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Intense stratification leads to phytoplankton nutrient limitation and reduced microzooplankton grazing in the southeastern Bering Sea

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ABSTRACT

During July and August 2004, we used the seawater dilution technique to investigate relationships among environmental conditions, phytoplankton growth, and microzooplankton grazing in the southeast Bering Sea. During summer 2004 the southeast Bering was unusually warm and strongly stratified. Compared with previous observations in the subarctic Pacific and Bering Sea, mixed-layer phytoplankton growth rates were typical (average 0.35 d^{-1}) while microzooplankton grazing rates were low (average 0.13 d^{-1}). Phytoplankton growth rates were strongly nutrient-limited, increasing to an average of 0.69 d^{-1} in response to N+P addition. The largest phytoplankton cells (>20 μm) grew at the highest rates both with and without added nutrients. However, all phytoplankton size classes (<5 μm, 5–20 μm, >20 μm) responded strongly to nutrient addition, and all showed equivalent growth increases in response to added ammonium versus nitrate. In contrast to growth, microzooplankton grazing rates did not vary with phytoplankton size class. Microzooplankton biomass ranged from 11 to 118 μg C L^{-1} and was dominated by ciliates and, especially, heterotrophic dinoflagellates. Estimated microzooplankton biomass-specific grazing on phytoplankton was generally low (<0.5 d^{-1}), a consequence of high microzooplankton biomass coupled with low grazing rates. Low ratios of grazing: growth (average 0.49) further indicated weak trophic coupling between phyto- and microzooplankton during summer 2004. Some regions near the Pribilof Islands contrasted with this scenario, exhibiting high phyto- and microzooplankton biomass and, in some cases, elevated growth and grazing rates. This lower trophic level enhancement was a response to natural nutrient addition events caused by flow–bathymetry interactions near the islands. These predictable sources of summer production are likely important to zooplankton and to the birds and mammals that breed on the Pribilofs. Comparison with a data set collected in the same region in 1999 (a cold, late ice year) showed that summer production at lower trophic levels can be strongly modified by environmental conditions that vary intra- and interannually. Warmer temperatures, weaker winds, and stronger stratification in 2004 likely led to nutrient limitation of phytoplankton growth, reduced microzooplankton grazing, and weak trophic coupling. Such responses at lower trophic levels could negatively affect zooplankton, birds and mammals dependent on summer production in the southeast Bering ecosystem.

1. Introduction

The broad, shallow continental shelf of the eastern Bering Sea supports a high production of commercially important fish and shellfish species (NRC, 1996; Bailey et al., 1999). The Pribilof Islands, perched near the shelf edge in the southeast Bering (Fig. 1), are breeding sites for large numbers of seabirds and marine mammals. These windswept outposts provide rookery sites with access to the rich resources of the eastern Bering shelf (Decker and Hunt, 1996; Byrd et al., 2008). Additionally, interaction of tides and currents with bathymetry may locally enhance production around the Pribilofs and at the shelf break (Springer et al., 1996; Stabeno and Van Meurs, 1999; Stabeno et al., 2008). The overall goal of our multi-investigator study was to investigate sources of new production for the summer ecosystem around the Pribilof Islands. We hypothesized that nutrients supplied by physical processes would enhance new production in the area, fueling secondary production of the zooplankton and fish on which birds and mammals feed while at island breeding sites. Within that larger study, the research presented here investigated lower trophic level processes: phytoplankton growth rates, the degree of phytoplankton nutrient limitation, and microzooplankton grazing and community composition.

The only other published data on phytoplankton intrinsic growth rates and microzooplankton grazing in the Bering were

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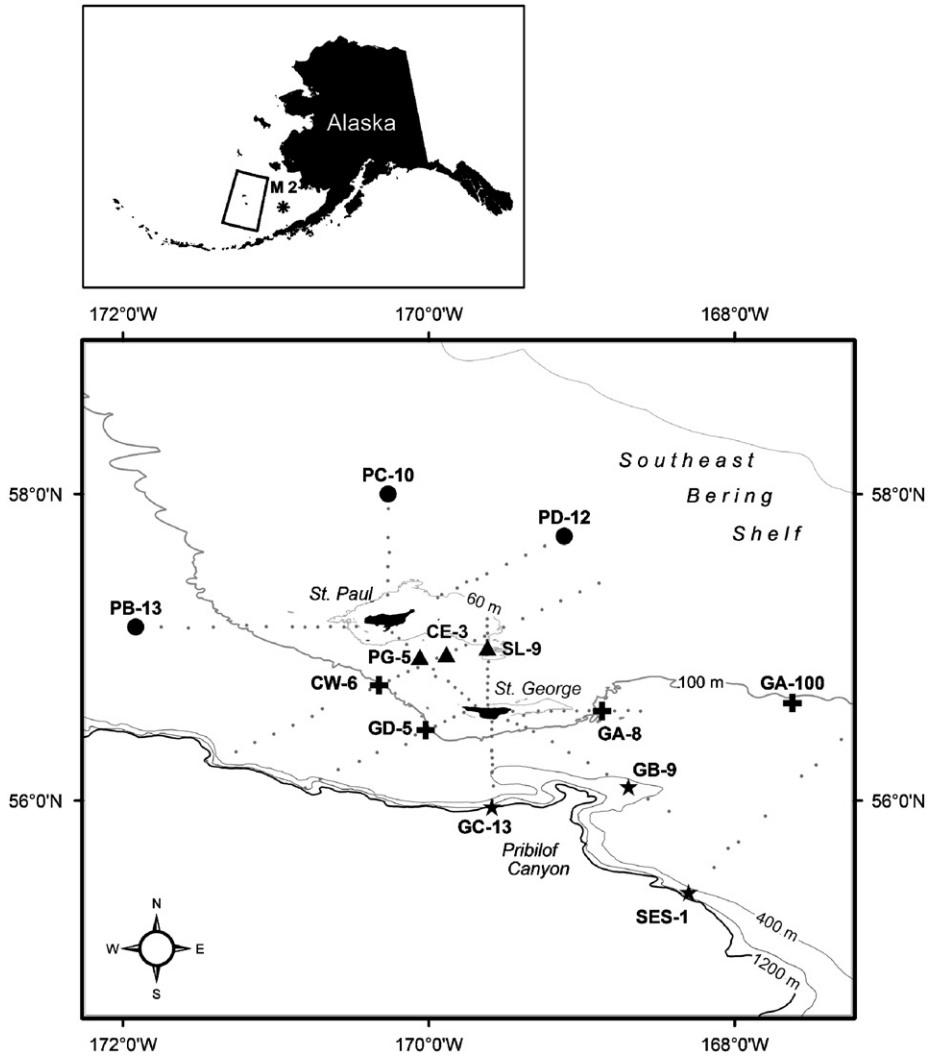

Fig. 1. Map of study area in the Pribilof Island region of the southeast Bering Sea. Major islands are St. Paul and St. George. Symbols indicate hydrographic sampling lines (small dots) and experiment stations in five regions: slope (stars); 100-m isobath (crosses); between islands (triangles); north and west of islands (circles) and M2 (asterisk, upper map).

collected in 1999 (Liu et al., 2002; Olson and Strom, 2002). Southeast Bering conditions in 1999 included a long ice season with heavy cover, late ice retreat, and cold winter and summer water temperatures. These contrasted strongly with conditions in 2004, which included limited ice cover, mid-season (average) ice retreat, and warm winter and summer temperatures (data sources: Stabeno and Overland, 2001; www.beringclimate.noaa.gov/data/). This contrast constitutes a natural experiment allowing us to examine the effects of interannual variability (and, by extension, longer-term climate change) on lower trophic level processes. The Bering Sea is hypothesized to be particularly sensitive to intra- and interannual climate variability, as opposed to longer-term (e.g., multi-decadal) climate 'regimes' (Bond and Overland, 2005). This is because the Bering Sea's latitude puts it at the conjunction of major climate modes, including the Pacific Decadal Oscillation and the Arctic Oscillation. In addition, the southeast Bering Sea historically has been at the southern reaches of winter ice cover (Hunt et al., 2002). The timing and duration of ice cover, dictated by winds and water temperature, play an important role in the physics and biology of this high productivity region (Hunt et al., 2002; Baier and Napp, 2003). Physical and biological responses to climate variation in the southeast Bering are thus magnified due to climate effects on ice cover.

Recent changes in the eastern Bering Sea illustrate the vulnerability of the ecosystem to climate variation. A large-scale bloom of coccolithophorids first appeared in 1997 (Sukhanova and Flint, 1998) and was nearly as extensive in the warm years of 1998 and 2000 (Iida et al., 2002). The 1997 bloom was associated with major ecosystem anomalies on the shelf, including increased abundance of small copepods, altered distribution of euphausiids, and mortality of short-tailed shearwaters (Baduini et al., 2001; Napp and Hunt, 2001; Stockwell et al., 2001). Variations in abundance of the copepod *Calanus marshallae* during the late 1990s have been linked to interannual differences in ice cover during that period (Baier and Napp, 2003). Large increases in jellyfish were observed throughout the 1990s as well (Brodeur et al., 1999). Mechanistic links between climate variation, attendant oceanographic conditions, and production at higher trophic levels have been proposed. Most conceptual models involve the timing of the spring bloom—as determined by the timing of ice retreat—and consequent effects on various food web processes, including timing of food availability for copepods, temperature for copepod development, and the abundance and distribution of predatory fish (Hunt and Stabeno, 2002; Hunt et al., 2002; Baier and Napp, 2003). Summer linkages also have been proposed, in which warm, low nutrient conditions favor

Table 1
Initial conditions for dilution experiments

Region	Station	Date	Depth (m)	I (mol m^{-2})	Temp (°C)	Sal (psu)	Nutrients (μM)				Total Chl (μg L^{-1})	Chl >20 μm (% Total)
							PO_4^{3-}	SiO_4^{2-}	NO_3^-	NH_4^+		
Slope	SES-1	07/27/04	3	24.7	10.5	32.29	0.23	4.83	0.11	0.20	1.21	22
Slope	GC-13	07/28/04	2.5	9.4	10.9	32.64	0.26	0.00	0.17	0.27	3.34	70
Slope	GB-9	07/29/04	3	12.3	10.2	32.74	0.60	9.51	5.75	0.13	2.94	67
Slope	SES-1	07/30/04	2.5	10.6	10.5	32.37	0.24	2.50	0.10	0.16	2.27	62
Mooring 2	M2	08/08/04	7	30.8	12.7	31.77	0.01	1.89	0.17	0.13	0.32	16
Mooring 2	M2	08/09/04	7	31.5	12.8	31.77	0.21	1.51	0.13	0.07	0.36	19
Mooring 2	M2	08/10/04	7	16.5	13.4	31.77	0.21	2.09	0.12	0.08	0.28	16
Between Isl.	PG-5	08/01/04	3	22.2	11.2	31.95	0.25	1.57	0.11	0.17	1.15	78
Between Isl.	CE-3	08/04/04	3	18.8	9.3	32.03	0.26	4.66	0.34	0.08	2.70	79
Between Isl.	SL-9	08/05/04	3	30.7	9.9	32.05	0.18	4.34	0.30	0.12	2.81	67
Between Isl.	PG-5	08/11/04	3	14.0	10.2	31.94	0.39	3.37	0.43	0.58	1.21	64
100 m Isobath	GD-5	07/31/04	4	25.3	10.7	32.04	0.50	8.99	1.49	0.73	1.34	30
100 m Isobath	CW-6	08/03/04	5	15.9	9.6	31.92	0.25	7.78	0.18	0.40	0.95	53
100 m Isobath	GA-100	08/06/04	7	21.1	12.2	31.66	0.12	2.88	0.19	0.08	0.23	31
100 m Isobath	GA-8	08/11/04	7	13.8	12.1	31.68	0.29	8.59	0.12	0.54	0.30	22
N&W of Isl.	PC-10	08/16/04	4	17.1	11.2	31.95	0.35	11.85	0.10	0.12	1.17	74
N&W of Isl.	PD-12	08/17/04	3	14.2	10.8	32.03	0.33	2.09	0.00	0.04	2.25	75
N&W of Isl.	PB-13	08/17/04	5	21.5	10.7	32.01	0.44	10.12	0.08	0.10	0.97	6

Water was collected from the depth corresponding to 50% surface irradiance. I: total incident irradiance (as photons of photosynthetically active radiation) received during incubation period. Temp: surface temperature at seawater collection site (representative of temperature during 24-h incubations). Sal: salinity at seawater collection depth. Chl: chlorophyll in experiment initial samples.

development of coccolithophorid blooms that in turn affect higher trophic levels through disruption of microzooplankton grazing and trophic transfer (Stockwell et al., 2001; Olson and Strom, 2002; Merico et al., 2004).

Microzooplankton grazers consume well over half of marine primary production globally, including in highly productive coastal waters (Strom et al., 2001; Calbet and Landry, 2004). As a significant, and sometimes the dominant, prey source for mesozooplankton (Stoecker and Capuzzo, 1990; Fessenden and Cowles, 1994; Liu et al., 2005), microzooplankton are a major trophic link between primary producers and consumers that can in turn be prey for fish, birds, and mammals. Understanding phyto- and microzooplankton responses to local nutrient enrichments and larger-scale variations in oceanographic conditions will be key to understanding the mechanisms that link climate variation to production at higher trophic levels. In this paper, we present data showing local enhancement of phytoplankton growth and microzooplankton grazing rates in response to flow past bathymetric features near the Pribilof Islands. This enhancement, however, was set against a backdrop of strong nutrient limitation of phytoplankton growth and low microzooplankton grazing over the wider southeast Bering region in 2004. Reduced lower trophic level activity was related to spring and summer weather conditions in 2004 that, in contrast to 1999, resulted in strong stratification and limited nutrient availability to surface waters. Phytoplankton nutrient limitation and reduced microzooplankton grazing must have strongly affected the transfer of primary production to higher trophic levels during 2004.

2. Methods

2.1. Station location and sampling program

Water column sampling and seawater dilution experiments were carried out between 27 July and 18 August 2004 in the southeast Bering Sea. All experiment stations were on hydrographic lines occupied by the program, and were distributed among five oceanographic regions (Fig. 1): the continental slope, the 100-m isobath that runs south-southwest of the Pribilof Islands, the region between St. Paul and St. George Islands, the region north and west of St. Paul Island, and station M2 in the middle of the Bering Sea shelf where a moored buoy has been collecting long-term data since 1995. Three or four experiments were performed in each region (Table 1).

Immediately prior to each experiment, water samples from eight depths were collected for determination of a chlorophyll vertical profile. Water samples from this profile and from initial and final dilution experiment samples (see below) were filtered using a fractionation cascade to yield <5, 5–20, and >20-μm size classes; total chlorophyll was estimated as the sum of the three size fractions. Filters were glass fiber (Osmonics GF-75, 25 mm) and polycarbonate (5 and 20 μm pore size, 47 mm). Chlorophyll samples were extracted in 90% acetone (−20 °C, dark, 24 h) and analyzed fluorimetrically (Turner Designs 10AU) using the acidification method (Welschmeyer, 1994).

2.2. Dilution experiments

We conducted a total of 19 experiments. One experiment (station GA-8, 6 August) gave substantially negative intrinsic growth rates in all phytoplankton size classes, and those data are not included here. We attributed the negative growth to inhibition by diatoms and their extracts released during preparation of filtered seawater with a cartridge filter used previously in diatom bloom waters. This effect was subsequently explored in manipulation experiments; those data will be presented elsewhere. Filtered seawater for all other experiments in low-chlorophyll waters was prepared with new, pre-cleaned cartridge filters.

In eight of the remaining 18 experiments, the seawater dilution technique was used to estimate phytoplankton growth and microzooplankton grazing rates (Landry and Hassett, 1982); methods are described in detail in Strom et al. (2006). Briefly, a range of whole seawater (wsw) percentages of approximately 5, 11, 25, 51 and 100 was used, each in 1.2-liter polycarbonate bottles, with 37% and 74% treatments added to two of the eight experiments. Intermediate dilution levels were in duplicate, while 5% and 100% treatments were in triplicate for consistency with the 2-point method (below). Net growth rates in each bottle (k, d^{-1})

were calculated from initial and final chlorophyll readings in each dilution treatment: $k = (1/t)(\ln[Pt/Po])$, where Pt = final chlorophyll concentration, Po = initial chlorophyll concentration, and t = incubation time in d.

For the remaining 10 experiments, a modification of the dilution technique (the 2-point method) was employed. Instead of using net growth in series of progressively dilute samples to estimate intrinsic growth and grazing mortality, net growth rates in two treatments consisting of 100% and 5% wsw were determined (Landry et al., 1984). The 100% wsw treatment contained all organisms smaller than 200 μm and provided a measure of phytoplankton growth rate in the presence of microzooplankton grazers (k = net growth). The 5% treatment was assumed to be sufficiently dilute that encounters between grazers and prey were effectively eliminated; i.e. net growth rate in those bottles was assumed to be equivalent to the intrinsic growth rate (μ) of the phytoplankton (see below). Using these two treatments, microzooplankton grazing rates (g, d^{-1}) were calculated from $g = \mu - k$. Estimates of g were occasionally negative (10 of 72 determinations). In most cases, these negative values did not differ significantly from zero. However, four determinations of grazing on the 5–20-μm size class were significantly negative. This may have resulted from variations in the efficiency with which cells were captured by the different filter membranes during the chlorophyll size fractionation process (note that this will not affect rate estimates based on total chlorophyll). Measured g values are reported in Table 2; however, subsequent analyses equate all negative estimates of g to zero.

Ratios of g:μ were computed to assess the grazing of microzooplankton as a fraction of phytoplankton production. For calculation of mean g:μ, ratios were arctan-transformed to minimize the effect of extreme values (Calbet and Landry, 2004).

The assumption that net growth rates in 5% dilution treatments provide a robust estimate of intrinsic growth rates was verified by comparing two different estimates of μ: one derived from the y-intercept of a linear regression analysis of full dilution series, the other derived from net growth rates in 5% treatments from the same dilution series. An analysis of 39 experiments conducted in the coastal Gulf of Alaska showed that the two approaches gave the same growth rate estimates (Strom et al., 2006). We conducted the same comparison with data from the eight full dilution experiments conducted in the present study (Table 3). Grazing rate estimates from the two methods were indistinguishable for all phytoplankton size classes; growth rate estimates were indistinguishable except for the 5–20 μm size class. In that case, a paired t-test showed a significant difference between the two sets of growth rates ($p = 0.03$). The offset, however, was slight, with growth rate averages from the two methods differing by only 0.03 d^{-1}.

Water for dilution experiments was collected from depths varying from 2.5 to 7 m, which corresponded to 50% surface irradiance. All collection depths were in the surface mixed layer. Water was gently siphoned from multiple Niskin bottles closed at a single depth and pooled into two 25-L polycarbonate carboys. To exclude macrozooplankton, one carboy (for wsw) was prescreened during filling from the Niskins with 200-μm Nitex mesh attached to the ends of the drain tubes. The other (unscreened) carboy was subsequently gravity-filtered through a 0.2-μm Gelman® pleated capsule filter to produce particle-free seawater (fsw) that was used as the diluent for the dilution series. For the full dilution series experiments, predetermined amounts of fsw were added to incubation bottles, then wsw was gently siphoned in to fill bottles completely. A separate 10-L carboy was used to make 5% wsw for both types of experiments: gentle siphoning was used to add a predetermined mixture of whole and filtered seawater to the carboy. Both full and 2-point dilution series had

Table 2
Phytoplankton growth and microzooplankton grazing rates (d^{-1}) for three chlorophyll size fractions and total chlorophyll, from seawater dilution experiments

Region	Station	Unenriched growth rates				NH_4^+ enriched growth rates				Grazing rates			
		>20 μm	5–20 μm	<5 μm	Total	>20 μm	5–20 μm	<5 μm	Total	>20 μm	5–20 μm	<5 μm	Total
Slope	SES-1	0.57 (0.02)	0.12 (0.05)	0.23 (0.09)	0.25 (0.02)	1.28* (0.10)	0.62* (0.07)	0.47* (0.10)	0.70* (0.08)	0.25 (0.05)	0.22 (0.05)	0.12 (0.03)	0.14 (0.03)
	GC-13	0.75 (0.05)	0.19 (0.09)	0.08 (0.01)	0.59 (0.05)	1.27* (0.05)	0.75* (0.14)	0.46* (0.12)	1.10* (0.03)	0.27 (0.03)	0.27 (0.01)	0.17 (0.03)	0.25 (0.02)
	GB-9	1.20 (0.01)	0.59 (0.14)	0.48 (0.17)	1.00 (0.02)	1.26 (0.05)	0.79 (0.14)	0.51 (0.18)	1.07 (0.03)	0.31 (0.01)	0.35 (0.13)	0.15 (0.08)	0.27 (0.01)
	SES-1	0.16 (0.05)	−0.04 (0.08)	0.19 (0.02)	0.14 (0.04)	0.98* (0.01)	0.48* (0.06)	0.54* (0.04)	0.82* (0.02)	0.28 (0.09)	0.17 (0.06)	0.32 (0.05)	0.27 (0.08)
Mooring 2	M2	0.11 (0.11)	−0.11 (0.14)	0.19 (0.04)	0.13 (0.06)	0.42 (0.19)	0.24* (0.10)	0.71* (0.03)	0.59* (0.03)	−0.06 (0.06)	−0.03 (0.04)	0.22 (0.01)	0.14 (0.02)
	M2	0.03 (0.09)	−0.23 (0.01)	0.23 (0.00)	0.13 (0.01)	0.34* (0.11)	0.12* (0.03)	0.58* (0.07)	0.47* (0.05)	0.07 (0.05)	−0.22 (0.09)	0.14 (0.01)	0.07 (0.03)
	M2	0.31 (0.17)	0.25 (0.03)	0.44 (0.11)	0.40 (0.07)	0.31 (0.10)	0.44* (0.03)	0.70* (0.03)	0.62* (0.03)	0.06 (0.03)	0.08 (0.05)	0.21 (0.07)	0.18 (0.06)
Between Islands	PG-5	0.62 (0.08)	0.05 (0.11)	0.27 (0.13)	0.51 (0.04)	0.89* (0.05)	0.37* (0.01)	0.37 (0.08)	0.76* (0.03)	0.16 (0.03)	−0.25 (0.18)	0.00 (0.08)	0.09 (0.01)
	CE-3	0.48 (0.06)	0.52 (0.11)	0.47 (0.12)	0.48 (0.03)	0.63* (0.05)	0.33 (0.18)	0.26 (0.13)	0.56* (0.02)	0.11 (0.03)	0.03 (0.19)	0.19 (0.09)	0.10 (0.05)
	SL-9	0.07 (0.03)	−0.18 (0.01)	−0.08 (0.18)	0.00 (0.02)	0.64* (0.07)	0.20* (0.10)	0.33 (0.02)	0.51* (0.03)	0.12 (0.00)	0.07 (0.14)	0.16 (0.02)	0.09 (0.01)
	PG-5	0.33 (0.07)	−0.16 (0.09)	0.26 (0.01)	0.24 (0.03)	1.15* (0.08)	0.25* (0.03)	0.49* (0.07)	0.91* (0.05)	0.13 (0.05)	−0.29 (0.16)	0.19 (0.04)	0.06 (0.05)
100 m Isobath	GD-5	1.14 (0.02)	0.20 (0.06)	0.53 (0.01)	0.76 (0.02)	1.17 (0.04)	0.31 (0.05)	0.58 (0.10)	0.80 (0.05)	0.07 (0.04)	0.08 (0.10)	0.16 (0.05)	0.02 (0.03)
	CW-6	0.02 (0.08)	0.05 (0.08)	0.18 (0.02)	0.08 (0.03)	0.58* (0.05)	0.34 (0.10)	0.32 (0.06)	0.46* (0.03)	0.24 (0.06)	0.26 (0.02)	0.38 (0.02)	0.27 (0.03)
	GA-100	0.46 (0.05)	0.22 (0.06)	0.41 (0.03)	0.39 (0.04)	1.01* (0.07)	0.37* (0.06)	0.65* (0.14)	0.70* (0.08)	−0.01 (0.05)	−0.02 (0.14)	0.12 (0.08)	0.01 (0.07)
	GA-8	0.48 (0.05)	0.43 (0.09)	0.44 (0.04)	0.45 (0.04)	0.57 (0.06)	0.49 (0.11)	0.61* (0.03)	0.57* (0.05)	0.17 (0.16)	0.15 (0.07)	0.16 (0.03)	0.16 (0.03)
N & W of Islands	PC-10	0.63 (0.12)	0.24 (0.16)	0.22 (0.04)	0.52 (0.09)	0.83* (0.03)	0.46 (0.36)	0.34 (0.09)	0.71* (0.03)	0.12 (0.05)	0.16 (0.00)	0.12 (0.03)	0.10 (0.04)
	PD-12	0.32 (0.01)	−0.34 (0.14)	−0.20 (0.07)	0.13 (0.02)	1.06* (0.05)	0.13* (0.02)	0.08* (0.03)	0.79* (0.04)	0.15 (0.03)	−0.34 (0.09)	−0.11 (0.01)	0.00 (0.03)
	PB-13	0.32 (0.18)	0.01 (0.00)	0.06 (0.01)	0.06 (0.02)	0.58 (0.11)	0.20* (0.05)	0.27* (0.05)	0.27* (0.04)	−0.02 (0.10)	0.09 (0.09)	0.30 (0.01)	0.18 (0.01)

Values in parentheses: 1 s.d. * denotes significant difference between enriched and unenriched growth rates (t-test, $\alpha = 0.05$).

Table 3
Comparison of estimates of phytoplankton growth and microzooplankton grazing rates derived from two different analysis methods

Rate	r^2	Slope	Intercept	p-Value
Growth				
>20 μm	0.947	1.02 (0.78, 1.26)	−0.01	0.82
5–20 μm	0.972	0.95 (0.76, 1.13)	0.06	0.03
<5 μm	0.951	0.93 (0.72, 1.14)	0.06	0.10
Total	0.957	1.15 (0.90, 1.39)	−0.08	0.29
Grazing				
>20 μm	0.935	1.28 (0.95, 1.62)	0.00	0.10
5–20 μm	0.972	0.98 (0.79, 1.17)	−0.02	0.29
<5 μm	0.908	1.10 (0.75, 1.45)	0.02	0.11
Total	0.919	1.26 (0.88, 1.63)	0.00	0.18

Data are shown for three phytoplankton size classes and for total phytoplankton, from eight experiments conducted in summer 2004. Rates from regression analysis of full dilution series were compared with those from 2-point analysis of the same experiments (see Section 2 for details). Tabulated values are correlation coefficients (r^2), slopes of the relationships between the two sets of rate estimates (with 95% confidence limits), y-intercepts of the relationships, and p values from paired two-way t-test comparisons. No slope values differed significantly from 1. Only 5–20 μm growth rate estimates were significantly different between the two methods ($p = 0.03$) as shown by t-test results; average 5–20 μm growth rates over the eight experiments were 0.41 d^{-1} (regression) and 0.38 d^{-1} (2-point).

three nutrient treatments: triplicate 100% and 5% bottles without nutrient addition, triplicate 100% and 5% bottles enriched with ammonium and phosphate (5 μM as NH_4Cl and 0.3 μM as Na_2HPO_4, respectively), and triplicate 100% and 5% bottles enriched with nitrate and phosphate (5 μM as $NaNO_3$ and 0.3 μM as Na_2HPO_4, respectively). Bottles at intermediate dilution levels in full dilution series were enriched with ammonium and phosphate. Experimental bottles were enclosed in one layer of neutral density screen, which simulated the light level at collection depth. Bottles were incubated for 24 h in on-deck flow-through seawater chambers.

During experiment setup, initial samples were taken from the wsw and 5% wsw carboys to determine concentrations of size-fractionated chlorophyll (in triplicate) and nutrients [ammonium, nitrate, nitrite, silicic acid and phosphate; see Mordy et al. (2008) and Sullivan et al. (2008) for details]. For some experiments, additional nutrient-spiked bottles (not incubated) were prepared and sampled to verify nutrient addition levels. Addition levels averaged 0.28 μM for phosphate, 5.02 μM for nitrate, and 4.84 μM for ammonium. The wsw carboy also was sampled in duplicate for microzooplankton identification and enumeration. After 24 h incubation, final samples were taken from each incubation bottle for size-fractionated chlorophyll, and from all nine 100% wsw bottles for nutrient analysis. Final nitrate or ammonium levels were >1.3 μM in enriched bottles in all experiments but one (GC-13, final nitrate 0.37 μM, final ammonium 0.67 μM).

2.3. Phyto- and microzooplankton identification and enumeration

Using inverted microscopy, larger microzooplankton were identified and counted from seawater samples preserved in amber glass bottles containing 10% acid Lugol's solution (final concentration). Epifluorescence microscopy was used for identification and enumeration of heterotrophic flagellates <20 μm; these samples were preserved in a final concentration of 0.5% glutaraldehyde and approx. 0.2 μg mL^{-1} DAPI stain. Glutaraldehyde-preserved samples were stored at 4 °C in the dark for 11–24 h, then filtered (0.8-μm pore-size polycarbonate filter, 1.0-μm pore-size MCE backing filter) and slide-mounted. Slides were stored frozen and transported back to a shore laboratory for analysis.

All ciliates regardless of size and all other microzooplankton >20 μm in largest dimension were enumerated and categorized from settled volumes of 3.6–50 mL of Lugol's-preserved sample, depending on microzooplankton density. Samples greater than 10 mL were preconcentrated by settling in a graduated cylinder. Inverted microscopy combined with a computer digitizing system was used to identify and measure individual microzooplankton and to convert linear dimensions to cell volumes (Roff and Hopcroft, 1986). Note that auto- and heterotrophic dinoflagellates cannot be distinguished in Lugol's-fixed samples, so all >20 μm dinoflagellates are included in our microzooplankton abundance and biomass estimates. Many if not most autotrophic dinoflagellates can feed (e.g., Jeong et al., 2005). Heterotrophic flagellates (including dinoflagellates) <20 μm were identified under blue and UV excitation using epifluorescence microscopy. Identification was based on morphology, nuclear characteristics, and lack of chlorophyll autofluorescence. An ocular grid was used to place flagellates in size classes. Cell volumes were estimated using standard geometric formulae; cell C content was then estimated from cell volume using the empirical relationships of Putt and Stoecker (1989) for ciliates, Menden-Deuer and Lessard (2000) for dinoflagellates, and Verity et al. (1992) for heterotrophic nanoflagellates. *Pseudo-nitzschia* spp. diatoms were identified based on morphological features (Hasle et al., 1996) as seen using scanning electron microscopy (SEM). SEM samples were prepared using a combination of methods in Miller and Scholin (1998) and Trainer et al. (2000). *Pseudo-nitzschia* spp. cells were enumerated from acid Lugol's-preserved samples using inverted microscopy (volume examined approx. 0.3 mL per sample).

Microzooplankton biomass-specific grazing rates (G_{MZ}) for feeding on phytoplankton were calculated for each experiment from chlorophyll-specific grazing rates (g), chlorophyll concentrations (Chl) and microzooplankton biomass (MZ) according to

$$G_{MZ} = ((g_{<5}\mathrm{Chl}_{<5}\mathrm{C} : \mathrm{Chl}_{<5}) + (g_{5-20}\mathrm{Chl}_{5-20}\mathrm{C} : \mathrm{Chl}_{5-20}) + (g_{>20}\mathrm{Chl}_{>20}\mathrm{C} : \mathrm{Chl}_{>20}))/MZ.$$

Carbon:chlorophyll (C:Chl) ratios were not measured during our program; rather, two different sets of assumed ratios were used to calculate G_{MZ}. Based on summer measurements in the coastal Gulf of Alaska (E. Lessard, personal communication), we first assumed a C:Chl of 65 for phytoplankton <20 μm, and 25 for phytoplankton >20 μm. Second, we assumed that strong N limitation might have led to elevated C:Chl ratios (Goldman, 1980). Occasional values >200 have been observed in high-latitude ecosystems (Booth and Smith, 1997); in one Antarctic study (Garibotti et al., 2003), the highest C:Chl values were associated with low phytoplankton growth rates and low chlorophyll levels. Based on these studies, we assigned a C:Chl ratio of 150 to the entire phytoplankton community in experiments exhibiting strong N limitation. Strong N limitation, observed in 12 of 18 experiments, was defined as a whole-community growth rate increase of >0.2 d^{-1} in response to N+P addition (Table 2). For the other six experiments, we assumed a C:Chl of 50 for the entire phytoplankton community.

3. Results

3.1. Phytoplankton community

The region around the Pribilof Islands supported a mosaic of phytoplankton biomass levels and community types during summer 2004 (Fig. 2; see also Sambrotto et al., 2008). Initial chlorophyll levels during our experiments ranged from 0.23 to 3.34 μg L^{-1} (Table 1), and integrated chlorophyll at experiment stations ranged from 13 to 202 mg m^{-2}. Highest integrated

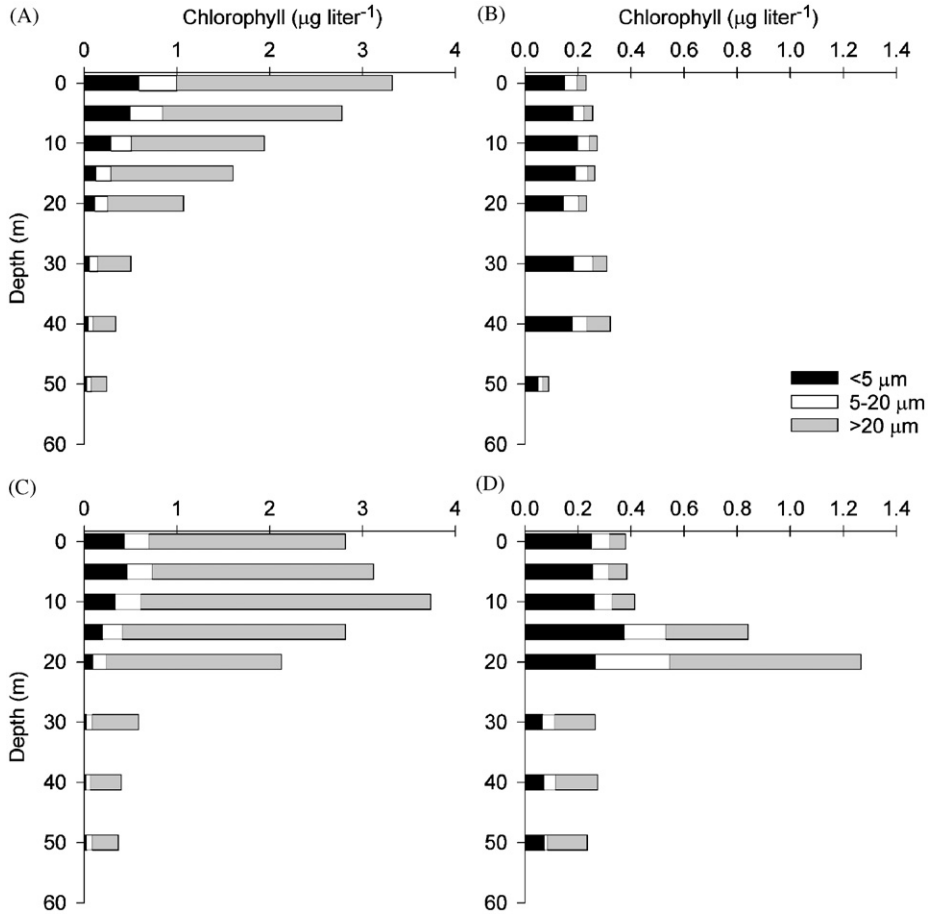

Fig. 2. Vertical profiles of chlorophyll concentration (total) as partitioned into three size fractions (<5, 5–20, and >20 μm) at stations in four different study regions. (A) GB-9; (B) GA-8; (C) PG-5; (D) M2.

chlorophyll levels were found between the islands (Fig. 3), in a 'green patch' that was visible on SeaWiFS ocean-color images at least several weeks before our study began, and persisted throughout the cruise period (Stabeno et al., 2008). Elevated chlorophyll levels were also observed on the slope (Fig. 3). A subsurface chlorophyll maximum was commonly observed (11 out of 18 stations, see Fig. 2C,D), as would be expected given the strong thermal stratification and low mixed-layer nutrient levels over much of the region (Whitledge et al., 1986; Sullivan et al., 2008). High chlorophyll levels were typically associated with large-cell-dominated phytoplankton communities, and low chlorophyll levels with small cell dominance (Fig. 3). However, small cells made substantial contributions to elevated surface chlorophyll levels at stations SES-1 (when first sampled) and GD-5 (Table 1). Most stations showed a consistent chlorophyll size distribution with depth. However, the highly stratified mid-shelf station M2 showed a transition from a surface community dominated by the smallest size class to a subsurface maximum dominated by the largest (Fig. 2D).

While we did not taxonomically characterize the phytoplankton community, we did note that *Pseudo-nitzschia* spp. diatoms were abundant at many of the stations with high chlorophyll levels. Light microscopy followed by SEM analysis showed that two cell types were present, a large cell identified as *P. seriata*, and a smaller cell consistent in frustule morphology with the *P. delicatissima* complex (Lundholm et al., 2006). *Pseudo-nitzschia* spp. abundances ranged from undetectable to $>1\times10^6$ cells L^{-1} at some slope stations (Table 4).

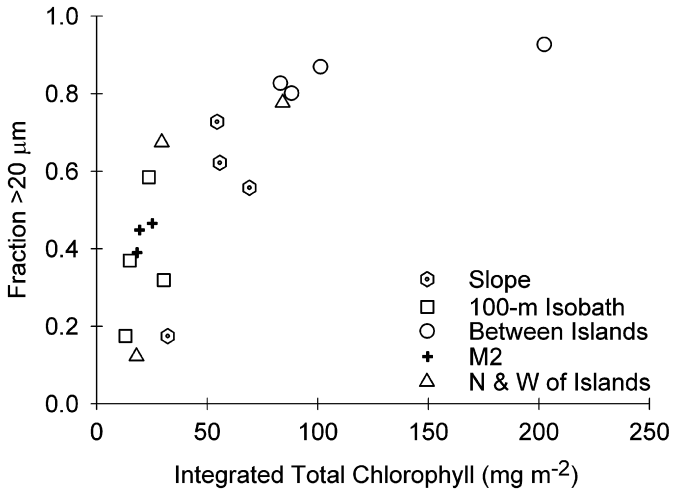

Fig. 3. Integrated chlorophyll (total) versus the fraction of total chlorophyll in cells >20 μm. Data shown for stations in the five study regions.

3.2. Phytoplankton growth rates and nutrient limitation

Phytoplankton intrinsic growth rates varied widely depending on sampling date and location. Unenriched rates based on total chlorophyll (representative of the whole phytoplankton community) ranged from 0.00 to 1.00 d^{-1}, and averaged 0.35 d^{-1} (Table 2).

Table 4
Abundance and distribution of *Pseudo-nitzschia* spp. cells during July–August 2004 in the study region

Region	Station	Date	*Pseudo-nitzschia* ($\times 10^3$ L^{-1})	
			seriata	cf. *delicatissima*
Slope	SES-1	27 July	0	67
	GC-13	28 July	852	417
	GB-9	29 July	638	436
	SES-1	30 July	44	120
M2	M2	8 August	0	7
	M2	9 August	0	3
	M2	10 August	0	14
Between Islands	PG-5	1 August	0	790
	CE-3	4 August	26	304
	SL-9	5 August	7	274
	PG-5	11 August	7	0
	PG-5	11 August	4	4
100-m Isobath	GD-5	31 July	0	732
	CW-6	3 August	0	291
	GA-100	6 August	0	0
	GA-8	11 August	0	11
N&W of Islands	PC-10	16 August	0	51
	PD-12	17 August	19	426
	PB-13	17 August	0	15

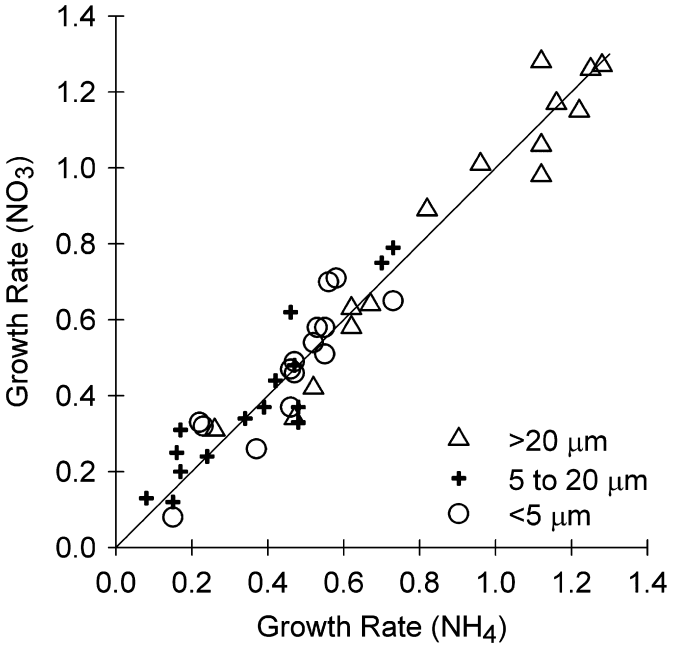

Fig. 4. Phytoplankton growth rates (d^{-1}) in three chlorophyll size fractions in incubations with nitrate versus ammonium as the added N source for growth. Line shows 1:1 relationship.

The largest cells (>20 μm) grew at higher rates than cells in either of the smaller size fractions (one-way anova, $p = 0.002$). Unenriched rates for the >20, 5–20, and <5-μm size fractions averaged 0.44, 0.10, and 0.24 d^{-1}, respectively. Nutrient limitation played a major role in the summer 2004 ecosystem. Growth rates increased in response to nutrient addition in all but two experiments, and whole-community rate increases were >0.2 d^{-1} in most cases (Table 2). As for the unenriched rates, the largest cells grew at the highest rates when enriched (one-way anova, $p < 0.001$). Nutrient-enriched growth rates for the >20, 5–20, and <5-μm size fractions averaged 0.83, 0.38, and 0.46 d^{-1}, respectively.

Our experiments explicitly compared the effect of added nitrate versus ammonium on phytoplankton intrinsic growth rate. No effect of N source was found (Fig. 4): rates of growth on nitrate+phosphate were the same as rates on ammonium+phosphate whether individual size fractions or total chlorophyll-based rates were considered (paired *t*-test, $n = 15$ pairs for each size fraction, all p values >0.30). Because ammonium additions were done in all 18 experiments, analyses of enriched growth rates throughout the remainder of the paper are based on data from ammonium enrichments.

The highest unenriched phytoplankton growth rates were measured on the slope and at station GD-5 on the 100-m isobath (Table 2, Fig. 5A). Unenriched rates exceeding 0.50 d^{-1} were occasionally observed elsewhere, but never at mid-shelf station M2. Slope phytoplankton also showed the highest growth rates in response to nutrient addition (Fig. 5A). The two stations showing no nutrient limitation of phytoplankton growth (GB-9 and GD-5) were both associated with Pribilof Canyon and associated transport of nutrients onto the slope and outer shelf.

Drifter studies before and during our cruise demonstrated persistent, strong flow from east to west along the 100-m isobath (Stabeno et al., 2008; Sullivan et al., 2008). To determine the effects of outer shelf physical processes on lower trophic levels, we sampled a series of stations along the 100-m isobath. Stations bracketed Pribilof Canyon (crosses, Fig. 1). Natural nutrient injections along this transect yielded responses similar to those seen in our nutrient-enriched experimental treatments. Elevated nitrate levels just west of the canyon (GD-5, Table 1) were associated with a diatom bloom (Table 4), a spike in intrinsic growth rate, and a reduction (to near zero) in the degree of nutrient limitation (Fig. 6A). Further west at station CW-6, nitrate levels were again very low, intrinsic growth rates were near zero, and the phytoplankton community was nutrient-limited, although the signature of the nutrient injection remained in the form of a high phytoplankton biomass. The microzooplankton community showed a classic successional response to the natural enrichment event, responding to the phytoplankton bloom with an increase in both biomass and grazing activity (Fig. 6B).

3.3. Microzooplankton community

Microzooplankton biomass ranged from 11.2 to 118.1 μg C L^{-1} and was positively related to total chlorophyll concentration (Fig. 7), so that highest biomass levels were found in phytoplankton bloom locations such as between the islands, station CW-6 on the 100-m isobath, and several of the slope stations (Fig. 8). Biomass in bloom locations was surprisingly high given the generally low microzooplankton grazing rates. In contrast, uniformly low microzooplankton biomass (<15 μg C L^{-1}) was observed at M2. In terms of community composition, heterotrophic nanoflagellates were most abundant on the slope and at two of the three stations north and west of St. Paul Is (Fig. 8A, C). Ciliates—mainly naked spirotrichs—and dinoflagellates—mainly aloricate *Gymnodinium* and *Gyrodinium* spp.—comprised most of the microzooplankton biomass. The largest ciliates and dinoflagellates (those >40 μm) were most abundant at bloom station CW-6 and at stations between the islands. In contrast, communities at slope bloom stations had a lower abundance of large microzooplankton (Fig. 8). Throughout the region, dinoflagellates were greater contributors to microzooplankton biomass than ciliates, with the ratio of dinoflagellate to ciliate biomass ranging from 0.95 to 4.17 (average 2.30).

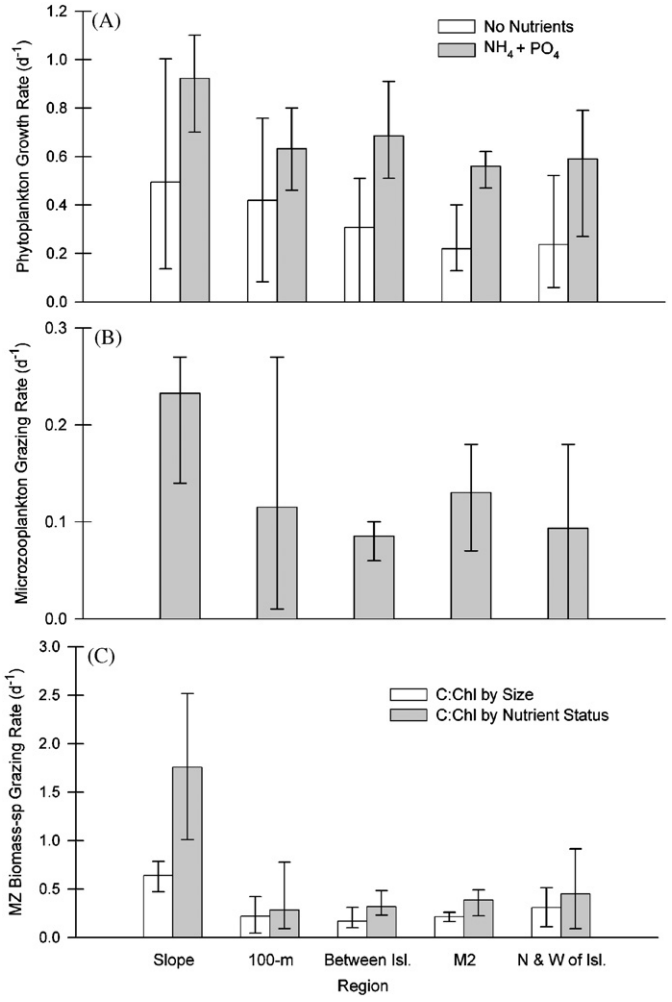

Fig. 5. Average rates of (A) phytoplankton growth (with and without added nutrients), (B) microzooplankton grazing, and (C) microzooplankton biomass-specific grazing (G_{MZ}) for different study regions. C:Chl by size: assumed ratio for phytoplankton $<20\,\mu m = 65$; for phytoplankton $>20\,\mu m = 25$. C:Chl by nutrient status: assumed ratio for nutrient-limited communities = 150; for non-limited communities = 50. Bars show range of data.

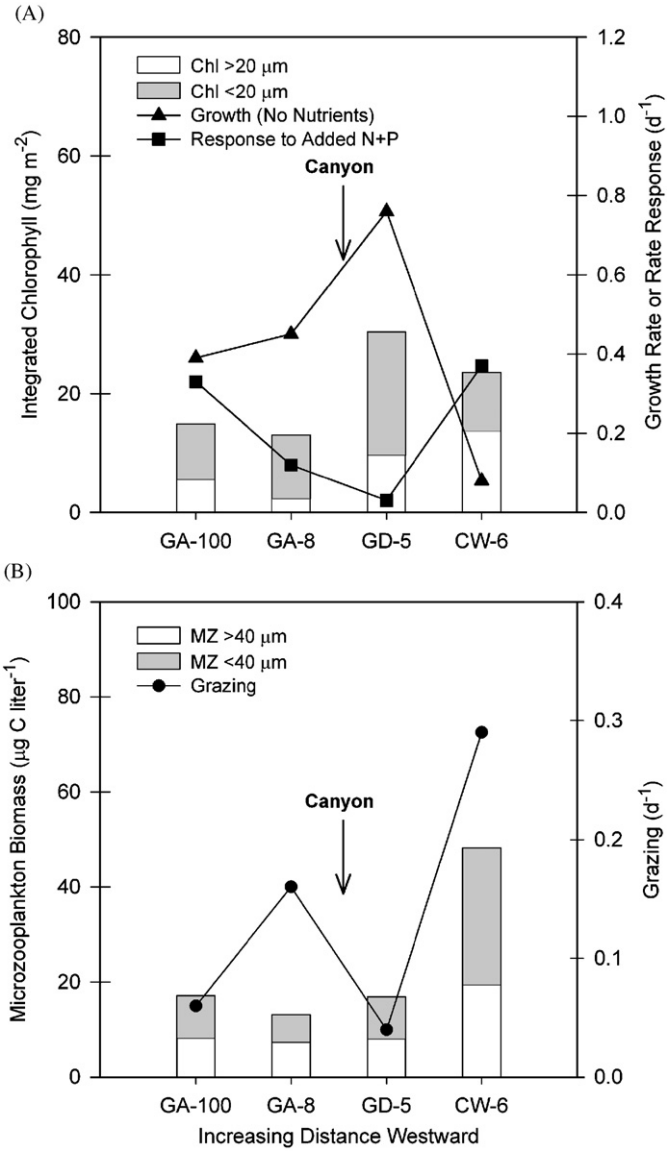

Fig. 6. Effects of nutrient inputs via Pribilof Canyon on lower trophic level communities along the 100-m isobath. Stations arranged from east to west along the *x*-axis, corresponding to mean flow direction during the study. (A) Phytoplankton stocks and processes, including water column chlorophyll content in small and large size fractions (bars), phytoplankton growth rates (triangles), and the growth rate response (= rate increase) in response to added N+P (squares). (B) Microzooplankton stocks and processes, including upper mixed-layer biomass in small and large size classes (bars), and rates of grazing on phytoplankton (circles).

3.4. Microzooplankton grazing on phytoplankton

Grazing rates were low across the entire summer 2004 ecosystem, ranging from 0.00 to 0.27 d^{-1} and averaging 0.13 d^{-1} (Table 2). Unlike phytoplankton growth, microzooplankton grazing rates did not vary with phytoplankton size class (one-way anova, $p = 0.16$). Rates of grazing on >20, 5–20, and <5-μm chlorophyll size fractions averaged 0.14, 0.11, and 0.17 d^{-1}, respectively. Only on the slope (3 out of 4 stations) and at station CW-6 on the 100-m isobath did we observe grazing rates $>0.2\,d^{-1}$ (Fig. 5B).

The ratio of grazing to growth is a measure of the fraction of primary production consumed by microzooplankton. We compared grazing with unenriched growth as the best measure of the relationship between the two processes in the 2004 Pribilof environment. Based on total chlorophyll, the grazing: growth ratio averaged 0.49 for the entire study. For specific chlorophyll size fractions, an average ratio of 0.65 was observed for the <5-μm phytoplankton, whilst lower ratios of 0.47 and 0.46 characterized the 5–20 and >20-μm size fractions. Grazing rates were more strongly correlated with growth rates in enriched bottles (from which they were derived) than in unenriched bottles. The only significant correlation with unenriched growth rates was in the 5–20-μm size fraction (linear regression, $r^2 = 0.24$, $p = 0.03$). For enriched growth rates, grazing was even more strongly related to growth in this intermediate size fraction ($r^2 = 0.66$, $p < 0.01$) and was also positively related for the >20-μm size fraction ($r^2 = 0.29$, $p = 0.02$). No relationship between growth and grazing was ever observed for the smallest ($<5\,\mu m$) size class.

We computed the microzooplankton biomass-specific grazing rate G_{MZ}, a measure of the activity level of individuals in the community, for feeding on phytoplankton. G_{MZ} values were low at most stations regardless of the assumed C:Chl ratio (Fig. 5C). The low values illustrate that the depressed community grazing rates we measured were due, at least in part, to reduced per capita feeding rates on phytoplankton. G_{MZ} was consistently higher on the slope than elsewhere (average = 0.6 d^{-1} with C:Chl based

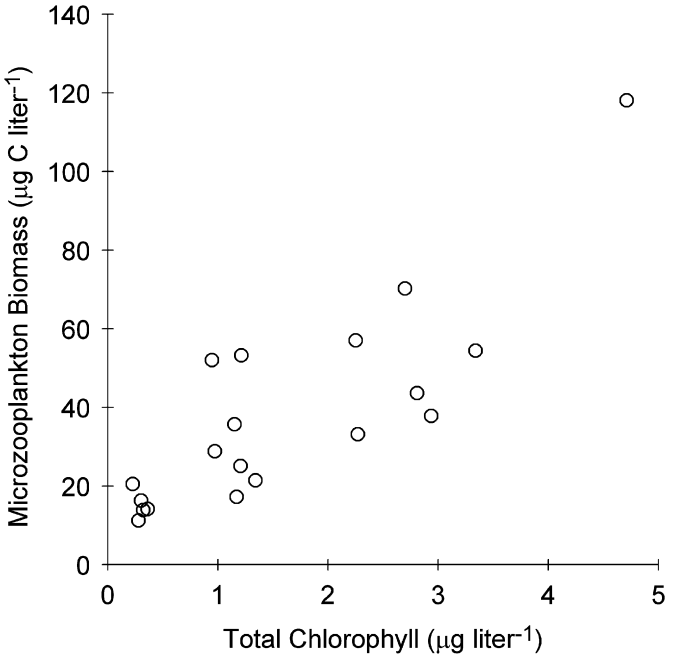

Fig. 7. Microzooplankton biomass (MZ, $\mu g\,C\,L^{-1}$) as a function of total chlorophyll concentration (CHL, $\mu g\,L^{-1}$) for all experimental stations. MZ = 17.3(CHL)+10.2; $r^2 = 0.69$; $p < 0.001$.

on phytoplankton size; average = $1.8\,d^{-1}$ with C:Chl based on phytoplankton nutrient status, Fig. 5C). Assuming a gross growth efficiency of 0.33 (Straile, 1997), and further assuming that microzooplankton feed only on phytoplankton (see discussion), the study-wide average G_{MZ} of $0.30\,d^{-1}$. This yields a very long community-average doubling time for microzooplankton of 1/0.30/0.33 = 10.1 d. This general conclusion is relatively insensitive to the assumed phytoplankton C:Chl ratio. Assuming a C:Chl ratio of 150 for nutrient-limited phytoplankton communities yields an average G_{MZ} of $0.66\,d^{-1}$, and a still lengthy microzooplankton community doubling time of 4.6 d.

4. Discussion

4.1. Phytoplankton growth rates: nutrient limitation and local mixing effects

Phytoplankton growth rates in the SE Bering averaged $0.35\,d^{-1}$ from late July to mid-August 2004. This value (equal to 0.5 doublings per d) is ~3× lower than the maximum (resource-saturated) rate of $1.1–1.3\,d^{-1}$ predicted by Eppley (1972) for temperatures of 10–13 °C. Nutrient limitation was the major factor causing relatively low growth rates during our study. Enrichment with N+P caused growth rates to increase to an average of $0.69\,d^{-1}$ (1.0 doublings per d), and was especially stimulatory to the largest phytoplankton cells, which sometimes reached the maximum

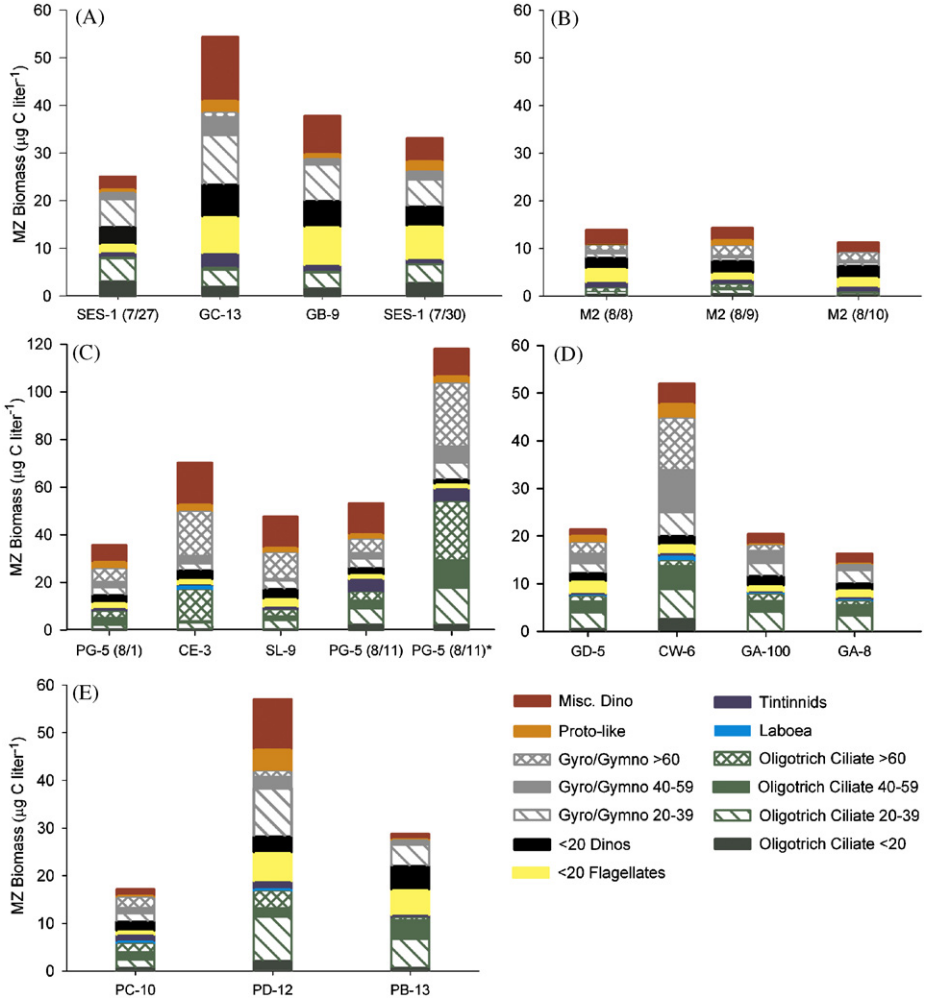

Fig. 8. Biomass of microzooplankton at experimental stations in five regions: (A) slope; (B) M2; (C) between the islands; (D) along the 100-m isobath; and (E) north and west of the islands. Biomass partitioned into taxonomic and size categories. Note *y*-axis scale difference in panel C. *: this sample was not associated with an experiment.

Table 5
Comparison of phytoplankton growth and microzooplankton grazing rates (d^{-1}, from seawater dilution technique based on total chlorophyll) and microzooplankton (MZ) biomass levels ($\mu g\,C\,L^{-1}$) among summer Bering Sea and subarctic Pacific studies

Location	Date	Growth	Grazing	MZ (all)	MZ (>20 μm)	Ref.
SE Bering	July–August 2004	0.00–1.00 **0.35** ($n=18$)	0.00–0.27 **0.13** ($n=18$)	11.2–118.1 **38.1** ($n=19$)	6.2–111.3 **30.0** ($n=19$)	1
SE Bering/WSG/ESG	June–July 1999	−0.30–0.50 **0.27** ($n=11$)	0.08–0.57 **0.26** ($n=11$)	nd	nd	2
SE Bering	July–August 1999	−0.07–0.60 **0.33** ($n=13$)	0.06–0.54 **0.29** ($n=13$)	nd	18.4–164.0 **56.8** ($n=13$)	3
CGOA	July 2001	−0.08–0.69 **0.28** ($n=9$)	0.14–0.54 **0.27** ($n=9$)	28.7–94.1 **48.1** ($n=9$)	9.7–70.5 **31.0** ($n=9$)	4
ESG	June, September 1987	0.24–0.67 **0.38** ($n=8$)	0.05–0.31 **0.16** ($n=8$)	nd	nd	5
ESG	June 1987	−0.05–0.72 **0.34** ($n=8$)	0.12–0.68 **0.33** ($n=8$)	nd	nd	6
ESG	August 1988	0.26–0.69 **0.55** ($n=13$)	0.04–0.38 **0.23** ($n=13$)	nd	nd	6

Upper water column observations only (>30% surface irradiance). Range and average (in bold) shown, with number of observations in parentheses. WSG: western subarctic gyre; ESG: eastern subarctic gyre; CGOA: coastal Gulf of Alaska
References: 1, this study; 2, Liu et al. (2002); 3, Olson and Strom (2002) (excluding four stations in nearshore waters north of the Aleutian Islands); 4, Strom et al. (2006, 2007); 5, Strom and Welschmeyer (1991); 6, Landry et al. (1993).

resource-saturated rates predicted by the Eppley data summary (Table 2). All size classes, however, showed a substantial response to nutrient addition. Nitrogen was most likely the proximate limiting nutrient during summer 2004. Inorganic N:P ratios in the surface mixed layer (from our initial samples, Table 1) ranged from 0.13 to 9.74, excluding a single sample with very low P levels (M2, 8 August). These ratios were mainly well below the Redfield ratio of 16, indicating an excess of P relative to N at least in terms of inorganic nutrients in the environment. Similarly, N:P utilization ratios (i.e. ΔNO_3+NH_4)/ΔPO_4 during the incubations) in our nutrient-enriched bottles were nearly all >16 (average 18.5, range 10.5–31.6, $n=44$).

Disruption of the intense summer stratification by mixing events introduced enough nutrients into the surface layer to stimulate high phytoplankton growth rates in a few locations. For example, flow up Pribilof Canyon delivered high-nutrient water to the region around station GB-9 (Stabeno et al., 2008), where we observed no nutrient limitation and a whole-community growth rate of $1.00\,d^{-1}$. Persistent westward flow along the 100-m isobath, as observed with drifters before and during our study (Stabeno et al., 2008), carried the high-nutrient water to the west. A bloom sequence corresponding to this nutrient injection was observed along our sampling trajectory from station GA-100 to CW-6 (Fig. 6), with a growth rate of $0.76\,d^{-1}$ measured at GD-5 just west of the canyon. Elevated primary and new production rates were also measured west of the Pribilofs along the 100-m isobath during this study by Sambrotto et al. (2008).

Moderate growth rates, above the regional average, were sometimes but not always observed in the high-chlorophyll waters between the islands (Fig. 5A). The nutrients fueling this persistent bloom came from both the east (deep middle shelf water) and the southwest (slope water advected up Pribilof Canyon and along the 100-m isobath). This nutrient-rich water was mixed to the surface by a combination of tides and winds in the shallow area between the islands (Stabeno et al., 2008). Persistent high chlorophyll in shallow waters around the islands (Sambrotto et al., 2008) likely resulted from tidal mixing and nutrient injection, although we have no growth rate data from the tidally mixed area. In general, flow–topography interactions that mix nutrients into surface waters were important to summer 2004 production near the Pribilofs. This predictable source of summer production is almost certainly an important aspect of the habitat for marine birds and mammals, abundant around the islands. For example, high densities of murres (Kokubun et al., 2008) were found around many of the high chlorophyll, high productivity features described above, including the tidally generated front near the islands, the northern edge of Pribilof Canyon, and the shelf break front (see below).

4.2. Microzooplankton grazing rates: chronically low

Phytoplankton growth rates, while low relative to potential physiological maxima, were typical of summer rates previously observed in the Bering Sea, open subarctic Pacific, and coastal Gulf of Alaska (Table 5). The comparison between our 2004 and the 1999 Bering Sea rates is explored below. Elsewhere, limitation by either macronutrients (N—as in our study) or micronutrients (Fe) is known to affect phytoplankton growth rates and production either seasonally or chronically across much of the subarctic (Harrison et al., 1999; Whitney et al., 2005). In contrast to phytoplankton growth, 2004 microzooplankton grazing rates in the Bering were anomalously low. Our study-wide average of $0.13\,d^{-1}$ was 2–3 × lower than summer averages from the Bering Sea in 1999, the western and eastern subarctic gyres, and the coastal Gulf of Alaska (Table 5).

As for phytoplankton growth, grazing rates increased in response to natural nutrient enrichment and consequent phytoplankton growth increases. Productivity 'hot spots' including the slope and the region northwest ('downstream') of Pribilof Canyon on the 100-m isobath sustained the highest microzooplankton grazing. Even in these regions, though, the rates we measured were modest, 2–3 × lower than the maxima observed in other comparable studies (Table 5). Furthermore, rates in the high-chlorophyll region between the islands were some of the lowest we measured anywhere.

Low microzooplankton biomass did not explain low community grazing rates. Our biomass estimates ranged from 11 to $118\,\mu g\,C\,L^{-1}$, and averaged $38\,\mu g\,C\,L^{-1}$. We did observe low biomass ($11–20\,\mu g\,C\,L^{-1}$) at M2 and east of the islands on the 100-m isobath, all in highly stratified, low-chlorophyll waters. These levels are similar to those reported by Booth et al. (1993) for iron-limited, low-chlorophyll waters of the eastern subarctic Pacific. Elsewhere in our study area, however, microzooplankton biomass during summer 2004 was quite high (Fig. 8), approximating that found in the summer coastal Gulf of Alaska, where grazing rates averaged 2 × higher (Table 5). (Note that our microzooplankton samples were taken from 200-μm-screened seawater, indicating that prescreening to exclude macrozooplankton did not cause large losses of protist grazers.) Given the relatively high biomass and the low grazing rates, clearly the microzooplankton biomass-specific feeding rates in the summer 2004 ecosystem were low (Fig. 5C). Many individual microzooplankton must have been relatively inactive. Another possibility, which we are unable to assess directly, is that removal of mesozooplankton from our incubation bottles led to enhanced growth of large microzooplankton populations, increased predation on small microzooplankton, and consequent suppression of grazing on

phytoplankton through alteration of a trophic cascade (Calbet and Landry, 1999; Strom et al., 2007). However, given the low summer 2004 mesozooplankton biomass on the shelf (Coyle et al., 2008), it seems unlikely that such a cascade would have been operating strongly in the natural environment. A third possibility is that microzooplankton were feeding substantially on non-phytoplankton prey such as bacteria, detritus, and heterotrophic protists (Diederichs et al., 2003; Jeong et al., 2004). Such prey could have been abundant in localized, high productivity regions such as the continental slope and the area between the islands. However, the generally low summer production rates elsewhere in the ecosystem (Sambrotto et al., 2008) were unlikely to have supported a vigorous bacterial or detritus-based food web. An unexplored possibility is the summer utilization (as bacteria or detritus) of residual spring bloom primary production by micrograzers.

4.3. Lower trophic level processes over the slope: support for the 'Green Belt' concept

Our data support the historical observation that southeast Bering slope waters sustain elevated primary and secondary production during summer in the southeast Bering Sea (Springer et al., 1996). This 'Green Belt' is likely supplied by a variety of nutrient transport and mixing mechanisms, including cross-shelf fluxes associated with mesoscale eddies (Stabeno and Van Meurs, 1999; Mizobata et al., 2008, and references therein). In addition to high chlorophyll 'green' waters at our slope stations, we observed elevated microzooplankton biomass and most of our highest microzooplankton grazing rates in this region. While rates of grazing, including on the largest phytoplankton cells, were high (for this study), the slope microzooplankton community contained strikingly fewer large ciliates and heterotrophic dinoflagellates than other high-chlorophyll regions that we sampled. This led to high estimated microzooplankton biomass-specific grazing rates on the slope (Fig. 5C). A low biomass of large microzooplankton coupled with high per capita grazing rates indicates rapid turnover. This is consistent with Coyle et al.'s (2008) observation that the slope zooplankton community contained a high abundance of large-bodied oceanic copepods (*Neocalanus plumchrus-flemigeri*, *N. cristatus*, *Metridia* spp., *Eucalanus bungii*) relative to the shelf. *Neocalanus* spp. in particular are known to be important consumers of large microzooplankton in the subarctic Pacific, and can feed at high rates on this prey type (Gifford, 1993; Liu et al., 2005). Aspects of phytoplankton community composition also support Coyle et al.'s finding that the slope community was separate and distinct from that on the shelf, with the boundary between the two located seaward of the 100-m isobath during our study. The large *Pseudo-nitzschia seriata* was found almost exclusively at slope stations, where we observed a maximum abundance of 8.5×10^5 cells L^{-1} (Table 3).

4.4. 1999–2004 comparison

An extensive study of phytoplankton growth and microzooplankton grazing was conducted in July–August 1999 in the southeast Bering Sea, using techniques comparable to those employed here (Olson and Strom, 2002). This allows us to examine the effects of contrasting physical conditions on lower trophic level processes in the region. Although conditions during 1999 did not stand out as unusual relative to the 1959–1999 climatological mean (Bond and Adams, 2002), upper mixed-layer temperatures in July–August 1999 averaged 4–5 °C lower than in 2004 (our data, Fig. 10); (Coyle et al., 2008). The mean water column stability parameter, a measure of stratification strength,

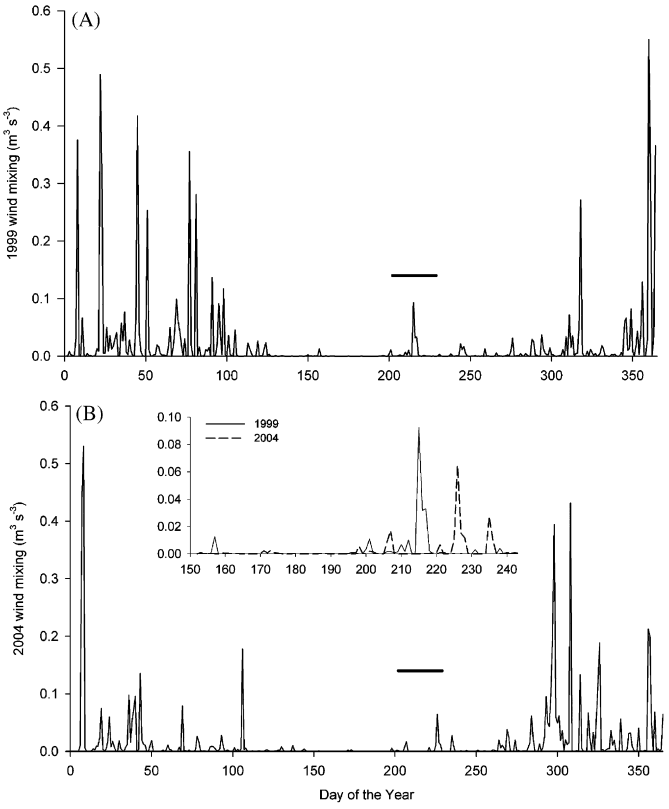

Fig. 9. Wind mixing (friction velocity cubed) at M2 for (A) 1999 and (B) 2004. Inset shows summer mixing (June 1–August 31) in both years. Solid horizontal lines show cruise periods. Wind data derived from NCEP reanalysis (see Bond and Overland, 2005).

averaged 2.5 × higher in 2004, indicative of the greater amount of energy that would be required to mix the 2004 water column (Coyle et al., 2008).

Conditions in 2004 appear to have been representative of the period 2000–2005, typified not only by warmer summer surface temperatures, but by reduced ice cover and/or early ice retreat in the southeast Bering (Stabeno and Overland, 2001; www.bering-climate.noaa.gov/data/). A close examination of the wind data reveals an additional contrast between 1999 and 2004 (Fig. 9). Wind mixing events were more frequent and more intense in winter and spring 1999. During summer 1999, a storm of moderate intensity occurred on 3–4 August, less than halfway through the 1999 cruise period. That storm was associated with mixing across the thermocline, surface cooling (Stabeno et al., 2002, their Fig. 4), and likely led to elevated surface nitrate and ammonium levels during the 1999 study (Olson and Strom, 2002). In contrast, summer 2004 was calm from mid-April until ca. 14 August, when a somewhat weaker summer storm interrupted sampling operations late in our cruise. Thus both multi-year climatological conditions and within-year weather events favored increased stratification, reduced availability of mixing energy, and reduced nutrient supply to surface waters in summer 2004 relative to 1999.

Consequences of this difference in conditions were severe. Although surface waters were 4 °C colder, average unenriched phytoplankton growth rates in 1999 (from Olson and Strom, 2002) were similar to those in 2004 (0.33 vs. 0.35 d^{-1}, Fig. 10A). Almost no nutrient limitation was evident in 1999, while nearly all sampled sites showed strong nutrient limitation in 2004. Addition of nutrients elevated 2004 rates relative to those in 1999 (0.69 vs. 0.42 d^{-1}, Fig. 10B), as would be expected given higher water

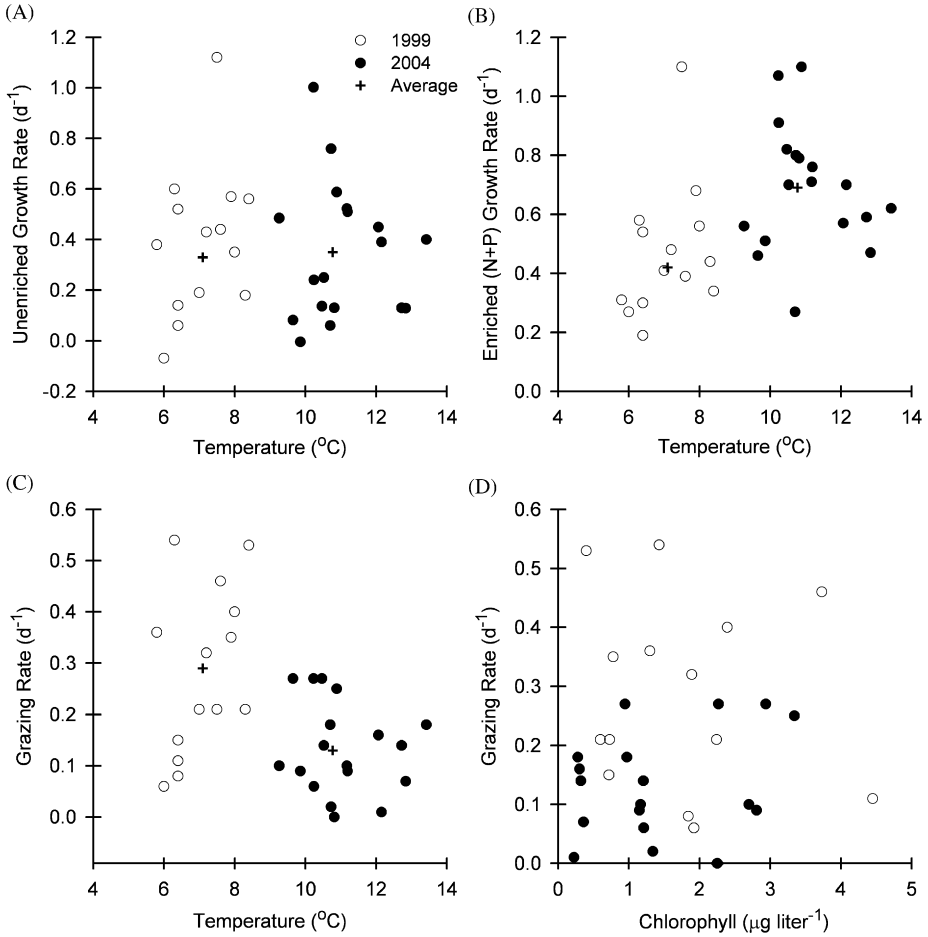

Fig. 10. Phytoplankton growth and microzooplankton grazing rates as a function of environmental conditions, for summer 1999 (open symbols) versus summer 2004 (filled symbols) in the southeast Bering Sea. Crosses show average values for each year. (A) Phytoplankton growth (unenriched); (B) phytoplankton growth (with added N+P); (C) microzooplankton grazing, all as a function of temperature. (D) Microzooplankton grazing as a function of total chlorophyll concentration. Summer 1999 data from Olson and Strom (2002), excluding four stations in nearshore waters north of the Aleutian Islands.

temperatures in 2004. The increase of $0.27\,d^{-1}$ over a 4° temperature range (see crosses, Fig. 10B) corresponds to a reasonable physiological Q_{10} for phytoplankton growth of 2.6.

Nutrient limitation and consequent reductions in phytoplankton growth rate appear to have profoundly affected the microzooplankton community. While biomass levels in the 2 years were comparable (Table 5), grazing rates were substantially lower in 2004 (average values 0.13 vs. $0.29\,d^{-1}$, Fig. 10C). Although inconsistencies in methodology make a direct comparison impossible (i.e. heterotrophic nanoflagellates were not enumerated in 1999; see Olson and Strom, 2002), it seems likely that microzooplankton biomass-specific grazing rates were considerably higher in 1999. When compared with chlorophyll concentration as a measure of prey availability, 2004 rates are seen to be generally lower than 1999 rates even for equivalent chlorophyll levels (Fig. 10D). Microzooplankton in 2004 appeared to be feeding at lower rates relative to physiological maxima (set in part by temperature), to grazing capacity (set in part by microzooplankton biomass), and to prey availability (set in part by phytoplankton biomass).

Low prey quality is a possible explanation for these reduced grazing rates. *Pseudo-nitzschia seriata* and species in the *delicatissima/pseudodelicatissima* complex can (but do not always) produce domoic acid, a toxin (Hasle, 2002). While acute toxicity should have reduced microzooplankton abundance and biomass levels, sublethal toxicity could explain at least some of the reductions in microzooplankton activity that we observed. Low grazing rates, however, were not confined to or even primarily associated with high *Pseudo-nitzschia* abundances; some of our highest grazing rates were in slope waters with high concentrations of *Pseudo-nitzschia*, while very low rates were observed at some stations with almost no *Pseudo-nitzschia*. *Pseudo-nitzschia* spp. have been reported previously from the southeast Bering Sea (Sukhanova et al., 1999), and it remains to be determined whether toxin production by these cells plays a role in bloom formation or other aspects of the summer ecosystem. An alternative and more general hypothesis for reduced grazing is that strong nutrient limitation of phytoplankton growth produced a prey community that was nutritionally poor for the microzooplankton. Low primary production levels also could limit production of bacteria dependent on phytoplankton and grazer-derived organic matter, reducing availability of bacterial prey.

Conditions in 2004 also impaired trophic coupling. Microzooplankton often consume most phytoplankton production in the sea; a recent data synthesis found that microzooplankton grazing (g) averaged 67% of phytoplankton growth (μ) on a worldwide basis (Calbet and Landry, 2004). Many larger zooplankton are known to feed more efficiently on microzooplankton than on phytoplankton (Gifford, 1993; Fessenden and Cowles, 1994; Liu et al., 2005). In 1999, the average ratio of g:μ in the southeast Bering in summer was 0.88, indicating that trophic efficiency was somewhat higher than the global average of 0.67. In 2004, however, g:μ averaged only 0.49. The fate of the remaining one-half of the primary production is unknown. If that half was

grazed directly by mesozooplankton such as the small *Pseudocalanus* and *Oithona* that dominated the 2004 shelf community, then food web efficiency could have been higher than in 1999 because the intermediate microzooplankton trophic link was weaker in 2004. However, given the dramatically lower 2004 mesozooplankton biomass (Coyle et al., 2008), it does not appear that mesozooplankton were directly consuming a large fraction of primary production. Alternative fates for the phytoplankton not removed by microzooplankton include direct sinking to the benthos, requiring replacement of nutrients to the summer euphotic zone through mixing events, or viral lysis. The latter would have fueled euphotic zone nutrient regeneration and bacterial production but would have greatly reduced transfer of primary production to the mesozooplankton.

Evidence that summer 2004 conditions were nutritionally depauperate was seen throughout the marine food web. Summer zooplankton biomass at M2 was approximately 7 × lower in 2004 than in 1999 (Coyle et al., 2008). Elevated stress hormone levels in birds captured on the Pribilof Islands indicated poor prey availability for breeding Least auklets by late July and thick-billed murres by early August 2004 (Benowitz-Fredericks et al., 2008). Our data reveal that reductions in prey availability and/or quality, evident throughout the 2004 food web, originated at the lowest trophic levels, with nutrient-limited phytoplankton, very low microzooplankton grazing, and reduced trophic coupling between phyto- and microzooplankton.

4.5. Summary

1. Rates of phytoplankton growth in summer 2004 were strongly nutrient-limited at nearly all sites.
2. Microzooplankton grazing rates in summer 2004 were low throughout the region. Low rates were not attributable to low microzooplankton biomass, which was equal to or greater than that in subarctic ecosystems supporting several-fold higher grazing rates. Low microzooplankton biomass-specific (i.e. per capita) feeding rates suggest that poor prey quality led to depressed feeding. Poor prey quality could have been a function of phytoplankton species composition and/or phytoplankton nutrient status.
3. Flow interactions with bathymetric features around the Pribilof Islands and on the slope injected nutrients into surface waters, stimulating phytoplankton growth and phyto- and microzooplankton biomass accumulation. Slope waters in particular showed evidence of elevated growth and grazing, and may have supported more efficient trophic transfer than other studied regions.
4. Comparison of 2004 with the cold, late ice retreat year of 1999 showed the profound effect of warming and stratification on lower trophic level processes. Compared with 1999, phytoplankton in 2004 were strongly nutrient-limited and thus grew at a lower fraction of their potential physiological (i.e. temperature-dictated) maximum rates. Phytoplankton were also grazed by microzooplankton at lower rates than in 1999. Trophic coupling was reduced, with grazing:growth ratios averaging only 0.49 in 2004 versus 0.88 in 1999. Depending on the fate of the ungrazed production, 2004 conditions may have decreased the availability of prey for zooplankton, birds, and mammals at higher trophic levels in the southeast Bering.

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