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Effects of Sediment Loading and Associated Turbidity on the Tropic Dynamics of a Central Oregon Reservoir
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ABSTRACT

During 1993 and 1994, phytoplankton and zooplankton population dynamics and sediment input were monitored in a central Oregon reservoir. In addition to seasonal differences in measures of productivity, distinct differences were noted between the uppermost area of the reservoir and lower reaches. Reservoir primary productivity, as measured by chlorophyll-α, was highest during spring-runoff and fall turnover; Area 4 (the uppermost study reach) was eutrophic in nature during these periods. For the remainder of the growing season, primary productivity in Area 4 and the rest of the reservoir was classified as mesotrophic and oligotrophic, respectively. Seasonal and spatial patterns in zooplankton community composition and abundance were also evident; the average density of zooplankton was 3-7 times greater in Area 4 than in the rest of the reservoir. Suspended non-biogenic turbidity could greatly affect the productivity and trophic dynamics of the reservoir. Zooplankton sampling for calculation of fishery management indices should occur in early- to mid-August for the hatchery rainbow trout program and between mid-May and mid-June for warmwater fish species.
INTRODUCTION

Trophic cascade and food web dynamics theories utilize the concept of energy flow to aid understanding of community interactions in aquatic systems (Wetzel 1983). Although the productivity of an aquatic system is ultimately limited by the supply of nutrients (Carpenter et al. 1985), the dynamics and allocation of those nutrients within the biological community often controls system productivity (Wurtsbaugh et al. 1990). Factors such as the form and timing of nutrient inputs, the size and morphology of the lake or reservoir basin, water chemistry, or the characteristics of mixing patterns can influence community structure and productivity. Turbidity associated with suspended sediments is one factor that can influence biological as well as physical and chemical processes in aquatic systems. The primary focus of this study was to identify how the dynamics and transport of suspended inorganic material - primarily colloidal montmorillonite clay - affected productivity at various trophic levels in a central Oregon reservoir.

Investigations into biological control of nutrient allocation within aquatic systems have illustrated the potential effects of "top-down" control of the structure and dynamics of lower trophic levels by planktivorous or predaceous fish (O'Brien 1979, Carpenter et al. 1985, Christoffersen et al. 1993, Gliwicz 1994, Hambright 1994;Ramcharan et al. 1995). In an effort to maintain desirable predator-prey balances for optimal gamefish production, fishery managers routinely sample the piscine community in a system. They often, however, do not have the time or resources to examine lower trophic levels. Such an examination could yield a better understanding of a system's complex food and energy dynamics (Carpenter et al. 1985) and, ultimately, the factors limiting the productivity of recreational fisheries (Oglesby 1977b). Development of easily obtained and calculated indices that use the linkage between trophic levels to identify potential imbalances between management expectations and biological potential could potentially very valuable. Mills and Schiavone (1982) showed that the size structure of zooplankton can be a good predictor of the growth potential of planktivorous fish related to warmwater fish associations in lakes. However, their research did not include fish associations containing salmonids. On the other hand, others have shown that the abundance of large daphnids (usually defined as zooplankters > 1.0 or 1.3 mm) is often highly correlated with the growth and survival of rainbow trout stocked into lakes and reservoirs (Galbraith 1975, Tabor et al. 1996, Wang et al. 1996). We wanted to investigate the feasibility of developing a similar index for management use. However, in order to develop a sampling protocol for such an index, we had to identify how seasonal variation in the abundance and species composition of the zooplankton community would affect our ability to obtain the most representative value.

In 1993 and 1994, ODFW personnel conducted a limnological investigation of the interspecific, seasonal, and interannual dynamics of phytoplankton and zooplankton in Prineville Reservoir. The objectives of this study were:

1. Examine the timing and magnitude of changes of zooplankton abundances and compare those to changes in the abundance of phytoplankton, as measured by concentration of chlorophyll-a.

2. Characterize sediment loading into and turbidity changes in the reservoir through time and
estimate their effects on the total production of fish in the reservoir.

3. Identify patterns of change in density and length frequency of cladocerans with respect to development of sampling protocol for management indices.

STUDY SITE

At full pool, Prineville Reservoir, located 27.4 km southeast of Prineville, Oregon at 986 m above sea level, is a 1,218 surface-hectare impoundment on the Crooked River (Figure 1). Bowman Dam, constructed in 1960, flooded 19.3 km of the Crooked River. Inundated lands were primarily juniper/sagebrush-covered, steeply sloping canyon lands with some pasture land in the upper reservoir area. Maximum depth of the reservoir is 70.1 m and maximum storage capacity is 191,208,000 m$^3$. Irrigation and flood control functions dictate control of reservoir levels, although stored water cannot exceed 114,724,800 m$^3$ between November 15 and February 15 (representing a drawdown of 7.2 m from full pool) to meet flood control requirements (Stuart et al. 1996).

Prineville Reservoir supports popular warmwater and coldwater recreational fisheries (Shrader 1998). However, several factors associated with normal reservoir operation impact the productivity of the system. Water level fluctuations, severe drawdown, very low abundance of

![Map of Prineville Reservoir showing study sections and limnological sampling stations.](image-url)
aquatic macrophytes, a lack of structural complexity, as well as limiting nutrients and high levels of suspended sediments, inhibit productivity at various trophic levels.

Productivity in Prineville Reservoir is severely impacted by the presence of inorganic turbidity (Johnson et al. 1985). Soils in the upper Crooked River and Bear Creek watersheds are formed of highly erodible material, including montmorillonite clay, and are subject to transport by heavy runoff (Silverdale et al. 1976). Streambanks degraded from timber harvest, livestock grazing, and road building contribute large quantities of turbid runoff in the spring. In addition, erosion of the reservoir shoreline (more than 90% of which are erodible soils) contributes significantly to amount of sediment suspended in the reservoir (Johnson et al. 1985, Silverdale et al. 1976). The fine clay particles stay in suspension for a long period resulting in turbid reservoir conditions long after the spring runoff (Herrig 1970, Silverdale et al. 1976).

Nutrient concentrations in Prineville Reservoir are elevated above levels common in other eastern Oregon reservoirs (Johnson et al. 1985). Orthophosphate phosphorus concentrations - measured at 0.047 mg/l in May of 1982, and 0.025 mg/l in July of 1982 – are indicative of an eutrophic system, but inorganic turbidity limits utilization by phytoplankton (Stuart et al. 1996). Chlorophyll-α levels, which are a measure of primary productivity, reflect the light limitation; concurrent samples in May and July, 1982 measured only 0.7μg/l and 1.5μg/l, respectively. These levels are very low and are characteristic of an oligotrophic system (Wetzel 1975).

High levels of suspended sediments are thought to affect phytoplankton ecology in the reservoir in several ways (Johnson et al. 1985). The annual bloom of blue-green algae *Aphanizomenon* in Prineville Reservoir is delayed until later in the season from other eastern Oregon reservoirs, presumably due to the turbidity. Suspended sediments may also affect phytoplankton species composition; periphytic diatoms not typically found in lakes dominate the algal community in Prineville Reservoir during the spring and summer (Appendix A). It is thought that these algae are probably associated with the suspended clay particles. Finally, phytoplankton densities are much lower than those suggested by nutrient levels presumably due to turbidity-related effects.

Zooplankton densities are generally low in the reservoir and reflect the poor phytoplankton production (Stuart et al. 1996). Zooplankton densities are generally much lower than in other eastern Oregon lakes (Appendix B); from May to September 1985, Prineville Reservoir had an average of 14,400 zooplankters per cubic meter.

**METHODS AND MATERIALS**

**Sediment Loading**

Sediment loading to Prineville Reservoir from April 1993 through March 1994 was calculated as the difference between sediment transport into the reservoir from the Crooked River and Bear Creek and sediment export in the Crooked River below Bowman dam. On each sampling occasion, replicate samples were analyzed for turbidity and total non-filterable residue
(assumed to be sediment) by standard methods (APHA 1976). Water samples were taken at each of three points: Bear Creek approximately 1200 meters upstream from its confluence with the Reservoir, the Crooked River upstream of the reservoir at the cattle guard on the north shore access road, and at the BLM campground approximately 3.2 kilometers downstream from Bowman Dam. Replicate 200-ml subsamples were filtered through the pre-weighed, oven-dried 200-micron pore size filter paper. Filtered samples were dried at 103°C for 24 hours and then cooled in a dessicator prior to being weighed to obtain the weight of the filterable residue. Sediment load was determined by multiplying the concentration of filtrable residue times the volume of discharge. Bear Creek discharge volume was determined by multiplying average water velocity by calculated cross-sectional area of flow. Crooked River flows were provided by COID and were obtained from USGS gauging stations.

**Reservoir Dynamics**

Prineville Reservoir at full pool was stratified lengthwise into four areas for sampling purposes (Figure 1). These areas corresponded with those used in the Prineville Reservoir Black Bass study (Shrader 1998). Sample stations were located approximately at the midpoint longitudinally and laterally within each area (except in Area 4 when reservoir drawdown in 1993 necessitated movement of that station down-reservoir later in the season and elimination of that station in 1994). Reservoir turbidity, phytoplankton (monitored by measuring chlorophyll-a concentration) and zooplankton density and distribution was determined for the 1993 growing season (April - October) on a biweekly basis. Zooplankton density and distribution were sampled again in 1994 but not as intensively as in 1993.

Replicate water samples for turbidity and chlorophyll analysis were collected using a 10-meter long, 2.54-cm diameter acrylic tube suspended vertically in the water column. Turbidity of the raw samples was measured in nephelometric turbidity units (NTU) with a turbidimeter. Samples for chlorophyll analysis were buffered with MgCO3, filtered through 0.45 μm filter paper, and stored in the freezer until processed. Spectrophotometric determination of concentrations of chlorophyll-a, b, and c, as well as pheophytin-a, were performed using standard methods (APHA 1976). Pheophytin-a, a degradation product of chlorophyll-a, can introduce error into chlorophyll-a determinations because it absorbs light at the same wavelength. The ratio of chlorophyll-a to pheophytin-a can range from 1.0 to 1.7 and serves as a good indicator of phytoplankton physiological condition (APHA 1976).

Changes in the relative abundance of the various types of chlorophyll can give insight into phytoplankton dynamics in Prineville Reservoir. The distribution of the different photosynthetic pigments is characteristic of certain algal phyla (Meeks 1974). Blue-green (Cyanophyceae) contain only chlorophyll-a, while green algae (Chlorophyta) and euglenophytes (Euglenophyceae) also contain chlorophyll-b. Other phyla of algae, such as yellow-green (Xanthophyceae) and golden-brown algae (Chrysophyceae), for instance, contain both chlorophylls a and c.

Zooplankton was sampled by making replicate 20-m vertical tows with a Wisconsin-type plankton net with 153 μm mesh and a 0.12 m diameter opening. In areas shallower than 20m,
tows started from just above the bottom. Zooplankton were preserved with 10% formalin and stained with rose bengal. Samples were later transferred to CAROSAFE (a nontoxic preservative) prior to analysis. Zooplankters were identified to the lowest practical taxonomic level, counted, and a subsample of the dominant taxa was measured. Zooplankton density was estimated as the quotient of the number of planktors counted divided by the volume of water sampled. Size-frequency distributions were determined for cladocerans by measuring from the anterior margin of the head to the base of the tail spine. Copepods were measured from the anterior margin of the head to the base of the caudal rami.

RESULTS

Sediment Flow and Turbidity

The period of peak sediment input into Prineville Reservoir (April and May) coincided with increased flows in Bear Creek and the Crooked River due to spring runoff (Figure 2). At times, Bear Creek sediment load exceeded that of the Crooked River above the reservoir (Figure 3). Later in the year, localized heavy precipitation associated with thunderstorms created short duration events characterized by increased flow rates and sediment load in the affected tributary. The net accumulation of sediment to the reservoir was affected by sediment input and reservoir operation (primarily irrigation withdrawals; Figure 4).

![Graph showing Crooked River and Bear Creek flow rates](image)

**Date**

Figure 2. Flow (c.f.s.) of major tributaries (Bear Creek and the Crooked River) to Prineville Reservoir and the Crooked River below Bowman Dam from April 20, 1993 to March 14, 1994.
Figure 3. Quantity of sediment transported by Bear Creek and the Crooked River (above and below Prineville Reservoir) from April 20, 1993 to March 14, 1994.

Figure 4. Amount of sediment deposited in Prineville Reservoir from April 20, 1993 to March 14, 1994.

Prineville Reservoir turbidity varied seasonally and by area. The sediment load of the two major tributaries affected the turbidity of contiguous areas of the reservoir (Figure 5). The peak in turbidity in Area 4 in late September - early October was due to reservoir drawdown exposing upper reservoir mudflats to erosion by the river (Figure 5). Sediment from Bear Creek affected the turbidity of Area 1 most significantly during spring run-off (Figure 6), although an intense storm event in the Bear Creek watershed on August 23 did result in increased sediment
input and turbidity in Area 1 (Figure 6). Area 1 turbidity remained slightly elevated over Area 2 values for much of the year, but it is questionable whether this was due to the low volume of sediment from Bear Creek.

Figure 5. Turbidity (ntu) in different study areas of Prineville Reservoir from April 20 to October 12, 1993.

Figure 6. Effect of Bear Creek on turbidity of lower Prineville Reservoir from April 20 to October 12, 1993.
Localized fall thunderstorms created a high flow event in Bear Creek that raised the turbidity in Area 1. The affect the Crooked River had on Area 4 turbidity was quite different due to its higher base flow (Figure 7). Early in the spring, during runoff, the turbidity in Area 4 was almost the same as in the incoming river water. Later in the season, increased turbidity in the in the Crooked River did not affect Area 4 turbidity to the same extent due to the decrease in river flow. The relationship between Crooked River and Area 4 turbidities is not as clear later in the season (September and October). The drop in reservoir elevation due to irrigation withdrawals meant that the Area 4 sample site was much closer to the river/reservoir interface. As a result, Area 4 water samples probably contained significant amounts of larger material displaced by the Crooked River as it flowed through exposed mud flats below the river sample site.

![Turbidity Graph](image)

**Figure 7.** Effect of Crooked River on turbidity of upper Prineville Reservoir from April 20 to October 12, 1993.

**Chlorophyll Dynamics**

Phytoplankton production in Prineville Reservoir in 1993, as measured by chlorophyll-α concentration, peaked on April 28 at 86.2 mg/m³ in Area 4 (Figure 8). Production then dropped precipitously and remained below 30 mg/m³ in the entire reservoir for most of May, June, and July. Chlorophyll-b and c levels followed this trend (Figures 9 and 10), although concentrations were higher than measured chlorophyll-α levels. Production in all areas increased again in August and remained high (with fluctuations) until mid-September when lower-reservoir production dropped.
Figure 8. Concentration of chlorophyll-α in different study areas of Prineville Reservoir from April 20 to September 25, 1993.

Figure 9. Concentration of chlorophyll-β in different study areas of Prineville Reservoir from April 20 to September 25, 1993.
Figure 10. Concentration of chlorophyll-c in different study areas of Prineville Reservoir from April 20 to September 25, 1993.

Seasonal succession of phytoplankton species composition in 1993 is similar to that observed in 1985 (Johnson et al. 1985; Figures 8-13). Changes in chlorophyll-a concentration during the spring phytoplankton bloom are mirrored by the levels of chlorophyll-b and c. The high concentration of chlorophyll-c relative to chlorophyll-b (Figures 9, 10, and 13) suggests that the main components of the spring bloom are diatoms (Bacillariophyceae), dinoflagellates (Dinophyceae), cryptomonads (Cryptophyceae), or brown algae (Phaeophyceae). Relative abundances of chlorophyll types remain relatively constant in June and July although at much lower absolute levels than seen in April and May. This suggests that the composition of the phytoplankton community did not change appreciably. A spike in the chlorophyll-b to chlorophyll-c ratio at the end of July and the beginning of August suggests a slight increase in the prevalence of green algae. This was followed by a dramatic increase in the measured concentration of chlorophyll-a (Figure 8), while chlorophyll-b and c levels remained relatively unchanged (Figures 9 and 10). This is almost assuredly due to a profusion of blue-green algae which generally occurs in the autumn in Prineville Reservoir.

Peaks in the chlorophyll-a to pheophytin-a ratio (Figure 14) correspond fairly closely to periods of maximal measured chlorophyll-a levels. When this ratio is 1.7, all the pigment (chlorophyll-a) is functional and associated with live plants. A value of 1.0 indicates that all the pigment has been degraded to pheophytin-a and is probably in the form of particulate detritus. Peaks in the chlorophyll-a - pheophytin-a ratio (Figure 14) show that phytoplankton production is probably highest during the spring runoff and highest for blue-green algae in the fall (Figure 15).
Figure 11. Ratio of chlorophyll-α to chlorophyll-β in different study areas of Prineville Reservoir from April 20 to September 25, 1993.

Figure 12. Ratio of chlorophyll-α to chlorophyll-ε in different study areas of Prineville Reservoir from April 20 to September 25, 1993.
Figure 13. Ratio of chlorophyll-\(b\) to chlorophyll-\(c\) in different study areas of Prineville Reservoir from April 20 to September 25, 1993.

Figure 14. Ratio of chlorophyll-\(a\) to pheophytin-\(a\) in different study areas of Prineville Reservoir from April 20 to September 25, 1993.
Figure 15. Concentration of physiologically-active chlorophyll-\(\alpha\) in different study areas of Prineville Reservoir from April 20 to September 25, 1993.

Zooplankton Dynamics

Zooplankton community composition and densities varied spatially and temporally during the study (Figures 16 and 17). Cladocerans and calanoid copepods were generally the most abundant zooplankton in Prineville Reservoir and their densities were generally higher in Area 4 than the rest of the reservoir (Table 1). In 1993, *Daphnia pulex* and *Diaphanosoma birgei* comprised almost 100% of the cladocerans in the zooplankton (Figures 18 and 19), while in 1994, *Ceriodaphnia* was much more prevalent and composed a significant percentage of the zooplankton community (Figures 20 - 22). *Leptodora kindti*, a large predatory cladoceran, was present but uncommon throughout the growing season. *Diaptomus* sp. were the prevalent calanoid copepod genus present in both years of the study (Figures 23 - 24). In contrast to other types of zooplankton, cyclopoid copepods were fairly abundant in the lower reservoir (Figures 25 and 26).

Table 1. Average total density of zooplankton (number per cubic meter) in different study areas of Prineville Reservoir during the period May 29 - Oct 4, 1993 and May 24 - Oct 12, 1994.

<table>
<thead>
<tr>
<th>Year</th>
<th>Average density Areas 1 - 3</th>
<th>Average density Area 4</th>
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<tr>
<td>1993</td>
<td>17,440</td>
<td>48,183</td>
</tr>
<tr>
<td>1994</td>
<td>13,011</td>
<td>89,228</td>
</tr>
</tbody>
</table>
Figure 16. Density of zooplankton in different areas of Prineville Reservoir, April 20 to October 4, 1993.

Figure 17. Density of zooplankton in different areas of Prineville Reservoir, May 24 to October 12, 1994.
Figure 18. Density of *Daphnia pulex* in different areas of Prineville Reservoir, April 20 to October 4, 1993.

Figure 19. Density of *Diaphanosoma birgei* in different areas of Prineville Reservoir, April 20 to October 4, 1993.
Figure 20. Density of *Daphnia pulex* in different areas of Prineville Reservoir, May 24 to October 12, 1994.

Figure 21. Density of *Daphanosoma birgei* in different areas of Prineville Reservoir, May 24 to October 12, 1994.
Figure 22. Density of *Ceriodaphnia* species in different areas of Prineville Reservoir, May 24 to October 12, 1994.

Figure 23. Density of calanoid copepods species in different areas of Prineville Reservoir, April 20 to October 4, 1993.
Figure 24. Density of calanoid copepods in different areas of Prineville Reservoir, May 24 to October 12, 1994.

Figure 25. Density of cyclopoid copepods in different areas of Prineville Reservoir, April 20 to October 4, 1993.
Figure 26. Density of cyclopoid copepods in different areas of Prineville Reservoir, May 24 to October 12, 1994.

Size distribution of *Daphnia* in Prineville Reservoir varied considerably during the 1993 and 1994 growing seasons (Figures 27 and 28). It is interesting to note that lowest mean size values on June 24 and August 23 are slightly after peaks in the abundance of nauplii (Appendix C). Mean size of *Daphnia* decreased steadily through the 1994-growing season. Whether or not

Figure 27. Size range (mean sized denoted by *) of *Daphnia pulex* in Prineville Reservoir, April 20 to October 4, 1993.
Figure 28. Size range (mean size denoted by *) of *Daphnia pulex* in Prineville Reservoir, May 27 to October 12, 1994.

This decrease is real or an artifact of the decreased sampling intensity is unknown. Identification of the timing of this variation is important if a standardized protocol is to be developed for sampling zooplankton for predator-prey balance (Figures 29 and 30).

Figure 29. Variation in potential indices of *Daphnia* size distribution in Prineville Reservoir, April 20 to October 4, 1993.
Figure 30. Variation in potential indices of *Daphnia* size distribution in Prineville Reservoir, May 27 to October 12, 1994.

**DISCUSSION**

**Community Structure and Trophic Dynamics**

There has been much debate in the recent ecological literature concerning the relative importance of "top-down" and "bottom-up" control mechanisms of aquatic community structure. Recent evidence suggests that these mechanisms are not mutually exclusive, rather that nutrient input into an aquatic ecosystem often determines the potential productivity of the system, while biological processes are the mechanisms that determine the community form or structure (Carpenter et al. 1985, Forrester et al. 1999). However, in systems with high external loadings of nutrients, such as Prineville Reservoir, algal populations may be more strongly influenced by the dynamics of the nutrient supply rather than by losses from zooplankton grazing (Ramcharan et al. 1995). Prineville Reservoir has historically been classified as a eutrophic system based primarily on limited light transparency and elevated phosphorus concentrations (Johnson et al. 1985). This classification may be misleading as inorganic particulate matter, i.e., sediment, not planktonic algae, is primarily responsible for the decreased light penetration (Grobbelaar and Stegmann 1976, Oglesby 1977a). A more realistic assessment of the trophic status of Prineville Reservoir should be based on the actual primary production of the system rather than the oft-confounding physical factors.

The seasonal pattern of phytoplankton abundance in Prineville Reservoir is typical of temperate dimictic lakes. Increases in primary production occur during the spring in the areas where there is significant input of nutrients, i.e., Area 4 where the Crooked River provides nutrients. Based on chlorophyll-*a* concentrations corrected for pheophytin-*a* concentrations
(Wetzel 1975), phytoplankton production in Area 4 could be classified as eutrophic briefly during the period of spring runoff. The spring maximum in phytoplankton production in Prineville Reservoir is dominated by diatoms - probably Melosira and Cocconetes (Johnson et al. 1985; Appendix A). Rapid growth of diatoms reduces available nitrogen and silica from the stratified epilimnion and results in reduced production in the summer (Wetzel 1975). As a result, for the majority of the growing season, the lower reservoir (Areas 1 and 2) and upper reservoir are generally oligotrophic and mesotrophic in nature, respectively, as measured by chlorophyll-α concentration. In the fall, the elevated phosphorus concentration noted in Johnson et al. (1985) and the decreased average size of Daphnia might have resulted in a small increase in the production of green algae (Schoenberg and Carlson 1984). The subsequent blue-green algae bloom was probably precipitated by a combination of factors. Increases in pH due to the increased green algae production and in turbidity in Area 4 favored the production of blue-green algae over diatoms and green algae (Shapiro 1973, Schoenberg and Carlson 1984). Additionally, favorable phosphate uptake kinetics and the ability to fix atmospheric nitrogen in the face of limited nitrate availability favor Cyanophyta over other forms of algae (Shapiro 1973, Fogg 1974, Boyd 1990). A large increase in measured levels of chlorophyll-α in Area 4 (Figure 8) reflect the fall blue-green algae bloom. Other forms of algae (diatoms, dinoflagellates, and cryptomonads) also increased slightly in abundance during this period (Figures 11 and 12), but not to the extent of the blue-green algae.

The methodology used to index phytoplankton production - spectrophotometric determination of chlorophyll-α concentration by acetone extraction- is not without problems. The ability of the solvent used (acetone) to extract chlorophyll from algae varies with the type of algae (Riemann and Ernst 1982). As a result, levels of blue-green algae may have been underestimated relative to green algae and diatoms due to limitations of the acetone extraction of chlorophyll-α in our methodology (Holm-Hansen 1977). Additional sources of error associated with this methodology would have greater implications to productivity estimates used in this study. As has been stated before, a large percentage of the algae, and therefore chlorophyll-α, in Prineville Reservoir is associated with sediment. When this sediment settles out of the photic zone, the algae dies but the chlorophyll-α associated with it is still included in the extraction with viable algae. Fortunately, this error can be minimized by procedures that correct for the degradation product- pheophytin-α. Another potential problem with the spectrophotometric methodology is that planktonic algae often increase the concentration of chlorophyll-α in their cells at low light intensities (Braun and Braun 1974), i.e., conditions which might occur during spring runoff. Uncorrected, these last two sources of error would tend to lead to overestimation of algal biomass and, consequently, reservoir productivity.

The pattern of zooplankton abundance in Prineville Reservoir was generally dicyclic in nature, i.e., possessing a spring maximum and a less-defined fall maximum (Pennack 1989). Diaphanosoma was the exception; it exhibited a classic single extended population "pulse" as suggested by Pennack (1989). In 1993, during the fall blue-green algae bloom, the density of Daphnia decreased and the density of calanoid copepods increased. This could be due to the competitive advantage calanoid copepods have over Daphnia. Calanoid copepods have a greater capability to select their food and avoid blue-green algae, whereas Daphnia growth, survival, and reproduction suffer when they attempt to process such food (Richman and Dodson 1983). Although we didn't measure chlorophyll-α in 1994, nutrient levels and, consequently,
zooplankton production were probably much higher in 1993 than in 1994 because of decomposition of terrestrial vegetation in the drawdown zone that had grown previously during several years of drought.

Sediment input and the associated turbidity may significantly affect energy allocation and transfer between trophic levels in Prineville Reservoir. The presence of large amounts of colloidal clay particles provides ample substrate for diatomaceous algae (Family Bacillariophyceae). These normally-benthic algae form the majority of the planktonic forms in Prineville Reservoir (Appendix A). This association is a dual-edged sword since sediment provides increased surface area for primary production in an otherwise light-limited environment but also reduces the nutritive value of the algae as zooplankters must consume large amounts on non-nutritive matter to obtain sufficient algal biomass to survive (Koenings et al. 1990). *Daphnia* fed amended sediments (those to which protein had been adhered) exhibited reduced growth and fecundity over *Daphnia* fed yeast, but they performed better than those fed only sediment (Arruda et al. 1983). Turbidities as low as 5-10 NTU increase *Daphnia* mortality and reduce recruitment rates because of the energetic cost of increased filtering and feeding rates necessary to overcome the insufficient energy extracted from ingested foods mixed with silt (Gliwicz 1986, Koenings et al. 1990). Arruda et al. (1983) showed that sediment concentrations of 50-100 mg/L reduced algal ingestion of *Daphnia* to near starvation levels. This response can be mediated if the sediment consumed has high levels of accompanying energy (chlorophyll-a, absorbed organic material, or detritus) associated with it (Cuker 1987).

In addition to population effects, inorganic turbidity can directly affect zooplankton community structure through differential ability of zooplankters to ingest different sizes of particles (Arruda et al. 1983). High levels of inorganic turbidity select against filter-feeders such as *Daphnia* (Loughheed and Chow-Fraser 1998), while calanoid copepods have a feeding strategy whereby they test each particle prior to ingestion therefore expending less energy (Pennack 1989). As a result, calanoid copepods are at an advantage over cladocerans in turbid situations (Richman and Dodson 1983, Koenings et al. 1990). Turbidity-induced changes in the production of *Daphnia* could, ultimately, affect recruitment of warmwater fish as *Daphnia* are prey critical for the survival of young-of-the-year warmwater fish.

**Management Implications**

**Effects of Sediment Loading and Turbidity on Production and Yield**

Land use and management practices in the Upper Crooked River watershed act in concert with soil conditions and hydrologic/climatic factors to affect transport of sediment into Prineville Reservoir. Although wave-induced erosion along the reservoir shoreline is a major contributor to turbidity problems in Prineville Reservoir, improvements in riparian conditions in the Upper Crooked River watershed would decrease sediment loading and turbidity in the reservoir (Silvernale et al. 1976). Soils in the Camp Creek and Eagle Creek watersheds containing significant amounts of montmorillonite clay (< 50 microns) with 30 to 60% amorphous material are likely the cause of much of the turbidity in the reservoir (Silvernale et al. 1976). Our results
suggest that an estimated 170,000 kg of sediment were deposited in the reservoir during the period from April 20, 1993 to March 14, 1994.

Numerous studies have demonstrated the relationship between phosphorus loading into a water body and the resultant productivity of that system (Dillon and Rigler 1974, Jones and Bachman 1976, Canfield 1983, McCauley et al. 1989, Prairie et al. 1989). Other investigations have illustrated the negative influence of non-volatile suspended solids on that relationship (Hoyer and Jones 1983, Knowlton and Jones 1993). Non-biogenic turbidity can decrease primary productivity of an aquatic system by decreasing light penetration (Grobbelaar and Stegmann 1979, Arruda et al. 1983), adsorbing phosphate to clay particles (Edzwald et al. 1976, Walmsley 1978, Hoyer and Jones 1983, Cuker 1987, Dokulil and Padisak 1994), and changing the heat budget and mixing depth of the lake (Cuker 1987, Mazumder et al. 1990).

Equations developed by Hoyer and Jones (1983) and Knowlton and Jones (1993) predict chlorophyll concentrations of 6.3 and 8.2 μg/L, respectively, for Area 1 in Prineville Reservoir when average total phosphorus concentration was 39 μg/L (Johnson et al. 1985) and average non-volatile suspended solids was ~20 mg/L (based on limited reservoir data in 1993). These values overestimate the actual average chlorophyll concentration (1.3 μg/L) measured by Johnson et al. (1985). Several factors may explain the discrepancy between the predicted and actual chlorophyll concentration in Prineville Reservoir. One potential source of error is the use of total phosphorus concentration to predict chlorophyll concentration because phosphorus adsorbed to clay particles is not available for utilization by algae (Oglesby 1977a). A more likely source of error was our estimate of suspended solids. The value of 20 mg/L nonvolatile suspended solids was undoubtedly low because a substantial amount of the sediments creating the turbidity were smaller than the 200-micron pore size of the filter used in standard methodology (Silvernale et al. 1976). In order to arrive at a value of 1.3 μg/L chlorophyll-a (using the equation developed by Hoyer and Jones (1983), the concentration of inorganic suspended solids must be closer to 45 mg/L. This suggests that solids < 200 microns must comprise approximately 50% of the turbidity-creating sediment.

Insight into the effect of inorganic turbidity on the fish yield of the reservoir can be accomplished by coupling the relationships developed by Hoyer and Jones (1983) with work by Oglesby (1977b). Oglesby (1977b) demonstrated a significant positive relationship between summer phytoplankton standing crop, as measured by chlorophyll-a concentration, and fish yield. Using the relationship he developed, a mean whole-reservoir chlorophyll concentration of 4.7 μg/L (based on 1993 data) yields a predicted fish yield of 0.07 g dry weight/square meter. Actual mean fish yield for Prineville Reservoir in 1993 and 1994 (minus weight of stocked fish) was 0.37 g dry weight/square meter of surface area based on creel survey results (Shrader 1998). Although this value is much higher than that predicted by Oglesby (1977b), it is still within the 95% confidence interval for the regression. By fixing total phosphate concentration at 39 μg/L, the regression developed by Oglesby (1977b) predicts that a 10% decrease in suspended solids would lead to an approximate 17% increase in fish yield from the reservoir.
Management Implications of Trophic Interactions

How does a better understanding of phytoplankton and zooplankton dynamics in Prineville Reservoir aid biologists in managing the fishery? First of all, the piscine community present in Prineville Reservoir in 1993 and 1994 was probably both a determinant of and reflective of the trophic structure below it. The effects of fish predation cascade through the community trophic structure in an aquatic system and are balanced by the carrying capacity as determined by the system's productivity (Ramcharan et al. 1995). There is ample evidence in the literature of "top-down" control of the structure and dynamics of lower trophic levels by planktivorous or predaceous fish (O'Brien 1979, Carpenter et al. 1985, Christoffersen et al. 1993, Gliwicz 1994, Hambright 1994, Ramcharan et al. 1996). Drenner et al. (1984) demonstrated the ability of a filter-feeding planktivorous fish (gizzard shad Dorosoma cepedianum) to shift the zooplankton community structure toward more evasive prey. Studies have also shown that particle-feeding planktivores can also shift zooplankton community structure toward smaller zooplankton (Lynch 1979, Hambright 1994, Ramcharan et al. 1996, Wang et al. 1996).

At the time of this study, the piscine community of Prineville Reservoir was dominated by top-level predators (smallmouth bass, largemouth bass, and rainbow trout). Except for juvenile bass (George and Hadley 1979, Jackson et al. 1990), zooplanktivorous fish capable of exerting "top-down" control of zooplankton were conspicuously absent. Trophic cascade theory suggests that such a community structure should result in large herbivorous zooplankton. Our investigations reveal that this is indeed the case with large Daphnia dominating the zooplankton community. Providing an example of "bottom-up" control, these large Daphnia are better adapted to utilize the colloidal clay-algae particles as food than smaller cladocerans would be (Knoechel and Holby 1986). As a result, present reservoir fish production is probably higher than if fish predation created a shift toward smaller zooplankton community. Black crappie were first detected in the reservoir by ODFW during the 1993 sampling and have become very abundant since that time. Increasing crappie abundance could, conceivably, alter the trophic equilibrium and energy flow in Prineville Reservoir by either 1) filling a vacant niche or 2) competing with established populations (Traxler and Murphy 1995). Although adult crappie generally do not utilize daphnids to any extent in their diet, young-of-the-year crappie are planktivorous for a period of time (Carlander 1977). Crappie predation could shift zooplankton size and species composition toward smaller individuals and affect the productivity of bass and trout in the reservoir.

Decreases in the size and abundance of Daphnia due to black crappie predation could alter the trophic equilibrium in Prineville Reservoir in many ways. Large-bodied Daphnia are able to utilize and in some cases, control blue-green algae blooms (Christoffersen et al. 1993, Schoenberg and Carlson 1984). Romare et al. (1999) showed a linkage between the predation pressure of juvenile European perch (Perca fluviatilis) on Daphnia and an increase in late-summer abundance of blue-green algae. Young-of-the-year perch predation decreased cladoceran biomass and size. This resulted in reduced grazing pressure and resulted in increases in blue-green algae abundance. To further complicate predicting the effects of black crappie, Daphnia were shown to be able to aggregate clay particles through consumption at a much greater rate than smaller zooplankton (Gliwicz 1986). These aggregated clay particles then settled out of suspension which lead to a decrease in turbidity and a substantial increase in
primary production. How these effects manifest themselves in Prineville Reservoir can only be speculated on.

Development of Fishery Management Indices

In Prineville Reservoir, large Daphnia constitute a large percentage of the zooplankton for most of the year, although the absolute abundance varies temporally and spatially. In addition, though there is no statistical difference between monthly mean Daphnia length in 1993 at the 0.05 level, there is a large change in the percentage of the population over 1.0 and 1.3 mm during the summer. In trying to develop a management index based on Daphnia abundance, the utility of such an index would depend, to a large extent, on the importance of Daphnia in the seasonal diet of the fish species of interest. While some investigators have shown a relationship between the abundance of large Daphnia and trout growth and survival (Galbraith 1975, Mills and Schiavone 1982, Tabor et al. 1996, Wang et al. 1996), others have suggested that Daphnia biomass would be a poor predictor of trout growth in systems where their diet is dominated by other prey (Johannes and Larkin 1961, Beauchamp 1990). Therefore, when developing a sampling strategy for an index based on zooplankton, the effects of the spatial distribution and behavior of the target fish on its potential diet must be considered (Wurtsbaugh et al. 1975, Jackson et al. 1990, Wang et al. 1996).

Galbraith (1975) suggested that indices for rainbow trout-managed waters should be calculated from sampling performed during August and September with a goal of 150 Daphnia per vertical tow (anoxic depth to surface) as a management goal. In waters that develop strong stratification, this period is when rainbow trout would probably be most dependent on zooplankton because of habitat limitations. In Prineville Reservoir, it appears that early- to mid-August is the period when Daphnia size and density would be most limiting to rainbow trout. Theoretically, indices for waters dominated by warmwater fisheries should be sampled in May or June because this is generally when young-of-the-year bass and panfish are utilizing large cladocerans. In Prineville Reservoir, sampling for this index should probably occur during the period from mid-May to mid-June.
LITERATURE CITED


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APPENDIX A

Phytoplankton Species Composition
in Prineville Reservoir, 1982

Appendix Figure A-1. Phytoplankton species composition in Prineville Reservoir in May, August, and November, 1982 (from Johnson et al. 1985). Number of species in "Other" category shown in parentheses.
APPENDIX B

Comparison of Zooplankton Densities in Select Central Oregon Lakes.

Appendix Table B-1. Comparison of zooplankton densities in select eastern Oregon lakes.

<table>
<thead>
<tr>
<th>Reservoir</th>
<th>Sampling Period</th>
<th>Average zooplankters/cubic meter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prineville Reservoir</td>
<td>May-September, 1985</td>
<td>14,400</td>
</tr>
<tr>
<td>Suttle Lake</td>
<td>May-September, 1982</td>
<td>34,100</td>
</tr>
<tr>
<td>Paulina Lake</td>
<td>May-September, 1982</td>
<td>33,300</td>
</tr>
<tr>
<td>North Twin Lake</td>
<td>May-September, 1982</td>
<td>37,800</td>
</tr>
<tr>
<td>East Lake</td>
<td>May-September, 1982</td>
<td>29,400</td>
</tr>
<tr>
<td>Phillips Reservoir</td>
<td>May 23, 1989</td>
<td>46,365</td>
</tr>
<tr>
<td>Thief Valley Reservoir</td>
<td>May 22, 1989</td>
<td>15,575</td>
</tr>
<tr>
<td>Unity Reservoir</td>
<td>May 23, 1989</td>
<td>26,400</td>
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<tr>
<td>Owyhee Reservoir</td>
<td>April-September, 1992</td>
<td>16,150</td>
</tr>
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</table>
APPENDIX C

Density of Zooplankton Nauplii
in Prineville Reservoir, 1993

(chart showing number per m³ over time for different areas)
APPENDIX D

Size Range of Selected Zooplankton in Prineville Reservoir, 1993

Appendix Figure D-1. Size range (mean size denoted by •) of *Diaphanosoma* in Prineville Reservoir in 1993.

Appendix Figure D-2. Size range (mean size denoted by •) of calanoid copepods in Prineville Reservoir in 1993.
Appendix Figure D-3. Size range (mean size denoted by *) of cyclopoid copepods in Prineville Reservoir in 1993.
APPENDIX E

Size Range of Selected Zooplankton in Prineville Reservoir, 1994

Appendix Figure E-1. Size range (mean size denoted by ●) of *Diaphanosoma* in Prineville Reservoir in 1994.

Appendix Figure E-2. Size range (mean size denoted by ●) of *Ceriodaphnia* in Prineville Reservoir in 1994.
Appendix Figure E-3. Size range (mean size denoted by ●) of calanoid copepods in Prineville Reservoir in 1994.

Appendix Figure E-4. Size range (mean size denoted by ●) of cyclopoid copepods in Prineville Reservoir in 1994.