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Microzooplankton grazing in the coastal Gulf of Alaska:Variations in top-down control of phytoplankton

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Abstract

Microzooplankton grazing rates on three phytoplankton size fractions (<5, 5–20, and >20 μm) were measured during spring and summer 2001 in the northern coastal Gulf of Alaska (CGOA). To a first approximation, microzooplankton consumed all production by phytoplankton <20 μm in size and nearly half the production by phytoplankton >20 μm, mainly diatoms. Microzooplankton (ciliate plus heterotrophic dinoflagellate) biomass ranged from 9.6 μg C L^{-1} to 82.2 μg C L^{-1}. The highest levels were associated with diatom blooms and equaled those previously reported for highly productive coastal upwelling regions. Regulation of microzooplankton grazing differed according to size class. Grazing on phytoplankton <5 μm in size averaged 0.48 d^{-1} and was closely correlated with phytoplankton growth rates in the same size class. In contrast, grazing on phytoplankton >20 μm averaged 0.17 d^{-1} and was unrelated to phytoplankton growth rate in this size class. Variations in grazing pressure on these largest phytoplankton arose mainly through variations in the biomass of the larger (>40 μm) ciliates and dinoflagellates. This biomass, in turn, became more closely correlated with >20 μm chlorophyll as the season progressed, indicating removal of top-down control on these ciliates and dinoflagellates as *Neocalanus* spp. copepods left the upper water column. Because microzooplankton directly consume much of the phytoplankton production in the CGOA, processes that regulate this trophic linkage have major implications for food web structure and secondary production in this coastal ecosystem.

There is growing recognition that microzooplankton consume a substantial fraction of marine phytoplankton production (Calbet and Landry 2004; Irigoien et al. 2005). The ubiquity of one or more microzooplankton trophic levels in planktonic food webs has major consequences for the amount and type of higher consumers that can be supported, including commercially important fish species (Pauly and Christensen 1995). The U.S. Global Ocean Ecosystem Dynamics (GLOBEC) program in the Northeast Pacific seeks to understand how environmental variability affects coastal food webs supporting salmon, other fish species, marine birds, and mammals. As part of this research effort in the northern coastal Gulf of Alaska (CGOA), we studied microzooplankton grazing on phytoplankton during spring and summer 2001. Our goals were to determine the amount and type of phytoplankton consumed by microzooplankton, to gain insight into the processes regulating consumption rates, and to understand the microzooplankton trophic link in the context of physical variability on the shelf.

The CGOA experiences physical forcing by a number of processes, including strong winter downwelling, weak and intermittent summer upwelling, a high volume of seasonally phased freshwater runoff, topographic complexity interacting with tides and alongshore currents, and long-lived mesoscale eddies (Royer 1982; Stabeno et al. 2004). Flow is dominated by westward currents, primarily the swift, nearshore Alaska Coastal Current (ACC) and the broader Alaska Current over the slope (Reed and Schumacher 1986). The region experiences a seasonal progression from deep winter mixing to spring onset of stratification, triggering a late April–May diatom bloom on the shelf. Strong summer stratification due to surface warming (over the entire shelf) and freshwater input (primarily retained in coastal embayments and on the inner shelf) leads to nutrient depletion and reduced chlorophyll levels (Childers et al. 2005; Weingartner et al. 2005).

Research on phytoplankton community structure, nutrient utilization, and growth was conducted in parallel with the microzooplankton studies presented here. Strom et al. (2006) present evidence that both temporal and spatial resource gradients affect CGOA phytoplankton. Temporally, some of the highest phytoplankton growth rates that we measured (>1.0 d^{-1}) were during April blooms of large chain-forming diatoms. However, macronutrient limitation of growth rates closely followed the onset of spring stratification and was evident nearshore as early as late April. The summer phytoplankton community was dominated by small (<5 μm) cells exhibiting varying degrees of macronutrient limitation depending on cross-shelf location. We did, however, observe an intense mid-summer diatom bloom in the ACC, perhaps in response to a series of upwelling events. Spatially, we identified a strong cross-shelf gradient consistent with progressively greater iron limitation as one moves offshore. This is consistent with known iron limitation in neighboring open subarctic Pacific waters and, likely, iron supply from terrestrial runoff (Martin et al. 1989; Boyd et al. 2004). Evidence for this iron limitation gradient was found in phytoplankton biomass and cell size (blooms of large cells confined to inner and mid shelf), nutrient

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utilization (inhibition of silicic acid uptake on the outer shelf), growth rate, and degree of macronutrient limitation (low to moderate outer shelf phytoplankton growth not responsive to added macronutrients).

In this article we demonstrate that microzooplankton community biomass and size structure during 2001 showed spatial and temporal gradients similar to those of phytoplankton in the CGOA. Whereas microzooplankton consumption of all phytoplankton was substantial, small cells (<20 μm) were consumed more readily than large cells (>20 μm). Thus, resource gradients influencing phytoplankton cell size indirectly but profoundly influenced the fate of phytoplankton production. Examination of relationships among biomass, growth, and grazing led us to conclude that fundamentally different processes regulate rates of microzooplankton grazing on small versus large phytoplankton, with consequences for the eventual fate of primary production.

Methods

Experiments were conducted during three 15-d cruises to the northern CGOA in 2001: 17 April to 01 May, 17 May to 31 May, and 12 July to 26 July. During each cruise we occupied four stations encompassing a cross-shelf gradient from Prince William Sound (PWS) in the north to the shelf break region in the south (Fig. 1). These stations were chosen to encompass anticipated cross-shelf physical and biological zonation (e.g., Fig. 2), including a protected fjord, the nearshore ACC, and the shelf break. For example, surface salinity increases seaward across the shelf (Weingartner et al. 2005), phytoplankton biomass typically decreases seaward but may be elevated across the outer shelf and slope (Dagg et al. 2006), and copepod species are distributed differentially across the inner, mid, and outer shelf (Coyle and Pinchuk 2005). We conducted two to four experiments at each station on each cruise for total of 40; the results of 39 are presented here. Data from one experiment (mid-shelf, 20 May) were not included in this analysis because the dilution plot was uninterpretable, likely because of very rough weather during water collection and incubation.

Experiments, described in detail in Strom et al. (2006), used the seawater dilution technique to estimate phytoplankton growth and microzooplankton grazing rates (Landry and Hassett 1982). The complete set of rate data can be obtained at http://globec.whoi.edu/jg/dir/globec/nep/cgoa/process/. Briefly, water drawn from multiple Niskin bottles closed at a single depth was pooled into two 25-liter polycarbonate carboys. Most often, water was collected from the depth corresponding to 50% of surface irradiance (50% I_o, 3–10 m). Water was collected from the depth of the subsurface chlorophyll maximum ([SCM] 12–25 m) once during April and once per station during July. The contents of one carboy were gravity-filtered (0.2 μm) to generate particle-free filtered seawater ([FSW] the diluent for the dilution series). The contents of the other were gently pre-screened through 200-μm Nitex mesh to exclude macrozooplankton ([WSW] the whole seawater for the dilution series). Using gentle siphoning and mixing techniques, FSW and WSW were combined in known proportions in 2.35-liter polycarbonate bottles to generate a dilution series consisting of 9, 16, 24, 41, 61, and 100% WSW (each in duplicate). An additional pair of bottles diluted to 4% was added during the May and July cruises, as well as an additional pair of 100% WSW bottles to

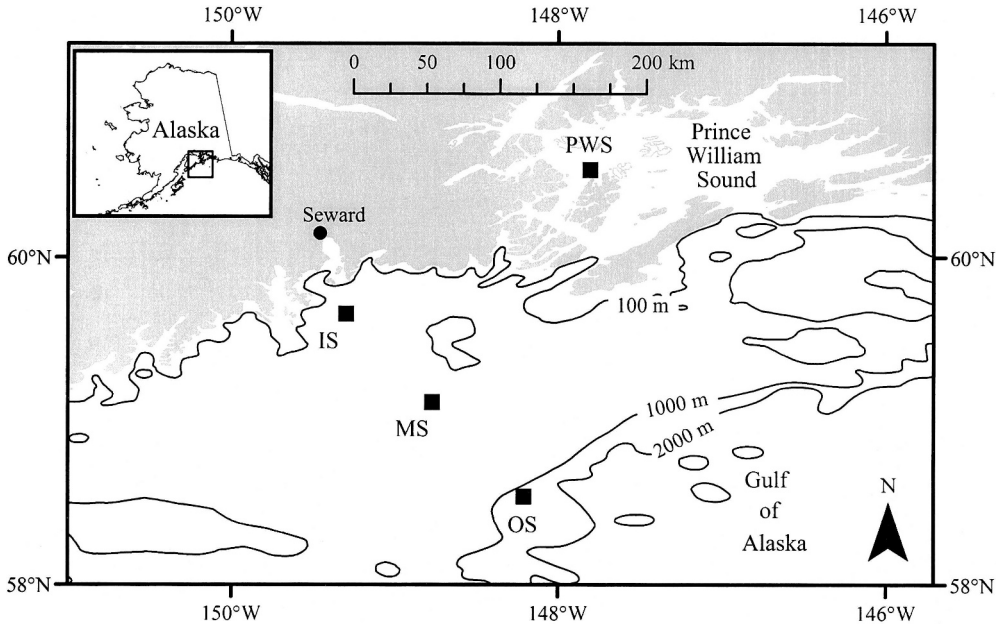


Fig. 1. Northern Gulf of Alaska study region. Squares show station locations for microzooplankton grazing rate determinations in 2001. OS, outer shelf; MS, mid shelf; IS, inner shelf; PWS, Prince William Sound.

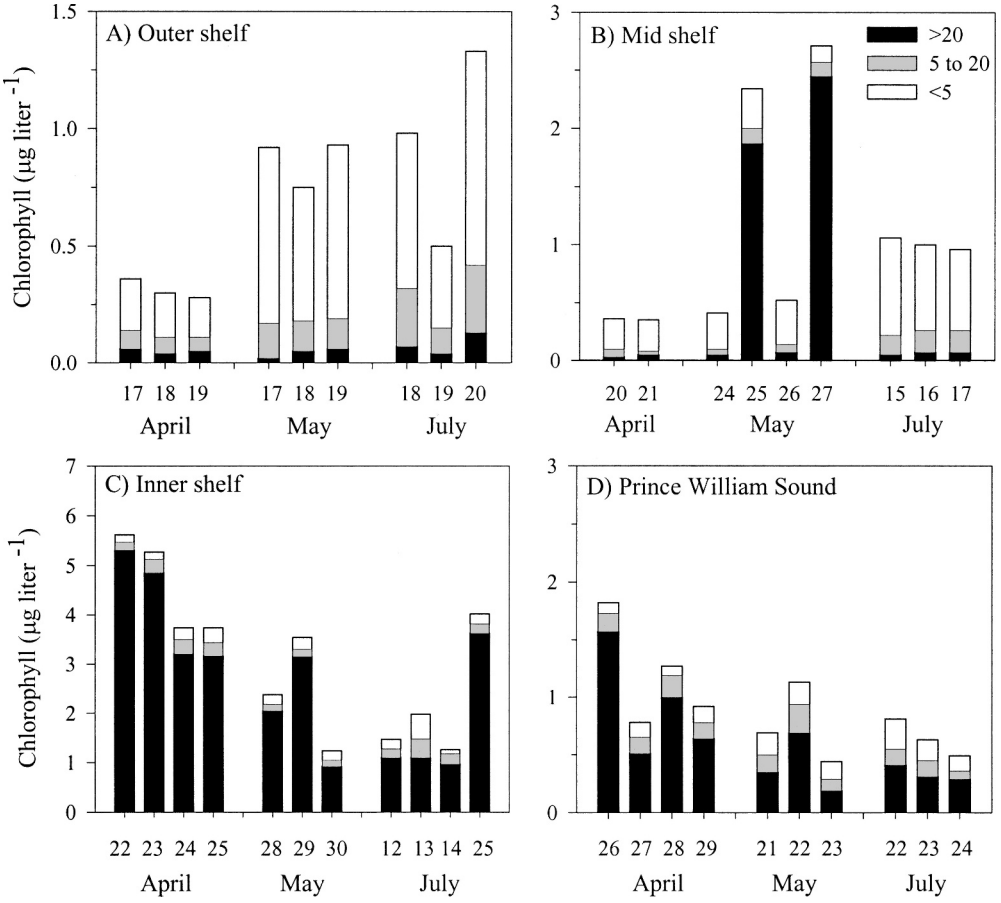


Fig. 2. Initial chlorophyll levels for experiments conducted on different dates at (A) outer shelf, (B) mid shelf, (C) inner shelf, and (D) Prince William Sound, showing size composition of total chlorophyll. Note differing y-axis ranges.

control for the effects of nutrient enrichment on phytoplankton growth rate. Clean techniques and inert materials (silicone, polycarbonate) were used throughout.

Initial samples for size-fractionated chlorophyll (<5, 5–20, and >20 μm, in quadruplicate), nutrients (nitrate, nitrite, silicic acid, and phosphate), and microzooplankton abundance and composition (in duplicate) were taken from the WSW carboy at intervals during experiment setup. Initial chlorophyll levels in diluted bottles were calculated from these measured WSW values and known dilution factors. Coefficients of variation for quadruplicate initial chlorophyll samples averaged 7.9%, 13.5%, and 8.9% for the <5 μm, 5–20 μm, and >20 μm size fractions, respectively. During May (all but outer shelf experiments) and July cruises, all diluted bottles and two 100% WSW bottles were enriched with nitrate (4.7 μmol L^{-1} as $NaNO_3$) and phosphate (0.27 μmol L^{-1} as Na_2HPO_4). The other two 100% WSW bottles were left unenriched. Bottles were screened to collection-depth light levels with neutral density screening and incubated on deck in seawater-cooled incubators for 24 h. All bottles were then sampled in duplicate for size-fractionated chlorophyll (filtration volumes ranged from 0.15 liter to 1.08 liters depending on WSW chlorophyll and dilution levels); 100% WSW bottles were additionally sampled for microzooplankton abundance and composition.

Net growth rates (k, d^{-1}) for total chlorophyll and individual chlorophyll size fractions were calculated as (1/t)(ln[Pt/Po]), where Pt is the final chlorophyll concentration, Po is the initial chlorophyll concentration, and t is incubation time in d. Intrinsic growth rates (μ, d^{-1}) of phytoplankton were estimated from the y-intercept of net growth rates regressed upon fraction WSW. For experiments exhibiting saturated grazing (i.e., a leveling of net growth rate across the least-dilute bottles), instrinsic growth rate estimates were based on regression of net growth rates in only the most dilute bottles (generally those with ≤40% WSW). Microzooplankton grazing rates (g, d^{-1}) were estimated from the slope of the regression for experiments with linear relationships between net growth and fraction WSW, and as $g = \mu_n - k_n$ (where k_n is net growth rate of phytoplankton in enriched, 100% WSW bottles) for experiments with saturated grazing. In experiments with nutrient enrichment, unenriched phytoplankton growth rates (μ_o) were calculated as $\mu_o = k_o + g$, where k_o is the net growth rate of phytoplankton in unenriched, 100% WSW bottles. Estimates of μ_o were used to compare microzooplankton

grazing to phytoplankton growth in situ ($g:\mu_o$). These ratios represent the fraction of primary production consumed each day by microzooplankton grazing. Ratios were arctan transformed for estimation of means and standard deviations.

Two types of preserved samples were taken for analysis of the microzooplankton community. The first, for identification and enumeration of ciliates and all other microzooplankton >20 μm in size by inverted microscopy, was preserved by adding the sample to acid Lugol's solution in an amber glass bottle (final Lugol's concentration: 10%). The second, for identification and enumeration of <20-μm heterotrophic dinoflagellates and phytoplankton by epifluorescence microscopy, was fixed by addition to cold 10% glutaraldehyde (final glutaraldehyde concentration 0.5%) and 4′6′diamidino-2-phenylindole ([DAPI stain] final concentration approximately 0.2 μg mL^{-1}). Glutaraldehyde samples were stored (4°C, darkness) for >11 h and <24 h; measured subsamples were then filtered (1.0-μm pore-size polycarbonate filters with 1.2-μm pore-size cellulose backing filters) and slide-mounted using Cargille Type B immersion oil. Slides were stored frozen and transported on dry ice to a shore laboratory for analysis.

Settled volumes (5–10 mL) of Lugol's-preserved samples were analyzed in their entirety. Occasional samples from low-chlorophyll environments had to be preconcentrated (10×) in a two-stage settling process. All ciliates, and all other microzooplankton >20 μm, were enumerated and placed in categories corresponding to size and taxon, and dimensions of each cell were recorded using a computerized digitizing system (Roff and Hopcroft 1986). The total number of microzooplankton enumerated and sized in each sample ranged from 65 to 425 (average 173). Slides for epifluorescence microscopy were examined under both blue and ultraviolet excitation to distinguish hetero- from autotrophic dinoflagellates (based on chlorophyll autofluorescence); dinoflagellate identification was based on nuclear and cell morphology. All cells encountered on one or more cross-filter transects (depending on abundance) were enumerated and placed in 5-μm size categories (<5 μm, 5–10 μm, etc.) based on maximum cell dimension.

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 and Menden-Deuer and Lessard (2000) for dinoflagellates. Reported abundance and biomass estimates are means of duplicate initial samples from each experiment; the difference between duplicate biomass estimates averaged 16% of the mean. Net microzooplankton growth rates (k_{MZ}; d^{-1}) were computed based on the biomass of ciliates plus >20-μm dinoflagellates (i.e., the cells counted using inverted microscopy), as well as for cells in separate size classes. Values of k_{MZ} were computed from (1/t)(ln[MZt/MZo]), where MZo is the average initial abundances in WSW carboys, and MZt is the average final abundances in unenriched 100% WSW bottles.

Results

Microzooplankton grazing rates—Across all sampled regions and months, microzooplankton grazing on total chlorophyll averaged 0.30 d^{-1} (Table 1). The largest phytoplankton (>20 μm, typically chain-forming diatoms) experienced the lowest microzooplankton grazing pressure, averaging 0.17 d^{-1}. Grazing rates on intermediate (5–20 μm) and small (<5 μm) phytoplankton were higher, averaging 0.39 d^{-1} and 0.48 d^{-1}, respectively (Fig. 3). In some instances, repeated experiments at a single station yielded consistent grazing rate estimates. We frequently observed, however, that rates could vary several-fold from one day to the next at a given site (note the differing sizes of range bars in Fig. 3).

Considering all chlorophyll size fractions, microzooplankton grazing rates ranged from a low of 0.00 d^{-1} to a high of 1.07 d^{-1}. Some of the highest rates were measured during April diatom blooms on the inner shelf and in PWS (Fig. 3C,D); relatively high rates were also seen on the inner shelf during the July ACC diatom bloom. These high rates, however, were sustained by the scarcer 5–20 μm and <5 μm cells in the community (Fig. 3C,D), and not by the abundant chain diatoms comprising the >20-μm size fraction. The timing of maximum grazing varied with location (Table 1). Rates were high in both April and May on the outer shelf, whereas the mid shelf and PWS exhibited maximum grazing in May. Only on the inner shelf were the rates highest in July.

We observed saturated grazing in a number of dilution experiments. Perhaps surprisingly, there was no relationship between the occurrence of saturated grazing in an experiment and the overall (or size fraction-specific) chlorophyll concentration in that experiment. Further, saturated grazing was no more likely to be observed in one month than another. However, grazing on the smallest phytoplankton cells was more frequently saturated than grazing on the largest (Fig. 4C). In addition, the incidence of saturated grazing varied with location, with the lowest

Table 1. Microzooplankton grazing rates (d^{-1}) on total chlorophyll by region and month for 2001 in the northern coastal Gulf of Alaska. Values are averages with 1 SD in parentheses. *See* Strom et al. (2006, Table 1) for a tabulation of associated environmental conditions.

	April	May	July	Overall
Outer shelf	0.39 (±0.22)	0.38 (±0.04)	0.21(±0.13)	0.33 (±0.16)
Mid shelf	0.30 (±0.19)	0.56 (±0.30)	0.38 (±0.15)	0.44 (±0.24)
Inner shelf	0.15 (±0.10)	0.17 (±0.15)	0.31 (±0.18)	0.21 (±0.15)
PWS*	0.26 (±0.08)	0.31 (±0.13)	0.18 (±0.07)	0.25 (±0.10)
Overall	0.26 (±0.15)	0.37 (±0.23)	0.27 (±0.15)	0.30 (±0.18)

* PWS, Prince William Sound.

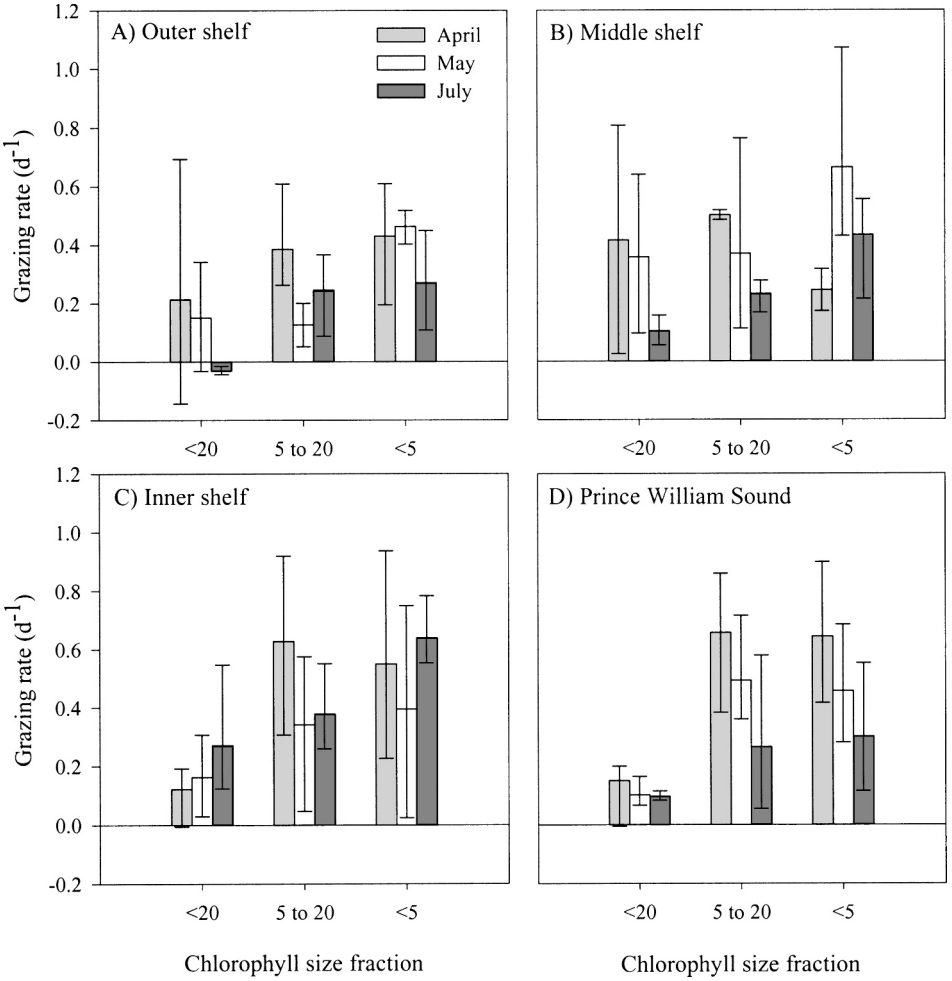


Fig. 3. Microzooplankton grazing rates by chlorophyll size fraction for experiments conducted during April, May, and July 2001 in the CGOA. (A) Outer shelf, (B) mid shelf, (C) inner shelf, (D) Prince William Sound. Values are averages of rates from 2–4 (usually 3) experiments conducted in a given region and month; error bars show range of observed rates.

occurrence on the outer shelf and the highest on the inner regardless of phytoplankton size fraction (Fig. 4C).

The ratio of microzooplankton grazing to phytoplankton growth ($g:\mu$) is equivalent to the fraction of primary production consumed daily by microzooplankton. For the whole phytoplankton community (i.e., total chlorophyll), $g:\mu$ averaged 0.75 across all regions and months (Table 2). Ratios on the outer shelf and in PWS declined from spring into summer, whereas ratios on the mid and inner shelf showed the opposite trend, reaching peak values in July (Table 2).

Considering the chlorophyll size fractions separately, $g:\mu$ averaged 1.02 ($\pm$0.32) for the intermediate (5–20 μm) phytoplankton size fraction, and 1.02 ($\pm$0.29) for the small ($<$5 μm) size fraction. Although day-to-day variability in both grazing and phytoplankton growth rates (*see* Strom et al. 2006) indicate transient imbalances between phytoplankton production and grazing losses, on average the fate of a $<$20-μm phytoplankton cell in this ecosystem was to be eaten by a micrograzer. For large phytoplankton, $g:\mu$ was lower, averaging 0.49 ($\pm$0.33). Thus, micrograzers consumed approximately half of $>$20 μm phytoplankton production during our study. Ratios for large cells in diatom blooms were somewhat lower than ratios for large cells in small cell-dominated, low-chlorophyll waters of the outer and mid shelf (0.41 ± 0.34 vs. 0.52 ± 0.33). A comparison across size fractions shows that the $g:\mu$ differences are due primarily to variation in g. In other words, phytoplankton growth did not vary significantly with size fraction, averaging 0.42, 0.34, and 0.44 d^{-1} for the $<$5, 5–20, and $>$20 μm chlorophyll size fractions, respectively. In contrast, microzooplankton grazing on $<$5-μm phytoplankton averaged 3$\times$ higher than on $>$20-μm phytoplankton.

Microzooplankton biomass and community composition—Total microzooplankton (ciliate + heterotrophic dinoflagellate) biomass in the water sampled for experiments ranged from 9.6 μg C L^{-1} to 82.2 μg C L^{-1}. The highest biomass levels were associated with diatom blooms (e.g., 27 May, mid shelf; 25 July, inner shelf; Fig. 5B,C), and these microzooplankton communities were dominated by large

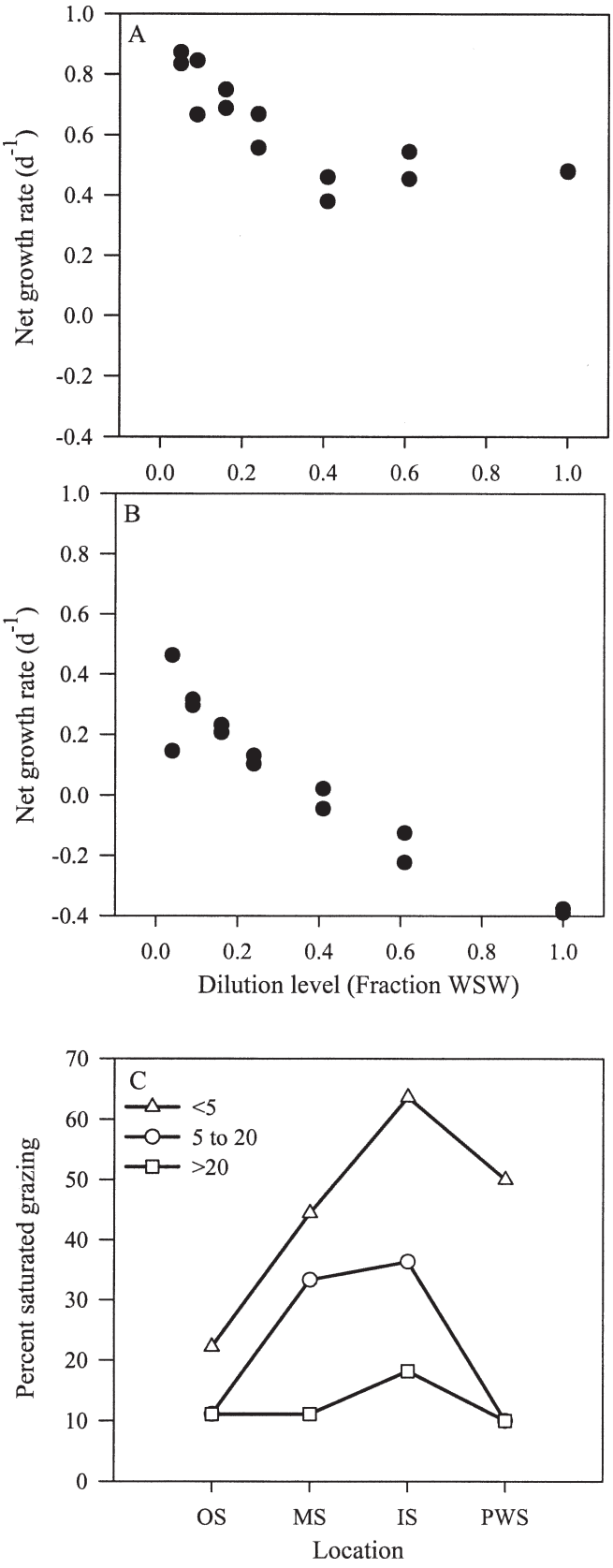


Fig. 4. Dilution plots (<5-μm chlorophyll size fraction) for inner shelf region on (A) 28 May (saturated grazing) and (B) 29 May (no saturated grazing). (C) Incidence of saturated grazing in <5 μm, 5–20 μm, and >20 μm chlorophyll size fractions, by shelf location (*see* Fig. 1).

dinoflagellates, which reached abundances of nearly 20 $\times$ 10^3 cells L^{-1} (Table 3). The smallest dinoflagellates (<20 μm) were sometimes abundant (range 3–698 $\times$ 10^3 cells L^{-1}; Table 3) but only contributed substantially to biomass on the outer shelf in summer (Fig. 5A). Ciliates were important in all regions at various times, but particularly so on the mid and outer shelf in spring and during some inner shelf diatom blooms (e.g., 29 May and 13 July, Fig. 5C). The overall range in ciliate abundance was 5.1–35.7 $\times$ 10^3 cells L^{-1} (Table 3).

A striking feature of the microzooplankton community is the degree of consistency within shelf regions and the strong contrasts among regions. With the exception of the two mid shelf diatom bloom stations (Fig. 2), the mid and outer shelf were dominated by naked spirotrich ciliates and small (<40 μm) heterotrophic dinoflagellates and exhibited low to moderate total biomass (range 9.6–33.7 μg C L^{-1}). Large heterotrophic dinoflagellates were much more important on the inner shelf and in PWS, with consistently large contributions of *Protoperidinium*-like cells in PWS (Figs. 5D, 6C). The miscellaneous dinoflagellate category in July PWS samples primarily comprised several species of *Ceratium*. Many of these cells contained large pigmented food vacuoles, evident when viewed under epifluorescence illumination. The inner shelf region was the most variable both in total biomass (range 12.8–76.0 μg C L^{-1}) and in community composition. Finally, although diatom blooms did not always support a high microzooplankton biomass (e.g., April inner shelf and PWS samplings), all observations of high microzooplankton biomass levels (>45 μg C L^{-1}) were made in diatom blooms.

In addition to the cross-shelf gradient in community composition, we observed a strong cross-shelf gradient in cell size. For microzooplankton >20 μm (i.e., those sized during inverted microscopy), average cell volume decreased from 20,150 μm^3 in PWS to 8,920 μm^3 on the outer shelf (Fig. 6A). This represents an equivalent spherical diameter range of 33.8–25.7 μm. This cross-shelf gradient in microzooplankton community size composition was remarkably consistent from one month to the next.

Microzooplankton growth rates reported here are net growth rates; that is, they are derived from biomass changes in 100% WSW bottles during the incubation period. These rates incorporate predation losses from within the microzooplankton. Final Lugol's-preserved samples were analyzed from a subset of all experiments, chosen to encompass a range of total chlorophyll levels and community types. Net growth rates were low in general, ranging from -0.86 to 0.24 d^{-1}. The three experiments with the lowest overall net growth rates (14 July: -0.86 d^{-1}; 16 July: -0.39 d^{-1}; 17 July: -0.26 d^{-1}) showed negative growth in all microzooplankton size categories. For the other six experiments (Fig. 7), growth rates increased with increasing microzooplankton size.

Table 2. Ratios of microzooplankton grazing : phytoplankton growth (g : μ_o, rates based on total chlorophyll) by region and month for 2001 in the northern coastal Gulf of Alaska. Values are averages with 1 SD in parentheses.

	April	May	July	Overall
Outer shelf	0.73 (±0.11)	1.67 (±0.06)	0.44 (±0.08)	0.83 (±0.29)
Mid shelf	0.65 (±0.11)	0.65 (±0.17)	1.28 (±0.31)	0.80 (±0.23)
Inner shelf	0.34 (±0.30)	0.53 (±0.50)	1.53 (±0.36)	0.65 (±0.47)
PWS*	0.80 (±0.33)	1.09 (±0.19)	0.36 (±0.6)	0.76 (±0.30)
Overall	0.61 (±0.28)	0.90 (±0.33)	0.80 (±0.38)	0.75 (±0.33)

* PWS, Prince William Sound.

Microzooplankton grazing and biomass relationships—During April and May, unenriched growth rates (μ_o) of the smallest phytoplankton were positively correlated with microzooplankton grazing on those phytoplankton (r = 0.860, $p < 0.01$ for April; r = 0.701, $p < 0.01$ for May). This rate correlation had disappeared by July (r = 0.178, p = 0.56), although July grazing rates were correlated with enriched growth rates (μ_n) if inner shelf data were excluded (r = 0.872; $p < 0.01$). In contrast to these smallest phytoplankton, correlations between growth and grazing were not significant for any other chlorophyll size fraction, whether considered by month or across the entire data set.

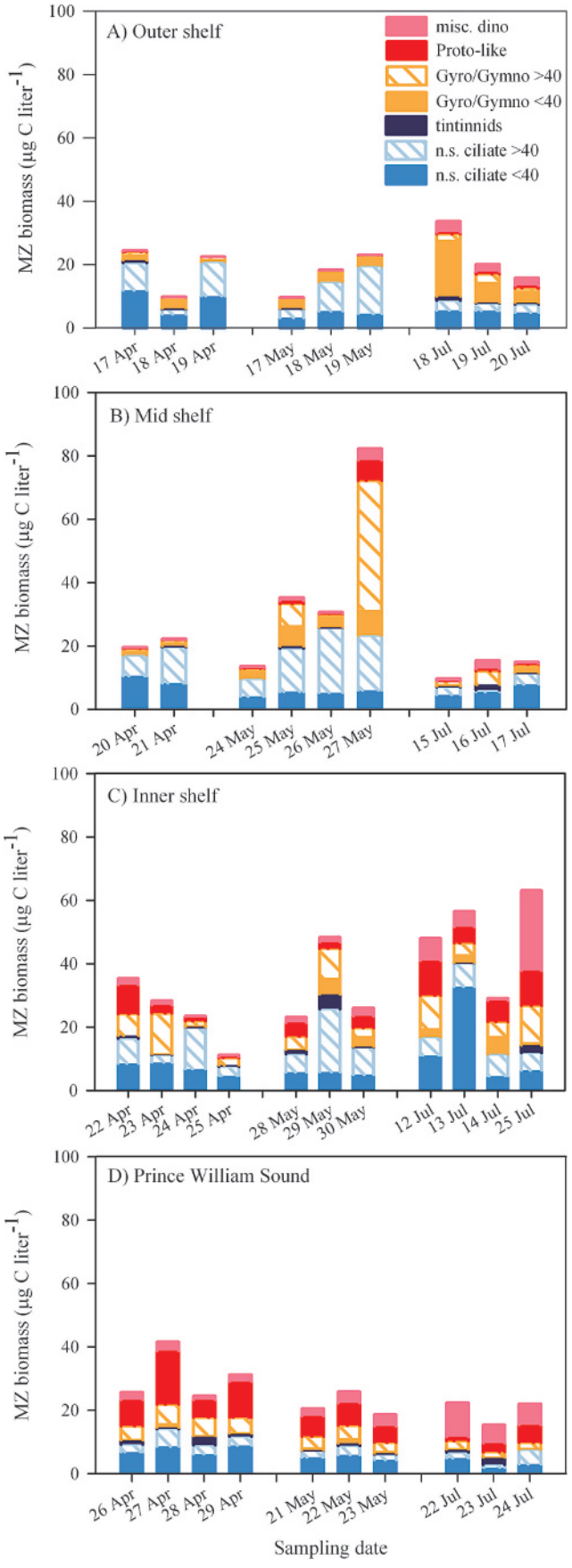
Microzooplankton grazing rates, which are chlorophyll-specific, might also be expected to increase with increasing prey and grazer biomass. For prey biomass, we related g values for each phytoplankton size fraction to chlorophyll concentration in that size fraction. There was no relationship between grazing rates and chlorophyll levels, whether we examined the data set as a whole or each shelf region separately. For grazer biomass, we compared g(total) with total microzooplankton biomass, and g(>20) with the biomass of microzooplankton >20 μm. For the total data set (all locations combined), no correlations were significant. By region, the only significant relationships were in nearshore waters and involved large cells. In PWS, g(>20) was positively correlated with the biomass of microzooplankton >20 μm (r = 0.690; p = 0.027). On the inner shelf, g(>20) was similarly correlated with the biomass of the >20-μm microzooplankton (r = 0.826; p = 0.002), and g(total) with total microzooplankton biomass (r = 0.839; p = 0.001). Clearly the variations in inner shelf biomass were driven almost entirely by variations in the larger microzooplankton (Fig. 8), with <20-μm ciliates and heterotrophic dinoflagellates remaining nearly constant at 2–7 μg C L^{-1} and 20–40 μm cells contributing only modestly to overall biomass increases. Overall, our analysis showed that microzooplankton grazing rates had no relationship to chlorophyll biomass and were related to grazer biomass only in regions (inner shelf, PWS) consistently dominated by large phytoplankton (Fig. 2) and large microzooplankton (Fig. 6).

In contrast to the weak correlations generally obtained when grazing rates were examined, biomass relationships between microzooplankton and chlorophyll were often strong. The smaller microzooplankton showed no significant correlation with either the <20-μm or the <5-μm chlorophyll concentration (Fig. 9). For both larger and total microzooplankton, correlation with the corresponding chlorophyll size class was weak to nonexistent in April and increased through May and July. By July, variation in total chlorophyll concentration explained 71% of the variation in biomass of total microzooplankton (Fig. 9), a relationship again driven by variations in the larger cells.

Discussion

Microzooplankton grazing effect on phytoplankton—Microzooplankton grazing rates in the CGOA during July 2001 averaged 0.27 d^{-1} (Table 1) and are similar to summer rates measured elsewhere in the subarctic Pacific and Bering Sea. Summer grazing rates averaging 0.16–0.38 d^{-1} have been reported across coastal and oceanic subarctic regions (e.g., Landry et al. 1993; Liu et al. 2002; Olson and Strom 2002). In contrast, spring 2001 rates in the CGOA (April average: 0.26 d^{-1}; May average: 0.37 d^{-1}) were lower than rates measured in the same region during April 1998 and May 1999 (average 0.51 d^{-1}; Strom et al. 2001). Conditions during May 1999, in particular, were quite different than in May 2001, with small cell-dominated communities nearshore and a bloom of small (<10 μm) autotrophic dinoflagellates seaward of the shelf break (Strom et al. 2001; Brickley and Thomas 2003).

A comparison of grazing (g) with phytoplankton growth (μ_o) reveals that microzooplankton grazing is one of the most important loss processes affecting phytoplankton in the northern CGOA. During spring and summer 2001, grazing rates by microzooplankton equaled growth rates of all phytoplankton <20 μm (average g : μ_o = 1.02). Thus, to a first approximation, all primary production by cells <20 μm during our study passed through a microzooplankton trophic level before reaching larger consumers. A lower but still substantial amount of >20 μm production was grazed by microzooplankton, with g : μ_o for this size class averaging 0.41 in diatom blooms. During our study, blooms were dominated by the chain-forming genera *Thalassiosira* and *Chaetoceros*, although pennates, including *Pseudo-nitzschia* and *Cylindrotheca*, could also be abundant (Strom et al. 2006). Heterotrophic dinoflagellates known to feed on chain diatoms, including the genera *Gyrodinium*, *Protoperidinium*, and related thecate species, were abundant in these bloom communities (Fig. 6B) and almost certainly played a major role in the consumption of diatoms. *Protoperidinium* and other thecate forms were particularly important in PWS in spring and on the inner



shelf in summer (Fig. 5C,D). Ciliates may also have fed on diatoms, as moderate grazing rates on >20-µm phytoplankton were sometimes associated with high ciliate biomass (e.g., 29 May and 13 July; Fig. 5C).

There is growing evidence that microzooplankton grazing is an important loss process affecting coastal diatom blooms, particularly in comparison with the grazing effects of larger zooplankton. Whereas copepods can occasionally consume a large fraction of bloom production (Rysgaard et al. 1999) and microzooplankton grazing in diatom blooms can be low to negligible (Gifford et al. 1995; Archer et al. 1996), high rates of microzooplankton grazing on diatoms have frequently been measured in coastal bloom waters at temperate and high latitudes worldwide (e.g., Neuer and Cowles 1994; Olson and Strom 2002; Umani and Beran 2003). When direct comparisons were done, consumption of bloom-forming diatoms by microzooplankton has frequently emerged as equivalent to or substantially greater than consumption by copepods (e.g., Nielsen and Hansen 1995; Landry et al. 2000; Vargas and Gonzalez 2004). In a number of studies this grazing pressure was directly attributable to heterotrophic dinoflagellates. They were found to be the major consumers of diatoms in blooms initiated by a variety of processes, including upwelling, river runoff, iron fertilization, and the arrival of spring (Neuer and Cowles 1994; Tiselius and Kuylenstierna 1996; Levinsen and Nielsen 2002). The idea that much coastal primary production passes through a microzooplankton trophic level is supported by a recent global data synthesis. Calbet and Landry (2004) reported that grazing by microzooplankton averages 67% of primary production across all marine ecosystem types, and 57% in the coastal ocean. This agrees well with our study-wide average of 75%, with percentages tending to be higher in the more oceanic waters of the mid and outer shelf and lower in waters closer to shore (Table 2).

Microzooplankton community structure and biomass—Both ciliates and heterotrophic dinoflagellates played important roles in spring and summer CGOA waters (Fig. 5, Table 3). Ciliates generally dominated the biomass in low-chlorophyll mid and outer shelf regions, whereas both dinoflagellates and ciliates were important in high-chlorophyll waters, including the mid shelf during the spring bloom and the inner shelf during all months. The PWS microzooplankton community was especially rich in dinoflagellates (Fig. 6B).

Total microzooplankton (ciliate + dinoflagellate) biomass on the outer shelf ranged from 9.7 µg C L^{-1} to 33.7 µg C L^{-1}. The outer shelf was, on average, the least

←

Fig. 5. Composition of microzooplankton (MZ) biomass (µg C L^{-1}) by taxon and size class (µm) during April, May, and July 2001 at (A) outer shelf, (B) mid shelf, (C) inner shelf, (D) Prince William Sound. Values are averages of duplicate samples taken from unfiltered seawater used to set up dilution experiments. proto-like, *Protoperidinium*-like; gyro/gymno, dinoflagellates in the *Gyrodinium*/*Gymnodinium* complex; n.s. ciliate, naked spirotrich ciliate

Table 3. Abundance of microzooplankton ($\times 10^3$ cells L^{-1}) in four coastal regions of the CGOA, for initial dilution experiment samples collected during April, May, and July. Abundances are means from two to four experiments in each region, with the range shown in parentheses. Dates for each set of experiments are shown above abundance values.

		Outer shelf		Mid shelf		Inner shelf		PWS*	
April	Dates:		17–19		20–21		22–25		26–29
	Dinos† <20	22.6	(5.9–52.8)	2.9	(2.5–3.3)	26.3	(14.8–40.3)	14.2	(8.9–18.9)
	Dinos >20	2.7	(1.6–3.7)	2.4	(2.3–2.5)	4.6	(2.3–8.3)	7.1	(5.7–9.0)
	Ciliates	17.4	(8.7–23.3)	16.7	(16.6–16.7)	15.1	(11.4–17.2)	17.0	(14.1–21.6)
May	Dates:		17–19		24–27		28–30		21–23
	Dinos <20	102.5	(92.5–111.1)	59.1	(26.3–105.9)	125.1	(85.8–173.1)	32.4	(24.4–41.6)
	Dinos >20	3.7	(3.1–4.2)	10.0	(4.0–19.9)	7.4	(6.4–8.2)	8.3	(7.4–9.5)
	Ciliates	13.1	(7.6–16.1)	15.2	(9.2–19.2)	16.0	(13.4–18.6)	10.3	(8.0–9.7)
July	Dates:		18–20		15–17		12–14, 25		22–24
	Dinos <20	322.4	(102.0–698.3)	138.8	(96.4–180.0)	93.3	(16.8–167.7)	46.9	(25.6–68.8)
	Dinos >20	7.6	(4.0–11.0)	7.2	(3.2–13.3)	12.1	(3.9–19.7)	5.3	(4.0–6.4)
	Ciliates	13.3	(12.8–13.8)	13.4	(12.2–14.8)	18.7	(7.6–35.7)	6.2	(5.1–7.1)

* PWS, Prince William Sound.
† Dinos, heterotrophic dinoflagellates (abundances for cells <20 μm and >20 μm shown separately).

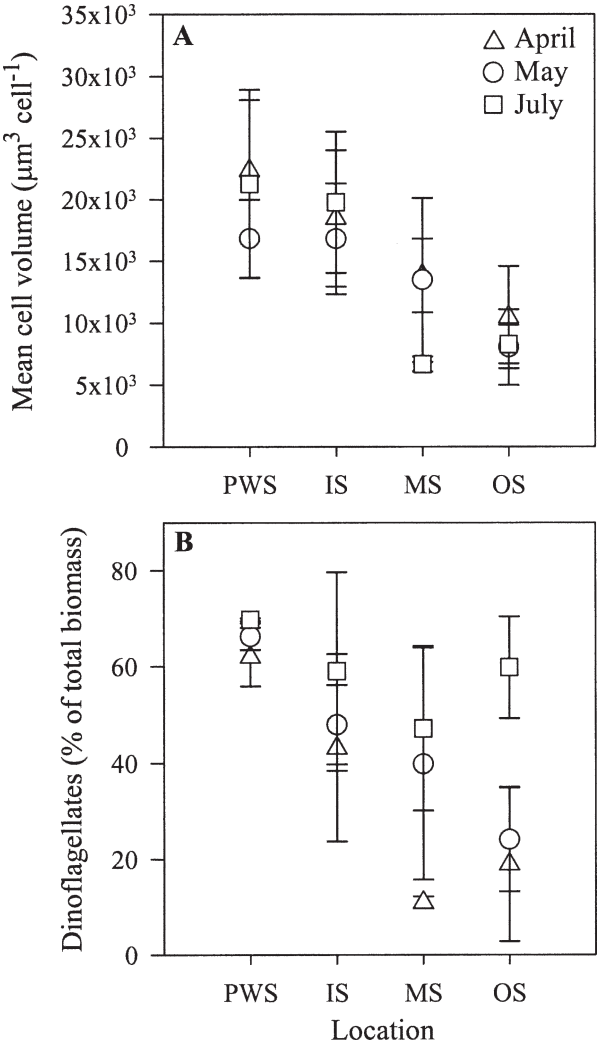


Fig. 6. Cross-shelf gradients in (A) microzooplankton mean cell volume (cells >20 μm only) and (B) percent contribution of dinoflagellates to total microzooplankton biomass. Values are averages ±1 SD.

productive of the regions we sampled. The outer shelf did, however, support a consistently higher microzooplankton biomass than the adjacent open subarctic Pacific in spring and summer. Ciliate + dinoflagellate biomass in the latter ranged from <5 μg C L^{-1} to approximately 20 μg C L^{-1} (Booth et al. 1993). The highest mid and inner shelf microzooplankton abundances during our study approximated or exceeded those found in the productive coastal upwelling region off the U.S. Washington and Oregon coasts (Table 4). The highest reported ciliate and dinoflagellate biomass levels there were 9.1 μg C $L^{-1}$and 66.6 μg C L^{-1} (Neuer and Cowles 1994), whereas our maxima reached 40.4 μg C L^{-1} and 58.9 μg C L^{-1}, respectively. For the larger North Pacific region, only the southeast Bering Sea supported greater microzooplankton biomass, with ciliates and dinoflagellates each occasionally exceeding 70 μg C L^{-1} (Olson and Strom 2002). The high microzooplankton biomass we found in portions of the CGOA supports the idea that much of the primary production in this region passes through a microzooplankton trophic level.

Environmental variability and the microzooplankton community—The physically dynamic CGOA environment leads to short-term variations in resource availability to phytoplankton, which are reflected in phytoplankton biomass, community composition, and in situ growth rate (Strom et al. 2006). This same physical variability affects the microzooplankton community. For example, the spatial mosaic of diatom blooms and low-chlorophyll blue waters that we observed on the May shelf (Fig. 2B) was reflected in the microzooplankton biomass and community composition (Fig. 5B) as well as in the community grazing rate (bloom average: 0.35 d^{-1}; blue water average: 0.77 d^{-1}; note large range bars for May, Fig. 3B). The July diatom bloom in the ACC, hypothesized to result from a series of upwelling events (Strom et al. 2006), was associated with both high microzooplankton biomass (Fig. 5C) and moderate to high grazing rates (Fig. 3C, Table 1). Overall, short-term environmental variability leading to blooms of large phytoplankton cells was

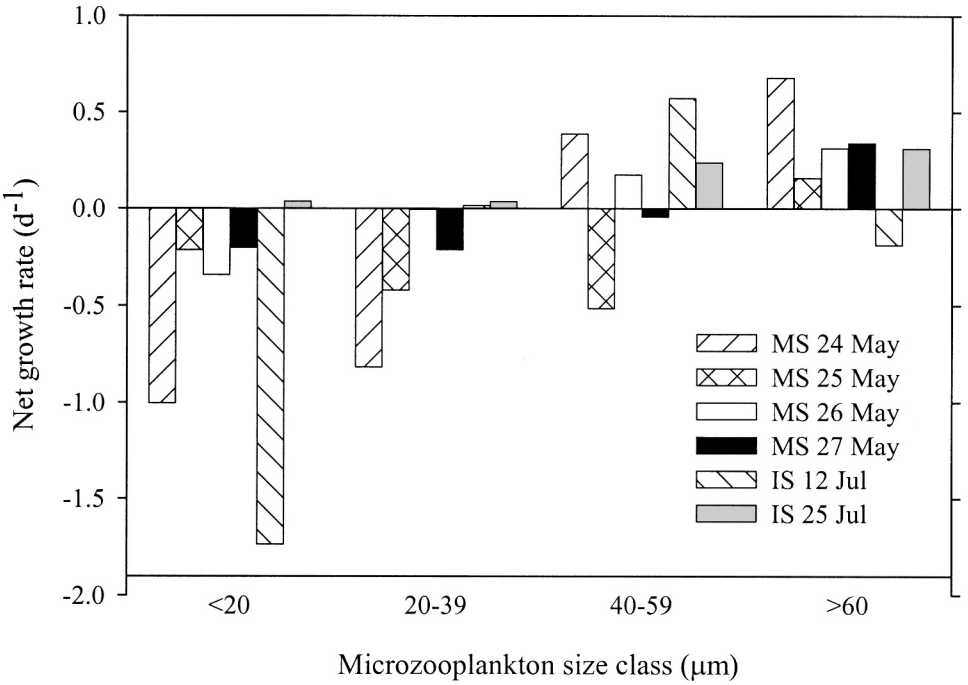


Fig. 7. Net growth rates (d^{-1}, average of duplicate determinations) for microzooplankton (all ciliates plus >20 μm dinoflagellates) in undiluted, unenriched seawater during 24 h dilution experiment incubations. Rates in four microzooplankton size classes shown for experiments initiated on six dates. MS, mid shelf; IS, inner shelf.

strongly correlated with increases in large-celled microzooplankton, particularly in May and July (Fig. 9). Thus environmental variability translated into variation in grazing potential within the large-celled community. Actual grazing rates, however, were seldom related to either prey or grazer biomass, and appeared to be modulated by other factors (*see* Regulation of microzooplankton grazing).

Over larger time and space scales, environmental conditions in the CGOA create persistent gradients in resource availability (Childers et al. 2005; Strom et al. 2006). These gradients will influence microzooplankton grazing through their effects on phytoplankton community composition. Our data show that small phytoplankton are more likely than large to be grazed by microzooplankton in the CGOA. Factors affecting phytoplankton cell size will therefore indirectly influence the fate of primary production. Because of their increased surface area : volume ratio, small cells tend to be competitively superior under

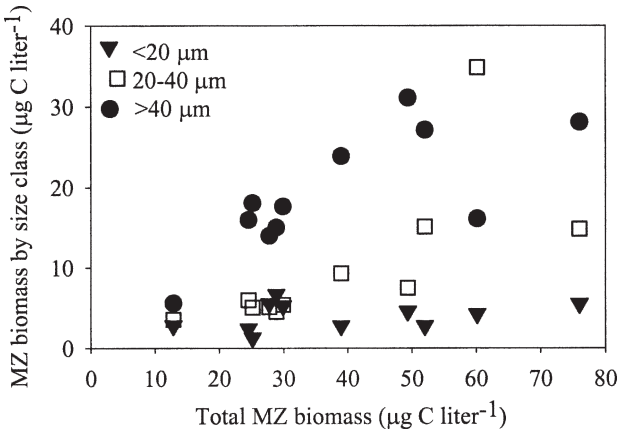


Fig. 8. Contribution of three microzooplankton size classes (<20, 20–40, and >40 μm) to total microzooplankton biomass on the inner shelf during 2001 microzooplankton grazing experiments.

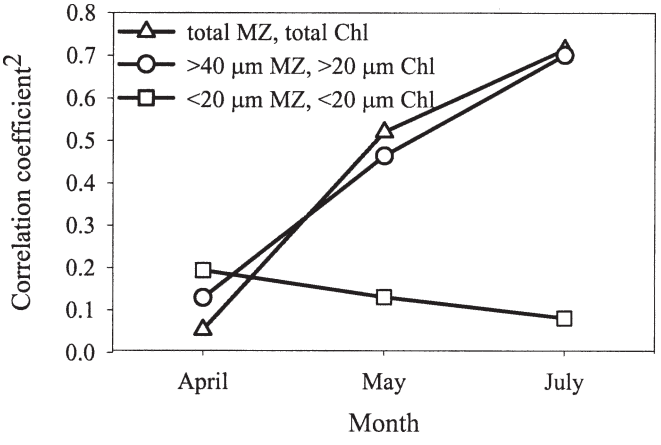


Fig. 9. Squared correlation coefficients (r^2) for relationships between chlorophyll biomass (Chl, μg L^{-1}) and microzooplankton biomass (MZ, μg C L^{-1}) during 3 months in the coastal Gulf of Alaska. Similarly low correlations within the smaller size classes (open squares) were obtained for <5 μm Chl versus <20 μm MZ, and <5 μm Chl versus <40 μm MZ.

Table 4. Spring and summer microzooplankton abundances ($\times 10^3$ cells L^{-1}) from the North Pacific and Bering Sea. Shown are ranges of reported abundances for ciliates (all) and dinoflagellates (>10 μm unless noted). Only studies that preserved ciliate samples in ≥2% acid Lugol's solution are reported; all samples were from upper 15 m of water column.*

Region	Ciliates	Dinoflagellates	Month(s)	Source
open subarctic				
WSP	6.3†	17.0†	May–Sep	Booth et al. 1993
WSP	3.4–28.0	nd	May–Sep	Strom et al. 1993
ESP‡	2.5–8.0	1.0–11.0	Jul	Saito et al. 2005
coastal subarctic				
Shelikof Strait	2.0–3.0	5.0–12.0§	May	Howell-Kubler et al. 1996
CGOA	1.9–16.9	2.1–36.9	Apr–May	Strom et al. 2001
CGOA	5.1–35.7	2.7–183.8	Apr–Jul	This study
coastal North Pacific				
US WA coast	3.0–27.8	nd	Oct	Landry and Hassett 1982
US OR coast	0.8–5.0	6.0–65.6	Apr–Sep	Neuer and Cowles 1994
Osaka Bay	0.1–1.0	nd	Jun	Uye et al. 1999
Bering Sea				
SE Bering	7.0–58.0	10.0–200.0	Jul–Aug	Olson and Strom 2002
SE Bering	4.2–63.3	10.2–139.2	Jul–Aug	Strom and Fredrickson unpubl. data

* WSP, western subarctic Pacific; ESP, eastern subarctic Pacific; CGOA, coastal Gulf of Alaska; nd, no data.
† Only average value reported.
‡ Data include response to iron fertilization of ESP region.
§ Abundance estimate includes only dinoflagellates >20 μm.

conditions of dissolved nutrient limitation. We have identified two modes of nutrient limitation in the CGOA that are associated with gradients in phytoplankton cell size (Strom et al. 2006). Seasonally, nitrogen limitation develops across portions of the shelf as stratification intensifies in spring and summer. Spatially, the CGOA appears governed by a persistent cross-shelf gradient in dissolved iron availability. The microzooplankton data reported here strongly support the hypothesis that a persistent cross-shelf gradient in resource availability drives the offshore ecosystem toward dominance by a low biomass of smaller cells (Fig. 6A).

Given these environmental gradients that influence cell size, phytoplankton susceptibility to microzooplankton grazing should increase overall with the spring–summer transition (increasing N limitation) and with distance offshore (increasing Fe limitation). Both trends are apparent in our $g:\mu_o$ ratios (Table 2). Furthermore, the contrasting microzooplankton communities supported across these gradients will influence the fate of the resultant microzooplankton production. The relatively large heterotrophic protists abundant in diatom blooms are important as prey for *Neocalanus* spp. and other coastal copepods (Gifford and Dagg 1991; Liu et al. 2005). Smaller microzooplankton associated with low-chlorophyll communities are less efficiently grazed by *Neocalanus* (Frost et al. 1983; Liu et al. 2005) and almost certainly introduce additional trophic levels into the food web supporting CGOA crustacean zooplankton.

Regulation of microzooplankton grazing—Grazing rates on the smallest phytoplankton were unrelated to microzooplankton biomass during our study. Thus, although microzooplankton biomass in small cell-dominated regions was variable (e.g., Fig. 5A), this variation was unrelated to grazing pressure. In contrast, increased grazing on <5-μm phytoplankton cells was strongly correlated with increased growth rates of these same cells. This suggests internal regulation of grazing by the growth state of the phytoplankton prey. Similar positive relationships between microzooplankton grazing and phytoplankton growth rates have been reported from both oceanic and coastal regions (Shinada et al. 2000; Strom 2002 and references therein; Verity et al. 2002), although the coupling can be disrupted by the presence of algal species that are toxic, unpalatable, or both (Irigoien et al. 2005).

The mechanism underlying the growth–grazing relationship could be regulation of feeding behavior by prey cell surface cues or prey-derived chemical signals, themselves related to phytoplankton nutritional (i.e., growth) condition (e.g., Monger et al. 1999; Matz et al. 2002; Strom et al. 2003). Worden and Binder (2003) showed short-term increases in microzooplankton grazing in response to changes in phytoplankton physiological state during dilution experiments in the Sargasso Sea and Gulf Stream. Alternatively, grazing rate variations could be driven by changes in microzooplankton community structure, as the abundances of specific micrograzer taxa wax and wane in concert with variations in the production of their prey. If community changes were occurring during our study they must have been rapid (to maintain the correlation with day-to-day changes in phytoplankton growth rates) and subtle (given the relative constancy in microzooplankton community composition at a given shelf location during our study).

Saturated grazing was the most prevalent in the grazing response to the smallest phytoplankton, reaching a frequency of 64% on the inner shelf (Fig. 4C). Prey concentrations had to be diluted at least two-fold (i.e., to ≤40% of ambient) before prey availability limited feeding rates in these saturated experiments (Fig. 4A). The inner shelf, which was experiencing a diatom bloom during all of our

cruises, also supported high rates of g(<5) and g(5–20) in most experiments (Fig. 3). Since the occurrence of saturated grazing was unrelated to <5-μm chlorophyll concentration, nonphotosynthetic organisms such as heterotrophic bacteria may have contributed to the diet of micrograzers feeding on the smallest phytoplankton. Bacterial production is often high in diatom blooms, and the abundance of bacteria in such blooms can be tightly controlled by nanoflagellates and other grazers (Brown et al. 2002; Hyun and Kim 2003 and references therein).

In contrast to the <5-μm phytoplankton, microzooplankton grazing on larger cells was apparently not regulated by the growth state of the prey, at least on the level of whole phytoplankton size classes. Growth and grazing rates were uncorrelated for 5–20 and >20-μm phytoplankton. On the other hand, g(>20) was positively correlated with microzooplankton biomass in PWS and on the inner shelf, a relationship driven by variation in abundance of larger microzooplankton (Fig. 8). Thus processes leading to an accumulation of large microzooplankton on the inner shelf should promote increased grazing on diatoms there. What are these processes?

As the 2001 season progressed from spring into summer, the biomass of large microzooplankton became increasingly correlated with the biomass of >20-μm phytoplankton (Fig. 9). This indicates a seasonal shift in the ability of large micrograzers to respond to increases in their prey. Warming temperatures may have enabled higher microzooplankton growth rates. Unfortunately there are few data available with which to evaluate this hypothesis. Hansen and Jensen (2000) report rates >1 d^{-1} for ciliates and heterotrophic dinoflagellates growing at 5°C. Other studies, however, suggest much lower dinoflagellate growth rates at low temperatures (Bjornsen and Kuparinen 1991; Archer et al. 1996), a constraint that may apply to heterotrophic protists generally (Rose and Caron 2007). An alternative explanation is a seasonal shift in top-down control of large microzooplankton. There are substantial decreases in crustacean zooplankton biomass between May and July in the CGOA (Coyle and Pinchuk 2005). The ontogenetic vertical migration undergone by *Neocalanus* spp., which removes them almost completely from surface waters by July, may release large microzooplankton from predation control and allow them to bloom in response to increases in their prey (e.g., Gifford and Dagg 1991; Liu et al. 2005).

Another way to examine whether micrograzer biomass controls rates of phytoplankton consumption is to compute biomass-specific grazing rates (G_{MZ}, the amount of phytoplankton C consumed per unit microzooplankton C per day) and compare them with theoretical values. Relatively high G_{MZ} values would indicate that microzooplankton were grazing at or near their potential per capita rates (such that community g might be regulated primarily by micrograzer biomass), whereas low G_{MZ} values would indicate that processes internal to the phytoplankton–microzooplankton relationship were acting to reduce per capita feeding rates. G_{MZ} values were calculated for microzooplankton feeding on all phytoplankton according to

$$G_{MZ} = (g)(Chl)(C : Chl)/MZ$$

C : Chl ratios of 65 and 25 were used for communities dominated by small and large phytoplankton, respectively, as determined for the CGOA environment during 2001 (E. Lessard pers. comm.). A ratio of 45 was used for PWS in May and July because that environment was in an intermediate condition (Fig. 2D). Biomass-specific ingestion rates measured during laboratory experiments are often higher than 2.0 d^{-1} and can be >5.0 d^{-1} (reviewed by Hansen et al. 1997, rates normalized to 20°C). In comparison, our rates were low, averaging 0.41, 0.75, and 0.64 d^{-1} for April, May, and July, respectively. The overall study average was 0.60 d^{-1} (SD 0.56; range 0.02 to 2.41). We did not quantify heterotrophic nanoflagellates in this study, although they were almost certainly important consumers of the smallest phytoplankton cells (e.g., *Synechococcus* and picoeukaryotes). Including these grazers in our estimate of the community biomass-specific ingestion rate would reduce the values further. This analysis indicates that CGOA microzooplankton were often feeding on phytoplankton at rates well below theoretical maxima.

Possible explanations for the low G_{MZ} values include low prey concentrations, feeding on alternative prey, and low prey quality. Low prey concentrations seem unlikely to explain low G_{MZ} for grazers of small prey, since these same grazers frequently exhibited saturated grazing functional responses (Fig. 4C). Larger dinoflagellates can be quite specific in their prey preferences (reviewed by Tillmann 2004) and may thus experience food limitation even in the midst of the seeming plenty of a diatom bloom. Ciliates and dinoflagellates of any size class might have fed on prey other than phytoplankton, including bacteria, detritus, or other microzooplankton. If alternative prey were significant in the diet, our phytoplankton-based g values would substantially underestimate total ingestion by microzooplankton. Finally, deterrent or grazing-resistant prey biochemistry or morphology might have reduced grazing rates relative to those in diet-optimized laboratory experiments.

The conclusion that microzooplankton were feeding at reduced per capita rates is supported by the low ciliate and dinoflagellate net growth rates that we observed (Fig. 7). Incubation artifacts and predation within the microzooplankton have been invoked as explanations for low net growth of ciliates and dinoflagellates (Hansen and Jensen 2000 and references therein). Although incubation artifacts may occur, experimental techniques similar to ours have yielded considerably higher rates in other regions, even in ecosystems dominated by the same taxa as the CGOA (e.g., Leakey et al. 1994; Strom and Strom 1996; Hansen and Jensen 2000). The decrease in net growth with decreasing microzooplankton cell size that we observed (Fig. 7) strongly suggests that larger microzooplankton preyed upon smaller cells during our incubations. This internal trophic link could be important in reducing the amount of CGOA primary production that is transferred to higher

trophic levels (e.g., metazoans). However, internal predation effects may have been exacerbated by the exclusion of meso- and macrozooplankton from our incubations. Copepods were shown to be important predators on larger CGOA microzooplankton during experiments conducted in parallel with ours (Liu et al. 2005).

Finally, our low per capita feeding rates refute the suggestion that the dilution technique systematically overestimates microzooplankton grazing rates. Dolan and McKeon (2005) used reported ciliate abundances (doubled to account for nano- and dinoflagellate contributions to grazing) and g values from dilution experiments to calculate per capita grazing rates. Because these rates were anomalously high in low-chlorophyll regions, they concluded that the dilution technique creates artifacts that can lead to large overestimates of microzooplankton grazing. In contrast, our biomass-specific grazing rates tended to be low. This demonstrates that the biomass of microzooplankton in the CGOA often exceeded that required to support measured rates of grazing on phytoplankton.

In summary, we found that, on average, microzooplankton consumed all production by phytoplankton <20 μm in size during our 2001 spring and summer studies in the CGOA. Microzooplankton communities dominated by heterotrophic dinoflagellates and, on occasion, large ciliates, also consumed approximately half the production by phytoplankton >20 μm, mainly diatoms. Little of the remaining diatom production was grazed by copepods during this study period (Liu et al. pers. comm.). Therefore microzooplankton were the major planktonic consumers of diatoms during spring and summer in the CGOA. Measured grazing rates, along with episodically high microzooplankton biomass levels, demonstrate that most CGOA primary production passed through at least one microzooplankton trophic level before reaching larger consumers.

The processes regulating microzooplankton grazing rates in the sea are poorly understood. Our data show that grazing on the smallest phytoplankton was tightly coupled to the growth rate of these cells, possibly through grazer behavioral responses to changes in prey physiological state. This coupling of rates likely resulted in the observed low biomass and low variability of <5-μm phytoplankton in the CGOA (Strom et al. 2006). Negative net growth rates of the smallest microzooplankton in our incubations indicate that they sustained substantial grazing pressure from the larger microzooplankton.

Large microzooplankton, in contrast, showed no response to the growth state of their prey, at least on the whole-community level. Changes in grazing pressure on >20-μm phytoplankton arose mainly through variations in the biomass of the largest ciliates and dinoflagellates. This biomass, in turn, became more closely correlated with >20-μm chlorophyll levels as the season progressed, possibly indicating the removal of top-down control on these ciliates and dinoflagellates as *Neocalanus* spp. copepods left the upper water column and overall mesozooplankton biomass decreased. Microzooplankton biomass-specific grazing rates during our study were low. This might have been due to prey scarcity, low prey quality, or other factors; the low rates indicate unrealized microzooplankton grazing capacity and suggest that, in combination with variable top-down control of large microzooplankton biomass, bottom-up influences strongly determine microzooplankton community grazing rates. Given the importance of microzooplankton grazing as a loss process affecting CGOA phytoplankton, gaining an understanding of these influences will be important to understanding the regulation and fate of production in this ecosystem.

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