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Phytoplankton blooms are strongly impacted by microzooplankton grazing in coastal North Pacific waters

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Abstract Phytoplankton growth and microzooplankton grazing were measured in two productive coastal regions of the North Pacific: northern Puget Sound and the coastal Gulf of Alaska. Rates of phytoplankton growth (range: 0.09–2.69 day^{-1}) and microzooplankton grazing (range: 0.00–2.10 day^{-1}) varied seasonally, with lowest values in late fall and winter, and highest values in spring and summer. Chlorophyll concentrations also varied widely (0.19–13.65 $\mu g\ l^{-1}$). Large (>8 μm) phytoplankton cells consistently dominated phytoplankton communities under bloom conditions, contributing on average 65% of total chlorophyll biomass when chlorophyll exceeded 2 $\mu g\ l^{-1}$. Microzooplankton grazing was an important loss process affecting phytoplankton, with grazing rates equivalent to nearly two-thirds (64%) of growth rates on average. Both small and large phytoplankton cells were consumed, with the ratio of grazing to growth (g:μ) for the two size classes averaging 0.80 and 0.42, respectively. Perhaps surprisingly, the coupling between microzooplankton grazing and phytoplankton growth was tighter during phytoplankton blooms than during low biomass periods, with g:μ averaging 0.78 during blooms and 0.49 at other times. This tight coupling may be a result of the high potential growth and ingestion rates of protist grazers, some of which feed on bloom-forming diatoms and other large phytoplankton. Large ciliates and *Gyrodinium*-like dinoflagellates contributed substantially to microzooplankton biomass at diatom bloom stations in the Gulf of Alaska, and microzooplankton biomass overall was strongly correlated with >8 μm chlorophyll concentrations. Because grazing tended to be proportionally greater when phytoplankton biomass was high, the absolute amount of chlorophyll consumed by microzooplankton was often substantial. In nearly two-thirds of the experiments (14/23), more chlorophyll was ingested by microzooplankton than was available for all other biological and physical loss processes combined. Microzooplankton were important intermediaries in the transfer of primary production to higher trophic levels in these coastal marine food webs.

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Introduction

Microzooplankton are now recognized as the dominant consumers of phytoplankton production in both oligotrophic and nutrient-rich regions of the open ocean (Capriulo et al. 1991; Sherr and Sherr 1992; Landry et al. 1997). The role of these grazers in the coastal ocean, especially in highly productive waters, is less clear. Do they feed primarily on bacteria and detritus, routing bacterial production to larger organisms in a "microbial loop" scenario? Or do microzooplankton play a significant role in the direct consumption of coastal phytoplankton? Significant microzooplankton grazing on coastal phytoplankton would influence the quantity and quality of the food supply to higher trophic levels. For example, overall food web efficiency (the proportion of primary production available to support organisms, such as fish, that occupy higher trophic levels) would be lowered by microzooplankton herbivory relative to a simpler "diatoms to copepods to fish" model of coastal food web function. On the other hand, there is growing evidence that heterotrophic protists, a major component of microzooplankton communities, are important nutritionally for coastal macrozooplankton (Stoecker and Capuzzo 1990). Several recent studies of coastal systems have demonstrated the importance of microzooplankton both as consumers of phytoplankton and as prey for mesozooplankton (Verity et al. 1993; Fessenden and Cowles 1994; Kiørboe and Nielsen 1994; Neuer and Cowles 1994; Lehrter et al. 1999; Levinsen et al. 1999). In our study, we wished to determine the

extent of microzooplankton grazing on phytoplankton in coastal waters of the eastern North Pacific.

Experiments to measure phytoplankton growth and microzooplankton grazing (23 total) were conducted in two productive ecosystems: northern Puget Sound and the coastal Gulf of Alaska (see Fig. 1). Northern Puget Sound is a deep, nutrient-rich estuary. Data from near the eastern end of the Strait of Juan de Fuca (available at http://www.ac.wwu.edu/~spmc/databases.htm) demonstrate that study site waters essentially never experience macronutrient depletion. Estuarine circulation, in conjunction with summer offshore upwelling, supplies nutrient-rich water from the outer coast, and additional nutrient inputs result from large rivers, primarily the Fraser (Harrison et al. 1994; Thomson 1994). Tidal mixing is vigorous due to large tidal exchange volumes and the complex topography and bathymetry of the area. In consequence, the region's waters are able to support a variable but typically high phytoplankton biomass throughout the spring and summer high-light season.

In contrast, the coastal Gulf of Alaska is a predominantly downwelling regime. Source waters for coastal downwelling, however, derive from the oceanic Gulf of Alaska, where surface macronutrient concentrations are persistently high (Wheeler 1993). In addition, coastal winds and consequent downwelling slacken during the summer high-light season, when weak upwelling can occur (Royer 1975). There is an enormous volume of freshwater run-off from streams and rivers along the entire southeast Alaskan coast, which can contribute to both stratification and to offshore transport and coastal upwelling (Royer 1979, 1982). Interactions between the various westward-flowing currents – the broad, diffuse Alaska Current and the swift, coastally confined Alaska Coastal Current – lead to formation of fronts, with associated convergent accumulation of plankton and/or entrainment of nutrients from depth. Relative to northern Puget Sound, little is known about seasonal cycles of nutrients and phytoplankton in this region. The waters are thought to be highly productive, at least episodically (Parsons 1986), although there are indications that nearshore waters can experience surface nutrient depletion in summer and fall (Reeburgh and Kipphut 1986; Whitledge, personal communication; for recent data see http://www.ims.uaf.edu:8000/globec/results/).

We used chlorophyll size-fractionation to determine the fate of small (<8 μm) and large (>8 μm) phyto-

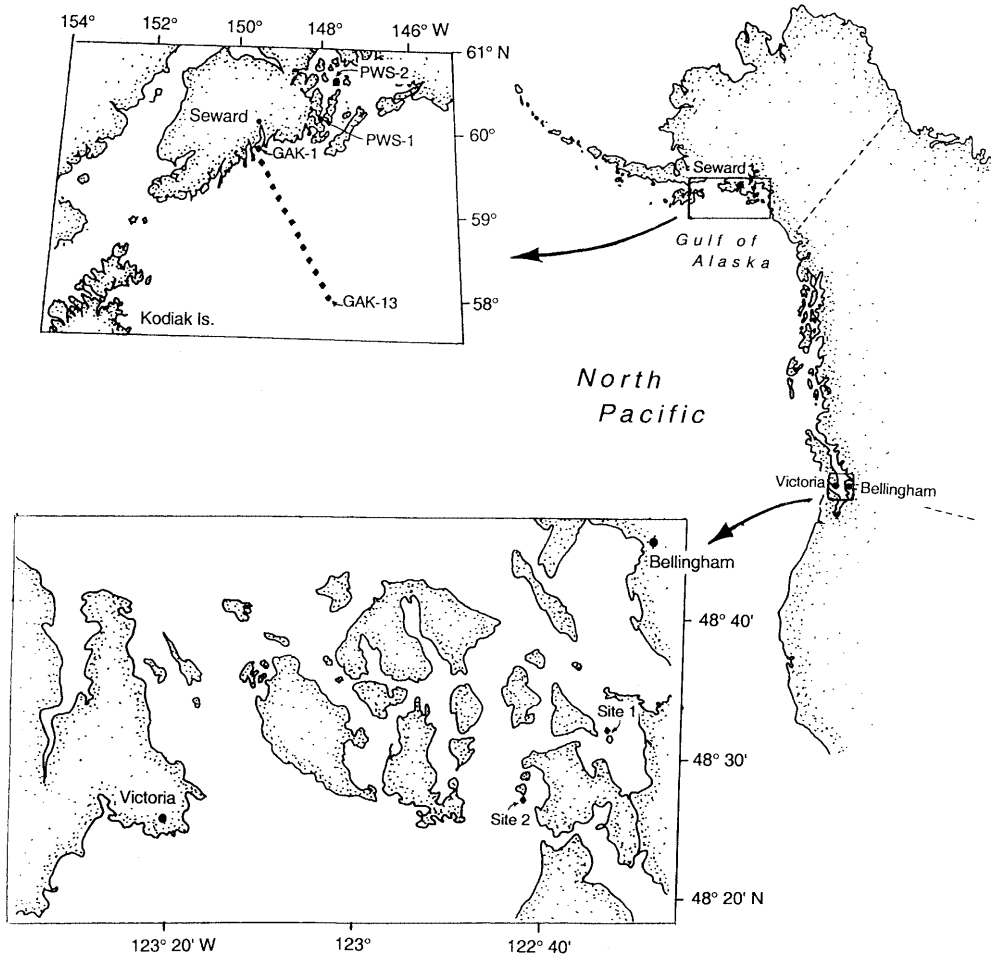

Fig. 1 Map of eastern North Pacific, with insets showing northern Puget Sound and coastal Gulf of Alaska sampling sites

plankton cells across a range of seasons and environmental conditions in the coastal North Pacific. As expected, microzooplankton grazing rates were equivalent to a substantial fraction (avg. 80%) of small phytoplankton growth rates. Our most important finding, however, was that microzooplankton grazing rates were always high during phytoplankton blooms dominated by large cells. At these times, grazing was equivalent to an average of 78% of phytoplankton growth, and the amount of chlorophyll ingested by microzooplankton generally exceeded that available for all other loss processes combined. These findings, in combination with other recent studies of coastal planktonic food webs, indicate that microzooplankton grazing constitutes a major loss process for phytoplankton in some coastal regions, and can play an important role in modulating blooms of large phytoplankton.

Materials and methods

Northern Puget Sound

Water was collected from site 1 (48°32′N; 122°34′W, between Hat and Saddlebag Islands) from November 1994 through August 1995, and from site 2 (48°29′N; 122°41′W, Burrows Bay) in August 1996 (Fig. 1). All carboys, bottles, and silicone tubing were precleaned by soaking in 10% HCl and rinsing in deionized water. Surface water was collected using a clean bucket and gently poured through Nitex screen (150 μm: site 1; 200 μm: site 2) into 23-l polycarbonate carboys. Approximately half of this water was gently filtered (peristaltic pump: 1994–1995; gravity: 1996) through a Gelman Versacap filter (pore size 0.2 μm) to prepare particle-free diluent for the dilution series. New Versacap filters were flushed with several liters of seawater before use. Dilution series were established by combining prescreened "whole" seawater with 0.2 μm filtered seawater in 2.3-l polycarbonate bottles. Filtered seawater was added to bottles first; whole seawater was then gently siphoned in using silicone tubing, the end of which was submerged in the filtered seawater. Source whole seawater carboys were periodically mixed by gentle manual agitation with a glass/Plexiglas "plunger". This was important in keeping large cells uniformly distributed in the source water.

For site 1 experiments, duplicate 2.3-l bottles were filled with each of the following fractions whole seawater: 1.0, 0.9, 0.6, 0.5, 0.3, 0.2, and 0.1 (total incubation bottles = 14). Initial chlorophyll levels were determined by sampling each bottle for total chlorophyll (50 ml sample filtered through glass fiber filter with nominal pore size of 0.7 μm) and by sampling the two undiluted bottles for chlorophyll in particles >8 μm (100 ml sample filtered through 8.0 μm pore size polycarbonate filter). After initial subsampling, bottles were refilled to the brim with whole seawater. Measured initial chlorophyll values were corrected for this refilling.

For site 2 experiments, 2.3-l bottles were filled with the following fractions whole seawater: 1.00, 0.75, 0.50, 0.35, 0.25, 0.20, 0.15, 0.10, and 0.05. Only the 1.00 treatment (undiluted) was duplicated (total incubation bottles = 10). Three additional 2.3-l bottles were filled with undiluted whole seawater and subsampled to determine initial chlorophyll levels (total and >8 μm chlorophyll, as above, in duplicate from each bottle). Initial chlorophyll levels in the incubation bottles were estimated from these measured values and theoretical dilution levels.

For all experiments, bottles were incubated in floating arrays moored just under the sea surface near the water collection sites. Nutrients were not added to these or to coastal Gulf of Alaska experiments because ambient nutrient levels are thought to be sufficient to saturate phytoplankton uptake (Harrison et al. 1994; Mackas and Harrison 1997). After 24 h, bottles were returned to the laboratory and sampled in duplicate for total and >8 μm chlorophyll concentration. Filters were immediately placed in 90% acetone and allowed to extract (−20 °C, dark) for 24 h. Chlorophyll levels were determined using a Turner model 112 fluorometer (Lorenzen 1966; Parsons et al. 1984) previously calibrated with pure chlorophyll *a*. Initial and final chlorophyll concentrations in the <8 μm ("small cell") size fraction were calculated from the difference between total and >8 μm ("large cell") chlorophyll concentrations. Net growth rates (k) for total, <8 μm, and >8 μm chlorophyll size fractions were then calculated assuming exponential growth and loss processes (Landry and Hassett 1982):

$$k = \frac{1}{t} \ln \frac{C_f}{C_i} \quad (1)$$

where t = incubation time and C_f and C_i = final and initial chlorophyll concentrations in each incubation bottle. Regression of net growth rate against dilution level allowed estimation of phytoplankton intrinsic growth rates (i.e. cell division rates, y-intercept of regression line) and microzooplankton grazing rates (slope of regression line). Occasionally (9 of 63 instances) regression analysis yielded negative rates of grazing. Because negative grazing is theoretically impossible, and because 95% confidence intervals for negative rates all include zero, negative rates were treated as zero in subsequent data analysis. In some cases, plots of net growth rate against dilution level showed evidence of saturated grazing (cf. Gallegos 1989). For these plots, phytoplankton growth rate (μ) was estimated from the regression intercept of the portion of the plot over which net growth increased linearly with increasing dilution; microzooplankton grazing rate (g) was then estimated as μ–net growth in undiluted bottles. For the Puget Sound experiment conducted 3 August 1995, apparently all but the two most dilute bottles had chlorophyll concentrations above grazing saturation levels. For this experiment, intrinsic growth rates (μ) were assumed to be equal to net growth rates in the two most dilute bottles (Gallegos and Jordan 1997), and microzooplankton grazing rates were estimated as described above.

Coastal Gulf of Alaska

Experiments were performed on two cruises of the R.V. "Alpha Helix" (HX205, early April 1998; HX 219, early May 1999). Most experiments were performed with water collected along the Seward line, extending southeast out of Seward, Alaska and across the continental shelf (Fig. 1). On each cruise, one additional station was sampled in Prince William Sound (PWS-1, southwest of Knight Island, 60°17′N; 148°01′W; PWS-2, west of Naked Island, 60°48′N; 147°35′W). Water was collected from a depth corresponding to 50% surface irradiance using precleaned (10% HCl) Niskin bottles rigged with silicone closure bands (30-l: 1998; 5-l: 1999). "Whole" seawater was prescreened by passage through a Nitex mesh (200 μm) as Niskin bottles were gently drained into polycarbonate carboys. Filtered seawater was prepared and incubation bottles filled as described above, except that 1.2-l polycarbonate incubation bottles were used for experiments in 1999. A preliminary experiment conducted with water from northern Puget Sound (April 1999, site 2) showed no significant difference between rates estimated using 1.2- versus 2.3-l bottles.

For experiments in 1998, dilution series consisted of duplicate incubation bottles at each of the following fractions whole seawater: 1.00, 0.79, 0.62, 0.49, 0.35, 0.22, and 0.10 (total incubation bottles = 14). For experiments in 1999, fractional whole seawater levels were 1.00, 0.75, 0.50, 0.35, 0.20, and 0.10, also in duplicate (total incubation bottles = 12). For all experiments, initial samples were taken from whole seawater source carboys during the bottle-filling process for chlorophyll analysis (total and >8 μm chlorophyll, filters as above, each in quadruplicate) and microscopy (500 ml preserved in acid Lugol's, 10% final conc.). Periodic checks for chlorophyll in source filtered seawater indicated levels that were below detection (1.2 l filtered). Bottles were covered with neutral

density screening to approximate 50% surface irradiance and incubated on deck in incubators flushed continuously with surface seawater. After 24 h, samples for final chlorophyll levels in each bottle were collected as described above. Filters were stored frozen (−20 °C, brief storage on dry ice during transport from Alaska) and analyzed within 1 month of sample collection as described above.

Time-averaged chlorophyll concentrations ($\bar{C}$, μg l^{-1}) in undiluted bottles were calculated according to Frost (1972):

$$\bar{C} = \frac{C_i\left(e^{(\mu-g)t} - 1\right)}{(\mu - g)t}$$

where μ = phytoplankton specific growth rate (day^{-1}) and g = specific grazing rate (day^{-1}). Microzooplankton ingestion rates (I, μg chl l^{-1} day^{-1}) were then calculated as:

$$I = g\bar{C}.$$

Preserved (Lugol's) microplankton samples were analyzed by inverted microscopy using a computer-aided digitizing system (Roff and Hopcroft 1986) to categorize and measure each cell. Samples from more dilute stations were preconcentrated four- to fivefold by settling in and siphoning from a graduated cylinder. Microzooplankton in 10-ml settling chambers were then enumerated in their entirety (>100 cells per sample counted and measured). Ciliates were identified as either tintinnids or aloricate choreotrichs ("oligotrichs") and further categorized by size; dinoflagellates were identified as belonging to one of four taxonomic groupings (*Gyrodinium*-like, *Protoperidinium*-like, *Gymnodinium*-like, and "other"). Only dinoflagellates >10 μm were included in this analysis (no ciliates <10 μm were encountered), and no attempt was made to separate dinoflagellates into autotrophic versus heterotrophic taxa (i.e. it was assumed that all >10 μm dinoflagellates feed, and thus constitute "microzooplankton"). Copepod nauplii were occasionally encountered, but were not included in the biomass and abundance estimates presented here. Measured linear dimensions were converted to cell volumes using standard geometric formulae; carbon biomass was then estimated from cell volume using the ratios 0.19 pg C μm^{-3} for ciliates (Putt and Stoecker 1989) and 0.14 pg C μm^{-3} for dinoflagellates (Lessard 1991).

Results

Chlorophyll stocks and size distributions

A wide range of initial chlorophyll concentrations (0.19–13.65 μg l^{-1}) was encountered over the course of these experiments. In northern Puget Sound, total chlorophyll varied seasonally, exhibiting a nearly 30-fold increase from late fall and winter to summer (Table 1). The percentage of total chlorophyll found in large (>8 μm) cells was nearly always high, particularly when overall chlorophyll biomass was high. Minimum contributions of large cells (avg. 30%) were observed at site 2 in August, whereas the site 1 average for the high-biomass summer period (May–August) was 78%. Nitrate and phosphate levels were high at all sites and seasons (Table 1), as is typical for this region (Harrison et al. 1994; Mackas and Harrison 1997).

In the coastal Gulf of Alaska, bloom conditions were found at the Prince William Sound station during April 1998 (Table 2), while oceanic conditions (total chlorophyll <0.5 μg l^{-1}, most chlorophyll in <8 μm cells)

Table 1 Water column conditions for microzooplankton grazing experiments conducted in northern Puget Sound. All experiments used surface water. Temperature and nutrient measurements for experiments in 1996 made at Shannon Point Marine Center, approximately 4 km from stn. 2

Date	Site	Temp. (°C)	Dissolved nutrients (μM)		Chlorophyll (μg l^{-1})	
			NO_3^-	PO_4^{3-}	Total	% >8 μm
15 Nov 94	1	8.5	35.9	2.14	0.81	41
21 Nov 94	1	8.0	40.0	3.28	0.67	58
28 Nov 94	1	7.8	36.0	2.82	0.49	45
21 Feb 95	1	6.0	36.9	2.14	0.47	nd
24 Feb 95	1	6.8	39.5	2.00	0.77	nd
18 May 95	1	9.5	23.1	1.60	2.32	87
30 May 95	1	11.5	16.5	1.20	3.99	74
2 Jun 95	1	10.9	14.5	0.90	6.14	82
18 Jul 95	1	13.5	15.0	0.02	11.50	55
31 Jul 95	1	13.2	24.5	0.02	13.65	89
3 Aug 95	1	14.5	17.5	0.02	12.97	81
1 Aug 96	2	10.0	29.9	1.97	1.03	27
8 Aug 96	2	12.6	22.4	1.76	0.93	32
21 Aug 96	2	11.1	25.3	2.36	1.42	30

Table 2 Water column conditions for microzooplankton grazing experiments conducted in the coastal Gulf of Alaska. See Fig. 1 for site locations (*PWS* Prince William Sound; *GAK* Gulf of Alaska). Depth column gives water collection depth followed by mixed layer depth in *parentheses*

Date	Site	Temp. (°C)	Depth (m)	Dissolved nutrients (μM)		Chlorophyll (μg l^{-1})	
				NO_3^-	PO_4^{3-}	Total	% >8 μm
3 Apr 98	PWS-1	4.8	5 (25)	2.05	0.57	6.58	50
31 Mar 98	GAK-1	5.1	10 (35)	5.44	0.68	1.12	54
2 Apr 98	GAK-4	6.0	10 (30)	13.89	0.94	0.26	19
5 Apr 98	GAK-11	5.6	10 (40)	12.68	1.67	0.42	10
10 May 99	PWS-2	5.2	20 (10)	6.77	0.50	0.19	4
9 May 99	GAK-1	5.2	20 (20)	8.14	0.69	2.04	3
9 May 99	GAK-4	5.5	20 (30)	15.79	0.84	1.93	6
8 May 99	GAK-9	6.4	10 (10)	3.84	0.45	3.60	51
7 May 99	GAK-13	5.7	17 (20)	9.55	0.72	3.11	14

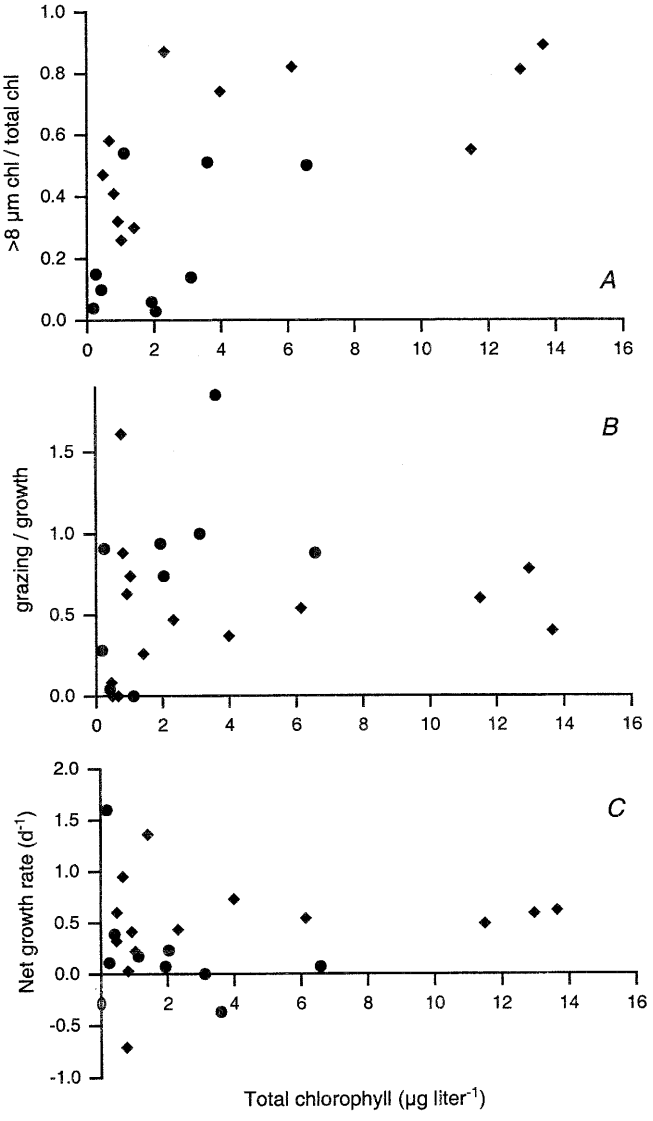

Fig. 2 **A** Proportion of total chlorophyll found in cells >8 µm. **B** Ratio of microzooplankton grazing rates (g) to phytoplankton growth rates (µ). **C** Average ($n = 2$) net growth rates of total chlorophyll in undiluted bottles as a function of total chlorophyll concentration (*diamonds* northern Puget Sound; *circles* coastal Gulf of Alaska). All chlorophyll data from initial dilution experiment samples

predominated on the middle and outer shelf. In May 1999, bloom conditions extended to outer shelf stations, while chlorophyll levels were extremely low at the innermost (Prince William Sound) station. Nitrate and phosphate levels were relatively high (>2.0 µM and >0.4 µM, respectively) during both months.

Taken together, the data from both sampling regions support the idea that addition of biomass to phytoplankton communities occurs through addition of cells in larger size classes, as opposed to increases in the abundance of small cells that dominate under "non-bloom" conditions (Fig. 2A). For experiments in which total chlorophyll was ≤ 2 µg l^{-1}, the percentage of total chlorophyll in large cells was low (avg. 27%), whereas experiments with total chlorophyll >2 µg l^{-1} had a greater proportion of chlorophyll in large cells (avg. 65%).

Phytoplankton growth

Phytoplankton growth rates in northern Puget Sound exhibited a seasonal cycle (Table 3; Fig. 3). Growth rates for the total chlorophyll size fraction increased from an average of 0.49 day^{-1} (range 0.25–0.92 day^{-1}) in late fall and winter, to an average of 1.30 day^{-1} (range 0.81–2.69 day^{-1}) in spring and summer. Phytoplankton growth rates were positively correlated with temperature in northern Puget Sound (Table 4). Similarly, in the coastal Gulf of Alaska (Table 5; Fig. 4), rates averaged higher in May (0.99 day^{-1}, range 0.54–2.21 day^{-1}) than in April (0.40 day^{-1}, range 0.09–0.65 day^{-1}). Differences between growth rates of <8 and >8 µm cells were not large in either environment. On the few dates when significant differences did exist (see marked values, Tables 3, 5), there was no indication that cells in one size class had consistently higher growth rates than cells in the other.

Microzooplankton grazing

In northern Puget Sound, microzooplankton grazing followed a seasonal cycle similar to that of phytoplankton growth (Table 3; Fig. 3). Rates were generally lower in fall and winter (avg. 0.35 day^{-1}, range 0.00–1.48 day^{-1}) and higher in spring and summer (avg. 0.71 day^{-1}, range 0.32–2.10 day^{-1}). As for phytoplankton growth, microzooplankton grazing in northern Puget Sound was positively correlated with temperature (Table 4). In the coastal Gulf of Alaska grazing also reflected phytoplankton growth, with rates increasing as the season progressed (Table 5; Fig. 4). Rates in May averaged 0.72 day^{-1} (range 0.51–1.20 day^{-1}) and were consistently higher than April rates, which averaged 0.24 day^{-1} (range 0.00–0.59 day^{-1}). As for phytoplankton growth, there was no clear pattern of consistently higher grazing on one phytoplankton size fraction relative to the other.

Growth–grazing relationships

Net growth rates (i.e. Eq. 1) in undiluted bottles most closely represent temporal changes in the natural <200 µm plankton community. That is, the rate of biomass accumulation in those bottles reflects the outcome of co-occurring growth and loss processes affecting the <200 µm plankton. As a measure of the robustness of the regression approach for estimating μ and g, we compared net growth rates as directly measured in undiluted bottles with net growth rates as predicted from μ–g for the corresponding dilution series (Fig. 5). Agreement between the two estimates was good

Table 3 Phytoplankton growth and microzooplankton grazing rates (±95% CL) for experiments conducted in northern Puget Sound. Rates are given for three chlorophyll size fractions (total, <8 μm, >8 μm) (*nd* not determined; *nc* not calculable: chlorophyll at the end of this experiment was almost all in the >8 μm size fraction, so that rates for the <8 μm fraction could not be estimated)

Date	Site	Phytoplankton growth (day^{-1})			Microzooplankton grazing (day^{-1})		
		Total	>8 μm	<8 μm	Total	>8 μm	<8 μm
15 Nov 94	1	0.25 (0.09)	0.37 (0.11)	0.14 (0.18)	0.22 (0.18)	0.05 (0.21)	0.38 (0.33)
21 Nov 94	1	0.70 (0.30)	0.70 (0.39)	0.79 (0.52)	−0.17 (0.68)	0.25 (0.90)	−0.58 (1.34)
28 Nov 94	1	0.23 (0.18)	0.22 (0.20)	0.19 (0.31)	−0.31 (0.32)	−0.25 (0.38)	−0.43 (0.59)
21 Feb 95	1	0.36 (0.10)	nd	nd	0.03 (0.16)	nd	nd
24 Feb 95	1	0.92 (0.40)	nd	nd	1.48 (0.63)	nd	nd
18 May 95	1	0.89 (0.17)	0.78 (0.15)	0.99 (1.29)	0.42 (0.32)	0.35 (0.28)	−0.09 (2.38)
30 May 95	1	1.10 (0.11)	1.18 (0.12)	1.06 (0.56)	0.41 (0.20)	0.51 (0.21)	0.42 (1.01)
2 Jun 95	1	1.25 (0.06)	1.21 (0.12)	1.13 (0.58)	0.67 (0.11)	0.51 (0.21)	0.75 (1.12)
18 Jul 95	1	1.21 (0.10)	1.33 (0.27)	1.05 (0.20)	0.72[a]	0.87[a]	0.52[a]
31 Jul 95[b]	1	0.81 (0.15)	0.65 (0.16)	1.61 (0.47)	0.32 (0.26)	0.35 (0.28)	0.42 (0.84)
3 Aug 95	1	2.69 (0.21)	2.74 (0.13)	3.00 (0.53)	2.10 (0.10)	2.10 (0.13)	2.09 (0.06)
1 Aug 96	2	0.86 (0.46)	2.20 (0.36)	nc	0.64[a]	0.60[a]	nc
8 Aug 96	2	1.10 (0.32)	1.38 (0.23)	0.93 (0.49)	0.69[a]	0.47[a]	0.89[a]
21 Aug 96[b]	2	1.83 (0.53)	3.06 (0.41)	1.08 (0.85)	0.47[a]	0.69[a]	1.05 (0.72)

[a] Saturated grazing observed on these phytoplankton size fractions; rates calculated as described in "Materials and methods"
[b] Difference between phytoplankton growth rates in <8 and >8 μm size fractions significant on these dates, as indicated by non-overlapping 95% confidence intervals

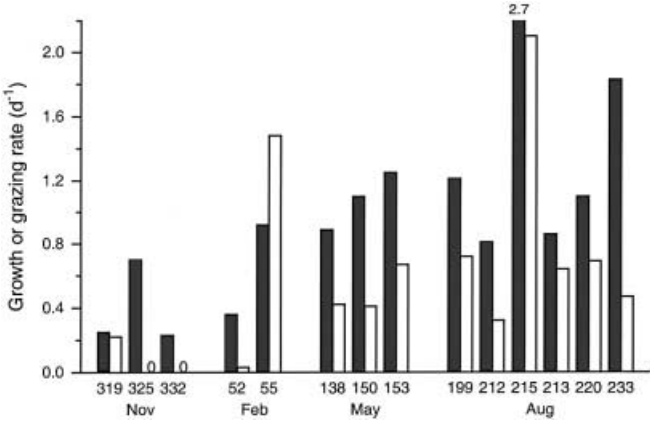

Fig. 3 Seasonal cycle in phytoplankton growth (*solid bars*) and microzooplankton grazing (*open bars*) in northern Puget Sound (data for total chlorophyll only). Compilation of data from two different years

(slope = 0.97, Pearson correlation coefficient = 0.987). The outlier from the 28 November 1994 experiment was apparently a consequence of the large negative grazing estimate from that date and was not included in either the correlation analysis or the following considerations of μ versus *g* relationships.

Overall, the proportion of phytoplankton growth removed by microzooplankton grazing in these experiments was substantial. That is, grazing rates often equaled or exceeded 50% of phytoplankton growth rates (Figs. 6, 7). Considering all experiments, the average ratio of grazing to growth (g:μ) for total chlorophyll was 0.64 (SD = 0.48, $n = 22$), indicating that, on average, microzooplankton consumed nearly two-thirds of the phytoplankton cells produced during these incubations. Furthermore, microzooplankton grazing was not associated solely or even predominantly with small (<8 μm) phytoplankton cells. Rates of grazing on large cells were often high, both in an absolute sense (Tables 3, 5) and relative to large cell growth rates (Figs. 6, 7). We hasten to add that there were exceptions to this general rule: on two occasions (1 August 1996 in Puget Sound, 8 May 1999 in the Gulf of Alaska), large excesses of μ over *g* for the >8 μm size fraction, coupled with high absolute growth rates, apparently allowed large cells to completely dominate phytoplankton biomass by the end of the incubations, rendering <8 μm chlorophyll undetectable within the precision of the size-fractionation method.

Microzooplankton grazing tended to be a larger proportion of phytoplankton growth when total chlorophyll biomass was high (i.e. during phytoplankton blooms, total chlorophyll >2 μg l^{-1}). That is, when biomass was low, *g* was a highly variable fraction of μ, but was frequently low or undetectable (Fig. 2B). For all low biomass experiments (total chlorophyll <2 μg l^{-1}), g:μ averaged 0.49 (range 0.00–1.61, SD = 0.51, $n = 11$). However, during blooms, grazing was always a substantial fraction of phytoplankton growth, with g:μ averaging 0.78 (range 0.37–1.85, SD = 0.42, $n = 11$).

Another way of examining the relationship between growth and grazing is to consider net growth rates as determined from chlorophyll accumulation rates in undiluted bottles (Eq. 1). If microzooplankton consume proportionally more phytoplankton production when biomass is high, then phytoplankton net growth rates should be lower during blooms than during non-bloom periods. This was the case for our data: net growth rates from bloom experiments averaged 0.31 day^{-1}, while rates from non-bloom experiments averaged 0.44 day^{-1}. There were also consistent differences in net growth rates between the northern Puget Sound and coastal Gulf of Alaska systems, even at a given chlorophyll level (Fig. 2C). Comparing all Gulf of Alaska rates with those

Table 4 Significance of linear relationships between temperature, biomass levels, and rate processes measured in coastal North Pacific grazing experiments. The relevant chlorophyll size fraction (total, <8 μm, or >8 μm) is indicated for each relationship (n no. of observations; r^2 coefficient of determination; P probability for slope of relationship)

	Equation	n	r^2	P
Northern Puget Sound				
Phyto. Growth (total) vs. temperature	$\mu = 0.17T–0.75$	14	0.49	0.005
Microzoo. Grazing (total) vs. temperature[a]	$g = 0.16T–1.15$	13	0.55	0.004
Microzoo. Grazing (total) vs. total chl		14	0.19	0.113
Microzoo. Grazing vs. phyto. Growth (both >8)[b]	$g = 0.43\mu + 0.01$	11	0.49	0.016
Microzoo. Grazing vs. phyto. Growth (both <8)[b]	$g = 0.64\mu–0.10$	10	0.60	0.009
Coastal Gulf of Alaska				
Microzoo. Biomass vs. total chl	$M = 5.12C + 6.50$	9	0.65	0.008
Ciliate biomass vs. >8 μm chl	$Cil = 5.23C_{>8} + 5.75$	9	0.70	0.005
Dinoflagellate biomass vs. >8 μm chl	$Din = 5.61C_{>8} + 3.99$	9	0.75	0.003
Ciliate biomass vs. <8 μm chl	–	9	0.25	0.170
Dinoflagellate biomass vs. <8 μm chl	–	9	0.25	0.166
Microzoo. Grazing (total) vs. total chl	–	9	0.06	0.535
Microzoo. Grazing vs. chl (both >8)	–	9	0.00	0.879
Microzoo. Grazing vs. chl (both <8)	–	8	0.02	0.718
Microzoo. Grazing (total) vs. microzoo. Biomass	–	9	0.01	0.785
Microzoo. Grazing vs. phyto. Growth (both >8)	$g = 0.84\mu–0.25$	9	0.91	<0.001
Microzoo. Grazing vs. phyto. Growth (both <8)		8	0.24	0.213

[a] Excluding 24 Feb 1995 outlier
[b] Excluding 28 Nov 1994 data

Table 5 Phytoplankton growth and microzooplankton grazing rates for experiments conducted in the coastal Gulf of Alaska. Rates (±95% CL) are given for three chlorophyll size fractions (total, <8 μm, >8 μm) (*nd* not determined; *nc* not calculable) (see Table 3 legend for further details)

Date	Site	Phytoplankton growth (day^{-1})			Microzooplankton grazing (day^{-1})		
		Total	>8 μm	<8 μm	Total	>8 μm	<8 μm
3 Apr 98	PWS-1	0.40 (0.10)	0.53 (0.07)	0.24 (0.22)	0.35 (0.17)	0.30 (0.13)	0.41 (0.37)
31 Mar 98	GAK-1	0.09 (0.05)	0.04 (0.11)	0.12 (0.15)	–0.06 (0.09)	–0.09 (0.19)	–0.04 (0.27)
2 Apr 98	GAK-4	0.65 (0.13)	0.84 (0.10)	0.60 (0.17)	0.59 (0.22)	0.43 (0.18)	0.62 (0.29)
5 Apr 98	GAK-11	0.46 (0.10)	0.62 (0.18)	0.44 (0.10)	0.02 (0.17)	0.17 (0.31)	0.00 (0.17)
10 May 99[b]	PWS-2	2.21 (0.21)	0.65 (0.55)	2.20 (0.18)	0.61[a]	0.16 (0.70)	0.58[a]
9 May 99[b]	GAK-1	0.88 (0.17)	2.23 (0.59)	0.70 (0.14)	0.65[a]	1.81[a]	0.53 (0.22)
9 May 99	GAK-4	0.54 (0.16)	0.57 (0.11)	0.54 (0.18)	0.51 (0.29)	0.04 (0.19)	0.55 (0.23)
8 May 99	GAK-9	0.65 (0.20)	1.05 (0.12)	nc	1.20 (0.35)	0.79 (0.21)	nc
7 May 99[b]	GAK-13	0.65 (0.20)	1.68 (0.98)	0.13 (0.14)	0.65[a]	0.92[a]	0.32 (0.24)

[a] Saturated grazing observed on these phytoplankton size fractions; rates calculated as described in "Materials and methods"
[b] Difference between phytoplankton growth rates in <8 and >8 μm size fractions significant on these dates, as indicated by non-overlapping 95% confidence intervals

collected during the same season (spring) in northern Puget Sound, Gulf of Alaska net growth rates were consistently lower (0.25 versus 0.57 day^{-1}).

Plankton community composition

The composition of the phytoplankton community in the coastal Gulf of Alaska (Table 6) varied from almost complete diatom dominance (stn. GAK-9, May 1999) to dominance by an assemblage of small (2–10 μm) flagellates (stns. GAK-1 and GAK-4, May 1999). The phytoplankton assemblage could vary dramatically over short time and space scales. For example, stations GAK-9 and GAK-13, sampled 1 day apart in 1999, separated by only 75 km, and supporting similar total chlorophyll levels, hosted entirely different communities during our study, the former dominated by *Chaetoceros* sp. diatoms (with 51% of chlorophyll in large cells) and the latter by small gymnodinioid dinoflagellates (with only 14% of chlorophyll in large cells). In general, stations with a large fraction of total chlorophyll in large cells (PWS-1 and GAK-1 in 1998, GAK-9 in 1999) had diatoms as a major component of the phytoplankton community.

Total microzooplankton biomass ranged from 3.25 to 41.60 μg C l^{-1} (Table 6) and tended to be partitioned nearly equally into dinoflagellates and ciliates. Exceptions were stations GAK-4 and GAK-11 in 1998. These stations exhibited oceanic conditions (low chlorophyll biomass, $>80\%$ of chlorophyll in small cells), and microzooplankton communities consisting largely of ciliates (Fig. 8). The highest percent contribution of dinoflagellates was at the diatom-dominated station, GAK-9 (Fig. 8), though, in general, relationships between microzooplankton taxonomic composition or cell size and phytoplankton community size structure were weak (data not shown).

Though higher microzooplankton stocks were associated with higher total chlorophyll levels in the coastal Gulf of Alaska (Table 4), this relationship did not apply

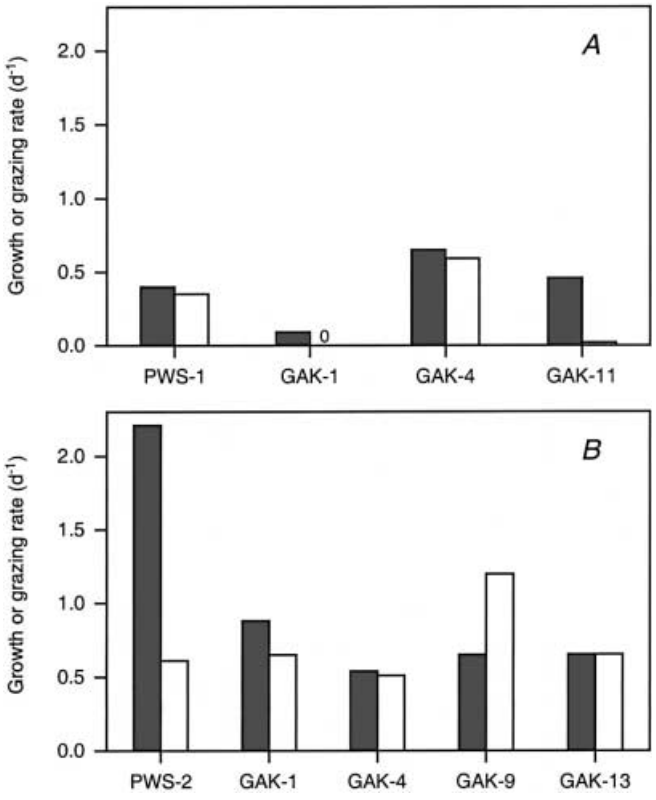

Fig. 4 Rates of phytoplankton growth (*solid bars*) and microzooplankton grazing (*open bars*) in the coastal Gulf of Alaska during **A** April 1998 and **B** May 1999. Data for total chlorophyll only

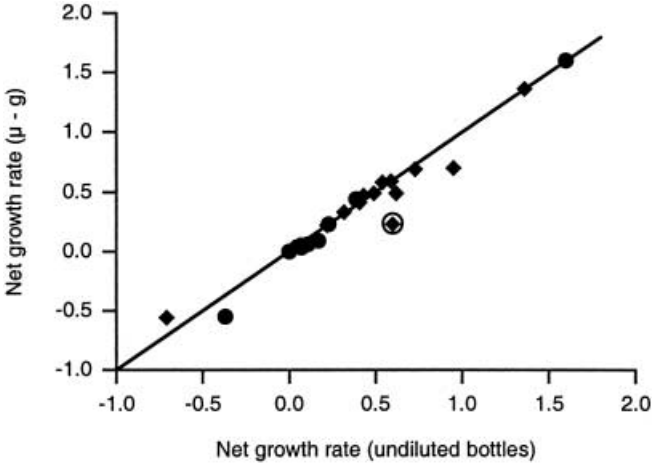

Fig. 5 Comparison between two different estimates of total chlorophyll-based net growth rate for each dilution experiment; *x*-axis: derived from rate of chlorophyll accumulation in duplicate undiluted bottles (see Eq. 1); *y*-axis: derived from the difference between phytoplankton intrinsic growth rates (μ) and microzooplankton grazing rates (g) as estimated from regression analysis of entire dilution series [*diagonal line* shows 1: 1 relationship; *encircled point* (outlier) excluded from all analyses of g:μ ratios; *diamonds* northern Puget Sound; *circles* coastal Gulf of Alaska]

uniformly to the individual phytoplankton size classes. There was a strong positive relationship between >8 μm chlorophyll concentrations and both ciliate and dinoflagellate biomass (Table 4; Fig. 9A, C). Curiously, however, this finding did not extend to <8 μm chlorophyll, which showed no clear relationship with the biomass of either microzooplankton group (Table 4; Fig. 9B, D).

Discussion

A major finding of our study is that microzooplankton grazers remove a substantial portion of phytoplankton production in coastal waters of the eastern North Pacific. On average, microzooplankton grazing was equivalent to 64% of phytoplankton growth. This means that nearly two-thirds of all phytoplankton cells produced during these experiments were consumed by microzooplankton grazers. Given that we conducted experiments across a wide range of seasons, phytoplankton biomass levels, and phytoplankton community types, we believe these results are representative of this coastal ecosystem as a whole.

Other investigators have measured microzooplankton grazing in coastal ecosystems ranging from polar to subtropical latitudes. We evaluated the extent to which our findings can be generalized by examining these published data on grazing rates. Nearly all studies show a substantial impact of microzooplankton grazing on coastal phytoplankton, with study-averaged grazing:growth ratios ranging from 0.17 to 1.15 (Table 7). The average value of g:μ taken across all experiments and studies was 0.71 ($n = 177$ experiments). This overall result demonstrates that microzooplankton grazing is an important – and often the dominant – loss process affecting phytoplankton in coastal waters around the world.

Phytoplankton growth rates from northern Puget Sound showed a pronounced seasonality. Rate increases were significantly related to temperature increases (Table 4), and undoubtedly also were driven by higher spring and summer light levels. Seasonal nutrient limitation is unlikely in these upwelling-supplied waters. A few of the measured phytoplankton growth rates (e.g. 9 May 1999 at GAK-1, several August rates from Puget Sound) were considerably higher than maximum rates predicted from empirical temperature versus growth rate relationships (e.g. Eppley 1972). This raises the possibility that the high growth rates were due in part to increases in chlorophyll per cell, perhaps as a photoadaptive response to changing light conditions during the incubation, rather than to true biomass increases (McManus 1995). Curiously, these exceptionally high growth rates were most often associated with the >8 μm chlorophyll size fraction, suggesting either that large cells are particularly prone to photoadaptive responses, or that published predictive relationships do not necessarily encompass the full range of physiological potential for certain large-celled taxa (see, for example, Sommer 1989). In any case,

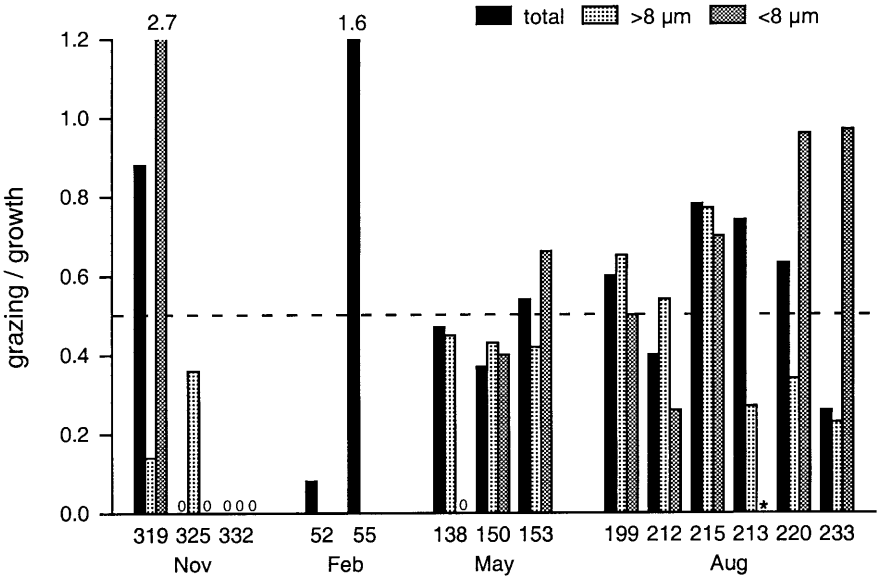

Fig. 6 Microzooplankton grazing as a fraction of phytoplankton growth for three chlorophyll size fractions (*solid bars* total; *lightly stippled bars* >8 µm; *heavily stippled bars* <8 µm) in northern Puget Sound (day of the year shown for each month). Measured values of zero are indicated above *x*-axis. *Dashed horizontal line* indicates grazing equivalent to half of phytoplankton growth. Size-fractionated rates were not measured during February experiments (*, not calculable)

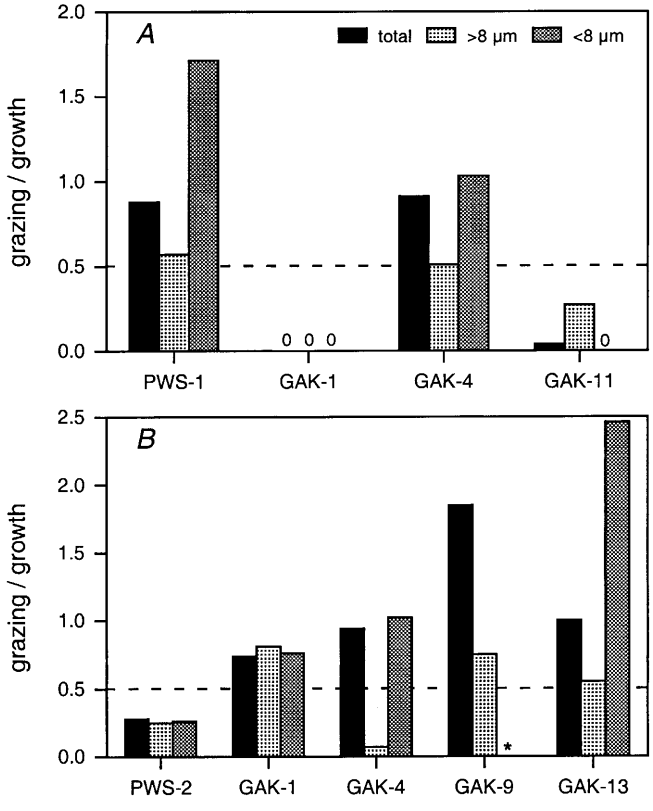

Fig. 7 Microzooplankton grazing as a fraction of phytoplankton growth for three chlorophyll size fractions (*solid bars* total; *lightly stippled bars* >8 µm; *heavily stippled bars* <8 µm) at various stations in the coastal Gulf of Alaska during **A** April 1998 and **B** May 1999. Measured values of zero are indicated above *x*-axis. *Dashed horizontal line* indicates grazing equivalent to half of phytoplankton growth (*, not calculable)

photoadaptation should not affect estimates of g, so that erroneously high growth rate estimates would yield erroneously low values of the $g{:}\mu$ ratio. Thus our argument that g averages a high fraction of µ would be a conservative one.

The partitioning of phytoplankton biomass, growth, and consumption into size classes during these experiments was extremely revealing of food web function. First, increases in phytoplankton biomass – blooms – seemed to occur through addition of "new" size classes of larger cells, rather than through accumulation of small cells (Fig. 2A). This same phenomenon has been reported for other ocean regions, including the Mediterranean, the Southern Ocean, and the western North Pacific (reviewed by Chisholm 1992), and is increasingly a fundamental assumption of planktonic food web models, particularly those using allometric scaling (e.g. Moloney and Field 1991; Carr 1998). In our observations, nearly all instances of initial chlorophyll concentrations exceeding 2 µg l^{-1} were associated with a large-cell-dominated phytoplankton community (i.e. $>50\%$ of total chlorophyll in the >8 µm size fraction, Tables 1, 2).

Models of high-productivity regions often go on to assume that a shift to larger phytoplankton cells gives rise to a corresponding shift in the grazer community, from micrograzers to macrozooplankton such as copepods (e.g. Moloney and Field 1991; Lalli and Parsons 1997). This fundamental change in grazer type is not supported by our data. We found microzooplankton grazing to be of greater importance, both proportionally and absolutely, when phytoplankton biomass was high and large phytoplankton were dominant (Fig. 2B). In other words, grazing:growth ratios were higher when chlorophyll biomass was high (avg. $g{:}\mu = 0.78$ for total chlorophyll >2 µg l^{-1}) than when chlorophyll biomass was low (avg. $g{:}\mu = 0.49$ for total chlorophyll <2 µg l^{-1}). These higher $g{:}\mu$ ratios applied to both phytoplankton size fractions. For small (<8 µm) phytoplankton cells, $g{:}\mu$ averaged 0.85 when total chlorophyll biomass was high, and 0.74 when biomass was low.

Table 6 Initial abundance (cells l^{-1}) and biomass (μg C l^{-1}) of ciliates (*C*) and >10 μm dinoflagellates (*D*), and phytoplankton community composition for experiments conducted in the coastal Gulf of Alaska

Date	Site		Microzooplankton		Phytoplankton
			Abund.	Biomass	
3 Apr 98	PWS-1	C	16,900	23.90	Many diatoms, incl. *Stephanopyxis*, *Coscinodiscus*, *Skeletonema*, *Nitzschia*, *Thalassiosira*; many small (<10 μm) *Gymnodinium*-like dinoflagellates, cryptomonads
		D	22,100	17.70	
31 Mar 98	GAK-1	C	8,890	8.43	Assemblage similar to PWS-1, but cells much less abundant
		D	12,900	10.40	
2 Apr 98	GAK-4	C	1,940	2.26	Small (3–5 μm) coccoid flagellates, a few *Nitzschia*-like pennate diatoms
		D	2,330	0.99	
5 Apr 98	GAK-11	C	7,690	15.00	Mixed assemblage of small (<10 μm) dinoflagellates, prasinophytes, cryptomonads, and prymnesiophytes; a few diatoms (*Chaetoceros*, *Thalassiosira*, *Thalassiothrix*, *Nitzschia*)
		D	2,130	2.38	
10 May 99	PWS-2	C	8,890	5.26	Mixed assemblage of small (2–10 μm) flagellates similar to GAK-11; diatoms including *Nitzschia*, *Chaetoceros*, *Lauderia*-like
		D	9,780	5.35	
9 May 99	GAK-1	C	4,780	3.19	Mixed assemblage of small (2–10 μm) flagellates similar to GAK-11
		D	10,800	3.39	
9 May 99	GAK-4	C	8,670	4.39	Mixed assemblage of small (2–10 μm) flagellates, very abundant, similar to GAK-11; a few *Nitzschia*
		D	7,330	1.96	
8 May 99	GAK-9	C	7,560	13.40	Many diatoms, dominated by small (10 × 15 μm), long-spined *Chaetoceros*; some *Nitzschia*, *Rhizosolenia*, and large *Chaetoceros* (many fragments of the latter two)
		D	36,900	21.30	
7 May 99	GAK-13	C	5,560	9.41	Dominated by small (<10 μm) *Gymnodinium*-like dinoflagellates; some prymnesiophytes; diatom assemblage similar to GAK-9, but less abundant
		D	14,700	8.32	

Similarly, $g{:}\mu$ for large (>8 μm) cells averaged 0.55 and 0.26 under high and low biomass conditions, respectively.

The significance of the above $g{:}\mu$ comparison, which is also borne out by observations of net growth in undiluted bottles, is twofold. First, small phytoplankton cells consistently experience a higher relative microzooplankton grazing pressure than large cells. This discrepancy has been reported previously (Strom and Welschmeyer 1991; Froneman et al. 1996) and is consistent with the observed dominance of blooms by large phytoplankton. This dominance also signifies that other loss processes (e.g. sinking, grazing by mesozooplankton or benthic organisms) are insufficient, at least episodically, to balance intrinsic rates of large-cell growth. At least in our study, consistently higher intrinsic growth rates for large phytoplankton were not observed, so growth rate differences apparently did not play a role in determining the composition of blooms.

A second important aspect of the $g{:}\mu$ ratios is their tendency to be higher during blooms. This suggests that blooms are better conceptualized as the persistent manifestation of a transient imbalance between production and loss, rather than as an ongoing disequilibrium. This is not to say that net growth rates are always zero (i.e. rates of intrinsic growth and grazing always equal) during blooms. In our data set, net growth rates for blooms in Puget Sound averaged 0.57 day^{-1} and were consistently higher than net growth rates for coastal Gulf of Alaska blooms. An earlier spring sampling time in Puget Sound might well have yielded rates more closely resembling those from April and May in the Gulf of Alaska. However, if data from these two regions are representative, the planktonic food webs in the two systems appear to function differently, with perhaps a greater degree of "top down" regulation of microzooplankton biomass in Puget Sound, or a phytoplankton flora there that is somehow (morphologically or chemically) less available to microzooplankton grazers.

Comparing rates of μ and g, the most direct way to assess relative rates of growth and grazing, does not indicate the quantity of phytoplankton biomass consumed. We prepared a budget to compare the amount of chlorophyll ingested by microzooplankton (Eq. 3) with the amount that accumulated in undiluted bottles during the incubation period (Table 8). Accumulated chlorophyll represents the phytoplankton biomass that would have been available for all other loss processes affecting phytoplankton in the water column, including consumption by other grazers (macrozooplankton, benthos) and physical export (sinking, advection). Note that phytoplankton mortality (e.g. lysis due to viral infection, natural mortality) is accounted for in our experiments (though not explicitly) as a negative component of the phytoplankton intrinsic growth rate, μ. Because grazing tended to be proportionally greater when phytoplankton biomass was high, the absolute amount of chlorophyll consumed by microzooplankton was substantial. In nearly two-thirds of the experiments (14/23), more chlorophyll was ingested by microzooplankton than was available for all other loss processes combined ($I/A > 1.0$, Table 8).

The responsiveness of the microzooplankton community to phytoplankton blooms is particularly evident in the microzooplankton biomass data. Both ciliate and dinoflagellate biomass showed strong positive relation-

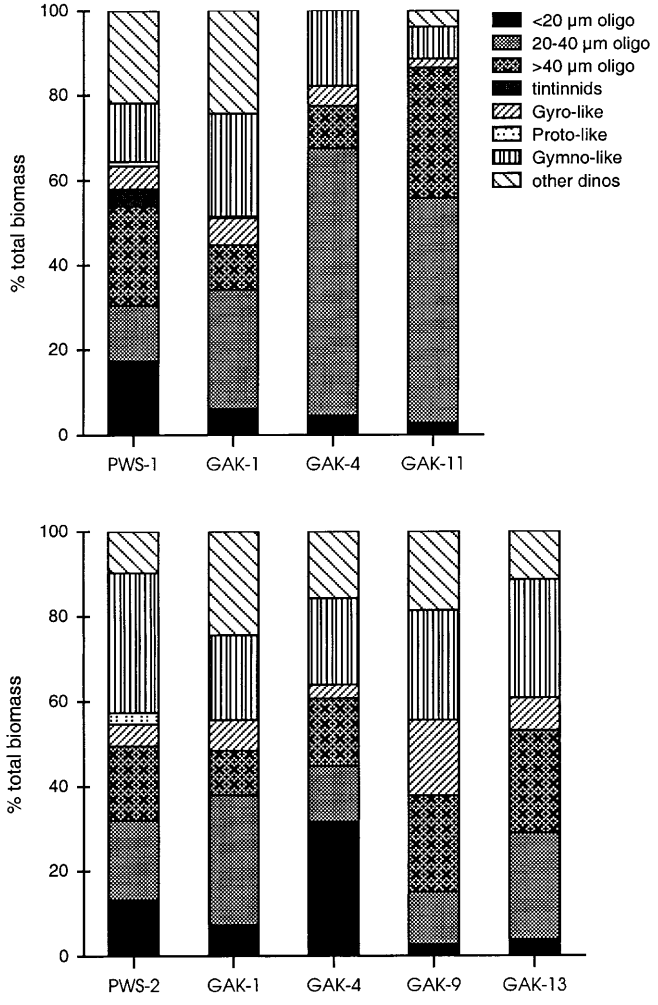

Fig. 8 Percent composition of microzooplankton biomass (µg C l^{-1}) for samples taken at the beginning of coastal Gulf of Alaska dilution experiments. *Upper plot*: 1998; *lower plot*: 1999. *Darker shading* shows ciliate contribution, while *lighter shading* shows >10 µm dinoflagellate contribution [oligo, oligotrich (aloricate choreotrich) ciliates; Gyro, *Gyrodinium*; Proto, *Protoperidinium*; Gymno, *Gymnodinium*]

ships to the biomass of large phytoplankton in the coastal Gulf of Alaska (Table 4; Fig. 9). While these microzooplankton might themselves be contributing some portion of the >8 µm chlorophyll (e.g. as photosynthetic dinoflagellates or chloroplast-retaining ciliates), our microscopic observations revealed a large diatom component to this size fraction as well (Table 6). Clearly microzooplankton biomass and grazing capacity was stimulated by increases in large-phytoplankton biomass, as has been seen in other productive coastal regions (Neuer and Cowles 1994; Nielsen and Kiørboe 1994; Levinsen et al. 1999). The lack of a relationship between microzooplankton biomass and <8 µm chlorophyll is somewhat at odds with the observed close coupling between µ and *g* for this chlorophyll size fraction. There may be an additional component to the microzooplankton community (e.g. <10 µm heterotrophic nanoflagellates) which was missed in our microscopy and was largely responsible for grazing on smaller phytoplankton. The dominant small phytoplankton taxa observed, however, including cryptophytes, prymnesiophytes, prasinophytes, and dinoflagellates, should have been readily available to most of the ciliate and dinoflagellate grazers enumerated (e.g. Strom and Morello 1998). Alternatively, production responses of the smaller microzooplankton might not have been expressed as biomass increases due to strong top-down control from within the <200 µm microzooplankton community (Calbet and Landry 1999).

The feeding and growth capabilities of protist grazers likely play a large role in the regulation of coastal phytoplankton blooms. Numerous protist species can consume "large" phytoplankton cells and may exhibit a preference for cells at the high end of the size spectrum available to them (Monger and Landry 1991; Hansen B et al. 1994; Hansen FC et al. 1996; Strom and Loukos 1998). Large oligotrich ciliates and tintinnids, both common in coastal waters (Lynn and Montagnes 1991; Pierce and Turner 1993), can feed at high rates on diatoms, cryptomonads, and autotrophic dinoflagellates in the 10–30 µm size range. Heterotrophic dinoflagellates, including *Gyrodinium* and *Protoperidinium* spp., common in temperate coastal waters (Jeong 1999), can consume and have been shown to prefer large diatoms, including chain-forming species (reviewed by Hansen and Calado 1999). They feed on phytoplankton dimensionally larger than themselves either by engulfing prey in a membrane extruded from the dinoflagellate cell ("pallium feeding", Jacobson and Anderson 1986) or by drawing in chains and compressing them in food vacuoles ("trash compacting," e.g. Buck and Newton 1995). Large ciliates and *Gyrodinium*-like dinoflagellates were associated with diatom blooms in our study (stns. PWS-1 and GAK-9, Fig. 8).

In addition to wide-ranging feeding capabilities, heterotrophic protists can have high growth rates, with the potential to double their population size rapidly given temperature and food levels representative of spring and summer in the coastal North Pacific (Verity 1986; Montagnes 1996; Strom and Morello 1998). Thus, when phytoplankton biomass is high, both enhanced per capita feeding rates and a large biomass of microzooplankton grazers may be supported (Table 4; Fig. 9). This high biomass, along with high potential population growth rates, leads to a high level of grazer community responsiveness to increases in prey biomass, i.e. a potentially close coupling between µ and *g*. On the other hand, when phytoplankton biomass is low, there are often fewer grazers (Table 4), and these are likely to be less active. There is evidence that some protist grazers enter metabolic "resting states" of various types when food is scarce (Fenchel and Finlay 1983; Finlay 1983). These resting states may be associated with very low rates of respiration and feeding, as well as reduced responsiveness to food concentration increases on both individual and population levels. Lowered metabolic rates and reduced responsiveness should lead to an uncoupling of μ and g.

Table 7 Compilation of published phytoplankton growth and microzooplankton grazing rate data for chlorophyll-based seawater dilution experiments conducted in coastal ecosystems. Studies (or data within studies) were excluded if (1) nutrient enrichment was used without simultaneous determination of unenriched (i.e. natural) phytoplankton growth rates, and (2) ambient nutrient levels were considered low enough to limit phytoplankton growth [*chlorophyll* range of initial chlorophyll concentrations measured ($\mu g\ l^{-1}$); *n* number of experiments conducted; *g*:μ ratio of microzooplankton grazing rate to phytoplankton growth rate – average for study, with range in *parentheses*]

Location	Chlorophyll	*n*	g:μ	Reference
Washington coast[a]	3.53–6.77	3	0.50 (0.28–0.76)	Landry and Hassett 1982
Halifax Harbor	0.3–2.2	5	0.44 (0.10–1.00)	Gifford 1988
Rhode River estuary	34.8–138.4	4	0.90 (0.67–1.10)	Gallegos 1989
Oslofjord[b]	1.14–7.30	6	1.03 (0.22–1.87)	Andersen et al. 1991
Chesapeake Bay[c]	2.18–22.96	9	1.15 (0.35–2.43)	McManus and Ederington-Cantrell 1992
Oregon coast	1.1–55.3	11	0.42 (0.08–1.33)	Neuer and Cowles 1994
Fourleague Bay	14.31–27.11	6	1.05 (0.68–1.44)	Dagg 1995
Ross Sea polyna[d]	1.3–10.6	10	0.65 (0.00–1.18)	Lessard et al. 1995
Gulf of Mexico[a]	0.10–0.78	8	0.89 (0.00–2.25)	Strom and Strom 1996
South African coast[e]	0.09–0.31	2	0.17 (0.08–0.27)	Froneman and Perissinotto 1996
Antarctic Peninsula[c]	0.08–2.28	12	0.90 (0.00–1.38)	Tsuda and Kawaguchi 1997
Gulf of St. Lawrence	0.35–2.05	4	0.72 (0.44–1.34)	Tamigneaux et al. 1997
San Francisco Bay[c]	0.4–16.0	19	0.37 (0.00–2.65)	Murrell and Hollibaugh 1998
Arabian Sea[a,c,e]	0.36–2.44	21	0.59 (0.40–2.41)	Landry et al. 1998
New Zealand coast	0.12–2.49	15	0.98 (0.15–2.13)	James and Hall 1998
Arabian Sea[e]	0.22–0.51	7	0.72 (0.42–1.10)	Edwards et al. 1999
Norwegian fjords	1.6–3.5	12	0.62 (0.47–0.78)	Archer et al. 2000
Coastal North Pacific[a]	0.19–13.65	23	0.64 (0.00–1.85)	present study

[a] Grazing (*g*) from nutrient-enriched dilution series; μ from net growth (in unenriched, undiluted bottles)–*g*
[b] Grazing (*g*) from N + P-enriched dilution series; μ from net growth (in P-enriched, undiluted bottles)–*g*
[c] High value (>3) of *g*:μ excluded (very low growth rates with measurable values of *g* will yield extremely high values of the ratio)
[d] Rates based on changes in *Phaeocystis* sp. cell number in *Phaeocystis*-dominated phytoplankton community
[e] Coastal stations only

Table 8 Comparison between quantity of chlorophyll accumulated (*A*) during incubation ($\mu g\ l^{-1}\ day^{-1}$) and quantity of chlorophyll ingested (*I*) by microzooplankton during incubation ($\mu g\ l^{-1}\ day^{-1}$). Values shown are for total (not size-fractionated) chlorophyll in undiluted bottles

Date	Site	*A*	I	I/*A*
Coastal Gulf of Alaska				
3 Apr 98	PWS-1	0.48	2.36	4.92
31 Mar 98	GAK-1	0.21	0.00	0.00
2 Apr 98	GAK-4	0.03	0.16	5.27
5 Apr 98	GAK-11	0.19	0.01	0.06
10 May 99	PWS-2	0.76	0.29	0.38
9 May 99	GAK-1	0.53	1.49	2.81
9 May 99	GAK-4	0.14	1.00	7.14
8 May 99	GAK-9	−1.13	3.32	–
7 May 99	GAK-13	0.08	2.04	25.44
Northern Puget Sound				
15 Nov 94	1	0.02	0.18	9.04
21 Nov 94	1	1.06	0.00	0.00
28 Nov 94	1	0.41	0.00	0.00
21 Feb 95	1	0.19	0.02	0.09
24 Feb 95	1	−0.39	0.87	–
18 May 95	1	1.20	1.24	1.04
30 May 95	1	4.31	2.36	0.55
2 Jun 95	1	4.38	5.58	1.27
18 Jul 95	1	7.34	10.68	1.46
31 Jul 95	1	11.91	5.64	0.47
3 Aug 95	1	10.47	22.79	2.18
1 Aug 96	2	0.25	0.74	2.95
8 Aug 96	2	0.48	0.79	1.64
21 Aug 96	2	4.09	1.42	0.35

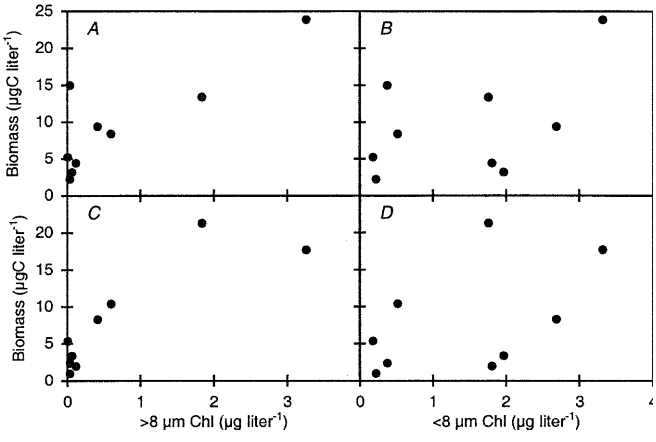

Fig. 9 Biomass of ciliates (**A**, **B**) and >10 µm dinoflagellates (**C**, **D**) as a function of chlorophyll concentrations in >8 and <8 µm size fractions. Data from coastal Gulf of Alaska experiments

In summary, our results show that microzooplankton grazing is an important loss process for phytoplankton production in coastal waters of the eastern North Pacific. On average, microzooplankton grazing was equivalent to nearly two-thirds of phytoplankton growth during our experiments. Periods of high phytoplankton biomass were associated with dominance by large phytoplankton cells in both northern Puget Sound and the coastal Gulf of Alaska. Surprisingly, coupling between microzooplankton grazing and phytoplankton growth was tighter (i.e. *g*:μ was higher) during high biomass periods than at other times, so that the proportion of total phytoplankton growth consumed by microzooplankton was highest during blooms. Because

of this, the absolute amount of chlorophyll ingested by microzooplankton often exceeded the amount of chlorophyll available for loss via other biological or physical processes. Thus it is not appropriate to characterize coastal microzooplankton solely as members of the "microbial loop," consuming only bacteria fueled by dissolved organic matter (e.g. Lalli and Parsons 1997). Nor do microzooplankton grazers feed primarily on small phytoplankton cells, with large-cell-dominated blooms necessarily giving rise to a macrozooplankton-dominated grazing community. A predictive understanding of coastal planktonic food webs and their eventual yield must take into account microzooplankton as important and sometimes dominant consumers of bloom-forming and other phytoplankton.

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