

Löder, M.G., Meunier, C., Wiltshire, K.H., Boersma, M, Aberle, N., 2011. The role of ciliates, heterotrophic dinoflagellates and copepods in structuring spring plankton communities at Helgoland Roads, North Sea. Mar. Biol. 158, 1551–1580.

Lomas, M.W., Moran, S.B., Casey, J.R., Bell, D.W., Tiahlo, M., Whitefield, J., Kelly R.P., Mathis J.T., Cokelet, E.D., 2012. Spatial and seasonal variability of primary production on the Eastern Bering Sea shelf. Deep-Sea Res. II, in press.

Menden-Deuer, S., Lessard, E., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol. Oceanogr. 45, 569–579.

Montagnes, D.J.S., Dower, J.F., Figueiredo, G.M., 2010. The protozooplankton–ichthyoplankton trophic link: an overlooked aspect of aquatic food webs. J Eukaryot Microbiol 57, 223–228.

Moran, S.B., Lomas, M.W., Kelly, R.P., Iken, K., Gradinger, R., Mathis, J.T., 2012. Seasonal succession of net primary productivity, particulate organic carbon export, and autotrophic community composition in the eastern Bering Sea. Deep-Sea Res. II, in press.

Neuer, S., Cowles, T.J., 1994. Protist herbivory in the Oregon upwelling system. Mar. Ecol. Prog. Ser. 113, 147–162.

Olsen, Y., Anderson, T., Gismervik, I., Vladstein, O., 2006. Protozoan and metazoan zooplankton-mediated carbon flows in nutrient-enriched coastal planktonic communities. Mar. Ecol. Prog. Ser. 331, 67–83.

Olson, M.B., Strom, S.L., 2002. Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: insight into the formation and temporal persistence of an *Emiliania huxleyi* bloom. Deep-Sea Res. II 49, 5969–5990.

Parsons, T., Maita, Y., Lalli, C., 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press, New York.

Putland, J.N., 2000. Microzooplankton herbivory and bacterivory in Newfoundland coastal waters during spring, summer, and winter. J. Plankton Res. 22, 253–277.

Putt, M., Stoecker, D.K., 1989. An experimentally determined carbon: volume ratio for marine ‘‘oligotrichous’’ ciliates from estuarine and coastal waters. Limnol. Oceanogr. 34, 1097–1103.

Raven, J.A., Waite, A.M., 2004. The evolution of silicification in diatoms: inescapable sinking and sinking as escape? New Phytologist 162, 45–61.

Roff, J.C., Hopcroft, R.R., 1986. High precision microcomputer based measuring system for ecological research. Can. J. Fish. Aquat. Sci. 43, 2044–2048.

Rose, J.M., Caron, D.A., 2007. Does low temperature constrain the growth rate of heterotrophic protists? Evidence and implications for algal blooms in cold waters. Limnol. Oceanogr. 52, 886–895.

Sherr, E.B., Sherr, B.F., 1993. Preservation and storage of samples for enumeration of heterotrophic protists. In: P. Kemp, B. Sherr, E. Sherr, and J. Cole (eds), Current Methods in Aquatic Microbial Ecology, Lewis Publ., New York, NY, pp. 207–212.

Sherr, E.B., Sherr, B.F., 2002. Significant of predation by protists in aquatic microbial food webs. Anton. Leew. Int. J. G. 81, 293–308.

Sherr, E.B., Sherr, B.F., 2007. Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Mar. Ecol. Prog. Ser. 352, 187–197.

Sherr, E.B., Sherr, B.F., 2009. Capacity of herbivorous protists to control initiation and development of mass phytoplankton blooms. Aquat. Microb. Ecol. 57, 253-262.

Sherr, E.B., Sherr, B.F., Hartz, A.J., 2009. Microzooplankton grazing impact in the Western Arctic Ocean. Deep-Sea Res. II 56, 1264–1273.

Smetacek, V., 1981. The annual cycle of protozooplankton in the Kiel Bight. Mar. Biol. 63, 1–11.

Stabeno, P.J., Kachel, N.B., Sullivan, M., Whitledge, T.E., 2002. Variability of physical and chemical characteristics along the 70-m isobath of the southeast Bering Sea. Deep-Sea Res. Pt. II 49, 5931–5943.

Stabeno, P., Kachel, N., Moore, S., Napp, J., Sigler, M., Zerbini. A.N., 2012. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep Sea Res. II, in press.

Straile, D., 1997. Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator–prey weight ratio, and taxonomic group. Limnol. Oceanogr. 42, 1375–1385.

Strom, S.L., Fredrickson, K.A., 2008. Intense stratification leads to phytoplankton nutrient limitation and reduced microzooplankton grazing in the southeastern Bering Sea. Deep-Sea Res. 55, 1761–1774.

Suffrian, K., Simonelli, P., Nejstgaard, J.C., Putzeys, S., Carotenuto, Y., Antia, A.N., 2008. Microzooplankton grazing and phytoplankton growth in marine mesocosms with increased $CO_2$ levels. Biogeosci. 5, 1145–1156.

Sukhanova, I., Semina, H., Venttsel, M., 1999. Spatial distribution and temporal variability of phytoplankton in the Bering Sea. In: Loughlin, T., Ohtani, K. (Eds.), Dynamics of the Bering Sea. University of Alaska Sea Grant, Fairbanks, pp. 453–484.
Sukhavona et al., 2006.

Tillmann, U., Hesse K.-J., Tillmann, A. 1999. Large-scale parasitic infection of diatoms in the Northfrisian Wadden Sea. J. Sea Res. 42, 255–261.

Verity, P.G., Wassmann, P., Frischer, M.E., Howard-Jones, M.H., Allen, A.E., 2002. Grazing of phytoplankton by microzooplankton in the Barents Sea during early summer. J. Mar. Syst. 38, 109–123.

Welschmeyer, N.A. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. Limnol. Oceanogr. 39, 1985–1992.

Table 1. Summary of dates, station locations, bottom depths, ice extent as visually estimated percent of sea surface cover, sampling depth, water temperature and nitrate concentration at the sampling depth, and light level during incubation as percent of incident light, for dilution assay experiments conducted during BEST spring cruises. In 2010, no quantitative assessment of ice cover was made, however notes were made as to no ice cover observed, when sampling was done at the ice edge (edge), or when ice floes were present (floes). Nitrate concentrations were provided by the BEST service team. nd = no data.

| Date | Lati-tude °N | Longi-tude °W | Bottom depth m | Ice cover % | Sample depth m | Temp. °C | Nitrate µM | Light % Io |
|---|---|---|---|---|---|---|---|---|
| 4/2/2008 | 57.895 | 169.246 | 67 | 90 | 15 | -1.3 | 12.8 | 15 |
| 4/5/2008 | 59.892 | 169.791 | 53 | 90 | 16 | -0.1 | nd | dark |
| 4/7/2008 | 59.878 | 172.680 | 76 | 100 | 10 | -0.1 | nd | dark |
| 4/8/2008 | 59.900 | 176.432 | 141 | 90 | 2 | -1.6 | 20.8 | 15 |
| 4/11/2008 | 62.204 | 175.099 | 80 | 70 | 10 | -1.6 | 16.4 | 15 |
| 4/13/2008 | 61.964 | 171.223 | 53 | 9 | 14 | -0.8 | 10.1 | 15 |
| 4/16/2008 | 59.904 | 171.257 | 74 | 80 | 2 | -1.0 | 9.7 | 25 |
| 4/18/2008 | 57.914 | 169.230 | 69 | 30 | 10 | -1.3 | 11.9 | 25 |
| 4/21/2008 | 57.827 | 171.734 | 101 | 0 | 14 | 1.8 | 8.9 | 25 |
| 4/23/2008 | 57.929 | 173.877 | 165 | 0 | 10 | -0.4 | 19.0 | 15 |
| 4/25/2008 | 59.206 | 175.906 | 139 | 0 | 20 | -0.3 | 16.0 | 25 |
| 4/28/2008 | 59.196 | 175.982 | 139 | 0 | 10 | nd | 14.8 | 25 |
| 4/29/2008 | 62.199 | 174.698 | 73 | 100 | 10 | -1.6 | 14.3 | 25 |
| 4/8/2009 | 59.902 | 170.39 | 62 | 80 | 10 | -1.4 | 5.0 | 25 |
| 4/10/2009 | 59.867 | 175.256 | 120 | 90 | 20 | -0.5 | 16.6 | 15 |
| 4/12/2009 | 59.901 | 178.905 | 504 | 90 | 16 | -1.3 | 23.9 | 15 |
| 4/14/2009 | 61.778 | 176.789 | 113 | 6 | 10 | -1.1 | 17.9 | 15 |
| 4/16/2009 | 62.077 | 173.275 | 60 | 10 | 10 | -1.0 | 11.2 | 15 |
| 4/18/2009 | 61.697 | 167.742 | 28 | 90 | 10 | -1.0 | 4.2 | 15 |
| 4/20/2009 | 59.457 | 167.786 | 38 | 60 | 10 | -0.6 | 0.9 | 25 |
| 4/22/2009 | 57.441 | 169.745 | 66 | 70 | 10 | -0.7 | 15.4 | 15 |
| 4/24/2009 | 56.974 | 170.273 | 72 | 0 | 10 | 0.6 | 17.0 | 25 |
| 4/26/2009 | 59.529 | 175.203 | 137 | 0 | 7 | -1.0 | 11.5 | 50 |
| 4/27/2009 | 59.540 | 175.077 | 130 | 0 | 7 | -0.8 | 6.0 | 50 |
| 4/29/2009 | 59.584 | 175.125 | 132 | 0 | 5 | -1.1 | 2.4 | 50 |
| 4/30/2009 | 59.546 | 175.143 | 133 | 0 | 5 | -1.1 | 3.7 | 50 |
| 5/2/2009 | 62.255 | 172.543 | 59 | 80 | 10 | -1.4 | 8.5 | 25 |
| 5/4/2009 | 62.183 | 175.131 | 80 | 90 | 10 | -1.2 | 14.4 | 25 |
| 5/6/2009 | 59.433 | 174.076 | 115 | 0 | 15 | -0.1 | 0.0 | 25 |
| 5/12/2010 | 56.283 | 171.051 | 140 | 0 | 15 | 3.5 | 9.4 | 15 |
| 5/13/2010 | 56.727 | 170.573 | 115 | edge | 40 | -0.4 | 6.9 | 15 |
| 5/15/2010 | 58.351 | 171.791 | 102 | 0 | 18 | 0.6 | 0.6 | 15 |
| 5/17/2010 | 59.329 | 175.606 | 142 | edge | 27.5 | 2.0 | 17.5 | 15 |
| 5/19/2010 | 59.899 | 178.898 | 485 | 0 | 5 | 1.3 | 0.2 | 15 |
| 5/21/2010 | 58.204 | 174.236 | 381 | 0 | 24 | 2.6 | 12.5 | 15 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 5/23/2010 | 59.072 | 170.170 | 67 | floes | 19 | 0.2 | 2.7 | 15 |
| 5/25/2010 | 56.917 | 167.317 | 78 | 0 | 22 | 1.8 | 7.0 | 15 |
| 5/27/2010 | 58.171 | 169.898 | 72 | 0 | 28.5 | 1.5 | 1.8 | 15 |
| 5/29/2010 | 55.432 | 168.061 | 204 | 0 | 12 | 3.4 | 9.7 | 15 |
| 5/30/2010 | 57.131 | 163.798 | 67 | 0 | 25 | 2.2 | 8.2 | 15 |
| 5/31/2010 | 56.853 | 164.506 | 73 | 0 | 15 | 1.9 | 0.1 | 15 |
| 6/2/2010 | 58.612 | 170.285 | 72 | 0 | 15 | 1.3 | 0.5 | 15 |
| 6/4/2010 | 61.411 | 173.735 | 76 | 0 | 25 | 2.6 | 1.0 | 15 |
| 6/5/2010 | 62.189 | 175.152 | 79 | 0 | 27 | 2.7 | 0.1 | 15 |
| 6/7/2010 | 59.893 | 178.898 | 666 | 0 | 17 | 3.6 | 10.1 | 15 |
| 6/9/2010 | 59.900 | 172.200 | 73 | 0 | 25 | 1.8 | 0.1 | 15 |
| 6/10/2010 | 58.830 | 168.159 | 46 | 0 | 35 | 2.3 | 0.1 | 15 |

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Table 2. Summary of results for dilution assay experiments conducted during BEST spring cruises. Where calculated MZP grazing rates were negative, i.e., k > kd, we assumed a grazing rate of 0.

| Date | Sample site | Chl-a µg $l^{-1}$ | Phyto. µ, $d^{-1}$ | MZP, m, $d^{-1}$ | Signifi-cance | µ/m |
|---|---|---|---|---|---|---|
| 4/2/2008 | NP-7 | 0.22 | 0.10 | 0.21 | P < 0.04 | 2.2 |
| 4/5/2008 | MN-4 | 0.15 | 0.04 | 0 | ns | 0 |
| 4/7/2008 | MN-8.5 | 0.11 | 0.08 | 0 | ns | 0 |
| 4/8/2008 | MN-15 | 1.0 | 0.14 | 0.50 | P < 0.06 | 3.6 |
| 4/11/2008 | SL-12 | 1.6 | 0.19 | 0.12 | P < 0.04 | 0.64 |
| 4/13/2008 | SL-6 | 0.8 | 0.12 | 0 | ns | 0 |
| 4/16/2008 | W7.5 | 0.15 | 0.14 | 0 | ns | 0 |
| 4/18/2008 | NP7 | 0.30 | 0.27 | 0 | ns | 0 |
| 4/21/2008 | BS1 | 21.4 | 0.31 | 0 | ns | 0 |
| 4/23/2008 | BS2 | 7.0 | 0.30 | 0 | ns | 0 |
| 4/25/2008 | ZZ14 | 6.4 | 0.23 | 0.08 | P < 0.02 | 0.36 |
| 4/28/2008 | ZZ27 | 9.7 | 0.12 | 0.10 | P < 0.02 | 0.31 |
| 4/29/2008 | 70m58 | 8.5 | 0.06 | 0.05 | ns | 0 |
| 4/8/2009 | MN5 | 0.3 | 0 | 0 | ns | 0 |
| 4/10/2009 | MN13 | 0.4 | 0.09 | 0 | ns | 0 |
| 4/12/2009 | MN19 | 0.9 | 0.25 | 0 | ns | 0 |
| 4/14/2009 | MN-SL4 | 0.2 | 0 | 0 | ns | 0 |
| 4/16/2009 | SL9 | 0.5 | 0.36 | 0.18 | P < 0.02 | 0.51 |
| 4/18/2009 | SL1 | 0.3 | 0.10 | 0.08 | P < 0.01 | 0.77 |
| 4/20/2009* | NP1 | 0.3 | 0 | 0.03 | ns | 0 |
| 4/22/2009 | NP9 | 1.1 | 0.15 | 0.03 | ns | 0 |
| 4/24/2009 | NP11 | 2.9 | 0.43 | 0.02 | ns | 0 |
| 4/26/2009 | BL1 | 10.3 | 0.38 | 0.14 | P < 0.02 | 0.36 |
| 4/27/2009* | BL4 | 23.6 | 0.27 | 0.14 | P < 0.02 | 0.54 |
| 4/29/2009* | BL15 | 20.9 | 0.47 | 0.17 | P < 0.01 | 0.36 |
| 4/29/2009* | BL15 | 20.9 | 0.40 | 0.08 | P < 0.01 | 0.21 |
| 4/30/2009* | BL20 | 21.4 | 0.27 | 0.07 | P < 0.06 | 0.26 |
| 4/30/2009* | BL20 | 21.4 | 0.31 | 0.10 | P < 0.02 | 0.30 |
| 5/2/2009* | BN-1 | 1.9 | 0.42 | 0.16 | P < 0.06 | 0.39 |
| 5/4/2009* | SL-12 | 0.6 | 0.36 | 0.27 | P < 0.01 | 0.76 |
| 5/6/2009* | B-21 | 38.1 | 0.18 | 0.17 | P < 0.02 | 0.91 |
| 5/12/2010 | NP-14 | 14.8 | 0.20 | 0.07 | P < 0.06 | 0.35 |
| 5/13/2010 | NP-12 | 8.1 | 0.16 | 0.09 | P < 0.001 | 0.57 |
| 5/15/2010* | Z-15 | 11.0 | 0.11 | 0 | ns | 0 |
| 5/17/2010 | IE-1 | 10.5 | 0.35 | 0.33 | P < 0.002 | 0.93 |
| 5/19/2010* | MN-19 | 24.3 | 0.15 | 0.15 | P < 0.01 | 1.0 |
| 5/21/2010 | NZ 11.5 | 1.2 | 0.18 | 0 | ns | 0 |
| 5/23/2010* | NZ 4.5 | 11.1 | 0.10 | 0.08 | P < 0.01 | 0.75 |
| 5/25/2010* | HBR1 | 31.6 | 0.04 | 0 | ns | 0 |
| 5/27/2010* | 70m26 | 5.6 | 0.10 | 0.15 | P < 0.01 | 1.6 |
| 5/29/2010 | CN17 | 7.8 | 0.38 | 0 | ns | 0 |
| 5/30/2010* | CN 5 | 3.5 | 0.06 | 0 | ns | 0 |
| 5/31/2010* | 70m4 | 7.5 | 0.24 | 0 | ns | 0 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 6/2/2010* | 70m29 | 0.5 | 0.39 | 0.14 | $P < 0.001$ | 0.36 |
| 6/4/2010* | 70m52 | 14.9 | 0.15 | 0.13 | $P < 0.04$ | 0.87 |
| 6/5/2010* | SL12 | 2.0 | 0.00 | 0 | ns | 0 |
| 6/7/2010* | MN-19 | 7.9 | 0.16 | 0.07 | $P < 0.03$ | 0.45 |
| 6/9/2010 | MN8 | 0.4 | 0.24 | 0.05 | $P < 0.02$ | 0.22 |
| 6/10/2010* | NP-3 | 1.2 | 0.07 | 0.21 | $P < 0.07$ | 3.0 |

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2 * Experiments in which nutrients were added.

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Table 3. Mean seawater temperature, Chl-a concentration, phytoplankton production and microzooplankton grazing rate as mg C $m^{-3}$ $d^{-1}$, and percent of phytoplankton production grazed by microzooplankton during spring; mean values ± one standard deviation. At bloom stations Chl-a concentrations were > 3.0 µg $l^{-1}$. All data, including experiments with non-significant grazing, were included.

| **Year** | **Surface seawater temp, $^{o}$C** | **Chl-a µg $l^{-1}$** | **Phyto. prod. rate mg C $m^{-3}$ $d^{-1}$** | **Microzoop. grazing rate mg C $m^{-3}$ $d^{-1}$** | **Percent of Chl-a grazed $d^{-1}$** | **Percent of phyto. prod. grazed $d^{-1}$** |
|---|---|---|---|---|---|---|
| *Spring 2008* | | | | | | |
| Non-bloom | -1.0 ± 0.6 | 0.6 ± 0.6 | 2.7 ± 3.0 | 4.6 ± 8.6 | 11 ± 17 | 86 ± 140 |
| Bloom | -0.4 ± 1.0 | 10.6 ± 6.2 | 135 ± 144 | 16 ± 13 | 4 ± 4 | 31 ± 31 |
| *Spring 2009* | | | | | | |
| Non-bloom | -1.0 ± 0.3 | 0.8 ± 0.8 | 14 ± 25 | 4.1 ± 6.6 | 9 ± 12 | 26 ±32 |
| Bloom | - 0.6 ± 0.7 | 22.4 ± 8.2 | 410 ± 127 | 67 ± 103 | 11 ± 10 | 45 ± 23 |
| *Spring 2010* | | | | | | |
| Non-bloom | 2.2 ± 0.6 | 1.1 ± 0.6 | 6.7 ± 5.2 | 4.6 ± 8.6 | 9 ± 10 | 69 ± 120 |
| Bloom | 1.9 ± 1.3 | 12.2 ± 7.8 | 104 ± 67 | 57 ± 72 | 9 ± 11 | 50 ± 50 |

Table 4. Values under non- bloom (Chl-a < 3.0 µg $l^{-1}$) and bloom (Chl-a > 3.0 µg $l^{-1}$) conditions during the three BEST spring cruises for Chl-a concentration, microzooplankton (MZP) biomass, fraction of MZP biomass composed of heterotrophic dinoflagellates (HDino), and fraction of MZP biomass composed of cells > 40 µm in longest linear dimension. Values are means ± one standard deviation, with range of values in parentheses.

| | **Chl-a** µg $l^{-1}$ | **MZP biomass** µg C $l^{-1}$ | **HDino fraction of MZP biomass** | **> 40 µm fraction of MZP biomass** |
|---|---|---|---|---|
| ***Dilution initial MZP depths*** | | | | |
| **Non-bloom** **17 stations** | 0.86 ± 0.72 (0.15- 2.9) | 9.2 ± 7.8 (2.0 – 27) | 0.65 ± 0.12 (0.42- 0.84) | 0.49 ± 0.21 (0.19 – 0.80) |
| **Bloom** **21 stations** | 16 ± 9 (5.6 – 38) | 42 ± 22 (15 – 109) | 0.67 ± 0.14 (0.45 – 0.86) | 0.66 ± 0.17 (0.31- 0.85) |
| ***Phytoplankton production profiles, 6 depths per profile*** | | | | |
| **Non-bloom** **16 stations** | 0.86 ± 0.83 (0.06- 2.95) | 11 ± 17 (0.2 – 71) | 0.75 ± 0.13 (0.43- 0.93) | 0.51 ± 0.23 (0.14 – 0.88) |
| **Bloom** **15 stations** | 15 ± 9 (3.5 – 40) | 23 ± 22 (5.5 – 100) | 0.72 ± 0.13 (0.40 – 0.93) | 0.62 ± 0.13 (0.33- 0.86) |
| ***Early spring, March 12 – April 3 2010*** | | | | |
| **Pre-bloom** **10 stations** | 0.28 ± 0.14 (0.17 – 0.59) | 3.2 ± 0.8 (2.0 – 4.4) | 0.81 ± 0.08 (0.40 – 0.93) | 0.52 ± 0.13 (0.37- 0.77) |

Table 5. Values under non-bloom and bloom conditions during the three BEST spring cruises for microzooplankton biomass-specific grazing rate, potential microzooplankton growth rates, and microzooplankton community doubling times. Values are means ± one standard deviation, with range of values in parentheses.

| | **MZP specific grazing rate $d^{-1}$** | **Potential growth rate $d^{-1}$** | **Doubling time days*** |
|---|---|---|---|
| **Non-bloom** | 1.0 ± 1.6 | 0.33 ± 0.50 | 3.3 ± 3.5 |
| **17 stations** | (0 – 4.8) | (0 – 1.45) | (0.5 – 8.5) |
| **Bloom** | 2.0 ± 1.6 | 0.43 ± 0.37 | 2.2 ± 1.7 |
| **21 stations** | (0 – 5.4) | (0 – 1.14) | (0.6- 6.0) |

*Doubling times only calculated for stations for which microzooplankton had non-zero potential growth rates.

Table 6. Comparison of phytoplankton growth and microzooplankton grazing rates, and percent of phytoplankton production grazed, found in this study with values for these parameters determined by the dilution technique in another Arctic system, and in general geographic regions of the world ocean. Values are means ± one standard deviation.

| Region | Temp $^{o}C$ | Chl-a µg $l^{-1}$ | Phyto. growth µ, $d^{-1}$ | MZP grazing g, $d^{-1}$ | % Phyto growth grazed | Reference |
|---|---|---|---|---|---|---|
| **Arctic/sub-arctic** | | | | | | |
| Barents Sea Early summer | -0.2 – 7.4 | 0.66 ± 0.20 | 0.32 ± 0.13 | 0.24 ± 0.11 | 77 ± 8 | Verity et al. 2002 |
| Western Arctic Ocean Spring | - 1.6 ± 0.1 | 2.1 ± 2.5 | 0.21 ± 0.15 | 0.07 ± 0.06 | 17 ± 21 | Sherr et al. 2009 |
| Western Arctic Ocean Summer | - 0.4 ± 2.0 | 3.4 ± 5.4 | 0.11 ± 0.13 | 0.06 ± 0.05 | 27 ± 33 | Sherr et al. 2009 |
| Southeastern Bering Sea Summer 1999 | 11.1 ± 1.1 | 1.4± 1.1 | 0.53 ± 0.21 | 0.43 ± 0.28 | 90 ± 56 | Olson & Strom 2002 |
| Southern Bering Sea Summer 1999 | 6.6 ± 0.9 | 1.2 ± 0.5 | 0.47 ± 0.15 | 0.27 ± 0.14 | 58 ± 31 | Liu et al. 2002 |
| Southeastern Bering Sea Summer 2004 | 6.8 ± 1.8 | 1.4 ± 1.0 | 0.35 ± 0.30 | 0.13 ± 0.09 | 49 | Strom & Frederickson 2008 |
| Eastern Bering Sea Spring, non-bloom | - 0.3 ± 1.4 | 0.8 ± 0.7 | 0.17 ± 0.14 | 0.08 ± 0.12 | 52 ± 100 | This study |
| Eastern Bering Sea Spring, bloom | 0.8 ± 1.7 | 14 ± 9 | 0.21 ± 0.12 | 0.09 ± 0.08 | 42 ± 42 | This study |
| **Other ocean regions** | | | | | | |
| Oceanic | | 0.58 ± 0.03 | 0.59 ± 0.02 | 0.39 ± 0.01 | 70 ± 2 | Calbet & Landry, 2004 |
| Tropical/subtropical | | 1.01 ± 0.21 | 0.72 ± 0.02 | 0.50 ± 0.02 | 74 ± 2 | " |
| Temperate/subpolar | | 5.18 ± 0.66 | 0.69 ± 0.03 | 0.41 ± 0.02 | 61± 2 | " |
| Polar (Southern Ocean) | | 0.62 ± 0.06 | 0.44 ± 0.05 | 0.41 ± 0.16 | 59 ± 3 | " |

**Figure legends**

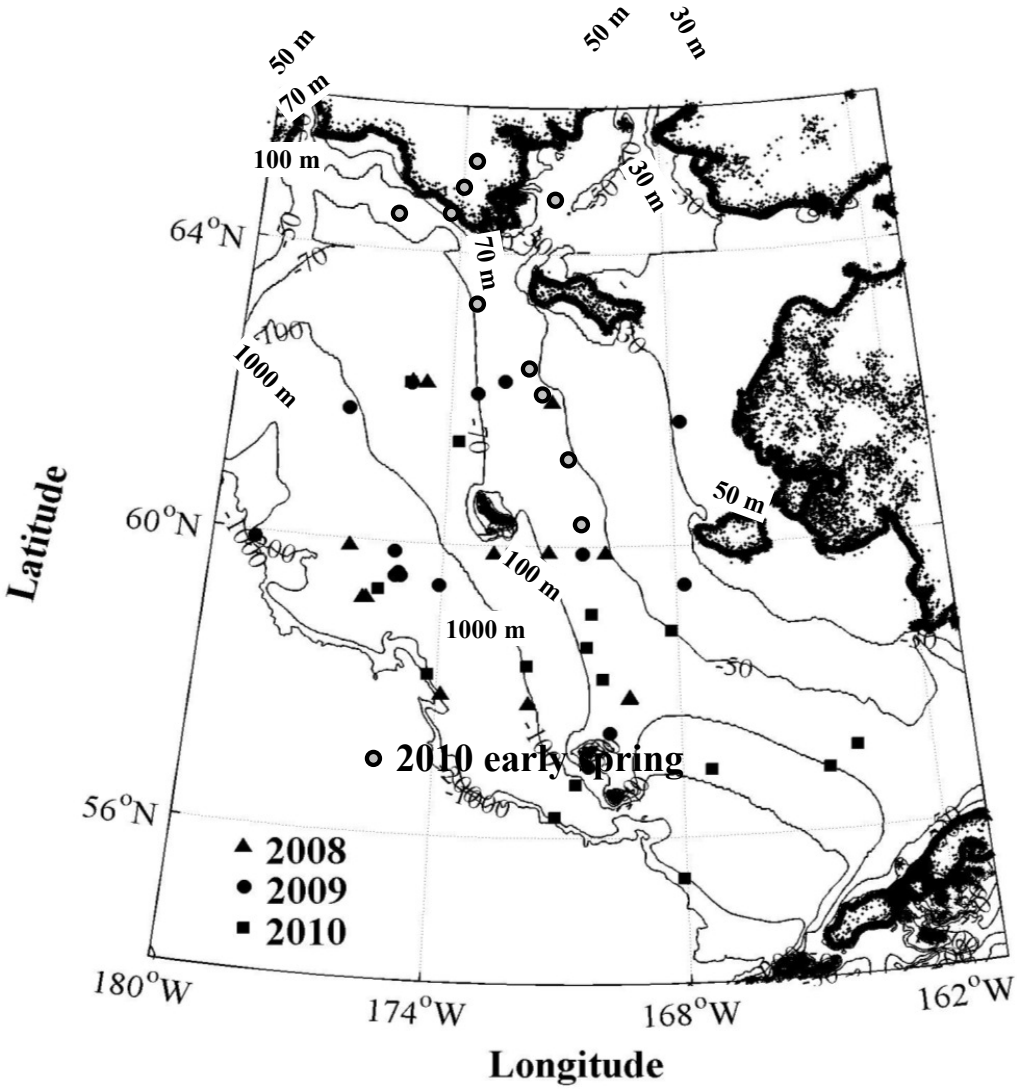
Fig. 1. Location of stations sampled in the eastern Bering Sea. Solid symbols denote stations at which water was collected to set up dilution assay experiments during the three spring BEST process cruises. Grey circles denote stations for which microzooplankton biomass was sampled in early spring 2010.

Fig. 2. Examples of protists observed feeding on diatoms in the Bering Sea during spring. A) heterotrophic athecate dinoflagellates, cf *Gyrodinium* sp., upper cell with no ingested prey, lower cell distended with ingested diatom chain, B) heterotrophic gyrodinoid dinoflagellate cell distended with ingested centric diatom, C) heterotrophic thecate dinoflagellate, cf *Protoperidinium* sp., attached to a diatom chain by an extruded pallium, D) spirotrichous ciliate with ingested diatom chain, E) three parasitoid heterotrophic flagellates on a pennate diatom chain, empty frustules suggest prior feeding by the flagellates, F) two testate amoeba feeding on a centric diatom cell. Scale bars = 50 µm.

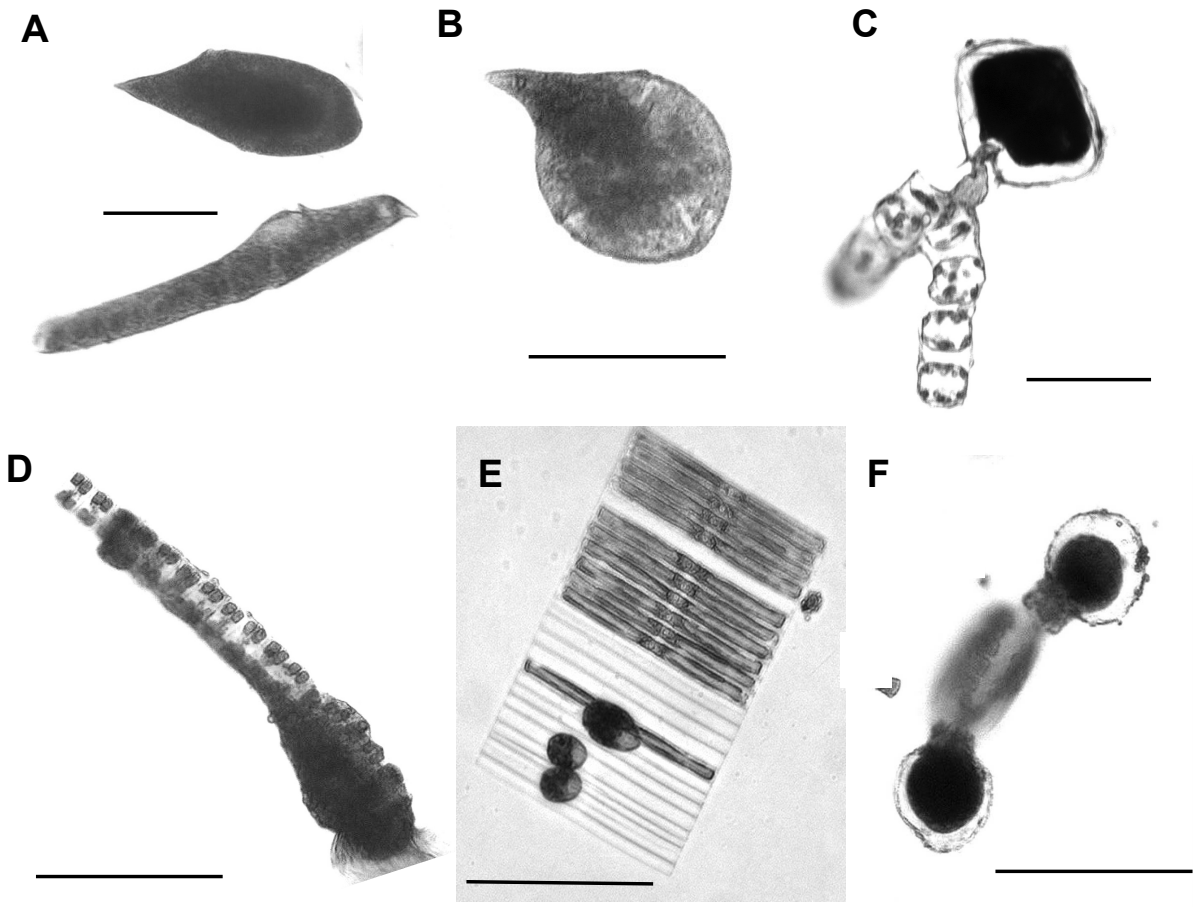
Fig. 3. Log-log relation of microzooplankton biomass (MZP, µg C $l^{-1}$) to Chl-a (µg $l^{-1}$). Dark grey symbols represent initial water samples collected for dilution assays, black symbols water samples from primary production profile depths, light grey symbols water samples from a 2010 early spring (13 March to 3 April) cruise. Polynomial curve equation: $\log_{10}$ MZP = 0.86 + 0.74 $\log_{10}$ Chl-a – 0.21 ($\log_{10}$ Chl-a)$^2$, $R^2$ = 0.44.

Fig. 4. Log-log relation of depth integrated microzooplankton biomass (MZP, gC $m^{-2}$) to integrated phytoplankton biomass (gC $m^{-2}$) for primary production casts. Regression equation: $\log_{10}$ MZP = -1.23 + 0.72 $\log_{10}$ phytoplankton, $R^2$ = 0.72.

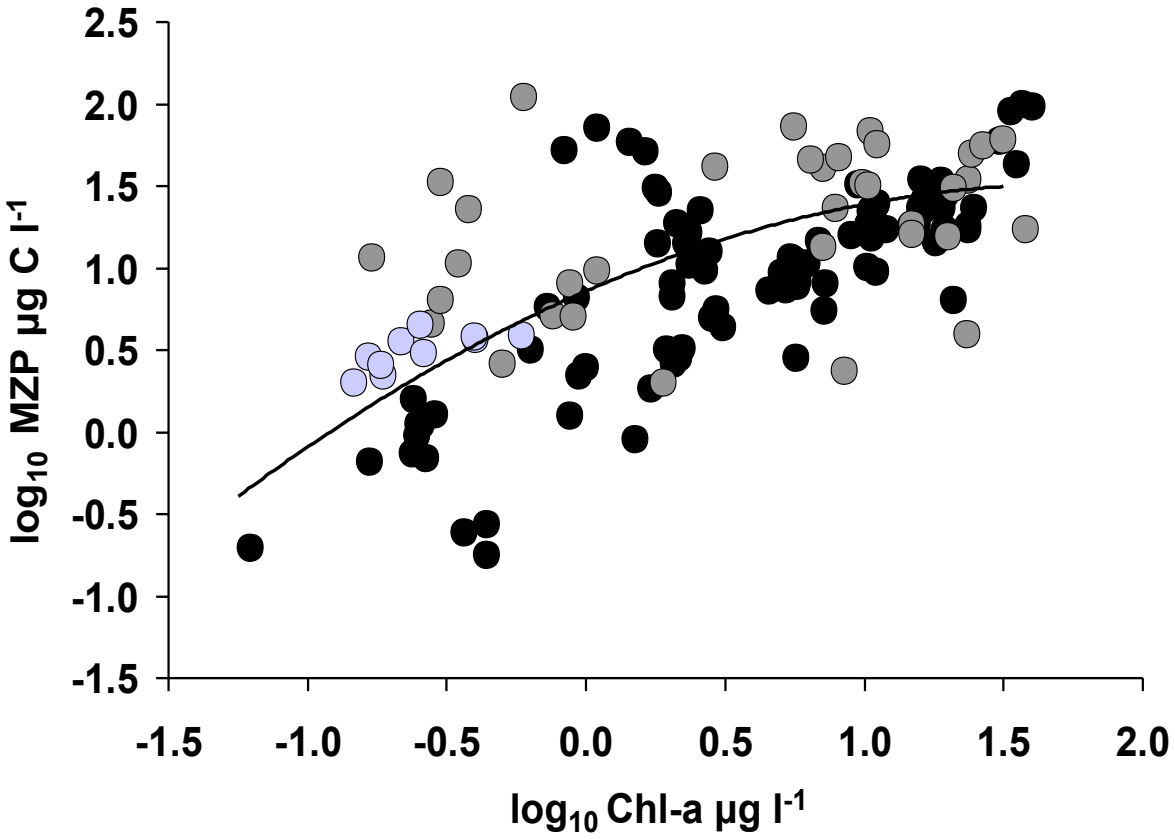
Sherr et al. Figure 1



Sherr et al. Figure 2



Sherr et al. Figure 3



Sherr et al. Figure 4