Abstract  The distribution of bacterial and archaeal species in Crater Lake plankton varies dramatically over depth and with time, as assessed by hybridization of group-specific oligonucleotides to RNA extracted from lakewater. Nonmetric, multidimensional scaling (MDS) analysis of relative bacterial phylotype densities revealed complex relationships among assemblages sampled from depth profiles in July, August and September of 1997 through 1999. CL500-11 green nonsulfur bacteria (Phylum Chloroflexi) and marine Group I crenarchaeota are consistently dominant groups in the oxygenated deep waters at 300 and 500 m. Other phylotypes found in the deep waters are similar to surface and mid-depth populations and vary with time. Euphotic zone assemblages are dominated either by β-proteobacteria or CL120-10 verrucomicrobia, and ACK4 actinomycetes. MDS analyses of euphotic zone populations in relation to environmental variables and phytoplankton and zooplankton population structures reveal apparent links between *Daphnia pulicaria* zooplankton population densities and microbial community structure. These patterns may reflect food web interactions that link kokanee salmon population densities to community structure of the bacterioplankton, via fish predation on *Daphnia* with cascading consequences to *Daphnia* bacterivory and predation on bacterivorous protists. These results demonstrate a stable bottom-water microbial community. They also extend previous observations of food web-driven changes in euphotic zone bacterioplankton community structure to an oligotrophic setting.

Keywords  Crater Lake · Bacterioplankton community structure · Multidimensional scaling · Green nonsulfur bacteria · Marine Group I crenarchaeota · *Daphnia* predation

Introduction

Crater Lake is a high-altitude, ultraoligotrophic lake in the Cascade Mountains of the Northwest-
ern United States. Formed by the catastrophic eruption and collapse of a volcanic mountain approximately 6500 years ago, Crater Lake has been the subject of a wide range of studies characterizing the physics, chemistry, biology and ecology of the system (Larson, 1996). An unusual community of planktonic bacteria and archaea was identified in the lake, based on phylogenetic analysis of SSU rRNA genes sampled during August of 1997 (Urbach et al., 2001). At that time, the upper water column was dominated by two groups of currently uncultivated bacteria: the CL120-10 evolutionary cluster in the Verrucomicrobiales, and the ACK4 cluster in the Actinomycetales. At the same time, the lower water column contained a novel group of green non-sulfur (GNS) bacteria (Chloroflexi), CL500-11, and archaea in the marine Group I crenarchaeota clade. The relative importance of these groups inferred from DNA analysis was confirmed by oligonucleotide hybridization to RNA from the same lakewater samples. Microbial populations in other aerobic lakes of many trophic levels and elevations, from the Alps to the Netherlands, are consistently dominated by β-proteobacteria, with significant populations of ACK4 actinomycetes and cytophaga/flavobacteria and other, minor groups (Bahr et al., 1996; Hiorns et al., 1997; Semenova & Kuznedelov, 1998; Methé & Zehr, 1999; Glöckner et al., 2000; Zwart et al., 2002b; Zwisler et al., 2003). Comparison of the physical, chemical and biological characteristics of Crater Lake to 13 other lakes characterized by rRNA gene analysis suggested that Crater Lake’s microbial communities were likely structured by low concentrations of available trace metals and dissolved organic matter, chemistry of infiltrating hydrothermal waters or high levels of ultraviolet light (Urbach et al., 2001).

Crater Lake is an extraordinarily oligotrophic, deep lake with deep penetration of ultraviolet light, an oxygenated hypolimnion, low concentrations of metals and dissolved organic carbon, and influx of hydrothermal fluids (R.W. Collier, pers. comm.; Collier et al., 1991, 1993; McManus et al., 1996; Nelson et al., 1996; Crawford & Collier, 1997; Hargreaves et al., this issue). At all depths, dissolved N/P molar ratios fall below the Redfield ratio of 16, suggesting that autotrophic growth may be N-limited (Redfield, 1958). Bioassay studies also suggest that phytoplankton productivity may be co-limited by N and trace metals, with different size fractions showing differences in growth stimulation by N and metal mixtures (Lane & Goldman, 1984; Groeger & Teitjen, 1993; Groeger, 2007). Crater lake shares a number of features with oligotrophic, open ocean waters, including oxygenated deep waters, the possibility of combined N and trace metal limitation, a deep chlorophyll maximum, and exceptionally high light transmittance (Urbach et al., 2001).

Organisms that live in Crater Lake must contend with the extreme and unusual environmental conditions: high fluxes of ultraviolet light, low concentrations of dissolved organic carbon, hydrothermal influx at the bottom of the lake and deep hydrography, combined with N and potentially trace metal limitations. Available data do not show much variation in these factors (with the possible exception of NH₄⁺ concentrations), and they are likely to be responsible for the unusual bacterioplankton taxa found in the lake. CL120-10 verrucomicrobia and CL0-1 OP10 bacteria have been found in low numbers near the mouth of the Columbia River and CL120-10 in a Siberian reservoir, but, at present, CL500-11 GNS and CL500-3 planctomycetes are unique to Crater Lake, and marine Group I archaea have not been found in other freshwater planktonic populations, though they have been reported to occur in sediments (MacGregor et al., 1997; Crump et al., 1999; Urbach et al., 2001; Trusova & Gladyshev, 2002). Our earlier study presented a snapshot of Crater Lake prokaryotic plankton and identified correlates with the unusual organisms found there.

Here we present analysis of Crater Lake bacterioplankton populations during July through September of 1997, 1998 and 1999, with comparison to time series measurements of physical, chemical and biological factors. These analyses suggest that depth and food web structure are major factors influencing Crater Lake bacterioplankton populations.