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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 µg 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 µg 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.

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; Kjørboe and Nielsen 1994; Neuer and Cowles 1994; Lehrer 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 (Reeburn 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.