

AN ABSTRACT OF THE THESIS OF

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From July 1985 to April 1987 the pelagic zooplankton community of Crater Lake, Oregon was studied to determine taxonomic structure, absolute and relative densities, and spatial and temporal distributional patterns. Samples were collected using vertically-towed zooplankton nets. The community structure consisted of two cladoceran and nine rotifer species, which were either phytophagous, polyphagous, or triptophagous; none was predaceous. The community numerically was dominated by rotifers, and the majority of the populations occurred within the hypolimnion. Taxonomic structure, abundance, and distribution of the zooplankton community were relatively stable. While the stability was attributed to the extremely high numerical dominance of the rotifer, Keratella cochlearis, some of the observed variations were attributed to depth and season. This stability may be

short-term. Historic data suggest that the density of the cladoceran, Daphnia pulicaria, is cyclic, being highly abundant in some years and rare in others. During this study, D. pulicaria abundances were low but appeared to be on an increasing trend. Changes in Daphnia densities may be due to fluctuations in food supply or in densities of the zooplanktivorous kokanee (Oncorhynchus nerka kennerlyi). Such fluctuations in the daphnid population may be related to and integrated with changes and fluctuations in the zooplankton and phytoplankton communities, primary production, and water clarity.

Structure, Abundance, and Distribution
of Pelagic Zooplankton
in a Deep, Oligotrophic Caldera Lake

by

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STRUCTURE, ABUNDANCE, AND DISTRIBUTION OF PELAGIC ZOOPLANKTON IN A DEEP, OLIGOTROPHIC CALDERA LAKE

INTRODUCTION

Zooplankton play significant roles in the general dynamics of lacustrine systems. Since they are primarily herbivores and a major food source of zooplanktivorous fish, zooplankton are a critical link between phytoplankton and fish communities. In addition to representing a key component in pelagic trophic interactions, zooplankton also influence water quality through their grazing activities and nutrient recycling. Thus, direct and indirect relationships for zooplankton have been established between water quality (e.g., Shapiro et al. 1975) and fish production (e.g., Mills and Schiavone 1982) in lake systems.

The notion that zooplankton communities reflect and influence both biotic and abiotic conditions was demonstrated by Hrbáček et al. (1961). In the presence of planktivorous fish, the zooplankton community consisted of small cladocerans and rotifers; and water transparency decreased due to an increase in nanoplankton abundance. When fish selectively were removed, the zooplankton community shifted to species of larger cladocerans and the phytoplankton composition shifted to lower densities of larger algal species; as a result, water clarity

increased. Subsequent studies have explored these fish-zooplankton-phytoplankton-water quality interactions with similar and consistent results (e.g., Straškraba 1965, Lampert 1978, Lampert and Schober 1978, Henrikson et al. 1980, Elliot et al. 1983, Shapiro and Wright 1984).

In the absence of invertebrate predation on zooplankton, the general pattern resulting from the interactions described above is represented in Figure 1. Predation by zooplanktivorous fishes causes a shift in zooplankton community composition from larger cladocerans to smaller cladocerans and rotifers. Preferential feeding by fish effectively reduces densities of zooplankton larger than about 1.0 mm, allowing smaller zooplankton to successfully compete for common food resources (e.g., Brooks and Dodson 1965, Hall et al. 1970; also, for review see de Bernardi et al. 1987). Fish-mediated changes in zooplankton community structure causes changes in phytoplankton species composition because of differences in nutrient regeneration rates and zooplankton grazing pressure: i) Zooplankton play a major role in lacustrine nutrient recycling (Lehman 1980). Recycling rates increase when the community consists mostly of smaller zooplankters (such as rotifers) because nutrient excretion rates are greater for smaller-bodied organisms (Ejsmont-Karabin 1983). Additionally, in the absence of larger cladocerans, nanoplankton production may be enhanced by

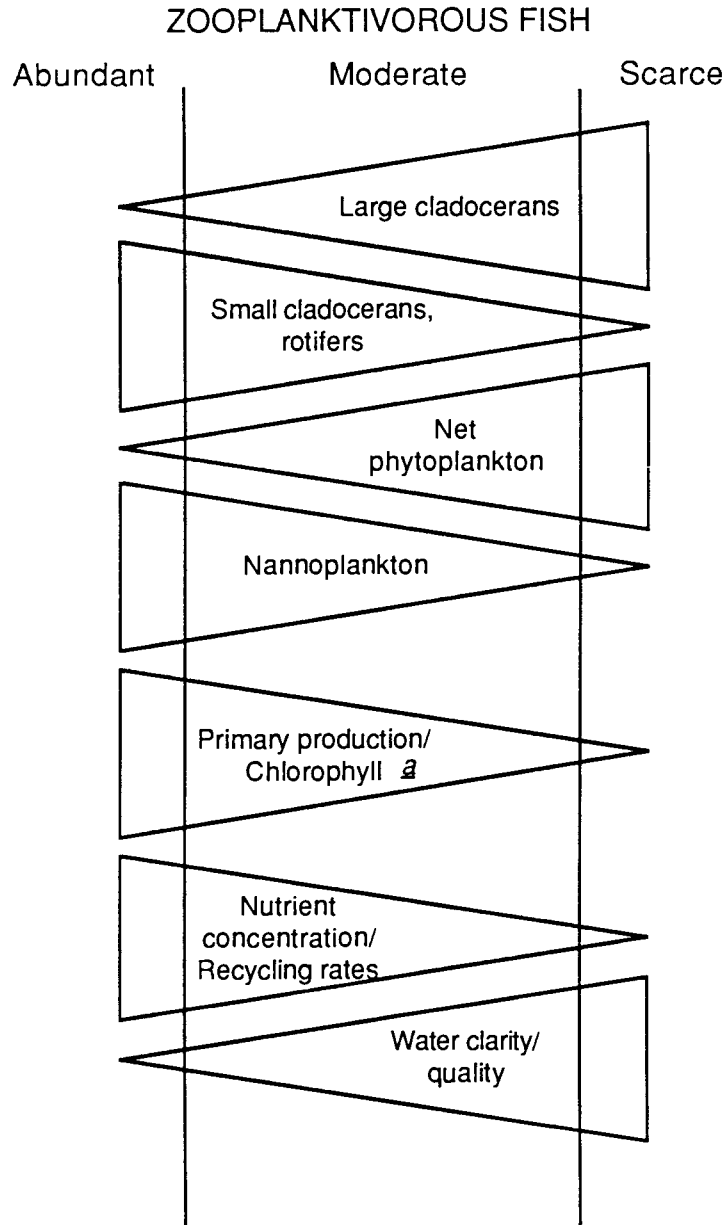


Figure 1. General framework of the relationship among zooplankton and phytoplankton communities, primary production, nutrients, and water clarity with a change in densities of zooplanktivorous fish.

fish excretions (Hillbricht-Ilkowska 1977) and fish decomposition (Neill 1984). ii) Large cladocerans exert a greater grazing pressure than small cladocerans and rotifers (Burns 1969, DeMott 1982, Peters and Downing 1984). When grazing pressure is reduced due to decreases in the densities of large cladocerans, nanoplankton--the size of phytoplankton preferred by zooplankton--increase in numbers over larger-sized phytoplankton (Berquist et al. 1985), presumably because nanoplankton are competitively superior to net plankton (McCauley and Briand 1979). Primary production increases because of higher nutrient availability through recycling and because nanoplankton have higher maximum growth rates than larger-celled phytoplankton (Banze 1976), enabling them to contribute significantly to community production (Gutelmacher 1975, Malone 1971, Kalff 1972). With the increase in primary production, water clarity and/or quality declines (Edmondson 1980). In the absence of zooplanktivorous fish, the pattern reverses itself. This pattern illustrates a "top-down" approach; that is, biotic interactions determine the production of a system rather than abiotic factors.

From 1896 to 1969 several short-term, independent studies provided baseline data on limnological conditions of Crater Lake; these data indicated an extremely deep and clear ultraoligotrophic lake. However, studies from 1978

to 1981 suggested a dramatic decrease in lake clarity and a change in phytoplankton community structure (Larson 1984). Because the data base proved inadequate in providing a conclusive evaluation as to the extent and causes of these changes, Congress mandated a 10-year study of Crater Lake in 1982 to i) develop a reliable limnological data base, ii) develop a more comprehensive understanding of the physical, chemical, and biological components, and iii) establish a long-term monitoring program (Larson 1987a). From 1982 to 1984 investigations centered on physical factors, chemical components, phytoplankton, and primary production. Preliminary investigations of zooplankton and fish began in 1985.

Because of the concern of possible decreased transparency and water quality, the obvious goal of a zooplankton study would be to determine the role this biotic component plays in the Crater Lake ecosystem. However, prior to 1985 little was known about the zooplankton community. Between 1896 and 1969 zooplankton sampling was undertaken in four studies (Table 1). Additionally, some zooplankton information is available from the 1930s and 1940s (Brode 1938, Hasler 1938, Hasler and Farner 1942); however, these studies focused on fish and did not give details as to how and to what extent zooplankton were sampled. A summary of previous Crater Lake zooplankton investigations follows:

Table 1. Summary of previous zooplankton studies at Crater Lake, Oregon.

Investigator(s)	Year(s) of study	Depth sampled (m)	Species noted
Evermann (1897)	1896	surface, littoral	<u>Daphnia pulex</u> <u>pulicaria</u> , Forbes <u>Cyclops (Macrocyclops)</u> <u>albidus</u> , Jurine <u>Cyclops serrulatus</u> (<u>Eucyclops agilis</u>), Fisher <u>Allorchestes dentata</u> , Smith ¹
Kemmerer et al. (1924)	1913	0-590	<u>Daphnia pulex</u> <u>Bosmina longispina</u> <u>Asplanchna</u> <u>Notholca (Kellicottia)</u> <u>longispina</u> <u>Anuraea oculata</u> (<u>Keratella quadrata</u>)
Hoffman (1969)	1967, 1968	0-125	<u>Daphnia pulicaria</u> ² <u>Bosmina longirostris</u> ²
Malick (1971)	1969	0-100	<u>Daphnia pulicaria</u> ² <u>Bosmina longirostris</u> ²

¹This species is misidentified; Allorchestes is a marine amphipod.

²These species originally were reported as Daphnia pulex and Bosmina longispina.

1. Evermann (1897) reported four species of crustaceans were sampled from surface and littoral tows in August 1896 using "fine-meshed surface towing nets." The dominant species was Daphnia pulex pulicaria (Forbes) and noted to be very abundant. Rare species consisted of Cyclops (Macrocyclops) albidus (Jurine), Cyclops serrulatus (Eucyclops agilis) (Fisher), and Allorchestes dentata (Smith). The last species is a misidentification; Allorchestes is a marine amphipod.

2. Kemmerer et al. (1924) reported two species of crustaceans and three species of rotifers from samples obtained using a closing net of No. 20 silk in August and September 1913 (Table 2). Numerically, Asplanchna was dominant, and Daphnia pulex was second in abundance with greatest densities at 40 to 80 m. Swarms of Daphnia also were noted along the shores of Wizard Island and were described as being "of unusually large size." No zooplankton were found in samples collected from the surface to 30 m interval or below 200 m.

3. Brode (1938) reported zooplankton were not present in limnetic tows until a depth of 15 to 22 m was reached; after that depth he encountered "practically a pure 'culture'" of Daphnia, with maximum numbers occurring between 38 and 53 m. Brode did not report the actual time of sampling, but this probably occurred sometime between

Table 2. Summary of zooplankton abundance and depth profiles in Crater Lake, Oregon, 1913 (data from Kemmerer et al. 1924).

Species	Sample date	Depth of occurrence (m)	Number per cubic meter
<u>Daphnia</u>	1 Aug	40-100	1,020
	5 Sep	30-150	4,010
<u>Bosmina</u>	1 Aug	100-150	20
	5 Sep	---	0
<u>Asplanchna</u>	1 Aug	30-200	2,960
	5 Sep	30-200	11,280
<u>Kellicottia</u>	1 Aug	40-200	520
	5 Sep	60-200	1,190
<u>Keratella</u>	1 Aug	60-80	100
	5 Sep	60-200	260

1934 and 1936. Hasler (1938) found that the maximum numbers of pelagic Daphnia occurred between 50 and 122 m in 1937; also, he noted the presence of Daphnia in the bays of Wizard Island. Hasler and Farner (1942) reported that Daphnia were not present either in 100 m to surface tows or around Wizard Island in 1940.

4. Hoffman (1969) studied horizontal distributions and vertical migrations of limnetic Daphnia pulicaria and Bosmina longirostris from June to August in 1967 and 1968.

Horizontal distributions: Using five sampling periods each year, Hoffman made 100 m vertical tows using a 05-m standard net with No. 20 mesh (75 microns). In 1967, 39 tows were made at 6 stations; in 1968, 54 tows were made at 9 stations. In 1967 Bosmina accounted for 98% of the total season densities; Daphnia accounted for 2%. In 1968 Bosmina accounted for 59% of the total densities; Daphnia accounted for 41%.

Vertical migrations: In 1967 and 1968, horizontal tows were made at station 13, site of the deepest basin in Crater Lake (Fig. 2). In 1967 a 0.5-m standard net with No. 6 mesh (about 260 microns) was used, and in 1968 high-speed Miller samplers with No. 12 mesh (about 115 microns) were used. Only a fraction of the Bosmina and Daphnia populations tended to migrate with an exception in August 1968 when nearly the entire adult population of Daphnia

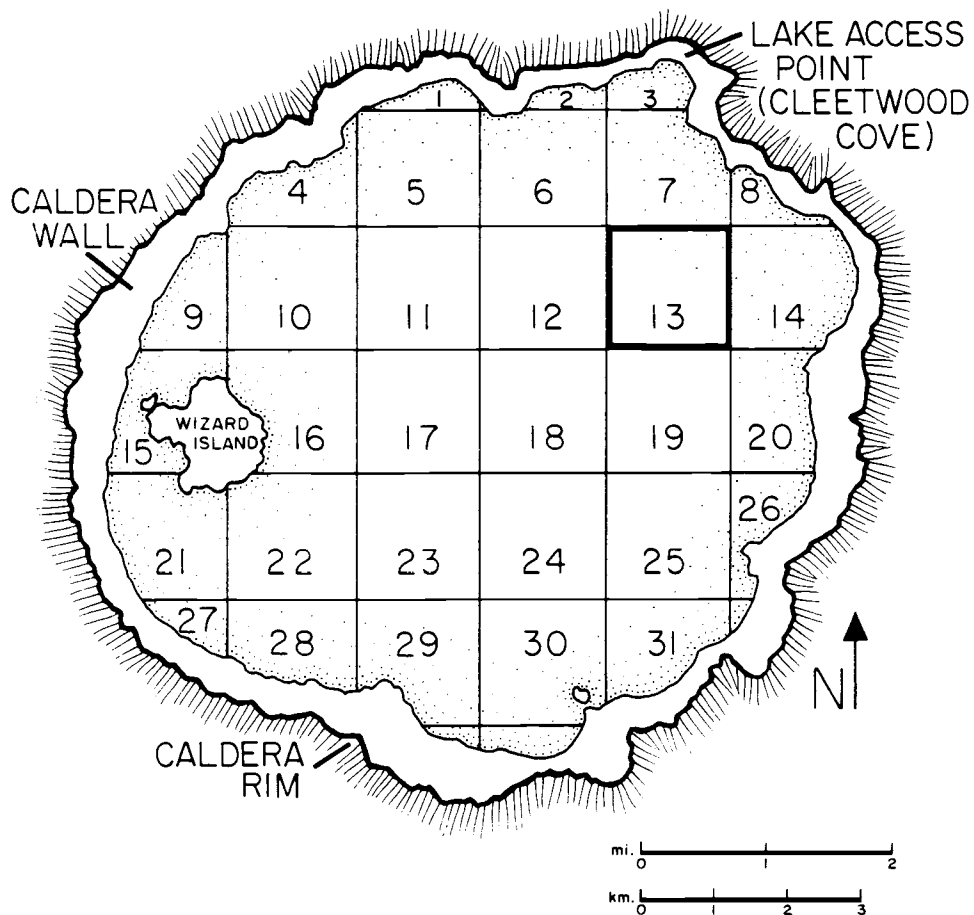


Figure 2. Station grid system for Crater Lake (after Hoffman 1969).

migrated to the surface waters. Greatest numbers of Bosmina occurred between 30 and 75 m; greatest numbers of Daphnia occurred below 50 m.

5. As part of a larger study, Malick (1971) investigated the population dynamics of Crater Lake's limnetic Daphnia pulicaria. He used Hoffman's 1968 data and additionally made 100 m vertical tows at three stations on 17 July and 31 August 1969, using a 0.5-m standard net with No. 6 mesh (about 260 microns). In contrast to conditions in 1968, Bosmina accounted for 2% of the total densities and Daphnia accounted for 98% in 1969. To evaluate instantaneous growth, birth, and death rates, Malick used the egg development time determined by Alevras (1970) for Daphnia pulex in East and Paulina lakes. He concluded that the results did not indicate heavy predation, and the Daphnia abundance appeared to be dependent on food supply.

The nature of the 1985-86 research was, by necessity, exploratory. A variety of methods and sampling designs were incorporated into the overall zooplankton investigations because of a lack of adequate historical information and the difficulties inherent in sampling a system such as Crater Lake. To bring coherency to this type of approach, my thesis focuses on samples taken biweekly from 24 June 1986 to 19 September 1986 at station

13. This station also is the main monitoring location for the mandated Crater Lake limnological studies and, as such, is sampled intensively and consistently. In addition to the biweekly samples obtained during 1986, I also will present and discuss the results of other sampling approaches for general, but inconclusive, observations and trends.

The main objective of this study was to describe taxonomic structure, densities, and distributional patterns of the Crater Lake pelagic zooplankton community during 1986. In doing so, hypotheses can be formulated as to why that particular structure occurred, how it might change through time, and what influence those changes might have on lake clarity. Specific objectives were to: i) describe the summer 1986 pelagic zooplankton community structure at station 13 in terms of species composition, relative and absolute abundances, and spatio-temporal distributions; ii) evaluate zooplankton distributional patterns relative to physical and chemical variables, chlorophyll a, and phytoplankton distributions and densities; iii) compare and evaluate the 1986 pelagic zooplankton community structure at station 13 relative to an additional pelagic location (station 23), the littoral zooplankton community, samples taken during the winter months of 1986 and 1987, and samples obtained from the 1985 pilot study; and iv) determine the most efficient

method and approach for sampling pelagic zooplankton
within the Crater Lake system.

STUDY SITE

Crater Lake exists within the collapsed caldera of Mount Mazama in the Cascade Mountain Range of southern Oregon. Volcanic events that led to the caldera formation occurred about 6600 years ago (Fryxell 1965), and the lake probably reached its present level of 1882 m about 700 to 1000 years ago (Nelson 1967). Near-circular in form, the lake has an area of 48 km², a maximum depth of 589 m, and a mean depth of 325 m (Byrne 1965). A high rim of steep caldera walls enclose the lake, resulting in a limited littoral zone. A secondary volcanic cone, Wizard Island, provides additional littoral habitat. Several springs and streams running down the caldera walls account for surface inflow, but no surface outlet occurs. The lake surface rarely freezes in winter because of strong wind action and a high heat budget.

General limnological features existing from 1982 to 1986 are reported by Larson (1987b). Thermal stratification tends to occur in August and September. The greatest epilimnion depth occurs in September, but this depth is variable, ranging from 9 m (1982, 1983) to 20 m (1985, 1986). A temperature profile taken in March 1986 was nearly isothermal, measuring 2.99°C at surface but increasing to 3.55°C at 250 m. During summer months lake surface temperature has ranged from 8.8 to 19.2°C and

at 100 m the range has been from 3.5 to 4.3°C. Less than 1°C in change occurred below 80 m in the March through September 1986 profiles. Selected temperature values from the summer of 1986 are listed in Table 3.

Although a high Secchi disk reading of 37.2 m occurred on 8 July 1985, values generally were in the high 20s and low 30s. The highest historical Secchi disk reading occurred at 40 m in August 1937 (Hasler 1938).

In terms of depth and season, the water column always is well oxygenated; for example, values ranged from 8.90 to 12.72 mg/l in 1986. The general pH range was from about 7.0 to 8.0. Total alkalinity and conductivity values have been fairly consistent; for example, the 1986 ranges were 25.7 to 27.5 mg/l and 112-120 micromhos/cm, respectively.

Nutrient concentrations are low. Nitrate-N is virtually nondetectable above 300 m. Below that depth a nitrocline occurs; in 1986 the range of values below 300 m was 8 to 16 micrograms/l. Orthophosphate, on the other hand, occurs throughout the water column and ranged from 12 to 19 micrograms in 1986.

Chlorophyll a occurs in low concentrations and tends to exhibit maxima between 100 and 140 m. The greatest

Table 3. Temperature values (Celsius) for selected depths at station 13, Crater Lake, during summer 1986.

Depth (m)	Sampling date			
	25 Jun	23 Jul	20 Aug	17 Sep
surface	12.4	14.1	16.4	12.8
20	5.5	6.9	8.4	12.8
40	4.3	5.3	5.8	6.9
80	3.9	4.0	4.2	---
120	3.8	3.8	3.8	---
200	3.6	3.7	3.7	---

value of 1.41 micrograms/l at 120 m occurred in August 1986.

METHODS

Zooplankton samples were collected from 1 July 1985 to 14 April 1987. Pelagic sampling stations were based on the grid system established by Hoffman (1969; Fig. 2).

Field Sampling

Overview

I used a variety of methods and approaches because of limited historical information on pelagic zooplankton, particularly regarding rotifers. Also, zooplankton investigations had to be adapted and modified to fit into the constraints imposed by a short sampling season, National Park Service operations and logistics, lake conditions, and schedules of other lake research projects.

A pilot study was conducted in the summer of 1985. Samples were taken on two dates: 23 July and 14 August. Information obtained from these samples was used to establish procedures for the 1986 summer sampling program.

Prior to 1986 the sampling at Crater Lake was restricted from late June/early July to late August/early September because weather conditions prevented lake access at all other times of the year. Research vessels had to be air-lifted from the caldera at the end of each summer to prevent their destruction by winter storms. Construction of a boat house on Wizard Island in 1985

provided over-winter storage of the vessels, and winter sampling began in 1986. Thus, this thesis documents the first winter and spring zooplankton samples taken from Crater Lake. In the winter and spring of 1986, zooplankton samples were obtained in March and May. Following the 1986 summer season, two additional sets of winter and spring samples were obtained in January and April 1987.

Sampling in the summer of 1986 focused on station 13, site of the monthly monitoring program of the Crater Lake limnological studies mandated by Congress. Zooplankton samples were taken biweekly during a period extending from 24 June to 16 September, resulting in seven sampling days. Four of the seven days coincided with the monitoring program, thereby incorporating environmental measures into zooplankton structure analysis. On the three intermittent, non-monitoring days an additional pelagic lake station was sampled so that comparisons between absolute abundances and community structure could be made, thus providing an indication of station 13's representativeness of the lake as a whole. Station 23, site of the second-deepest basin in the lake, was chosen as the comparison station; this station is the site most likely to reflect any anthropogenic effects due to its proximity to Rim Village.

Littoral samples were taken from seven transects during two days in early August 1986 for general comparison to the pelagic zooplankton structure occurring during the same time frame.

Night tows were taken to determine if any organisms capable of day-time net avoidance existed in the zooplankton community.

Two field experiments were undertaken in the summer of 1986. One involved testing flowmeters for extraneous readings; this experiment evolved from observations made during the 1986 sampling program. The other experiment was a comparison of sampling methods to determine the best and most efficient procedure in terms of data accuracy and field operations.

Equipment and Techniques

Two nets were used: i) a 0.75-m with a 64-micron mesh and closing apparatus and ii) a 0.50-m with 64-micron mesh; this net was not equipped with a closing apparatus until summer 1986. Both were "Puget Sound" nets, designed by Karl Banse of the University of Washington and built by Research Nets, Inc. in Bothell, Washington. Most samples were obtained using the 0.75-m net; however, the small net was used when dealing with adverse, difficult, or uncertain conditions (e.g., winter, littoral, and night

sampling). Van Dorn bottles with a 4-l capacity were used in the study to compare sampling methods.

The "Puget Sound" nets are designed to maximize sampler filtration efficiency by using a 1:4 ratio of mouth diameter to length of net. The net structure consists of a nonporous collar attached to a conical net, a plankton collecting bucket, and three weight lines. Two ring sets are used. The first ring includes the cross tow bar and is attached to the mouth of the collar; the second ring is attached to the bottom of the collar--where the collar and net are joined--and includes an attachment for a trip line. To close the net at a specific depth, a messenger unit trips a single release mechanism on the main cable tow line and the attachment point of the net to the line is then transferred from the tow bar on the first ring to the second ring. In this way, the collar folds down to close the net. Weights were used for both nets--13.6 kg was attached to the large net and 9.1 kg to the small.

Because the hauling and towing capacities of Crater Lake research vessels were limited, I incorporated only vertical tows into sampling designs. The 0.75-m net always was towed using a gasoline-powered winch, allowing for a constant tow speed of 0.75 m/s. The 0.50-m net was used with the power winch whenever possible; otherwise,

this net was towed by a hand-cranked winch. Both winches were equipped with meter wheels. Nets always were thoroughly rinsed after each tow.

Accurate estimates of water volume sampled are necessary for determining the field density of zooplankton captured by a specific sample. Volume of water sampled by a net system can be determined by multiplying the area of the mouth of the net by the distance the net was towed. Net clogging, however, introduces an error into this calculation, and filtration efficiency must be evaluated for each net haul. Therefore, to estimate filtration efficiency I used two Tsurumi Seiki Kosakusho (TSK) flowmeters, which record on a series of dials the number of revolutions of impeller blades. As recommended by Gehringer and Aron (1968), an inner flowmeter was located mid-way between the net center and the rim to evaluate the effect of the net on water flow. The outer flowmeter was located 0.3 m from the outside of the rim to evaluate free-flow. By using the ratio of inner to outer flowmeter readings, a net filtration factor was obtained for each tow.

Test for Extraneous Flowmeter Readings

The TSK flowmeters I used incorporate a locking device so that they turn only on net ascent and not during net descent. However, during the summer of 1986, while

obtaining pelagic samples with the 0.75-m net, I suspected the flowmeters might be accumulating turns during the net's descent. The procedure for evaluating the possibility of extraneous flowmeter readings, and the effect it might have on final readings, consisted of lowering the 0.75-m net to a specific depth, immediately closing the net at that depth, and towing the net vertically back to surface. Any readings greater than zero were considered extraneous and were recorded for both the inner and outer flowmeters following each tow. This procedure was followed on a calm day (i.e., lake surface flat to nearly flat) and a rough day (i.e., 0.15 to 0.30 m swells). On the calm day, the net was lowered to 20, 40, 60, 80, 100, and 140 m; on the rough day, the net was lowered to 20, 40, 60, and 80 m. Logistic limitations did not allow more extensive experimentation.

In addition to the above procedure, I calibrated the flowmeters in the field, and apart from the net, to compare the readings of the two meters and to equate impeller revolutions to specific depths in a free-flow situation. This was done by attaching the flowmeters, one on either side, to a 5 cm by 30 cm metal plate. This device then was lowered to various depths and retrieved at the designated sampling tow speed of 0.75 m/s. Because no net system was attached, I assumed no extraneous readings occurred during the flowmeter calibration tows. I used a

paired t-test (Sokal and Rohlf 1981) to determine if any differences in readings occurred between the two flowmeters.

Sampling Designs

1985 Pilot Study: Vertical tows were made using the 0.75-m closing net. Samples were taken on 23 July and 14 August at station 13 by dividing the water column into discrete intervals. Eight intervals, with one tow per interval, were sampled in July and covered a depth range from surface to 400 m; the intervals were: 0-20, 20-40, 40-80, 80-120, 120-160, 160-200, 200-300, and 300-400 m. Nine intervals, with two tows per interval, were sampled in August and covered a depth range from surface to 500 m; the intervals were the same as in July but with the addition of a 400-500 m interval.

Winter-Spring 1986: Vertical tows were made using the 0.50-m net and the hand-crank winch system on 5 March and 29 May. Three tow lengths were used: 50 m to surface, 100 m to surface, and 300 m to surface. Except for duplicating the 50 m to surface tow on 3 March, only one tow was made for each distance.

Summer 1986, Station 13: Using the 0.75-m net, I made three replicate tows from three intervals (20-80, 80-120, and 120-200 m) on 24 June, 2 and 22 July, 4 and 19

August, 2 and 16 September. Except for 2 July and 4 August, single tows also were taken from 40 m to surface and from 500 up to 200 m. Samples taken on 24 June, 22 July, 19 August, and 16 September were in conjunction with the Crater Lake limnological monitoring program; thus, environmental data were available. Factors used to evaluate zooplankton structure within the three intervals were temperature (range and mean), chlorophyll a (mean and total), light intensities (percent incident light), and phytoplankton densities and distributions. Phytoplankton species were grouped based on length in the longest dimension (1-10, 11-20, 21-50, 51-70, 71-90, 91-150, and >150 microns), potential use as a food source to zooplankton (edible or inedible), and whether flagellated or not (Appendix I). Food use was determined based on information in the literature: Algal species with rigid cell walls or protrusions, that are large-sized or form large colonies or filaments, or that produce unpalatable chemicals were classed as inedible (Porter 1977). The single tow taken from 40 m to surface was of special interest since 40 m represents the historical maximum in Secchi disk readings. Therefore, zooplankton densities and environmental factors were evaluated in relation to Secchi disk readings for that interval.

Summer 1986, Station 23: Vertical tows were made with the 0.75-m net. As with station 13, I took three

replicate tows from each of three intervals (20-80, 80-120, and 120-200 m) on 2 July, 4 August, and 2 September. A single tow from 40 m to surface was obtained on 2 September.

Summer 1986, Littoral: Seven transects were chosen to sample littoral areas (Fig. 3). Location choices were made to represent a variety of factors including shore vegetation, littoral gradient, presence or absence of rim springs, rim substrate, and bottom substrate. Each transect extended from near-shore out to the pelagic area, and vertical tows were made using the 0.50-m net. A tow was taken from near-bottom to surface at each of these depths: 10, 30, 60, and 100 m. Temperature profiles were taken at the 10 and 100 m stations. Secchi disk readings were taken at all depth stations.

Summer 1986, Night: Using the 0.50-m net and the hand-cranked winch, I took night tows on 25 July along a transect running south-east from Wizard Island's Fumerole Bay. Four depths were sampled: 15, 30, 50, and 75 m. A tow also was taken at station 23 to a depth of 100 m.

Winter-Spring 1987: Winter samples were obtained on 19 January and 14 April using the 0.50-m net with the gasoline-powered winch. On each date the following tows were made: 50 m to surface, 100 m to surface, and 200 m

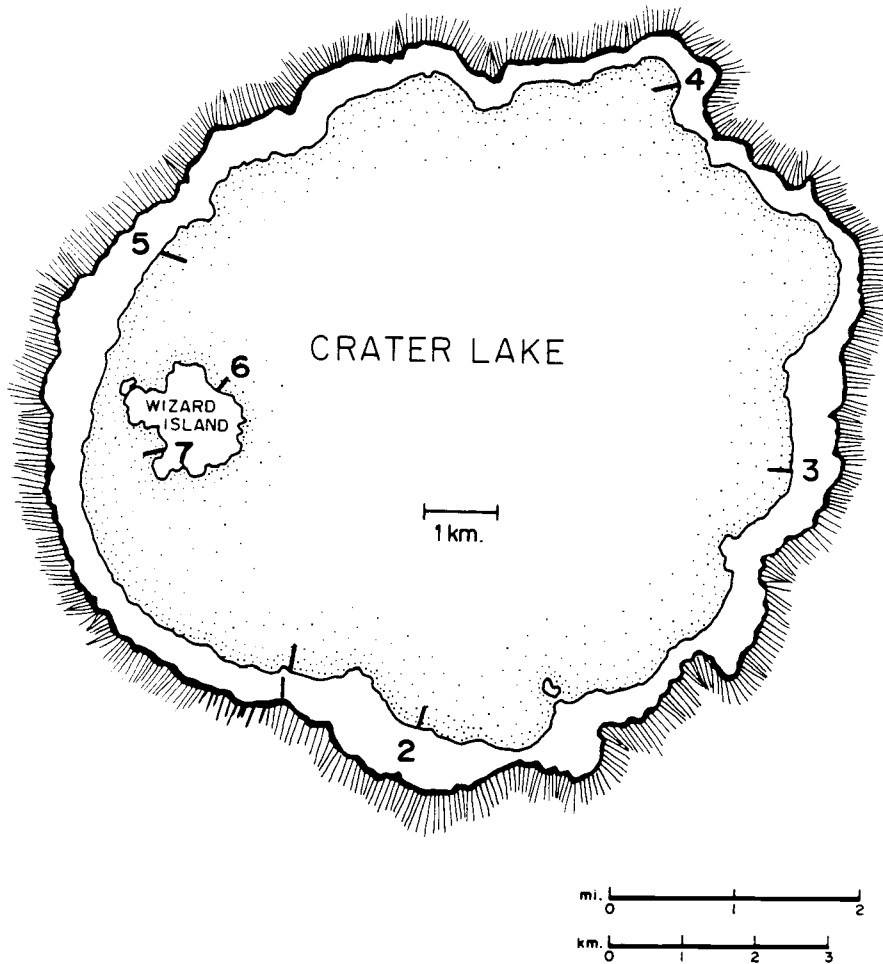


Figure 3. Locations of transects for littoral samples. Key to locations is: 1 = Spring 42, 2 = Spring 20 (Chaski Slide), 3 = Cloud Cap, 4 = Cleetwood Cove, 5 = Devil's Backbone, 6 = Wizard Island (NE), and 7 = Wizard Island (SW).

to surface. A duplicate tow was taken at the 100 m to surface interval for both dates.

Test to Compare Sampling Methods: On 29 July 1986 four sampling methods were evaluated: i) vertical tows using the 0.75-m net with 64-micron mesh, ii) vertical tows using the 0.50-m net with 64-micron mesh, iii) discrete samples using 4-l Van Dorn bottles and 64-micron mesh, and iv) discrete samples using 4-l Van Dorn bottles and 35-micron mesh. Both nets were towed from 80 to 40 m at a constant speed of 0.75 m/s. Eleven Van Dorn bottles were evenly spaced within the 40 to 80 m interval, and 3 l of water were strained from each bottle. Three sampling sets were taken for each of the four methods.

Sample Processing and Analysis

Verifications of species identification were requested from authorities in Cladocera and Rotifera taxonomy.

Samples were preserved in a 4% sucrose-formaldehyde solution and enumerated by subsampling. Specifically, field samples were diluted to acceptable concentrations and two 2-ml subsamples were counted for each concentration. Valid use of this subsample approach requires that i) individual species have a random dispersal pattern within the diluted sample and ii) the

subsample mean is a good estimate of the sample mean for any given species. Verification of random dispersal, the first requirement, particularly is important for rotifers as many have spines, or other protrusions, that induce clumping in preserved samples (e.g., see Ruttner-Kolisko 1977a). I tested for random dispersal by enumerating five replicate subsamples (without replacement) and comparing the observed distribution to a Poisson series (Lund et al. 1958, McCauley 1984, Prepas 1984). Most species tested positive for random dispersal at the 5% level of significance. If densities were great enough, the rotifers Synchaeta, Polyarthra, and Filinia tested positive at the 1% level of significance. To meet the second requirement, acceptable counting precision for each species was defined as a coefficient of variation equal to or less than 0.20 (Cassie 1971, McCauley 1984, Prepas 1984). This often required subsamples for species at low densities in a particular sample to be drawn from lesser concentrations than the dominant species. That is, to ensure counting precision for individual species, any given field sample usually was diluted to and subsampled from more than one concentration.

Samples were stained with Eosin Y to facilitate counting. Subsamples were counted in a rectangular chamber consisting of discrete rows separated by ridges.

Organisms were counted using a dissecting scope set at 40X magnification.

Counts obtained from subsamples were arithmetically expanded to estimate number of organisms per cubic meter of lake water filtered:

$$N = \frac{nV_s}{SV_f}$$

where N = number of organism per m³
 n = average number of organisms per subsample
 V_s = concentrated volume of sample, ml
 S = subsample size, ml
 V_f = volume of lake water filtered, m³ = (net surface area, m²)(depth of tow, m)(net filtration factor)

Data Analysis

Because the main objective of this study was to describe structure, abundance, and distributional patterns within observed field data sets, I used statistical programs that analyze taxonomic structure: AID1, AIDN (Overton et al. 1987), and CLUSB3 (Smith 1987).

I used Simpson's Diversity Index (SDI; AID1, AIDN) to express community structure in terms of species richness and relative abundances:

$$SDI = 1 - \sum_i (n_i/N)^2$$

where n is the number of zooplankton in the i-th species and N is the total number of zooplankton in the sample.

In addition to the diversity measure, I used a dominance measure, R (AID1):

$$R = (SDI_{\max} - SDI) / (SDI_{\max} - SDI_{\min}),$$

where SDI_{\max} and SDI_{\min} are, respectively, the maximum and minimum possible values for SDI, given the number of species in a sample of size N. SDI is the measured diversity of the sample, and R is a measure of dominance.

Seasonal and vertical distributional patterns of the pelagic zooplankton were expressed as absolute abundances in terms of density. Distributional patterns also were analyzed by a resemblance measure, SIMI (AIDN), which expressed the degree of similarity in taxonomic structures between individual samples within replicated tows, pooled replicated samples within a specific depth interval, and pooled samples within an entire water column:

$$SIMI(a,b) = (\sum_i p_{ai}p_{bi}) / [(\sum_i p_{ai}^2)(\sum_i p_{bi}^2)]^{1/2}$$

where $SIMI(a,b)$ is the taxonomic similarity between samples a and b, and p_{ai} and p_{bi} are the proportional abundances of the i-th species in samples a and b, respectively. A SIMI value of 1.0 indicates species compositions and relative abundances between two samples are identical. A value of 0 denotes no similarity.

To further elucidate structure and abundance distribution patterns I used CLUSB3, a cluster analysis program. CLUSB3 implements a divisive, nonhierarchical

algorithm to generate discrete groups of samples. To also assist in the interpretation of pelagic zooplankton structure and distribution, I considered zooplankton in terms of functional groups based on food preferences and additionally performed correlation analyses (Pearson product moment) on zooplankton densities and selected environmental variables.

To compare absolute densities between stations 13 and 23, I used profile analysis, a multivariate technique (Johnson and Wischern 1982). This procedure incorporates covariances in its analysis, thereby avoiding the assumption of independence, and is thus sensitive to the realities and conditions imposed by limnological sampling. To apply this method, the number of replicate samples taken from a specific depth interval must equal the number of depth intervals into which the water column has been divided; in this study, three replicates were taken at three depth intervals (20-80, 80-120, and 120-200 m) on three separate dates. To determine if differences in densities exist, profile analysis imposes three consecutive tests; if, for any test, the hypothesis of no difference is rejected, results of the remaining test(s) cannot be used or interpreted. The first test determines if the profiles established by the mean values along the three depth intervals at both stations are parallel to each other; that is, the change between mean values from

one interval to the next is the same at both stations. If the first test establishes that the profiles are parallel, the second test determines if the profiles between the two stations are the same; that is, there is no significant difference between the means of any of the three depth interval pairs of the two stations. If the second test establishes that the two profiles are the same, the third test determines if the profiles are level; that is, the means at all three depth intervals are equal. If, for any sampling date, the first test could not be passed I then applied an unpaired t-test (Sokal and Rohlf 1981).

Although the t-test does not provide the full dimension of a profile analysis, some insight nonetheless is gained.

The unpaired t-test also was used to determine if differences in absolute densities existed in samples when different sampling gear was used. Prior to applying either profile analysis or the unpaired t-test, I determined if population variances between samples were equal by using the F test (Sokal and Rohlf 1981).

RESULTS

Species Identification

Rotifer species from 1985 and 1986 were identified by Dr. Walter Koste of West Germany. Cladocera specimens from 1968, 1969, 1985, and 1986 were identified by Dr. Vladimír Kořínek of the Katedra Parasitologie a Hydrobiologie, Czechoslovakia. Cladocera from the 1960s were verified as Daphnia pulicaria and Bosmina longirostris, rather than D. pulex and B. longispina as previously reported by Hoffman (1969) and Malick (1971). Dr. Edward S. Deevey, Jr. of the University of Florida confirmed the bosminid identification. A list of species is presented in Table 4.

Flowmeter Experiment

In the flowmeter calibration tows, the flowmeters were pulled simultaneously through the water column in a free-flow situation; that is, without net attachment. With the information obtained from these tows, I was able to: i) determine if any differences in revolution reading between the flowmeters were occurring and ii) establish the relationship between tow depth and number of revolutions for each flowmeter. I found that while the outside flowmeter tended to read slightly higher than the inner flowmeter (Table 5), the differences were not

Table 4. Species list of pelagic zoolankton, Crater Lake, Oregon, 1985-1987.

Phylum or Order	Species
Cladocera	<u>Daphnia pulicaria</u> (Forbes 1893), (<u>emend.</u> Hrbacek, 1959) <u>Bosmina longirostris</u> (<u>senso lato</u>)
Rotifera	<u>Keratella cochlearis</u> (Gosse 1851) morphe <u>macracantha</u> (Lauterborn 1900) <u>Keratella quadrata</u> var. <u>dispersa</u> (Carlin 1943) <u>Polyarthra dolichoptera dolichoptera</u> (Idelson 1925) <u>Philodina</u> cf. <u>acuticornis</u> (Murray 1902) <u>Filina terminalis</u> (Plate 1886) <u>Synchaeta oblonga</u> (Ehrenberg 1831) <u>Conochilus unicornis</u> (Rousselet 1892) <u>Collotheca pelagica pelagica</u> (Rousselet 1893)

Table 5. Calibration values for the number of revolutions per depth for inner and outer flowmeters in a free-flow situation. Statistics for a paired t-test also are given (Sokal and Rohlf 1981).

Depth of tow (m)	<u>Number of revolutions</u>		Difference, D (outer - inner)	D ²
	outer	inner		
20	131	129	2	4
40	258	259	4	16
40	250	251	-1	1
50	315	312	3	9
60	374	374	0	0
60	372	370	2	4
80	509	509	0	0
80	499	493	6	36
100	633	632	1	1
			D = 17	D ² = 71

$$t_s = \frac{\bar{D} - 0}{s_{\bar{D}}} = 2.623$$

$$t_{c.01,8} = 2.896$$

significant ($p < 0.01$). I also found that a strong correlation ($r = 0.999$) existed between depth of tow and number of revolutions for both flowmeters (Fig. 4a and b).

When the flowmeters were attached to the net, I found extraneous revolutions occurred during net descent. I also found that the inner flowmeter recorded more descending revolutions than the outer for both rough and calm lake conditions. Inner flowmeter readings were greater on rough days than on calm, and the outer flowmeter readings for both calm and rough days were somewhat similar (Fig. 5a-d).

The y-intercepts of regressions between descending (i.e., extraneous) revolutions and the depth of the net at closing were greater than zero for both flowmeters under calm and rough conditions (Fig. 5a-d). Further, the y-intercepts for the inner flowmeter were particularly high--26.4 revolutions for calm conditions and 42.2 for rough. The possibility that the lack of zero y-intercepts could be a result of regression calculations did not seem likely because zero intercepts were obtained for the calibration tows (see Fig. 4a and b). Rather, this lack of zero y-intercepts appeared to be associated with net attachment and indicated that the majority of the problem, i.e., the greatest rate of extraneous revolutions, might be occurring within the upper 20 m of the water column.

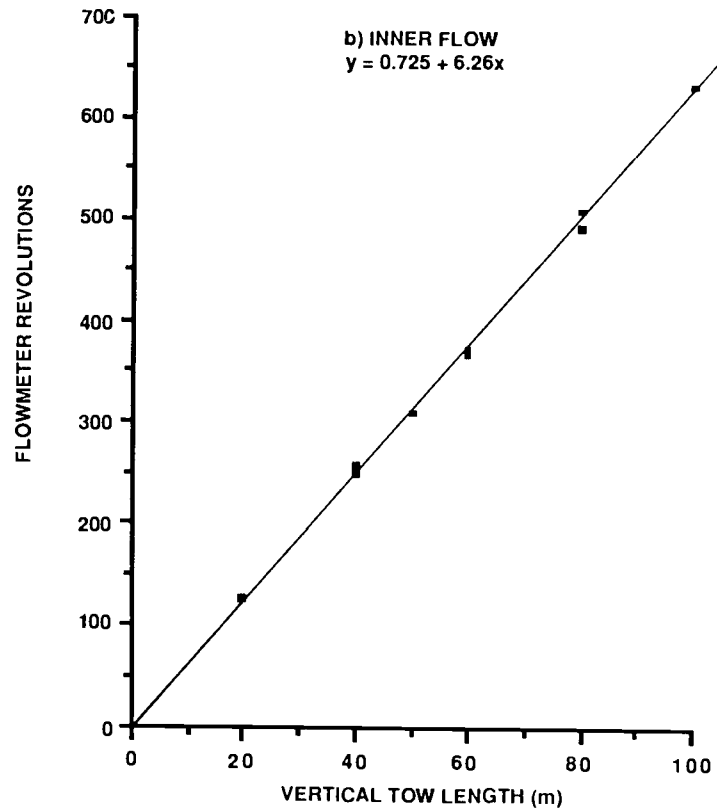
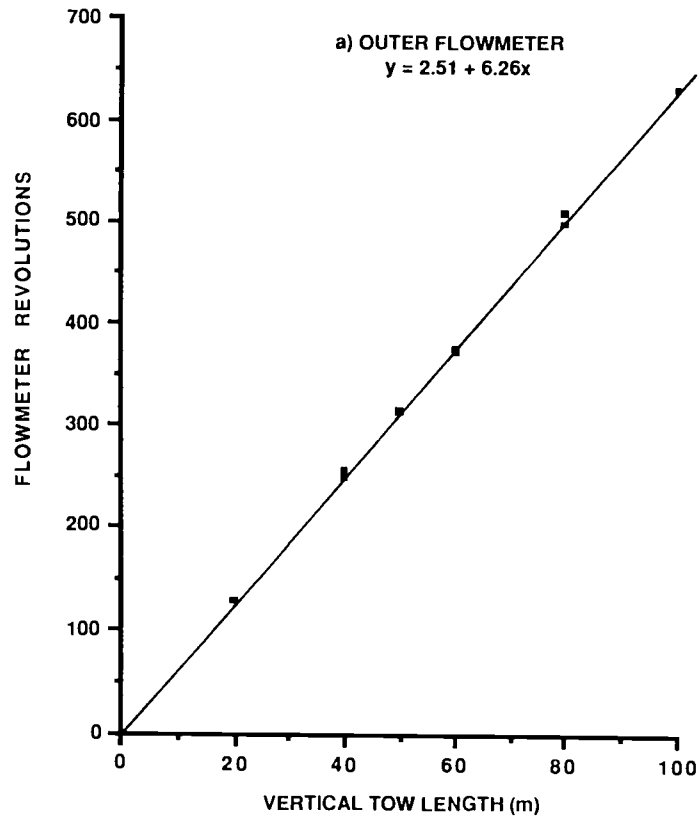


Figure 4. Relationship between tow length and flowmeter revolutions in a free-flow situation (i.e. without net attachment) for the outer (a) and inner (b) flowmeters.

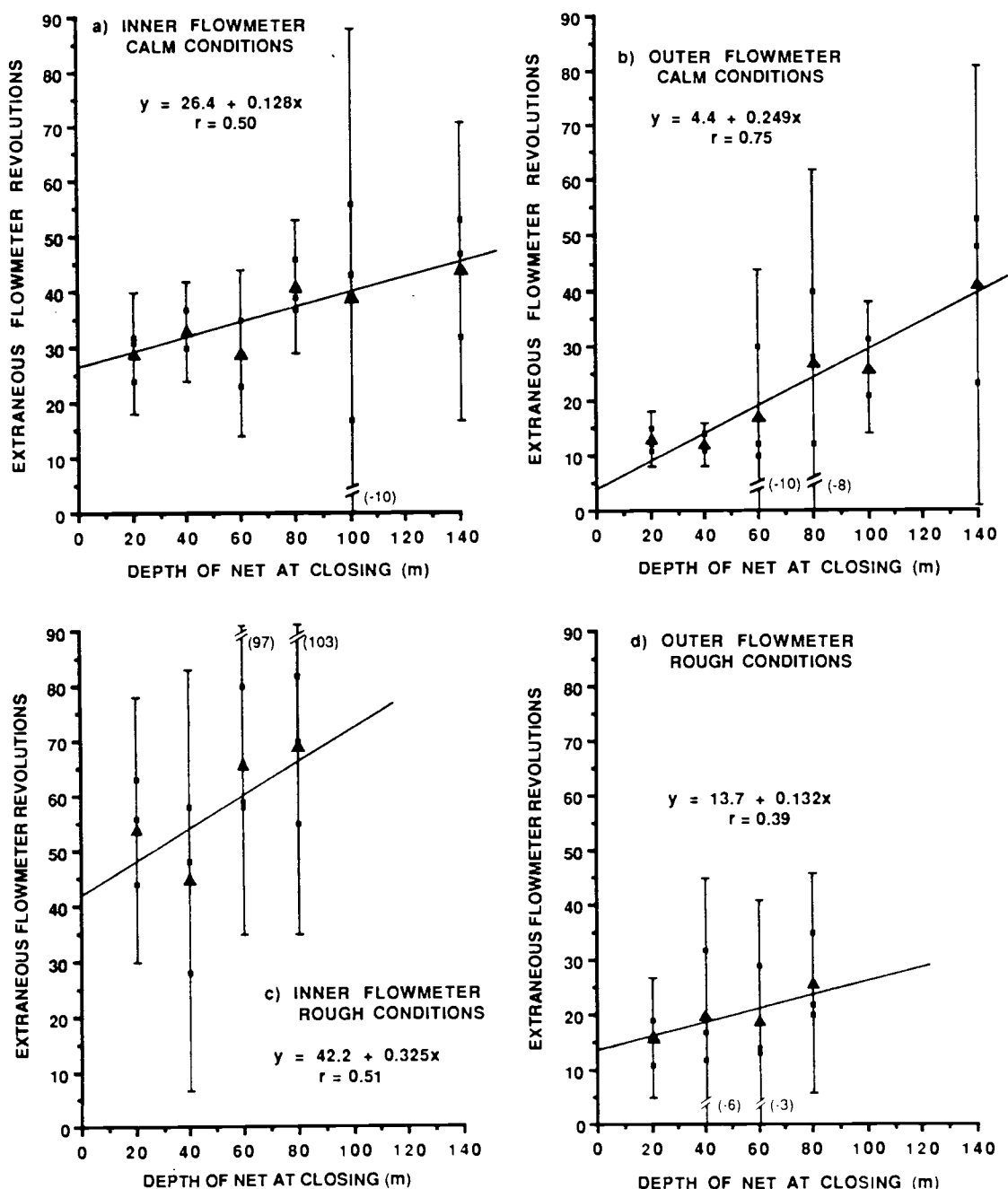


Figure 5. Relationship between depth of net at closing and extraneous flowmeter revolutions that occurred during net descent for the inner (a,c) and outer (b,d) flowmeters during calm (a,b) and rough (c,d) lake conditions. Calm = lake surface flat to nearly flat; rough = 0.15 to 0.30 m swells. Large triangle symbol = mean value; small square symbol = individual value. Vertical lines indicate 95% confidence intervals.

To evaluate this possibility, I calculated the percent bias from total revolutions expected for a given depth in two ways: i) by assuming the bias occurred only in the upper 20 m and, therefore, was being "diluted" by tows of greater depths (i.e., no extraneous revolutions occurred after 20 m) and ii) by using the regressed descending revolution values (see Fig. 5a-d) to estimate the probable number of extraneous revolutions that would occur at each depth if no dilution was occurring. Because of the high variability of the raw data, I used regressed descending revolution values rather than the mean values as the best estimate of the probable number of revolutions. For example, the expected number of revolutions reading on the inner flowmeter in a free-flow situation for an 80 m tow would be 501 (Fig. 4b). Based on the regression relationship established for the inner flowmeter while attached to a net system on a calm day, I can expect, on the average, 36.6 extraneous revolutions to occur during the net's descent to 80 m (Fig. 5a). If no readings occurred on descent, no bias would occur. But since readings did occur on descent, the percent bias from total revolutions is calculated as $(36.6 - 0/501) \times 100 = 7.3\%$. In comparing a possible "dilution" effect to the estimate of probable values for calm and rough conditions, I found that although the problem of extraneous revolutions occurred at all depths, the bias occurred

mainly in the first 20 m (Fig. 6a and b). Thus, at greater depths a tendency to partially "dilute" the number of extraneous revolutions does exist.

To determine what pattern might exist for these biases and to evaluate whether biases obtained were consistent for the inner and outer flowmeters, extrapolating percent bias values from the empirical data was necessary. I obtained the extrapolated values for percent bias on a calm day by computing the regressed descending revolution value for a specific depth on a calm day (Fig. 5a and b), dividing that value by the number of expected revolutions in a free-flow situation (Fig. 4a or b), and multiplying by 100. With this value, I then computed the corresponding percent bias for a rough day based on a linear regression relationship established between the empirical percent bias values for calm and rough conditions. To estimate intermediate lake conditions (i.e., rippled surface), I computed the average of the calm and rough percent error values. This assumes a linear relationship between calm and rough conditions; if the relationship is actually curvilinear, the error for intermediate conditions would most likely be less than estimated.

Patterns for percent bias for the inner flowmeter, which is susceptible to net influences, indicated that the

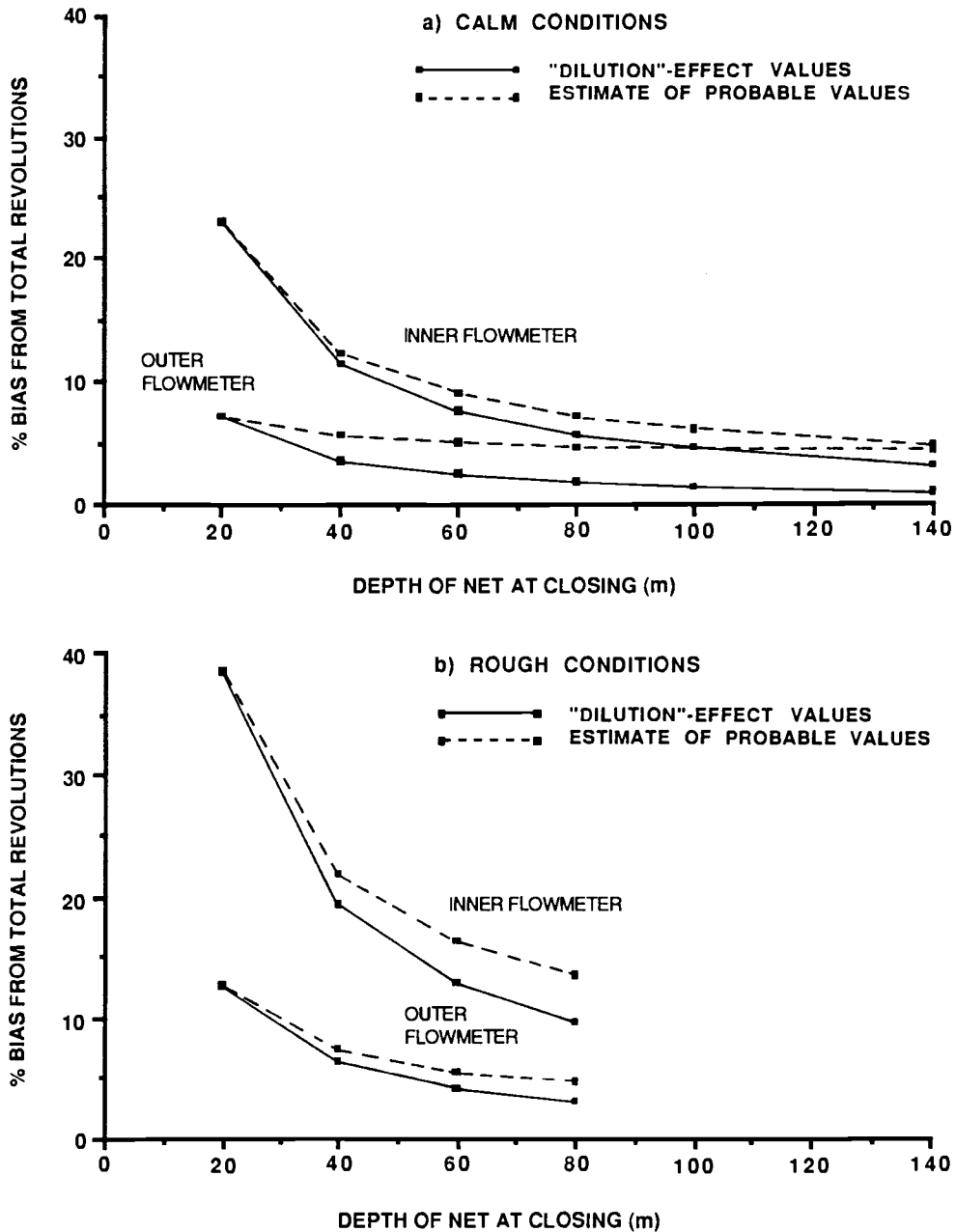


Figure 6. Comparisons between a possible "dilution" effect and the estimate of probable values under calm (a) and rough (b) lake conditions. The above patterns indicate that the inner flowmeter is affected more than the outer and that although the greatest number of extraneous revolutions appears to occur in the upper 20 m, the problem continues to occur at lower depths.

percent bias for both calm and rough conditions consistently decreased as depth increased and the difference between calm and rough values consistently decreased with increasing depth (Fig. 7a). Patterns for percent bias for the outer flowmeter, which evaluated free-flow, indicated that the bias decreased with increasing depth but that a change in slope occurred after 80 m (Fig. 7b). This slope change is most probably an artifact of insufficient data to fully assess bias patterns, particularly since a much smaller difference in mean values occurred between calm and rough conditions for the outer flowmeter. (Differences in mean values between calm and rough conditions were 3, 8, 2, and 1 for depths of 20, 40, 60, and 80 m, respectively; Figures 5b and 5d).

Since a consistency in bias is indicated for the inner flowmeter, I established correction values for a range of lake conditions--calm, intermediate, rough (Table 6). The correction values are the regressed descending revolution values that can, on the average, be expected for each specific tow depth. Table 6 lists only those tow depths used in the 1986 study.

The outer flowmeter requires a different correctional approach because the margin of bias between calm and rough conditions is small, particularly at depths of 80 m and greater. Also, the purpose of the inner flowmeter is to

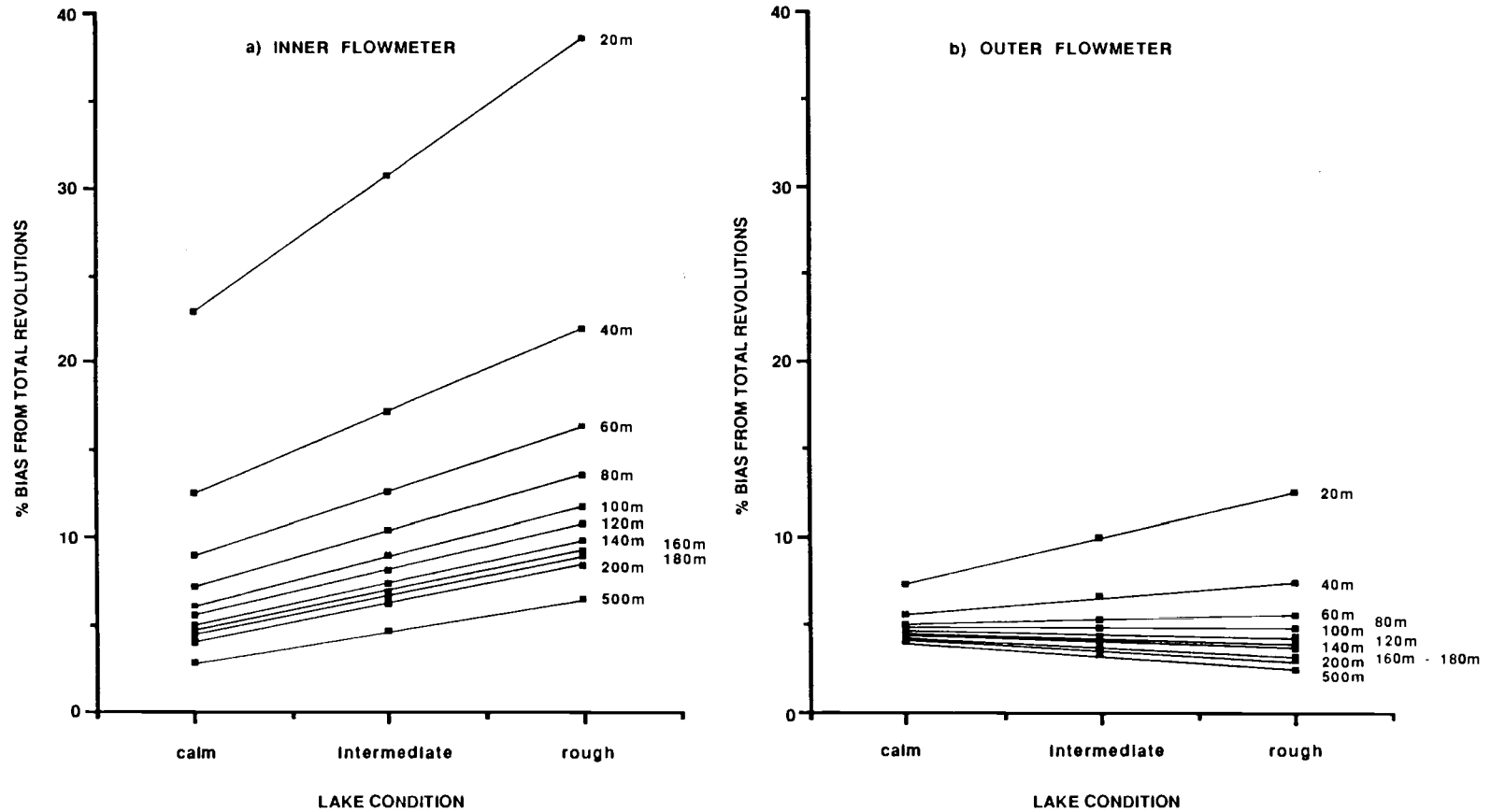


Figure 7. Changes in bias from calm to rough lake conditions for the inner (a) and outer (b) flowmeters. The above patterns indicate the inner flowmeter is more likely to be affected by extraneous revolutions and that the bias is consistent for the inner, but not the outer, flowmeter.

Table 6. Correction values for the inner flowmeter.

Lake condition	Depth of tow (m)	Correction value (= regressed extra- neous revolution)	Percent bias from calm value
Calm	40	32	---
	80	37	---
	120	42	---
	200	52	---
	500	90	---
Intermediate	40	43	4.8
	80	52	3.1
	120	62	2.6
	200	80	2.2
	500	148	1.8
Rough	40	55	9.5
	80	68	6.3
	120	81	5.3
	200	107	4.4
	500	205	3.7

evaluate net filtration efficiency, which is a function of tow length, mesh size, and zooplankton field densities, whereas the purpose of the outer flowmeter is to evaluate free-flow, which is a function of tow length only. For the outer flowmeter, then, I chose to use the regression relationship (established in Fig. 4a) between depth of vertical tow and number of flowmeter revolutions.

Application of the correction values is based on the relationship between inner and outer flowmeter readings. The outer flowmeter reading evaluates a free-flow situation and is a function of tow length (Fig. 4a), while the inner flowmeter reading reflects the influence of a net sampler on water flow; thus:

$$\text{inner flowmeter reading} = \text{outer flowmeter reading} \times \text{net filtration factor (NFF)}$$

Because the net filtration factor is simply the ratio of inner to outer readings, dividing both sides of this equation by the outer flowmeter reading gives the net filtration factor. But first, to account for extraneous flowmeter revolutions, the above equation can be modified:

$$\text{actual inner flowmeter reading} = \text{regressed outer flowmeter reading} \times \text{NFF} + \text{regressed extraneous revolutions for inner flowmeter}$$

This simply results in adjusting the inner flowmeter reading by a correction value that is the regressed

extraneous revolutions for the inner flowmeter for a specific depth:

$$\frac{\text{actual inner flowmeter reading} - \text{correction value}}{\text{regressed outer flowmeter reading}} = \text{NFF}$$

Thus, by using the correction values (Table 6), the ratio of adjusted inner reading to the regressed outer reading can be used to estimate a net filtration efficiency value that has accounted for the tendency of the flowmeters to accumulate turns on descent.

I applied correction values to tows made with the 0.75-m net in both 1985 and 1986 with the exception of the study comparing different sampling gear. For replicated samples taken in the three intervals comprising the 20 to 200 m range, a mean bias of 16.3% occurred between corrected and uncorrected density computations. Both corrected and uncorrected densities are listed in Appendix II.

1985 Pilot Study

The rotifer, Keratella cochlearis, numerically was the most abundant zooplankter, comprising 61.2% and 54.5% of the community in July and August, respectively (Tables 7a and b). In order of numeric importance, subdominant species were: Polyarthra, Kellicottia, Bosmina, Filinia,

Table 7a. Number of organisms per cubic meter of water sampled at station 13, Crater Lake, on 23 July 1985. Relative abundances per depth interval for each species is given in parentheses. Data presented are from nonreplicated tows and were corrected for extraneous flowmeter readings. + = present.

Depth interval (m)	Species									Totals
	<u>Bosmina</u>	<u>Keratella cochlearis</u>	<u>Keratella quadrata</u>	<u>Filinia</u>	<u>Kellicottia</u>	<u>Polyarthra</u>	<u>Synchaeta</u>	<u>Collotheca</u>	<u>Philodina</u>	
0- 20	+	+	+		+					
20- 40	1 (+)	1 (+)	+		1 (+)	2,334 (0.99)				2,337
40- 80	3,333 (0.09)	14,234 (0.40)			2,113 (0.06)	15,105 (0.43)	697 (0.02)			35,482
80-120	11,544 (0.07)	114,925 (0.69)	210 (+)	14,230 (0.09)	16,077 (0.10)	1,763 (0.01)	6,465 (0.04)	378 (+)	84 (+)	165,676
120-160	1,312 (0.04)	14,840 (0.50)	7,002 (0.23)	1,772 (0.06)	3,629 (0.12)	153 (0.01)	545 (0.02)	358 (0.01)	230 (0.01)	29,841
160-200	620 (0.11)	2,313 (0.40)	167 (0.03)	143 (0.02)	644 (0.01)	48 (0.01)	48 (0.01)	207 (0.04)	1,598 (0.28)	5,788
200-300	93 (0.13)	159 (0.23)	112 (0.16)	23 (0.03)	107 (0.16)			9 (0.01)	187 (0.27)	690
300-400	13 (0.11)	41 (0.35)			19 (0.16)	2 (0.02)			41 (0.35)	116
Totals	1,707 (0.07)	14,681 (0.61)	766 (0.03)	1,620 (0.07)	2,278 (0.09)	1,824 (0.08)	776 (0.03)	97 (+)	248 (0.01)	

Table 7b. Number of organisms per cubic meter of water sampled at station 13, Crater Lake, on 14 August 1985. Relative abundances per depth interval for each species is given in parentheses. Data presented are mean values from duplicated tows and were corrected for extraneous flowmeter readings. + = present.

Depth interval (m)	Species									Totals
	<u>Bosmina</u>	<u>Keratella cochlearis</u>	<u>Keratella quadrata</u>	<u>Filinia</u>	<u>Kellicottia</u>	<u>Polyarthra</u>	<u>Synchaeta</u>	<u>Collotheca</u>	<u>Philodina</u>	
0- 20	26 (0.02)					1,164 (0.98)				1,190
20- 40	9 (+)	+	+			37,705 (0.99)				37,714
40- 80	16,196 (0.31)	6,375 (0.12)		1,109 (0.02)	9,709 (0.19)	17,252 (0.33)	1,132 (0.02)			51,773
80-120	8,692 (0.05)	123,485 (0.76)	1,466 (0.01)	10,682 (0.07)	13,770 (0.09)	362 (+)	3,263 (0.02)			161,720
120-160	932 (0.02)	37,958 (0.68)	10,934 (0.20)	1,212 (0.02)	3,091 (0.06)	137 (0.02)	464 (+)	413 (+)	327 (+)	55,468
160-200	247 (0.12)	462 (0.23)	117 (0.06)	68 (0.03)	85 (0.04)	213 (0.11)	55 (0.03)	73 (0.04)	665 (0.34)	1,985
200-300	54 (0.23)	40 (0.17)	1 (+)	15 (0.06)	8 (0.03)	6 (0.03)	11 (0.05)	4 (0.02)	100 (0.42)	239
300-400	9 (0.20)	10 (0.23)	+	4 (0.09)	3 (0.07)	10 (0.23)	1 (0.02)	7 (0.16)		44
400-500	3 (0.13)	14 (0.58)	+	+			3 (0.13)	4 (0.17)		24
Totals	2,100 (0.08)	13,475 (0.54)	1,002 (0.04)	1,049 (0.04)	2,135 (0.09)	2,995 (0.18)	395 (0.02)	40 (+)	102 (+)	

Keratella quadrata, Synchaeta, Philodina, and Collotheca. Daphnia was rare. Distinct vertical zonation was evident with the majority of organisms occurring in the 80 to 120 m interval. In July, 98.7% of the zooplankton densities occurred in the 20 to 200 m range; in August, 99.5% occurred in this range. SDI values for pooled samples in the 20 to 200 m range were 0.60 in July and 0.63 in August. The SIMI value for the comparison of the July and August samples from the 20 to 200 m range was 0.994, indicating similar taxonomic structures between the two months.

Summer 1986, Station 13

Because the 1985 data indicated almost 100% of the zooplankton community existed between 20 and 200 m, I concentrated sampling efforts in this range during 1986; but whenever time allowed, I also took a single tow from 40 m to surface and from 500 to 200 m for reference purposes. Only Polyarthra occurred in any appreciable numbers in the 40 m to surface tow. However, in relation to the 20 to 80 m interval, an unusually high percent of Polyarthra occurred in the 0 to 40 m interval on 16 September. In considering the 1985 (Table 7a and b) and 1986 (Table 8) data, I found what appeared to be an upward migration by this species into the 0 to 20 m interval during the latter part of summer. Overlapping of the 0 to

Table 8. Number of Polyarthra per square meter of water sampled in two overlapping tow intervals in 1986, Crater Lake. Percent of sample for each interval on a given date also is given in parentheses.

Sampling date	Interval (m)	
	0 to 40	20 to 80
24 Jun	229,360 (15)	1,314,480 (85)
22 Jul	2,273,840 (44)	2,849,700 (56)
19 Aug	1,022,440 (53)	897,300 (46)
2 Sep	948,600 (46)	1,092,540 (54)
16 Sep	882,240 (66)	460,680 (34)

40 m and 20 to 80 m intervals prevents knowing the actual numbers existing in the 0 to 20 m, 20 to 40 m, and 40 to 80 m ranges. Nonetheless, clues are afforded by studying the percent values between the 0 to 40 m and 20 to 80 m intervals: i) 100% in the 0 to 40 m interval would indicate all Polyarthra occurred between the surface and 20 m, ii) 100% in the 20 to 80 m interval would indicate all Polyarthra occurred between 40 and 80 m, iii) a 50-50 trend would indicate all or most of Polyarthra occurred between 20 and 40 m, iv) a high percent in the 0 to 40 m tow would indicate greater numbers of Polyarthra occurred in the 0 to 20 m range, and v) a high percent in the 20 to 80 m interval would indicate greater numbers in the 40 to 80 m range. As the percentage trends in Table 8 indicate, Polyarthra was concentrated in the 40 to 80 m range in June. From July to early September their preferred range was 20 to 40 m. By 16 September, high densities occurred in the 0 to 20 m interval. The results for 1986 are based on zooplankton densities in the 20 to 200 m range. Based on the above observations, however, I have included an estimate of Polyarthra densities in the 0 to 20 m range for the 16 September calculations of absolute abundances.

Absolute Abundances

Zooplankton densities were stable throughout the summer sampling season, ranging from a mean of 60,360 to

83,518 zooplankton/m³ (Fig. 8). Coefficient of variation, which is the ratio of standard deviation to mean and provides a relative measure of dispersion, was low at 0.11. Individual species fell into one of three density-based categories: dominant, subdominant, and rare (Table 9). K. cochlearis accounted for 70.2% of the season density total and consistently was the most dominant species (Table 9).

Based on coefficient of variation values, individual species displayed one of three patterns of seasonal abundance changes: low, moderate, or high variation (Table 10). Densities for K. cochlearis, Kellicottia, Bosmina, and Sychaeta remained relatively stable throughout the season. K. quadrata steadily decreased as summer progressed. Both Filinia and Philodina increased as the season progressed. Polyarthra displayed a maximum density on 22 July. Daphnia, though low in numbers, had small peaks in late August and September. Conochilus was present only in the 16 September samples and was low in density.

Definite vertical zonation was displayed by zooplankton throughout the summer. In considering total summer densities, I found 36.9% of zooplankton numbers occurred in the 20 to 80 m interval, 51.8% occurred in the 80 to 120 m interval, and 11.3% occurred in the 120 to

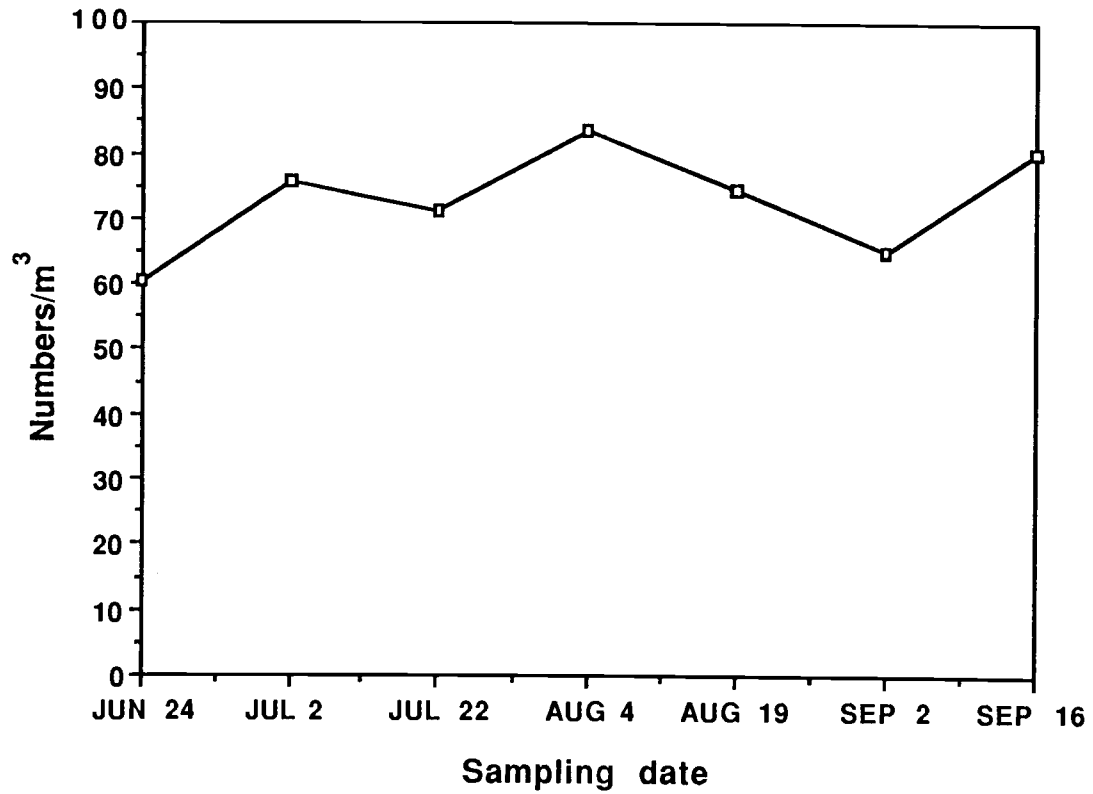


Figure 8. Total densities of zooplankton throughout the summer of 1986 at station 13, Crater Lake.

Table 9. Density classes of pelagic zooplankton from 24 June to 16 September 1986 at station 13, Crater Lake. See Appendix III for species-specific abundance values for this time period.

Abundance	Species	Percent of total season densities
Dominant	<u>K. cochlearis</u>	70.2
	<u>Polyarthra</u>	13.6
Subdominant	<u>Philodina</u>	5.9
	<u>Filinia</u>	3.8
	<u>Bosmina</u>	2.1
	<u>Synchaeta</u>	1.7
	<u>Kellicottia</u>	1.7
	<u>K. quadrata</u>	1.0
Rare	<u>Daphnia</u>	<0.05
	<u>Conochilus</u>	<0.05

Table 10. Descriptive statistics for pelagic zooplankton densities (as numbers per m²) at station 13 from 24 June to 16 September 1986, Crater Lake.

Species	Mean	Standard deviation	Coefficient of variation	Pattern of variation
<u>K. cochlearis</u>	9,218,380	1,121,428	0.12	low
<u>Polyarthra</u>	1,781,986	742,632	0.42	moderate
<u>Philodina</u>	767,949	258,130	0.34	moderate
<u>Filinia</u>	500,397	180,457	0.36	moderate
<u>Bosmina</u>	272,877	69,736	0.26	low
<u>Synchaeta</u>	222,589	63,049	0.28	low
<u>Kellicottia</u>	220,411	37,689	0.17	low
<u>K. quadrata</u>	136,649	138,763	1.02	high
<u>Daphnia</u>	1,906	1,645	0.86	high
<u>Conochilus</u>	326	862	2.64	high

200 m interval. On any particular sampling date, total densities in the 120 to 200 m interval never exceeded 13.4% of the sample. However, densities in the 20 to 80 m interval ranged from 21.8% (19 August) to 50.7% (16 September) of the total sample on a particular date, and the 80 to 120 m interval ranged from 41.8% (16 September) to 66.4% (19 August) (Table 11). The relatively high percentages exhibited within the 20 to 80 m and 80 to 120 m intervals on 16 September and 19 August, respectively, were due to increases in K. cochlearis densities.

Based on depths at which the majority of individual abundances occurred during the summer of 1986, a general pattern of species-specific vertical zonation existed (Fig. 9). In this generalization, Polyarthra, Conochilus, and Bosmina were the main species existing in the 20-80 m interval; K. cochlearis, K. quadrata, Filinia, Kellicottia, and Synchaeta were the main species in the 80-120 m interval; and Philodina was the main species in the 120-200 m interval.

A few species showed depth-specific preferences throughout the season (Fig. 10). K. quadrata occurred mainly in the 80 to 200 m range, with greater densities in the 80 to 120 m interval; Polyarthra occurred mainly in the 20 to 80 m interval, with an apparent migration into the 0 to 20 m interval at the end of the season; and

Table 11. Percent of zooplankton densities occurring in the three depth intervals for each sampling date during summer 1986 at station 13, Crater Lake.

Sampling date	Depth interval (m)		
	20-80	80-120	120-200
24 Jun	34.3	52.3	13.4
2 Jul	34.9	52.1	13.0
22 Jul	42.3	45.2	12.5
4 Aug	34.7	53.0	12.3
19 Aug	21.8	66.4	11.8
2 Sep	39.6	51.1	9.3
16 Sep	50.7	41.8	7.5

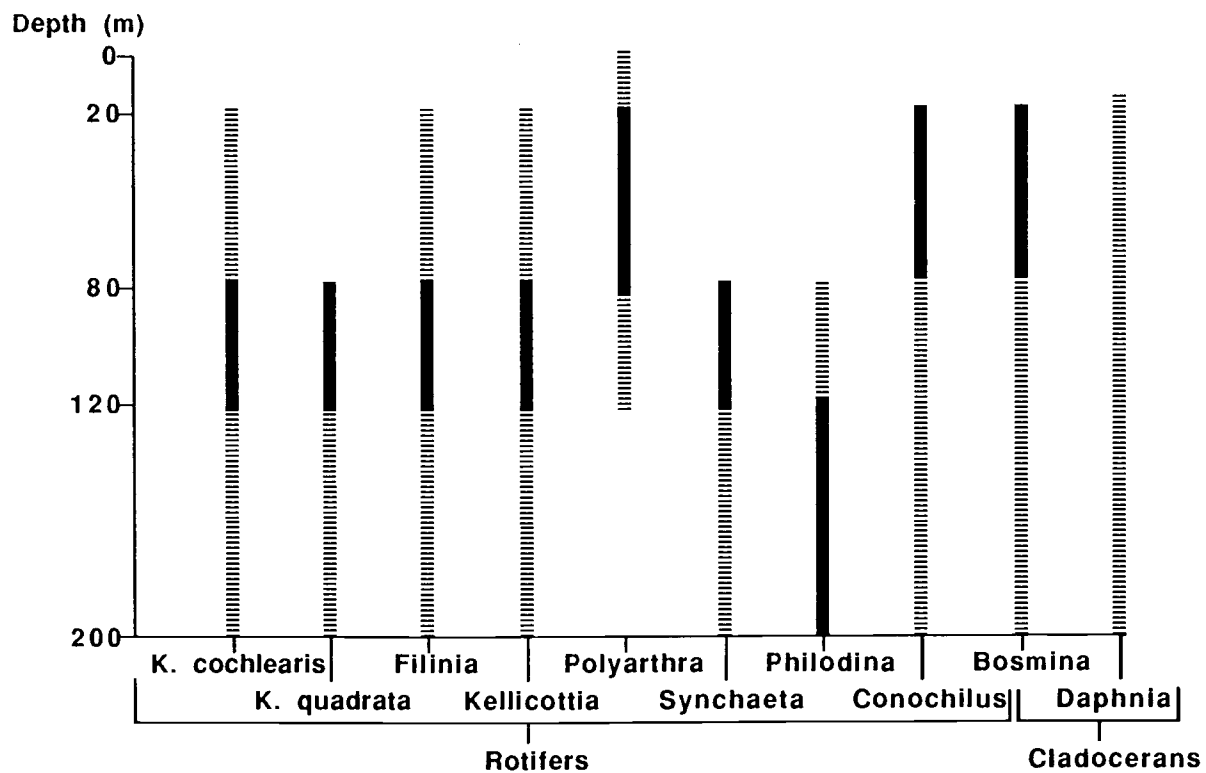


Figure 9. A general representation of species-specific depth occurrences during summer 1986 at station 13, Crater Lake. Solid lines indicate the depth at which the majority of individual abundances occurred. Broken lines indicate depths where lesser individual numbers occurred throughout the summer or depths where individual numbers increased during the latter part of summer.

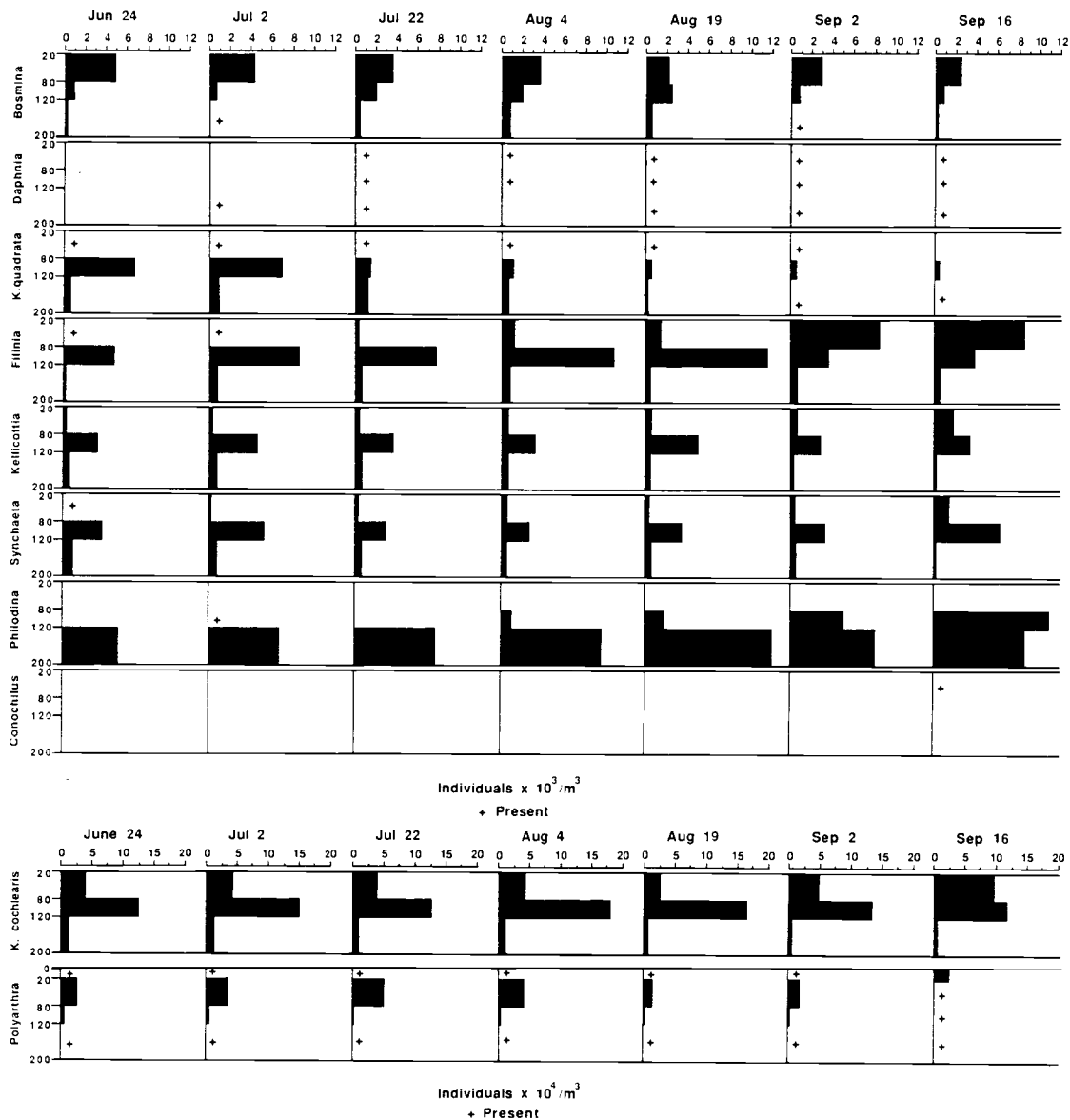


Figure 10. Densities of zooplankton, by species and depth interval, for seven sampling dates from 24 June to 16 September 1986, at station 13, Crater Lake.

Conochilus was found only in the 20 to 80 m tows of 16 September. Other species displayed more flexibility in vertical ranges (Fig. 10). The greatest numbers of Bosmina occurred mainly in the 20 to 80 m interval, although from 22 July to 19 August their densities increased appreciably in the 80 to 120 m interval and to some extent in the 120 to 200 m interval. Daphnia, though low in numbers, was present in all three intervals. Maximum numbers of Filinia occurred in the 80 to 120 m interval until September when maximum numbers occurred in the 20 to 80 m interval. Philodina showed a preference for the 120 to 200 m range until August when they extended their range into the 80 to 120 m interval. Kellicottia and Synchaeta showed similar patterns, with maximum numbers in the 80 to 120 m interval; they also occurred in the upper and lower intervals, with significant increases in the 20 to 80 m range on 16 September. Although K. cochlearis displayed maximum numbers in the 80 to 120 m interval, this species also had high densities in the 20 to 80 m interval, particularly in September.

Community Structure

Species diversity, as expressed by Simpson's diversity index (SDI), was relatively stable (coefficient of variation = 0.12) and low (SDI < 0.5) for pooled samples within the 20 to 200 m range throughout the summer

season (Table 12). This pattern was related closely to the high dominance and absolute abundances of K. cochlearis.

Within each of the five depth intervals, redundancy measures reflected the dominance of one or two species (Table 13): i) The 0 to 40 m interval had the highest dominance measure of the five intervals due to the almost exclusive use of that part of the water column by Polyarthra. A decrease in dominance between 2 September and 16 September corresponded to the first occurrence of Conochilus in the samples and the increase in numbers of K. cochlearis, Bosmina, Filinia, Kellicottia, and Synchaeta in the upper portion of the 20 to 80 m interval, which overlaps the 0 to 40 m interval in this study. ii) In the 20 to 80 m interval, redundancy measures fluctuated between 0.3389 and 0.3868 from 24 June to 2 September; this corresponded to codominance between Polyarthra and K. cochlearis. However, dominance increased ($R = 0.6179$) at the end of the season when K. cochlearis increased and Polyarthra decreased in numbers. iii) In the 80 to 120 m interval dominance was high, with redundancy values fluctuating between 0.6258 and 0.7643; this corresponded to K. cochlearis being the only dominant species within the 80 to 120 m interval. iv) In the 120 to 200 m interval, redundancy values ranged between 0.2652 and 0.4588. In this interval, K. cochlearis shared dominance

Table 12. Simpson's Diversity Index (SDI) values for pelagic zooplankton community occurring between 20 to 200 m at station 13, Crater Lake, 24 June to 16 September 1986. Statistics for these SDI values are: $n = 7$, $\bar{x} = 0.4209$, $s = 0.0486$, and $CV = 0.12$.

Sampling date	SDI value
24 Jun	0.4199
2 Jul	0.4601
22 Jul	0.4980
4 Aug	0.4342
19 Aug	0.3596
2 Sep	0.4037
16 Sep	0.3711

Table 13. Redundancy measures, $R(SDI)$, for the pelagic zooplankton community occurring within five depth intervals at station 13, Crater Lake, from 24 June to 16 September 1986. A value of 0 indicates maximum evenness; a value of 1.0 indicates maximum dominance.

Sampling date	Depth interval (m)				
	0-40	20-80	80-120	120-200	200-500
24 Jun	0.9601	0.3586	0.6925	0.3426	0.5343
2 Jul	---	0.3590	0.6383	0.3103	---
22 Jul	0.9965	0.3724	0.7238	0.2652	0.4585
4 Aug	---	0.3394	0.7643	0.2802	---
19 Aug	0.9941	0.3868	0.7500	0.3942	0.5949
2 Sep	0.9866	0.3389	0.7587	0.3684	0.3295
16 Sep	0.8619	0.6179	0.6258	0.4588	0.3583

with Philodina: K. cochlearis had greater abundance between 24 June and 22 July, numbers for each species were about equal on 4 August, and then Philodina increased to greater abundances between 19 August and 16 September.

v) In the 200 to 500 m interval, redundancy values ranged between 0.3295 and 0.5949. Philodina was dominant in this part of the water column.

In comparing species compositions between individual samples within replicated tows, I found all replicates within a specific interval for a specific date to be nearly identical ($SIMI > 0.858$; Table 14). In a sample size of 63 replicated tows, the mean SIMI value for all possible pairs was 0.989 with a standard deviation of 0.022 and a coefficient of variation was 0.02.

In comparing species compositions based on pooled replicate samples within a specific depth interval, most SIMI values for the paired depth intervals for any given date were between 0.351 and 0.756 (Table 15). In general, lowest similarities ($SIMI > 0.351$) occurred between the 20 to 80 m and 120 to 200 m intervals, where two different species codominated with K. cochlearis; that is, Polyarthra codominated in the 20 to 80 m interval while Philodina codominated in the 120 to 200 m interval. Low similarities ($SIMI > 0.437$) also occurred between the 80 to 120 m and 120 to 200 m intervals from 19 August through

Table 14. Comparisons of Crater Lake zooplankton community structure at station 13 for replicated tows from 24 June to 16 September 1986, using a similarity index (SIMI). A value of 1.0 indicates identical structures; a value of 0 denotes no similarity.

Sampling date	Interval(m)	Paired replicated tows		
		first-second	first-third	second-third
24 Jun	20- 80	0.986	0.998	0.990
	80-120	0.999	0.999	0.999
	120-200	0.995	0.997	0.999
2 Jul	20- 80	0.988	0.999	0.982
	80-120	0.999	0.999	0.999
	120-200	0.993	0.998	0.997
22 Jul	20- 80	0.996	0.994	0.999
	80-120	0.999	0.999	0.999
	120-200	0.947	0.993	0.977
4 Aug	20- 80	0.999	0.987	0.992
	80-120	0.999	0.999	0.999
	120-200	0.858	0.941	0.979
19 Aug	20- 80	0.998	0.949	0.959
	80-120	0.999	0.999	0.999
	120-200	0.964	0.998	0.974
2 Sep	20- 80	0.978	0.958	0.996
	80-120	0.999	0.999	0.999
	120-200	0.999	0.992	0.993
16 Sep	20- 80	0.997	0.996	0.988
	80-120	0.995	0.994	0.999
	120-200	0.991	0.976	0.995

Table 15. Comparisons of Crater Lake zooplankton community structure at station 13 for three depth intervals from 24 June to 16 September 1986 using a similarity index (SIMI). A value of 1.0 indicates identical structures; a value of 0 denotes no similarity.

Sample date	Paired intervals (m)		
	20-80/80-120	20-80/120-200	80-120/120-200
24 Jun	0.846	0.756	0.894
2 Jul	0.808	0.695	0.872
22 Jul	0.635	0.490	0.753
4 Aug	0.726	0.545	0.706
19 Aug	0.895	0.396	0.440
2 Sep	0.924	0.437	0.496
16 Sep	0.990	0.351	0.437

16 September. This pattern corresponds to the period when Philodina was more abundant than K. cochlearis in the 120 to 200 m interval. High similarities (SIMI > 0.895) occurred between the 20 to 80 m and 80 to 120 m intervals from 19 August through 16 September when K. cochlearis was dominant in both depth intervals.

In pooling all samples within the 20 to 200 m range for a given date and comparing community structure between pairs of sampling dates, SIMI values were greater than 0.954 for pooled samples obtained between 24 June and 16 September (Table 16).

In using CLUSB3 to group samples with the most similar taxonomic structure, I found clustering was based on depth- and season-related dominance (Table 17): i) The 80 to 120 m interval for all seven sampling dates was contained in one cluster; this was the interval where K. cochlearis remained dominant throughout the summer. ii) The 120 to 200 m interval was split into two subclusters. One group represented samples from 24 June to 4 August and corresponded to high densities of K. cochlearis; the other group was comprised of samples from 19 August to 16 September and corresponded to Philodina's increase in densities. iii) The 20 to 80 m interval was divided into two subclusters. The first group including all samples from 24 June to 14 August and corresponded to the

Table 16. Comparisons of Crater Lake zooplankton community structure at station 13 for a depth range of 20 to 200 m for 1986 using a similarity index (SIMI). A value of 1.0 indicates identical structures; a value of 0 denotes no similarity.

Date	2 Jul	22 Jul	4 Aug	19 Aug	2 Sep	16 Sep
24 Jun	0.998	0.984	0.996	0.994	0.995	0.988
2 Jul		0.992	0.999	0.990	0.993	0.982
22 Jul			0.994	0.968	0.976	0.954
4 Aug				0.989	0.993	0.999
19 Aug					0.981	0.998
2 Sep						0.995

Table 17. Clustering patterns (CLUSB3) of 21 zooplankton samples taken from station 13, Crater Lake, during summer 1986. Individual samples are identified by depth interval and date.

Cluster	Dominant species
Cluster 1	
80-120 m, 24 Jun	<u>K. cochlearis</u>
80-120 m, 2 Jul	
80-120 m, 22 Jul	
80-120 m, 4 Aug	
80-120 m, 19 Aug	
80-120 m, 2 Sep	
80-120 m, 16 Sep	
Cluster 2	
Subcluster 2a	
120-200 m, 24 Jun	<u>K. cochlearis/Philodina</u>
120-200 m, 2 Jul	
120-200 m, 22 Jul	
120-200 m, 4 Aug	
Subcluster 2b	
120-200 m, 19 Aug	<u>Philodina/K. cochlearis</u>
120-200 m, 2 Sep	
120-200 m, 16 Sep	
Cluster 3	
Subcluster 3a	
20-80 m, 24 Jun	<u>K. cochlearis/Polyarthra</u>
20-80 m, 2 Jul	
20-80 m, 22 Jul	
20-80 m, 4 Aug	
Subcluster 3b	
20-80 m, 19 Aug	<u>K. cochlearis</u>
20-80 m, 2 Sep	
20-80 m, 16 Sep	

codominance of K. cochlearis and Polyarthra. The second group was comprised of samples from 19 August to 16 September and corresponded to K. cochlearis' dominance and the progressively increasing representations of Bosmina, Filinia, Kellicottia, and Synchaeta in the 20 to 80 m interval during the latter part of summer.

Associations Between Zooplankton and Environmental Variables

Correlation analysis between zooplankton pairs occurring from 20 to 200 m throughout the summer revealed seven groups of associations (Table 18). The first group was comprised of K. cochlearis, Filinia, Kellicottia, and Synchaeta. This complex displayed positive correlations between their pairs, ranging from $r = 0.45$ to $r = 0.88$. A second association group was formed between Polyarthra and Bosmina ($r = 0.85$). The five remaining groups revealed moderate, but significant, associations. In one, Philodina was negatively correlated with four other species: Filinia ($r = -0.49$), Polyarthra ($r = -0.50$), Bosmina ($r = -0.59$), and K. cochlearis ($r = -0.64$). In another association, K. quadrata was positively correlated with Kellicottia ($r = 0.56$) and Synchaeta ($r = 0.58$), while Polyarthra was negatively correlated with Kellicottia ($r = -0.46$) and Synchaeta ($r = -0.47$). Filinia and Conochilus were positively correlated

Table 19. Correlations (Pearson product moment) between zooplankton and environmental factors from surface to 200 m at station 13 on 24-25 June, 22-23 July, 19-20 August, and 16-17 September 1986, Crater Lake. Values greater than the correlation coefficient at the 5% level of significance ($r = 0.50$, $n = 16$ and $r = 0.71$, $n = 8^a$) are boldfaced. BOSM = Bosmina, COCH = K. cochlearis, QUAD = K. quadrata, FILI = Filinia, KELL = Kellicottia, POLY = Polyarthra, SYNC = Synchaeta, PHIL = Philodina, CONO = Conochilus, TEMPMN = temperature mean, TEMPRG = temperature range, CHLMN = chlorophyll a mean, CHLTOT = chlorophyll a total.

Species	TEMPMN	TEMPRG	CHLMN	CHLTOT	Percent of incident light ^a			
					RED	BLUE	GREEN	CLEAR
BOSM	-0.07	-0.11	0.16	-0.25	-0.56	-0.10	-0.34	-0.41
DAPH	-0.26	-0.19	0.47	0.40	-0.44	-0.15	-0.30	-0.35
COCH	-0.36	-0.35	0.65	0.37	-0.52	-0.50	-0.53	-0.53
QUAD	-0.37	-0.40	0.30	0.22	-0.46	-0.65	-0.58	-0.55
FILI	-0.18	-0.13	0.52	0.33	-0.46	-0.55	-0.53	-0.51
KELL	-0.47	-0.47	0.81	0.57	-0.55	-0.66	-0.63	-0.61
POLY	0.60	0.50	-0.63	-0.68	0.52	0.80	0.71	0.68
SYNC	-0.49	-0.51	0.90	0.66	-0.58	-0.73	-0.68	-0.65
PHIL	-0.52	-0.54	0.44	0.75	-0.39	-0.60	-0.50	-0.47
CONO	0.50	0.30	-0.18	-0.25	---	---	---	---

^aIncident light data were available only in July and August; therefore, sample size for these variables is 8 rather than 16.

densities, and chlorophyll a variables within the 0 to 40 m interval. For zooplankton densities, the correlation coefficient was 0.09. Correlation coefficients for nanoplankton densities ($r = 0.72$), net phytoplankton densities ($r = -0.35$), chlorophyll a mean ($r = -0.74$), and chlorophyll a total ($r = -0.72$) were not significant at the 5% level of significance for sample sizes of 3 each. Lack of significant correlations between Secchi disk readings and the biological variables may be due to insufficient sample sizes. Further, lack of correlations may reflect the need to relate Secchi values either to changes in zooplankton and phytoplankton structures, rather than densities, or to abiotic variables, such as particles or sediment.

Placement of phytoplankton occurring in the 20 to 200 m range into functional groups based on size, edibility, and whether flagellated revealed that, over the season, nanoplankton (i.e., cells 1 to 50 microns in length) accounted for 84.7% of phytoplankton densities. Also, 87.6% of the total densities were edible species, and 23.0% were flagellated taxa.

The size range useable as a food resource by all zooplankton (1 to 20 microns) accounted for 77.8% of the total season densities. Of the nanoplankton within the 1 to 20 micron range, 98.2% were edible and 20.5% were

flagellated. On a monthly basis, these nanoplankton were numerically dominant within the 20 to 200 m range, with the greatest densities occurring in June and the lowest densities occurring in August (Fig. 11). The size class of phytoplankton useable to grasping zooplankton (21 to 50 microns) and the size class generally not useable to zooplankton (51 to >150 microns) had relatively low densities throughout the summer (Fig. 11).

Generally, phytoplankton densities in size classes greater than 20 microns remained relatively stable throughout the season with a few exceptions (see Table 20): i) In July the 20 to 50 micron size class increased to 11.6% of the total density due to increases in Gymnodinium inversum and a pyrophyte statospore within the 20 to 80 m depth interval; ii) in July and August the 70 to 90 micron size class reached 14.0% and 15.6%, respectively, of each month's total density due to high numbers of Nitzschia gracilis in the upper portion of the 20 to 80 m interval; and iii) in September the >150 micron size class increased to 12.6% of the sample due to an increase of Asterionella formosa (Mary Debacon, personal communication).

To illustrate vertical distribution (Fig. 12), I grouped the phytoplankton based on their possible use or non-use as a food resource to the coexisting zooplankton

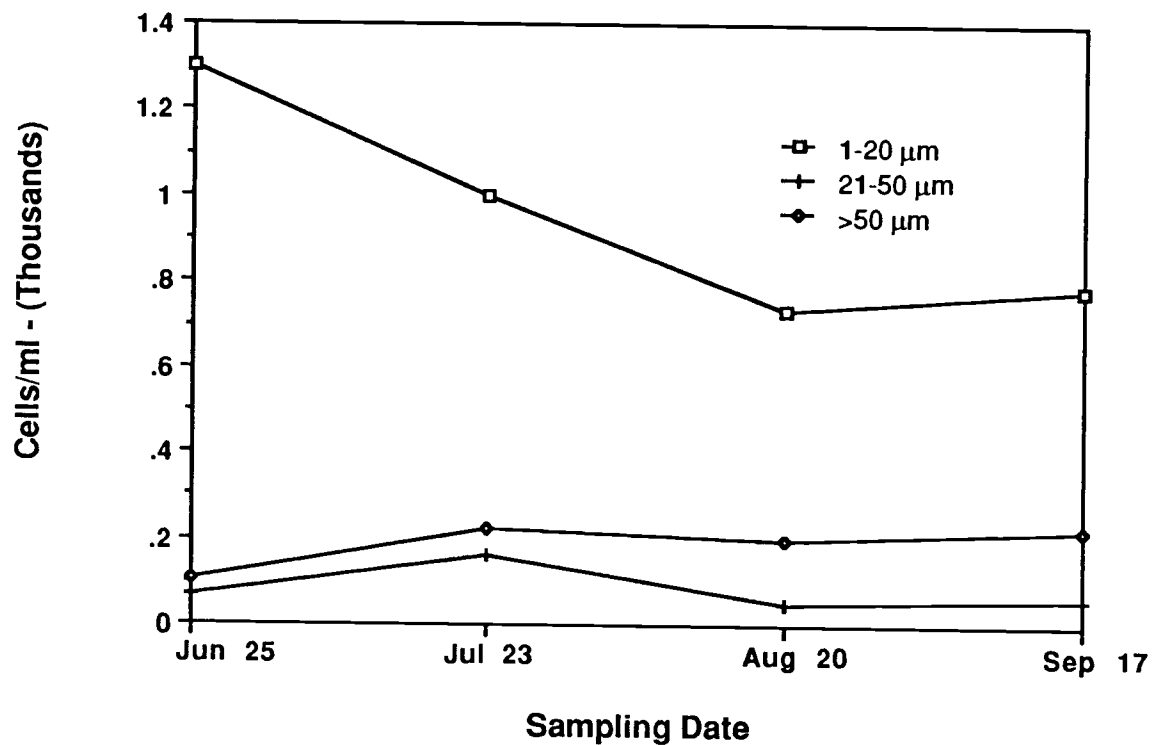


Figure 11. Monthly densities of phytoplankton sampled from 20 to 200 m at station 13, Crater Lake, during summer 1986. Phytoplankton are grouped into three size classes: 1 to 20 microns, 21 to 50 microns, and >50 microns.

Table 20. Densities (cells/ml) of phytoplankton based on size class. Samples were taken at station 13 from 20 to 200 m during summer 1986, Crater Lake. Percent of monthly total for each size class is given in parentheses.

Sampling date	Size category (microns)							Total
	1-10	10-20	20-50	50-70	70-90	90-150	>150	
25 Jun	1158(78.6)	144(9.8)	69(4.7)	25(1.7)	62(4.2)	2(0.1)	14(0.9)	1474
23 Jul	812(58.7)	186(13.4)	161(11.6)	13(0.9)	193(14.0)	3(0.2)	16(1.2)	1384
20 Aug	520(53.7)	203(21.0)	47(4.9)	18(1.9)	151(15.6)	2(0.2)	27(2.7)	968
17 Sep	343(32.1)	443(41.4)	62(5.8)	22(2.1)	62(5.8)	2(0.2)	135(12.6)	1069

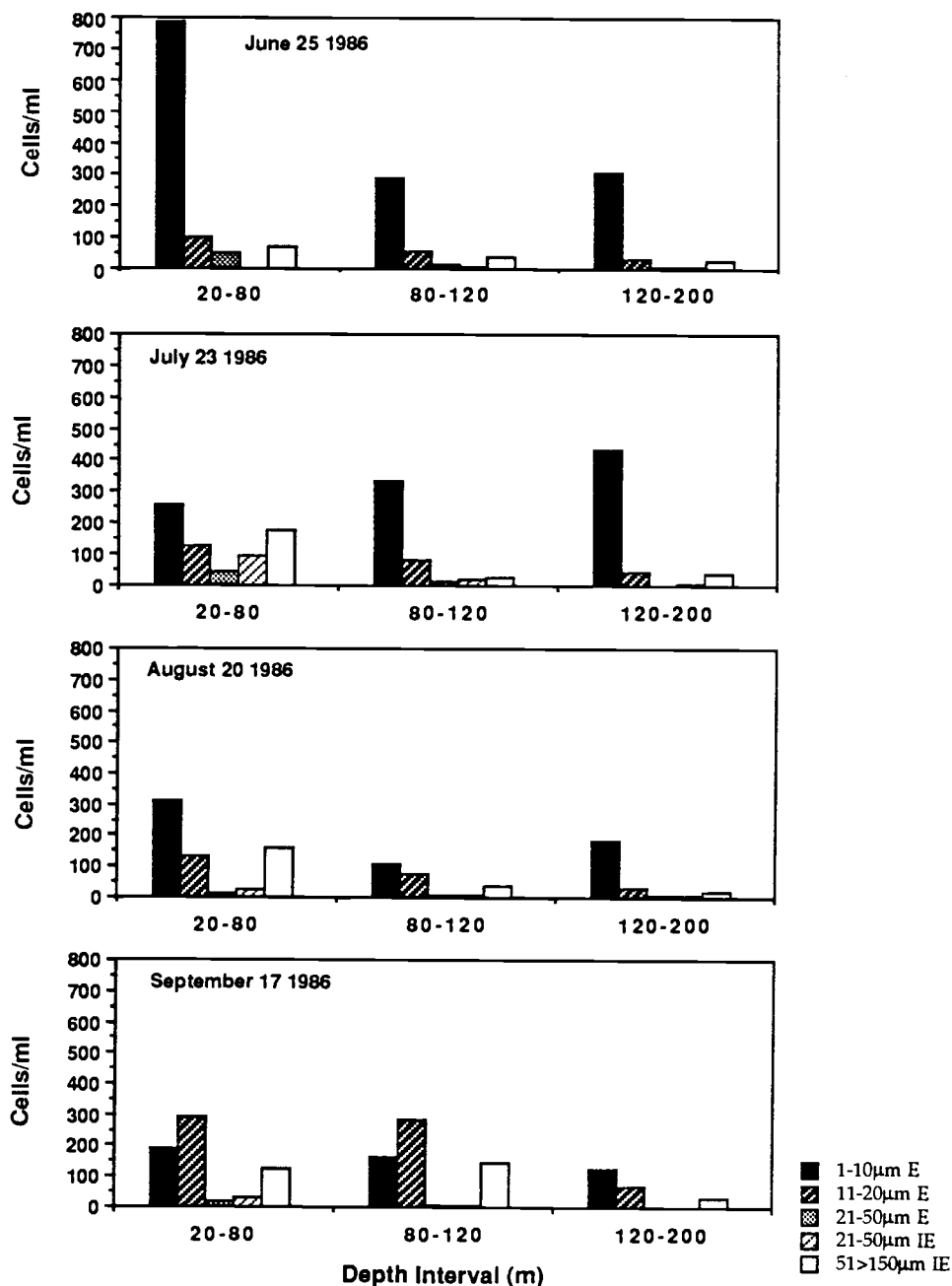


Figure 12. Distributions by depth and month of phytoplankton sampled from 20 to 200 m at station 13, Crater Lake, during summer 1986. Phytoplankton species are grouped into five classes: 1 to 10 microns, edible; 11 to 20 microns, edible; 21 to 50 microns, edible; 21 to 50 microns, inedible; 51 to > 150 microns, inedible.

community. Since 97.6% of the 1 to 10 micron size class were edible species, their total densities are depicted. Within the 10 to 20 micron size class, all species were edible. The 20 to 50 micron size category was subdivided into edible or inedible species because zooplankters with grasping abilities (i.e., Polyarthra, Synchaeta, Bosmina) could use food in this size range. All species greater than 50 microns were grouped together; these were considered to be unlikely food resources due to size. The preferred phytoplankton size ranges (1 to 20 microns) for zooplankton foraging were well represented within the three depth intervals throughout the season and dominated in all intervals for all four dates.

All phytoplankton considered to be edible flagellates were from 1 to 50 microns; no edible flagellates occurred in any size category greater than 50 microns. In the 20 to 200 m range, densities of edible flagellates increased throughout the season and reached a maximum in September (Table 21). Numbers in the 1 to 10 micron size class were stable during most the summer but decreased in September; numbers in the 10 to 20 micron size class were low in June but steadily increased through the summer and accounted for 77.6% of the total sample in September; flagellates in the 20 to 50 micron size class accounted for 59.3% of the total sample in June but steadily decreased as summer progressed (Table 21). Within the surface to 20 m

Table 21. Densities of edible flagellates in the 20 to 200 m range at station 13 during 1986, Crater Lake. Edible flagellates did not exceed 50 microns in length.

Sampling date	Densities (cells/ml)	Percent of sample in size class		
		1 to 10	10 to 20	20 to 50
25 Jun	100	34.3	6.4	59.3
23 Jul	147	43.3	21.0	35.7
20 Aug	165	41.0	49.2	9.8
17 Sep	474	17.0	77.6	5.4

interval, numbers of edible flagellates also increased as the season progressed (Table 22). Densities indicated in the September sample are underestimated as two of the four samples within that interval were not obtained in September. Edible flagellates in the 10 to 20 micron size class did not occur in the surface to 20 m samples until September; at that time, they represented the greatest numbers of the three size classes (Table 22). In terms of vertical distribution, the greatest numbers of edible flagellates occurred in the 20 to 80 m interval. Densities of edible flagellates increased in the 80 to 120 m interval during August and September, and their numbers consistently were lowest in the 120 to 200 m interval (Table 23).

Based on food preferences, I categorized the pelagic zooplankton into three feeding groups: i) phytophagous--those zooplankters that feed exclusively on phytoplankton, ii) triptophagous--those zooplankters that feed exclusively on detritus and bacteria, and iii) polyphagous--those zooplankters that exhibit generalist tendencies and consume algae, detritus, and bacteria (Table 24). The polyphagous groups included K. cochlearis--numerically the most dominant zooplankton, two other rotifer species, and both cladocerans. All five species feed by filtering; Bosmina also has grasping abilities. This group consistently dominated the

Table 22. Densities of edible flagellates within the surface to 20 m interval at station 13 during summer 1986, Crater Lake.

Sampling date	Numbers of flagellates (cell/ml)			Total
	1 to 10 um	10 to 20 um	20 to 50 um	
25 Jun	11	0	17	28
23 Jul	9	0	17	26
20 Aug	41	0	7	48
17 Sep ^a	12	56	14	82

^aSeptember values lack two of the four samples normally taken in the surface to 20 m interval and, therefore, are under-estimated.

Table 23. Proportions of edible flagellates within three depth intervals at station 13 during summer 1986, Crater Lake.

Sampling date	Percent of sample in interval (m)		
	20 to 80	80 to 120	120 to 200
25 Jun	68.4	21.1	10.5
23 Jul	63.3	21.3	15.4
20 Aug	50.5	32.5	17.0
17 Sep	47.4	41.0	11.6

Table 24. Pelagic zooplankton of Crater Lake categorized into functional groups based on food preferences. Type of food capturing method also is noted.

Functional group	Species	Food capturing method
Polyphagous	<u>K. cochlearis</u>	filtering
	<u>Philodina</u>	filtering
	<u>Bosmina</u>	filtering, grasping
	<u>K. quadrata</u>	filtering
	<u>Daphnia</u>	filtering
Phytophagous	<u>Polyarthra</u>	sucking, grasping
	<u>Synchaeta</u>	sucking, grasping
	<u>Kellicottia</u>	filtering
Triptophagous	<u>Filinia</u>	filtering
	<u>Conochilus</u>	filtering

zooplankton structure and represented 79.2% of the total season densities (Table 25). The phytophagous group was comprised of three rotifer species, one which feeds by filtering and two which feed by sucking and grasping. This group represented 17.0% of the season's total densities (Table 25). The triptophagous group essentially was represented by only one rotifer, Filinia, as Conochilus appeared in low numbers during the last sampling date. This group comprised 3.8% of the total densities (Table 25).

Although differing in orders of magnitude, the polyphagous and triptophagous groups displayed similar seasonal patterns. Both groups tended to increase in numbers through the summer with slight declines during late July and, for the polyphagous group, early September (Fig. 13a and b). The phytophagous group, however, peaked during late July and then continued to decline until numbers began to slightly increase in late summer (Fig. 13c).

The polyphagous and triptophagous groups also displayed similar patterns of vertical distribution (Fig. 14). The polyphagous group showed greatest numbers in the 80 to 120 m interval until late summer. Numbers were fairly constant in the 20 to 80 m interval except for a dramatic increase in late summer due to K. cochlearis's

Table 25. Number of zooplankton/m³ occurring within each of three functional feeding groups at station 13, Crater Lake, in 1986. Percent of sample for each date and for season total is given in parentheses.

Sampling date	Feeding group		
	Polyphagous	Phytophagous	Triptophagous
24 Jun	49,287 (81.7)	9,918 (16.4)	1,155 (1.9)
2 Jul	58,490 (77.3)	14,887 (19.7)	2,300 (3.0)
22 Jul	50,650 (71.3)	18,395 (25.9)	2,023 (2.8)
4 Aug	64,356 (77.1)	16,110 (19.3)	3,052 (3.6)
19 Aug	63,310 (84.9)	8,038 (10.8)	3,211 (4.3)
2 Sep	52,730 (81.3)	8,337 (12.8)	3,831 (5.9)
16 Sep	65,494 (81.6)	10,843 (13.5)	3,900 (4.9)
Totals	404,317 (79.2)	86,528 (17.0)	19,472 (3.8)

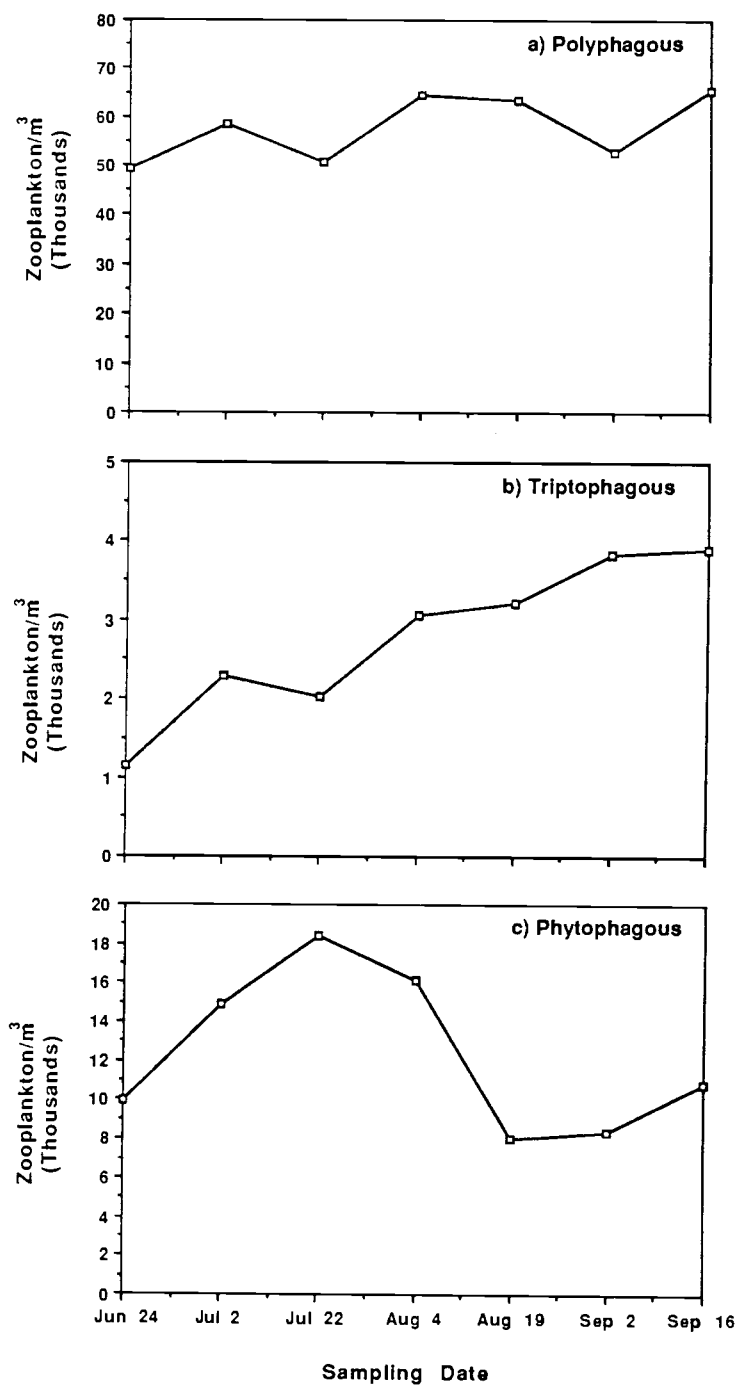


Figure 13. Seasonal densities of the three zooplankton feeding groups from 20 to 200 m at station 13, Crater Lake, during summer 1986. (Note: Y-axis values are different for the three graphs.)

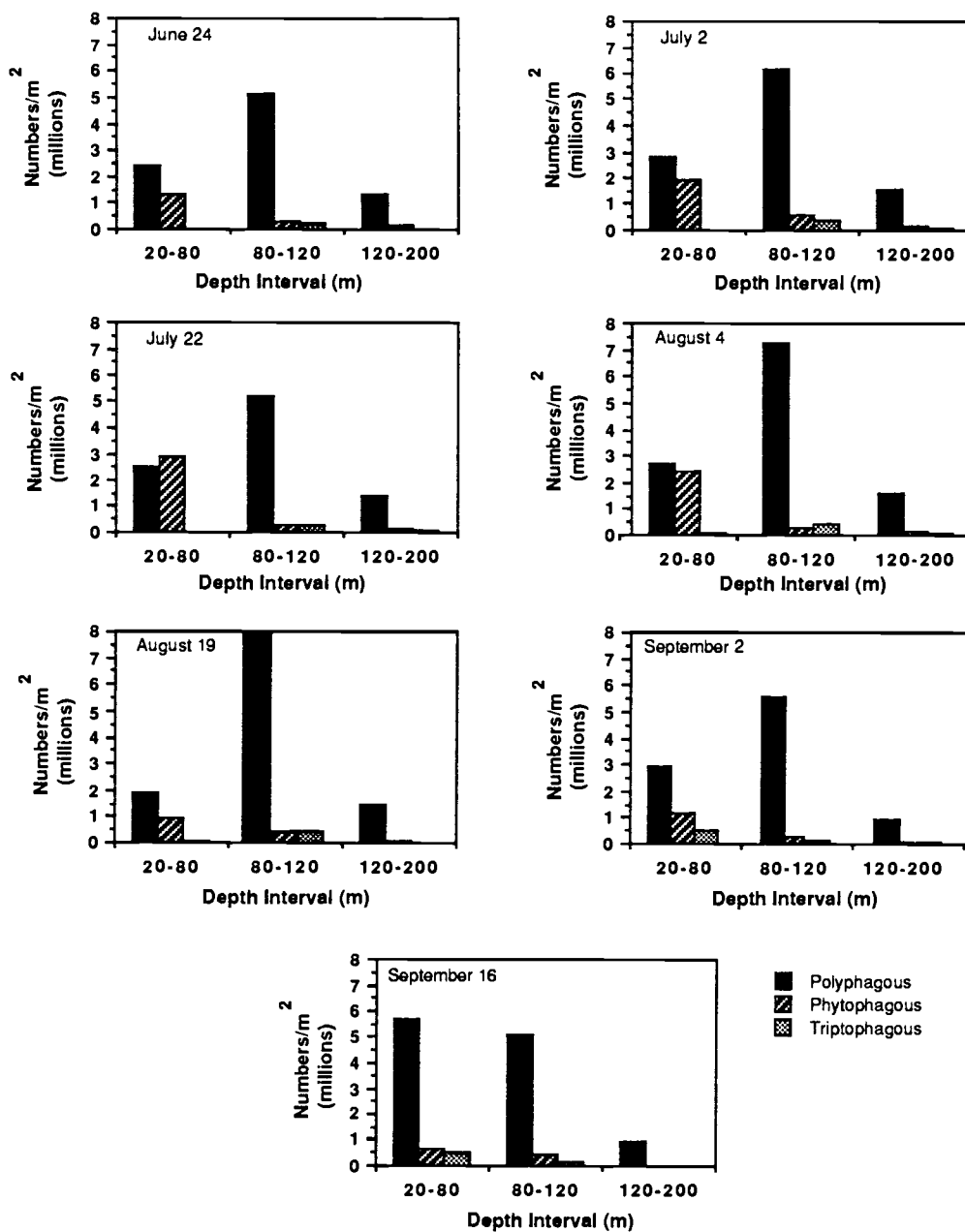


Figure 14. Seasonal densities, by depth interval and sampling date, of the three zooplankton feeding groups from 20 to 200 m at station 13, Crater Lake, during summer 1986.

density increase in that part of the water column. Numbers were lowest, but fairly constant, in the 120 to 200 m interval. The triptophagous group had greatest numbers in the 80 to 120 m interval until September, when the greatest numbers occurred in the 20 to 80 m interval. Numbers always were lowest in the 120 to 200 m interval. Throughout the season, the phytophagous group displayed greatest densities in the 20 to 80 m interval due to the numerical dominance of Polyarthra.

In relating densities of zooplankton within a particular feeding group to densities of nanoplankton (1 to 50 microns) for the four sampling dates when phytoplankton data were available, I found the polyphagous and triptophagous groups again displayed similar patterns. Progressing from June to August, nanoplankton numbers decreased as zooplankton numbers increased; in September both nanoplankton and zooplankton numbers slightly increased (Fig. 15a and b). The phytophagous group showed a different pattern. From June to July, nanoplankton numbers decreased as zooplankton numbers increased; from July to August, both groups decreased in numbers; from August to September nanoplankton numbers slightly increased as zooplankton numbers continued to decrease (Fig. 15c).

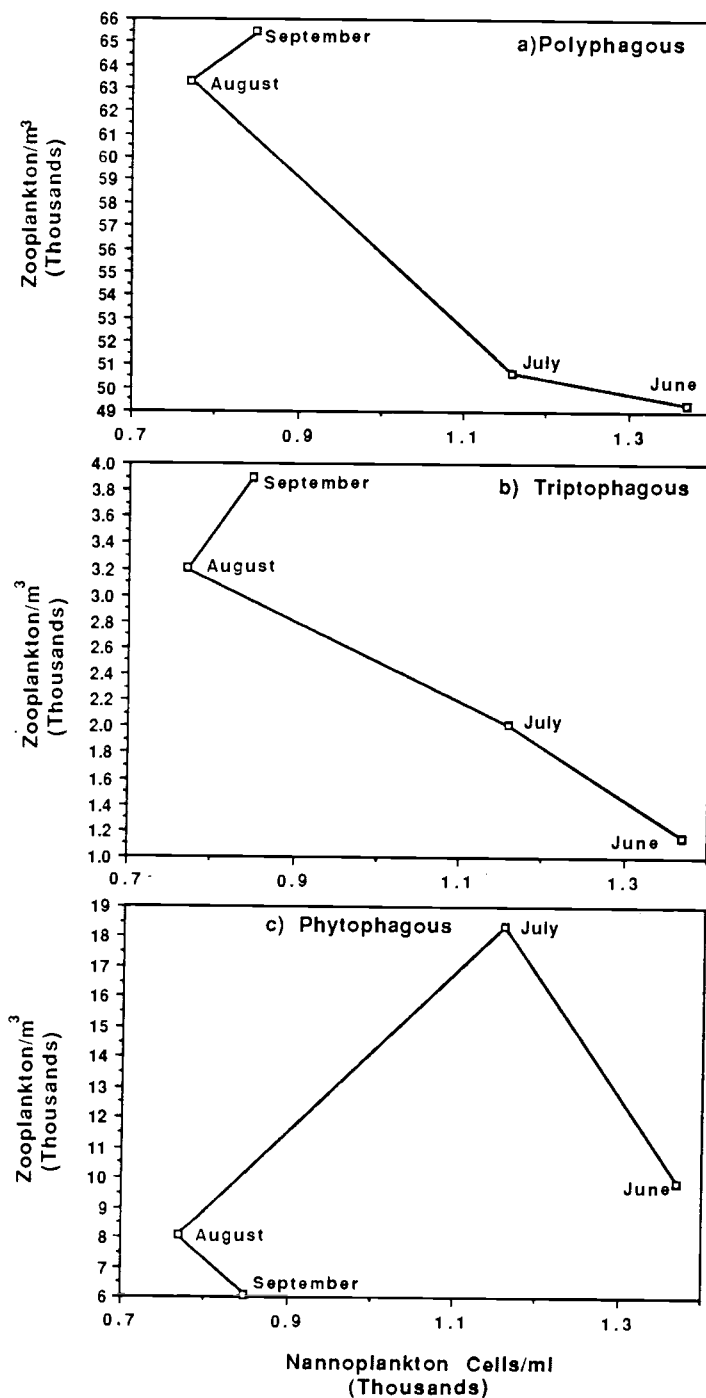


Figure 15. Relationships between densities of nanoplankton and the three zooplankton feeding groups. Data are from samples taken from 20 to 200 m at station 13, Crater Lake, during summer 1986. (Note: Y-axis values are different for the three graphs.)

Summer 1986, Comparison of Stations 13 and 23

The two criteria for determining whether differences existed between the zooplankton structures at stations 13 and 23 were based on comparing absolute densities and community compositions (i.e., species richness and relative abundances). I used a profile analysis and unpaired t-test to determine if density differences existed and SIMI, a resemblance measure, to determine if community composition differences occurred.

Correct application of profile analysis and an unpaired t-test requires normal distribution and equal variances for replicated samples. Although normality for small sample sizes is difficult to prove or disprove, normal distribution was a reasonable assumption for the Crater Lake zooplankton samples because similar counts were obtained among all replicates (data not shown). Also, population variances for replicates all tested for equality when an F test was applied at the 5% level of significance.

Profile analysis revealed that for July and September there were no significant differences in absolute densities between stations 13 and 23 (Table 26). The analysis also indicated that zooplankton numbers were not equally distributed among the three depth intervals.

Table 26. Profile analysis for stations 13 and 23 to determine if differences between mean densities exist. This statistical approach incorporates three tests. If, for any test, the hypothesis of no difference is rejected, results of the remaining test(s) cannot be used or interpreted. The 5% level of significance was used.

Test question	Sampling date		
	2 Jul	4 Aug	2 Sep
1. Are profiles parallel?	yes	no	yes
2. Are profiles the same?	yes	--	yes
3. Are profiles level?	no	--	no

Because the profile analysis for August indicated a significant difference between the two stations, I applied an unpaired t-test to each of the three pairs of intervals. At the 0.05 level of significance, no difference occurred between the mean absolute densities at station 13 and 23 for the 80 to 120 m and 120 to 200 m intervals. However, for the 20 to 80 m interval the mean densities between stations 13 and 23 were significantly different, with the mean density at station 13 higher than that at station 23.

Taxonomic structure was nearly identical (SIMI > 0.973) when samples from corresponding depth intervals for the two stations were paired for a specific date with one exception, the 20 to 80 m interval in August (SIMI = 0.733) (Table 27). Nonetheless, when all samples within a given station for a specific date were pooled to represent the water column as a whole, structure was nearly identical between the two stations for all three sampling dates (SIMI > 0.991) (Table 27).

By comparing the structures occurring within the 20 to 80 m interval at stations 13 and 23 on 4 August, I found that at station 13, K. cochlearis accounted for 47.5% of the pooled replicates and Polyarthra accounted for 45.8%. At station 23, however, K. cochlearis accounted for only 5.0% and Polyarthra represented 89.5%

Table 27. Similarity indices (SIMI) between stations 13 and 23. A value of 1.0 indicates species richness and relative abundances are identical; a value of 0 denotes no similarity.

Depth interval (m)	Sampling date		
	2 Jul	4 Aug	2 Sep
20 to 80	0.994	0.733	0.994
80 to 120	0.999	0.999	0.999
120 to 200	0.973	0.990	0.931
20 to 200 ^a	0.993	0.991	0.997

^aIntervals pooled to represent water column as a whole.

of the pooled samples. This difference also was reflected in the individual samples of the 20 to 80 m intervals. The absolute densities within the 20 to 80 m interval at station 13 was 42.7% greater than station 23; and actual mean numbers of K. cochlearis and Polyarthra at station 13 were 41,342/m³ and 39,839/m³, respectively, while at station 23 mean numbers were 2,499/m³ for K. cochlearis and 44,651 for Polyarthra. At the 5% level of significance, unpaired t-tests indicated that the mean values between the two stations were significantly different for K. cochlearis but not for Polyarthra.

Summer 1986, Littoral

All zooplankton species occurring in the pelagia were present, in varying degrees, in the littoral samples. Species adapted specifically to a littoral habitat were found only in the 10-m depth samples and were extremely low in numbers. Littoral zooplankton represented were cyclopoids, ostracods, chydorids, and the rotifer, Lecane. Littoral species associated with the benthos were not collected because of the sampling method used.

With the exception of the 10-m depths, a distinct structure characterized each tow depth, regardless of transect location. In pairing transects by corresponding depths, I found the taxonomic structures were highly similar among the 30-m depth samples (mean SIMI = 0.998),

the 60-m depth samples (mean SIMI = 0.955) and the 100-m depth samples (mean SIMI = 0.985) (Table 28). Samples from the 10-m depth, on the other hand, had a mean SIMI value of 0.756 and ranged from 0.246 to 0.999 (Table 28).

In general, the community structure for the 10-m depths was characterized by a dominance of K. cochlearis with the exception of transect 2, which had a dominance of Bosmina. All 30-m depth samples exhibited a high dominance of Polyarthra. At all 60-m depths, Polyarthra remained dominant, and an increase in species richness occurred. At all 100-m depths, K. cochlearis became dominant and species richness was greatest.

Each transect displayed the same pattern of taxonomic structure change from near-shore to open-water zones: Structures were dissimilar between the 10-m and 30-m depth samples (SIMI > 0.001), similar between the 30-m and 60-m depth samples (SIMI > 0.881), and dissimilar between the 60-m and 100-m depth samples (SIMI > 0.117) (Table 29). Additionally, taxonomic structures for the littoral, 100-m depth samples were similar to structures occurring in the 20 to 200 m range at the pelagic stations (13 and 23) during the same time period (SIMI > 0.977) (Table 29).

Absolute densities of organisms sampled tended to increase as distance from shore increased (Table 30). No

Table 28. Similarity indices (SIMI) for zooplankton tows taken at four depth stations along seven transects extending from near-shore out to open waters on 5 and 6 August 1986, Crater Lake. A value of 1.0 indicates species richness and relative abundances are identical; a value of 0 denotes no similarity.

Transect pairs being compared	Depth range of tow (m)			
	0 to 10	0 to 30	0 to 60	0 to 100
1 and 2	0.246	0.996	0.939	0.997
1 and 3	0.709	0.999	0.885	0.999
1 and 4	0.999	0.999	0.999	0.998
1 and 5	0.981	0.999	0.999	0.986
1 and 6	0.997	0.999	0.998	0.965
1 and 7	0.999	0.999	0.991	0.998
2 and 3	0.855	0.996	0.911	0.998
2 and 4	0.249	0.996	0.941	0.993
2 and 5	0.252	0.996	0.937	0.976
2 and 6	0.649	0.996	0.940	0.952
2 and 7	0.250	0.995	0.936	0.997
3 and 4	0.711	0.999	0.893	0.998
3 and 5	0.694	0.999	0.881	0.985
3 and 6	0.948	0.999	0.904	0.966
3 and 7	0.712	0.999	0.932	0.998
4 and 5	0.981	0.999	0.999	0.993
4 and 6	0.896	0.999	0.999	0.978
4 and 7	0.999	0.999	0.993	0.995
5 and 6	0.876	1.000	0.998	0.995
5 and 7	0.979	0.999	0.990	0.977
6 and 7	0.897	0.999	0.996	0.953

Table 29. Similarity indices (SIMI) for zooplankton tows taken at four depth stations along seven littoral transects and two pelagic stations from 4 to 6 August 1986, Crater Lake.

Tran- sect	Comparison between				
	10 and 30 m	30 and 60 m	60 and 100 m	100 m and station 13	100 m and station 23
1	0.007	0.999	0.117	0.995	0.986
2	0.145	0.963	0.137	0.990	0.977
3	0.006	0.881	0.538	0.995	0.986
4	0.032	0.999	0.186	0.998	0.993
5	0.188	0.999	0.272	0.994	0.998
6	0.001	0.998	0.411	0.981	0.993
7	0.032	0.994	0.198	0.991	0.977

Table 30. Number of zooplankton/m² sampled at specific depths along transects extending from near-shore out to open water on 5 and 6 August 1986, Crater Lake.

Transect number	Depth (m)			
	0 to 10	0 to 30	0 to 60	0 to 100
1	92,770	1,436,940	2,194,620	7,325,100
2	14,330	528,960	1,826,220	6,032,700
3	11,760	401,040	1,678,200	9,457,000
4	23,580	160,410	1,114,860	5,186,700
5	7,560	88,680	2,427,120	8,113,400
6	30	172,530	2,407,260	10,514,800
7	27,220	82,830	699,360	5,644,500

one transect consistently had greater numbers for any specific depth.

Temperature profiles were similar for all transects and depths. Any variations could be explained by time of day and varying wind conditions. The mean temperatures (Celsius) for each depth were: surface = 16.5, 10 m = 12.9, 30 m = 6.5, 60 m = 4.5, and 100 m = 4.0. Secchi disk readings for transects 1, 5, 6, and 7 ranged from 21.1 to 22.0 m. Secchi disk readings were 26.1, 29.3, and 28.9 m at transects 2, 3, and 4, respectively.

Winter-Spring 1986 and 1987

Tows within discrete depth intervals were not possible during winter months because a net-closing device was not used. In general, tows over long distances (i.e., 100, 200, and 300 m) would be more susceptible to net clogging than short-distance tows. This would result in underestimating densities of zooplankton in the upper portion of the water column; however, no strong evidence of this can be seen in the winter data (Table 31). Regardless of tow length, all tows within a given date had high similarity indices ($SIMI > 0.990$; Table 32). Clustering analysis (CLUSB3) emphasized the similarity of community structure within a given month: A four-cluster grouping divided samples into classes based on month of sample (e.g., cluster 1 included all March 1986 samples,

Table 31. Densities of zooplankton per square meter occurring in winter samples from station 13, Crater Lake.

Depth of tow (m)	Sampling date			
	Mar 1986	May 1986	Jan 1987	Apr 1987
50	12,762,050 ^a	787,850	1,419,500	1,213,750
100	23,014,200	3,892,500	4,607,900 ^a	2,227,300 ^a
200	---	---	7,859,000	4,522,600
300	34,450,395	8,871,800	---	---

^aMean of two samples

Table 32. Similarity indices (SIMI) between tows taken during winter months at station 13, Crater Lake.

Tow depths (m) being compared	Sampling date			
	Mar 1986	May 1986	Jan 1987	Apr 1987
50 and 100	1.000	0.998	0.991	0.996
50 and 200/300	0.999	0.999	0.992	0.990
100 and 200/300	0.999	0.999	0.998	0.990

cluster 2 included all May 1986 samples, and so on). This suggested, then, that during the winter months a uniform community structure occurred throughout the water column for a particular date.

Species diversity was low in March and May 1986 (mean SDI = 0.03 and 0.17, respectively), but increased to moderate values in January and April 1987 (mean SDI = 0.53 and 0.65, respectively) (Table 33). Changes in diversity values can be attributed to K. cochlearis. This species represented 98.3% and 90.8% of the March and May 1986 samples, respectively, but decreased in dominance during January and April 1987, representing 68.5% and 49.9% of the samples, respectively. All pelagic species that were present in the summer 1986 samples were present during the winter.

Summer 1986, Night

The purpose of night tows was to determine if any previously unsampled organisms could be captured, indicating daytime avoidance abilities. However, no new organisms were collected.

Table 33. Statistics for Simpson's Diversity Index (SDI) values computed for pelagic zooplankton samples taken during winter months at station 13, Crater Lake.

Sampling date	Sample size	Mean	Standard deviation	Coefficient of variation
5 Mar 1986	4	0.03	0.003	0.11
29 May 1986	3	0.17	0.021	0.13
19 Jan 1987	4	0.53	0.063	0.12
14 Apr 1987	4	0.65	0.023	0.04

General Trends: 1985 to 1987

Although sampling approaches differed during summer 1985, winter 1986, summer 1986, and winter 1987, evidence for general trends in species-specific abundances were observed.

Bosmina numbers were higher in summer 1985 than in summer 1986, averaging $1,115,330/\text{m}^2$ for two samples in 1985 but $293,363/\text{m}^2$ for seven samples in 1986. Numbers were lowest during winter and spring months, with the exception of January 1987 (Fig. 16a). Daphnia rarely was observed in summer 1985 and winter 1986 samples. Beginning in the summer of 1986, however, this species appeared to be on an increasing trend, averaging $1906/\text{m}^2$ in summer 1986 and also appearing in relatively high numbers during the winter of 1987 (Fig. 16b).

Patterns were varied for the nine rotifer species. K. cochlearis abundances appeared to be relatively stable from 1985 to 1987; however, extremely high numbers occurred in March 1986, and the lowest densities occurred in April 1987 (Fig. 17a). Polyarthra abundances also appeared to be similar during both summers; compared to summer time, this species' densities were extremely low in winter and spring months (Fig. 17b). Philodina appeared to have greatly increased in numbers from summer 1985 (with an average of $114,480/\text{m}^2$) to summer 1986 (averaging

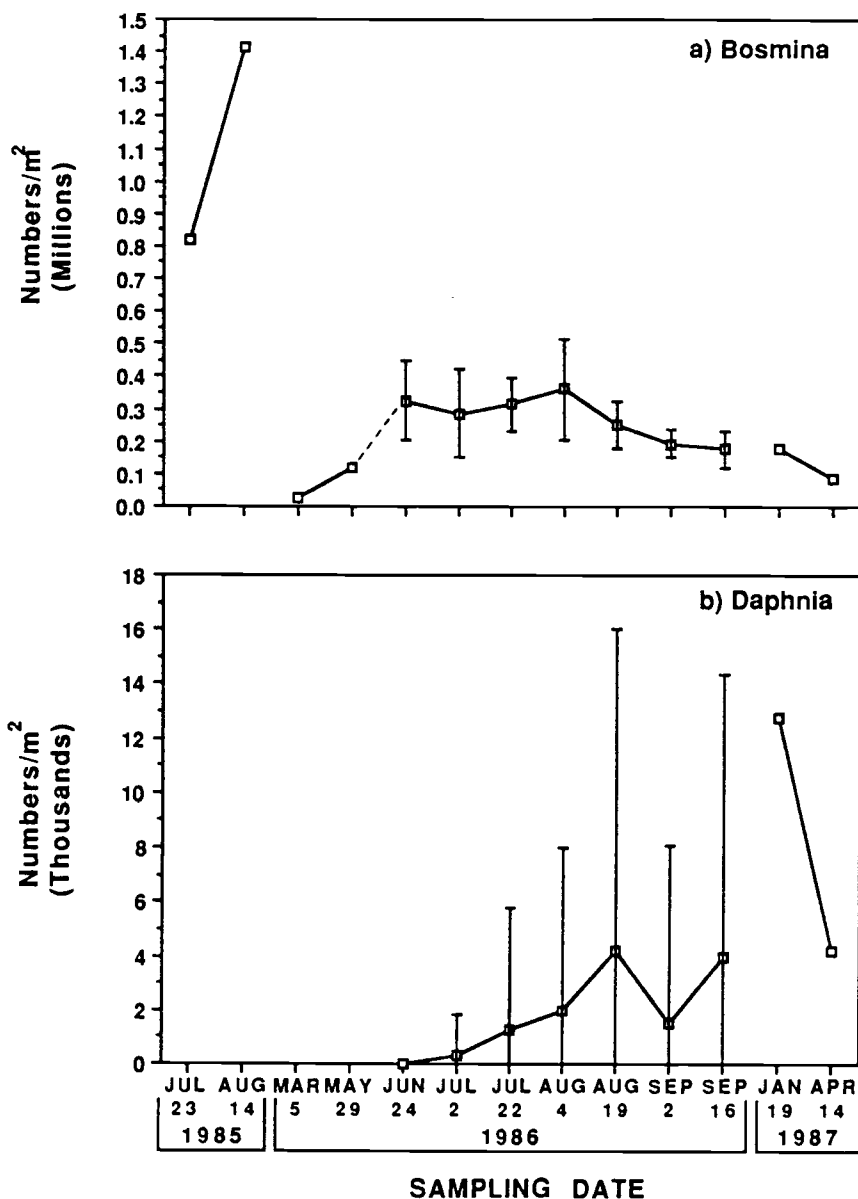
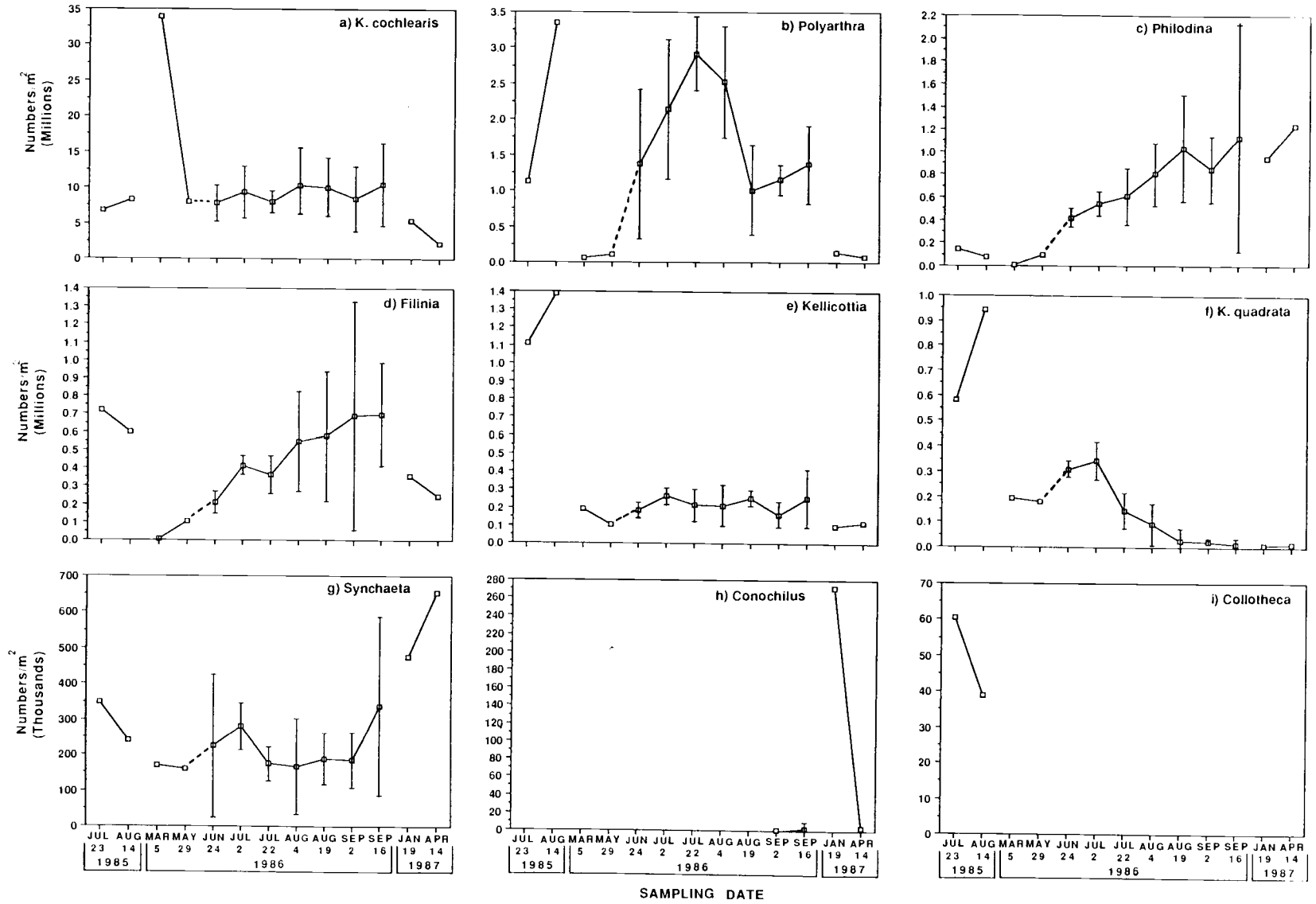


Figure 16. Densities of *Bosmina* and *Daphnia* in numbers per square meter for samples taken from 23 July 1985 through 14 April 1987 at station 13, Crater Lake. Winter values were obtained from 200 m to surface tows. Summer values were obtained from integrated tows that covered from 20 to 200 m. Vertical lines indicate 95% confidence intervals for summer 1986 samples. (Note: Y-axis values are different for the two graphs.)

Figure 17. Densities of individual rotifer species in numbers per square meter for samples taken from 23 July 1985 through 14 April 1987 at station 13, Crater Lake. Winter values were obtained from 200 m to surface tows. Summer values were obtained from integrated tows that covered from 20 to 200 m. Vertical lines indicate 95% confidence intervals for summer 1986 samples. (Note: Y-axis values are different on all graphs.)

Figure 17.



767,949/m²); also, where winter and spring 1986 numbers were low, Philodina's densities during winter and spring 1987 were comparable to summer 1986 (Fig. 17c). Filinia appeared to have similar densities for both summers, with its population minima possibly occurring in the winter and spring (Fig. 17d). Kellicottia exhibited a pattern similar to Bosmina and averaged 1,249,590/m² during summer 1985, but dropped to an average of 220,411/m² during summer 1986. However, numbers occurring during winter and spring months were within the confidence interval ranges for summer 1986 (Fig. 17e). K. quadrata appeared to be in a declining trend, averaging 762,320/m² in summer 1985 and 136,649/m² in summer 1986; numbers continued to decline during winter and spring 1987 (Fig 17f). Synchaeta displayed the most stable density trend of all the zooplankters: Mean values during summer 1985 and winter and spring months occurred within the confidence interval ranges for summer 1986, with the exception of a population maximum that occurred in April 1987 (Fig. 17g). Conochilus did not appear in samples until 16 September 1986, with a low density of 2280/m²; in January 1987 its numbers increased to 271,000/m², then decreased to 3,600/m² in April 1987 (Fig. 17h). Collotheca was present only in summer 1985 and averaged 49,600/m² (Fig. 17i).

Sampling Methods Experiment

As with the comparisons between stations 13 and 23, the criteria for determining whether differences occurred among sampling methods were based on absolute abundances and community composition.

Mean values for each sampling method were $40,485/\text{m}^3$ for the 0.75-m net; $38,843/\text{m}^3$ for the 0.50-m net; $13,940/\text{m}^3$ for the Van Dorn bottles with water samples strained through 64 micron mesh; and $22,268/\text{m}^3$ for the Van Dorn bottles using 35 micron mesh. Accepting the normality assumption as reasonable for the zooplankton samples, I used the F test to determine equality among population variances and the t-test to determine if differences occurred between mean densities. Population variances all tested for equality at the 0.05 level of significance except for the variances occurring between samples obtained for the 0.75-m net and the Van Dorn bottles with 35-micron mesh. Therefore, I could not test for differences between means for that particular pair of sampling devices. At the 5% level of significance, no differences occurred between the mean densities of the 0.75-m and 0.50-m nets, the 0.50-m net and the Van Dorn bottles with 35-micron mesh, and the Van Dorn bottles with 35- and 64-micron meshes (Table 34). Mean densities were significantly different between the 0.75-m net and the Van

Table 34. Differences in mean densities and similarity indices (SIMI) between sampling methods for samples taken from 40 m to 80 m at station 13, Crater Lake, on 29 July 1986.

Methods being compared	Difference in mean?	SIMI
0.75-m net and 0.50-m net	no	0.884
0.75-m net and Van Dorn, 64-micron mesh	yes	0.754
0.75-m net and Van Dorn, 35-micron mesh	---	0.769
0.50-m net and Van Dorn, 64-micron mesh	yes	0.949
0.50-m net and Van Dorn, 35-micron mesh	no	0.975
Van Dorn, 64 micron mesh and Van Dorn, 35-micron mesh	no	0.985

Dorn bottles with 64-micron mesh, and the 0.50-m net and Van Dorn bottles with 64-micron mesh (Table 34).

Taxonomic structures were similar between samples taken using the 0.75-m and 0.50-m nets (SIMI > 0.884), the 0.50-m net and the Van Dorn bottles with both mesh sizes (SIMI > 0.949), and between the two mesh sizes using the Van Dorn bottles (SIMI > 0.985) (Table 34).

DISCUSSION

This section is presented in three parts--sampling methods, historical perspectives, and community perspectives. Sampling methods presents justifications for 1986 methods and recommendations for the best and most efficient zooplankton sampling approach to use in the ongoing Crater Lake limnological study. Historical perspectives provides a brief review of the zooplankton history of Crater Lake based on past records and current taxonomic interpretations. Community perspectives i) describes the summer 1986 pelagic zooplankton structure and explores possible reasons as to why that structure occurred and ii) considers how the pelagic zooplankton community might change through time and what these changes might mean within the context of the Crater Lake ecosystem.

Sampling Methods

Sampling zooplankton communities presents many challenges. Zooplankton tend to vary spatially and temporally. Distribution usually is patchy, and discrete samples may easily over or underestimate abundances. Ability to avoid capture varies both among and within species. Size of zooplankters can range from a few microns to about 15 mm. Thus, use of different sampling gear and mesh sizes can result in differing estimates of

abundance and community structure (de Bernardi 1984). Choice of proper sampling gear should be based on: i) type of lake environment (e.g., deep and oligotrophic vs. shallow and eutrophic); ii) the target species (e.g., size, high or low avoidance tendencies); iii) study objectives; and iv) practicalities and logistics (time, cost, effort) (Green 1977, Ruttner-Kolisko 1977a, de Bernardi 1984).

Because the 0.75-m net sampled the greatest volumes of water, rare species were well represented; however, the size of the net made it awkward to operate and, as a result, this method was time consuming. Also, filtration efficiency was lowest using this method because of the amount of water sampled (data not shown).

Mesh size is a critical factor, particularly when sampling rotifers, because the mesh must be small enough to retain all rotifers but large enough to prevent clogging. Likens and Gilbert (1970) found 35 microns to be an acceptable and practical compromise among sizes. However, I found no differences in density and community structure between samples strained through either 35 and 64 micron mesh sizes when using the same gear and method, i.e., the Van Dorn bottles. This possibly was because extremely small-sized species of rotifers did not occur in the pelagia of Crater Lake. Although the Van Dorn bottles

have the advantage of sampling discrete parcels of water and thereby avoid the clogging problems of towed nets, they were the most laborious and time consuming of the three types of gear. Also, because they sampled the smallest volumes of water, rare species were not captured.

The 0.50-m net showed no density differences when compared to either the 0.75-m net or the Van Dorn bottles with 35-micron mesh. Community structure of samples obtained with the 0.50-m net was highly similar to those of the other three methods and approaches. In particular, excellent similarity values were obtained between the 0.50-m net samples and those obtained using the Van Dorn bottles, which represent 100% filtration efficiency. Filtration efficiency of the 0.50-m net was improved over that of the 0.75-m net because a lesser volume of water was filtered. This method was the least time consuming and the easiest to apply and operate.

Based on the above, I recommend use of the 0.50-m net in the Crater Lake monitoring program. Although the 0.75-m net was used in 1985 and 1986, results were compatible between the two nets in terms of absolute abundances and community structure.

A good estimation of filtration efficiency for each net tow is necessary to determine zooplankton field densities. While sampling in 1986, I discovered

extraneous flowmeter revolutions were occurring. The actual mechanisms causing this problem are not known; however, my experiments indicated the effect was mostly on the inner flowmeter and that the number of extra revolutions were greatly affected by lake conditions, with the problem being intensified during rough lake conditions as opposed to calm. Extraneous revolutions, particularly of the inner flowmeter, leads to an overestimation of the volume of water filtered and thus an underestimation of the numbers of organisms sampled. The question remains, then, as to how serious this problem might be. Ruttner-Kolisko (1977a) noted that field population densities increase and decrease over several orders of magnitude and, because of this, density trends can be followed even if sampling error amounts to 100% or more. I found that, on the average, the extra revolutions caused only a 16.3% bias in the data. However, because of the frequency of sampling and the high number of samples taken in 1986, I choose to apply correction values to dampen the effects of changing lake conditions. The main value of recognizing this problem is that it identified a source of sampling error previously not discussed, to my knowledge, in the literature.

To optimize estimates of zooplankton field densities, a specific number of replicate samples must be taken. The number of required samples generally is based on variance

estimates obtained from a pilot study (Prepas 1984). However, my choice of three replicated samples for each depth interval in 1986 was based on time constraints. To determine if three replicates were, in fact, adequate for reasonable density estimates, I applied the approach developed by Downing et al. (1987) where the required number of samples is a function of population density, volume of water sampled, and the desired level of precision. In reviewing my data, I found three replicates were sufficient at the precision of $p = 0.2$ (where $p = SE/m$, $SE = s/n^{0.5}$, $m = \text{mean of replicates}$, $s = \text{standard deviation of replicates}$, and $n = \text{number of replicates}$). The high similarity values obtained between all pairs of replicated samples also indicated that three replicates were sufficient in optimizing community structure estimates.

Frequency of sampling is an important consideration in zooplankton, particularly because rotifers generally are thought to have rapid development potentials during summer months. For this reason, sampling intervals of a week or less are recommended (Berner-Fankhauser 1987, Herzig 1987). However, Crater Lake sets an unusual environment for its biota. The majority of zooplankton occur in a depth zone characterized by a low, relatively constant temperature. This, in addition to low food concentrations, results in slowed metabolisms, delayed

onset of maturity, and prolonged juvenile growth periods (Ruttner-Kolisko, personal communication). Hence, the biweekly samples in 1986 most likely provided a realistic picture of zooplankton community structure in terms of absolute density trends and species diversity. The biweekly frequency would not, however, be adequate for information regarding population parameters such as fertility and mortality.

Historical Perspectives

Historical reconstruction of pelagic zooplankton community structures is difficult because of taxonomic revisions and lack of preserved reference specimens. Taxonomic confusions particularly are common among cladocerans due to polymorphism, cyclomorphosis, and early descriptions based on insufficient, and often inadequate, morphological characteristics (Goulden and Frey 1963, Deevey and Deevey 1971, Dodson 1981, Schwartz et al. 1985). Nonetheless, the pelagic zooplankton community structure of Crater Lake well may have consisted of one daphnid, one bosminid, and several rotifer species since before the turn of the century. Some evidence also exists that Daphnia densities are cyclic, being highly abundant in some years and rare in others.

The daphnid sampled in 1896 was identified as Daphnia pulex var. pulicaria (Evermann 1897). Forbes (1893), a

colleague of Dr. Evermann's, originally described this species from Yellowstone National Park samples and considered it to be a variation of Daphnia pulex. Later, Brooks (1957) synonymized D. pulicaria with D. pulex in his taxonomic revision of North American daphnids. However, Hrbáček (1959, as cited by Brandlova et al. 1972) found specific morphological differences in the males of this "variation," recognized a distinct rostrum reticulation pattern on the heads of females, and noted adult females never produced the head projection common in D. pulex; hence, D. pulicaria was recognized as a separate species. Ecological differences between D. pulex and D. pulicaria also have been noted (Hrbáčková-Esslová 1963, Hrbáček and Hrbáčková-Esslová 1966). These studies demonstrated that: i) D. pulicaria readily fed on detritus and algae, whereas D. pulex was able to eat only algae, and ii) D. pulicaria was adapted to lower temperatures than D. pulex. I was able to verify that daphnids in 1960s and 1980s samples were D. pulicaria. Most likely, then, the D. pulex referred to in previous studies (Kemmerer et al. 1924, Brode 1938, Hasler 1938, Hasler and Farner 1942) actually was D. pulicaria.

The bosminid sampled in 1913 was reported as Bosmina longispina (Kemmerer et al. 1924). However, bosminids from 1960s and 1980s samples were verified as B. longirostris. In light of more recent taxonomic

revisions, the 1913 specimen most likely was B. longirostris.

Of the three rotifers noted in 1913 (Kemmerer et al. 1924), Kellicottia and K. quadrata still exist in the lake today. Asplanchna is no longer present. Again, verification of these species is not possible due to lack of preserved reference specimens. Nine rotifer species were identified in the 1985 to 1987 samples.

Community Perspectives

Community Structure: Summer 1986

In 1986 the pelagic zooplankton taxonomic structure of Crater Lake was relatively simple, consisting of two cladocerans and eight rotifers, and uncomplicated because of no invertebrate predation. None of the rotifers was predaceous, and no other invertebrate predators occurred in the pelagia (e.g., cyclopoids, mysids, Chaoborus larvae). Only one vertebrate predator, the zooplanktivorous kokanee (Oncorhynchus nerka kennerlyi), occurred in the open waters (Mark Buktenica, personal communication).

From 24 June to 16 September 1986, the zooplankton community exhibited a remarkably stable structure in terms of species richness, relative abundances, and absolute densities. This stability was due, in part, to the

consistently high dominance of K. cochlearis.

Numerically, rotifers accounted for 97.9% of the summer samples, and K. cochlearis accounted for 70.2% of the total summer numbers. Cladocerans accounted for 2.1% of the zooplankters; Bosmina longirostris accounted for 99.3% of the cladoceran numbers and Daphnia pulicaria accounted for 0.7%. In essence, then, a rotifer-dominated community existed in the Crater Lake pelagia during 1986.

To explore why such a stable structure occurred in 1986, I will consider both abiotic and biotic factors that influence zooplankton abundances and regulate community structure. But first, a brief review and description of the unusual pelagic environment of Crater Lake will be useful. Because of the lake's high transparency, the photic zone is extensive, and 1% incident light transmissions range from 80 to 100 m. A relatively stable physio-chemical environment existed within the surface to 200 m range during the summer 1986 (Larson 1987b). Very little variation occurred among nutrients (nitrate-N and orthophosphate), silica, elements (calcium, magnesium, potassium, sodium, and sulfur), total alkalinity, conductivity, pH, and dissolved oxygen. Chlorophyll a peaks, although low in concentration, occurred from 100 to 140 m. During the summer surface temperature had a range of about 4°C, a low value of 12.4°C was measured on 25 June, and a high value of 16.4°C was measured on 20

August. A 20-m epilimnion was measured on 17 September; temperature was 12.8°C. During winter and summer, temperature became relatively constant at 80 m and below.

Two additional characteristics of the 1986 Crater Lake pelagia are noteworthy. First, the lake environment appeared to be horizontally homogeneous. That zooplankton tend to be "patchy" in distribution due to heterogeneous environments is considered the norm, rather than the exception, in lakes (see Miracle 1977a). However, by comparing two pelagic stations on three separate occasions in 1986, I found that only one interval (20-80 m) on one date showed a significant difference in absolute densities and community structure. Second, 99+% of the zooplankton densities occurred in the hypolimnion--that is, below 20 m--rather than the epilimnion. Because of a relatively shallow epilimnion, Crater Lake is mostly hypolimnic in the summer and, thereby, offers more thermal stability than is found in most lakes.

Temperature and oxygen are major abiotic factors regulating zooplankton abundance, succession, and distribution (e.g., Hutchison 1967, Kibby 1971, Hofmann 1977, Heisey and Porter 1977, Radwan 1984, Orcutt and Porter 1984, Herzig 1987). In Crater Lake, however, dissolved oxygen was not limiting because the water column was well oxygenated throughout the summer of 1986.

Within the general scope of this study, the influence of temperature on zooplankton abundance, succession, and distribution is difficult to assess. Temperature can have ambiguous effects on abundance. For example, increased temperature can decrease egg development time but also decrease life span (Hofmann 1977). Additionally, the synergistic effects of temperature and food concentration, particularly in environments of low-food concentration, may influence life history parameters (Orcutt and Porter 1984). Temperature generally influences succession. In temperate waters, for example, an annual succession of zooplankters is common; and species are classed as perennial (i.e., eurythermal) or seasonal (i.e., stenothermal). Cladoceran and rotifer perennial species tend to exhibit low populations in the winter (Miracle 1977a, Wetzel 1983); while seasonal or aestival species exhibit distinct temperature ranges, outside of which populations cannot be maintained (e.g., Elliott 1977, May 1983, Herzig 1987, Luxhaber 1987). In Crater Lake only two rotifer species, Polyarthra and Filinia, are considered cold-water stenotherms and, thereby, seasonal (Rutter-Kolisko 1974, Ruttner-Kolisko 1980, May 1983). For rotifers, different temperature preferences also can induce congeneric succession; that is, a succession of species within some genera, such as Synchaeta and Polyarthra (Carlin 1943, as cited by Herzig 1987; Berner-

Fankhauser 1987). In Crater Lake, however, temperature appeared to have little influence on zooplankton succession, because all species sampled in 1986--with the exception of the rare species, Conochilus--occurred during both winter and summer, including the stenothermic taxa. Also, no congeneric succession was apparent. Although temperature can influence vertical distribution, only two zooplankters showed correlations to temperature mean and range: Philodina, which occurred mainly in the lower depths, had a negative correlation; Polyarthra, which occurred mainly in the upper waters, had a positive correlation. Polyarthra dolicoptera, the cold-water stenotherm rotifer, has a reported temperature optimum of 5 to 15°C (May 1983). Specific information on Philodina acuticornis was not, to my knowledge, available. That temperature, of itself, may not have played a significant role in zooplankton distribution within the Crater Lake system in 1986 was emphasized by Polyarthra--as a cold-water stenotherm--being the only zooplankter effectively inhabiting the warmer upper 40 meters during the summer months. The extensive and relatively stable temperature regime of the hypolimnion may explain the apparently minor role of temperature in the Crater Lake system.

Light intensity is a cue for diel vertical migration in zooplankton populations (for review, see Hutchison 1967) and, thereby, can influence distribution. Rotifers,

however, generally exhibit weak migratory movements (for review, see Miracle 1977a). Maximum migrations in a 24 h period have been noted for Polyarthra vulgaris at 5.6 m (George and Fernando 1970) and Euchlanis sp. at 10.0 m (Cruz-Pizarro 1978). For cladocerans, maximum migration in a 24 h period have been noted for Daphnia hyalina at 50.0 m (Stich and Lampert 1984). Hoffman (1969) indicated that the vertical migrations of Daphnia and Bosmina in Crater Lake were not consistent and that Daphnia exhibited a greater magnitude of migration than Bosmina. He further suggested that migration might occur only during certain times of the year, such as late summer. In my study, I was unable to detect phototaxic movement because of the sampling design.

Light intensity may have directly influenced zooplankton distribution in Crater Lake because of the high amount of transmission. Polyarthra was the only zooplankter to have a positive correlation to light intensity and, again, to effectively inhabit the upper 40 meters during the daytime. All other zooplankton species had a negative association, suggesting the possibility of a light-inhibiting effect within the upper strata. Again, determining such an influence was beyond the scope of my study.

Biotic factors affecting zooplankton structure are i) food availability and exploitative competition, ii) predation, iii) mechanical interference, and iv) parasitism (Herzig 1987).

The effect of parasitism on rotifers has not been studied, but field observations suggested that parasitism decimated the populations of two species, C. unicornis (Ruttner-Kolisko 1977b) and F. terminalis (Miracle 1977b). I have no evidence of the effect, or lack of effect, of this factor in Crater Lake.

Mechanical interference, as a form of competition, was first noted by Gilbert and Stemberger (1985); they found that K. cochlearis typica was swept into the branchial chambers of large-sized daphnids, causing injuries and mortalities to the rotifer. Further experimentation by Burns and Gilbert (1986) prompted them to suggest that field populations of K. cochlearis, and possibly other rotifers, may often be suppressed by daphnids. This factor, however, would have had little, if any, effect on the 1986 Crater Lake zooplankton structure because of the extremely low daphnid densities.

Vertebrate predation may have played a major role in the 1986 zooplankton structure. Feeding preferences toward large crustaceans, such as Daphnia spp., by zooplanktivorous fishes, such as kokanee, is well

established (see review by de Bernardi 1987). The presence of kokanee in Crater Lake may have influenced the low densities of Daphnia in 1986. Crater Lake studies have indicated that Daphnia is a preferred food item of kokanee (Brode 1935 and 1938); and Hasler and Farner (1942) noted that, even when Daphnia did not appear in zooplankton tows during the summer of 1940, Daphnia was present in fish stomach samples. Because of the size-selective tendencies of zooplanktivores, rotifer populations appear to be exempt from direct negative impacts when these fishes are present (Herzig 1987). Conversely, invertebrate predators prefer smaller-sized prey, such as rotifers (for review, see Williamson 1983); however, invertebrate predators did not exist in the Crater Lake pelagia during summer 1986. Further, only one invertebrate predator--the rotifer, Asplanchna--has ever been noted in the Crater Lake pelagia (Kemmerer et al. 1924). The apparent absence of this large-sized rotifer since the 1913 samples may be due to the presence of fish, which were introduced into Crater Lake. Stenson (1982) indicated that Asplanchna is heavily preyed on by fish.

Food availability and exploitative competition can affect zooplankton structure. As a group, rotifers consume a variety of foods (algae, detritus, bacteria) ranging from about 1 to 20 microns (Edmondson 1965, Dumont 1977, Pourroit 1977). However, within that spectrum of

foods, rotifers tend to partition resources; different species feed preferentially based on type of food, food size, and food-gathering method (Dumont 1977, Pourroit 1977, Bogdan et al. 1982, Starkweather and Bogdan 1980, DeMott 1986). Because of this ability to partition food resources, rotifer species are able to reduce exploitative competition and coexistence is favored if the habitat offers a suitable spectrum and sufficient quantities of edible foods. Such appeared to be the case in Crater Lake during the summer 1986, because edible phytoplankton in the 1 to 20 micron range were well represented throughout the summer and the seasonally progressive increase of Filinia, which is exclusively triptophagous, suggested that detritus and bacteria were sufficiently available. Also, evidence exists that rotifers are capable of feeding efficiently at low food levels, suggesting that they are well adapted to oligotrophic environments (Stemberger and Gilbert 1985).

The two cladocerans, Daphnia and Bosmina, are polyphagous but have different abilities for exploiting food resources. Daphnia is a nonselective filter-feeder (DeMott and Kerfoot 1982), has grazing rates 20 to 1300 times greater than those of rotifers (Burns and Rigler 1967, Herzig 1987), and has the ability to feed on a broader range of food sizes than either rotifers or Bosmina (Burns 1968, DeMott 1982). Thus, Daphnia species

are capable of removing disproportionate amounts of the food resources (Gilbert 1985); and field and experimental studies indicate that when daphnids reach significant numbers, rotifer and small cladoceran populations become numerically depressed, suggesting competition (e.g., for rotifers: Neill 1984, Herzig 1987; for Bosmina: DeMott and Kerfoot 1982, Vanni 1986). Bosmina, on the other hand, has both filtering and grasping abilities, can feed selectively on flagellates, and appears to be able to feed efficiently at low food concentrations (Gilbert and Bogdan 1981, DeMott 1982, DeMott and Kerfoot 1982). Further, Bogdan and Gilbert (1982) found that Bosmina longirostris had clearance rates similar to K. cochlearis. Bosminids, then, are less likely to indiscriminately depress total food resources (DeMott 1986, Kerfoot 1987); and Gilbert (1985) suggested small cladocerans, with their lower clearance rates, are more likely to coexist with rotifers than are large cladocerans.

Food resource partitioning and spatial similarities may explain the positive correlations among some of the zooplankton species. As a group K. cochlearis, Filinia, Kellicottia, and Synchaeta were positively correlated. These species had their greatest densities in the 80 to 120 m interval throughout the summer, with increasing numbers occurring in the 20 to 80 m interval during September. The populations of K. cochlearis, Kellicottia,

and Synchaeta remained stable throughout the summer, while Filinia--which feeds exclusively on detritus and bacteria--increased. Both K. cochlearis and Kellicottia are filter-feeders and feed on the same range of particle sizes (<12 microns, Pourroit 1977); however, K. cochlearis is polyphagous and Kellicottia feeds exclusively on algae. Synchaeta also feeds exclusively on algae but--in difference to Kellicottia--feeds by sucking and grasping and specializes on large flagellates (Stemberger and Gilbert 1985). The positive correlation of the polyphagous filter-feeder, K. quadrata, to both Kellicottia and Synchaeta also suggested resource partitioning. However, K. quadrata steadily declined over the summer, indicating possible competitive interactions with K. cochlearis; both species are polyphagous, are filter-feeders, have malleate trophi, and feed on the same range of particle size. A strong and positive correlation occurred between Polyarthra and Bosmina. These two species had a strong preference for the 20 to 80 m interval, are capable of grasping food items, and selectively feed on large flagellates. However, Bosmina also is capable of filtering smaller food particles and detrital material. A fourth positive correlation occurred between Filinia and Conochilus. Both species are triptophagous, are filter-feeders, have malleoramate trophi, and feed on the same range of particle size.

Conochilus, however, did not appear in samples until September and appeared to have no direct effect on Filinia densities.

Three groups of negative associations occurred. Generally, these associations appeared to be based on spatial differences. In the first, Philodina was negatively correlated with Polyarthra, Bosmina, K. cochlearis, and Filinia. Unfortunately, little is published about the autecology of this species, and that it exists in the pelagia of Crater Lake is puzzling. Philodina belongs to a class of rotifers that prefers littoral habitats and that has well developed abilities for substrate attachment. Yet, in Crater Lake this species was numerically dominant in the 120 to 200 m interval from August to September. Philodina's negative correlation with four species might be explained by spatial differences. Philodina preferred the lower depths, while Polyarthra and Bosmina occurred mainly in the upper waters. Also, Philodina did not extend into the 80 to 120 m interval until September, when K. cochlearis and Filinia densities decreased in the 80 to 120 m range and increased in the 20 to 80 m interval. Whether competitive interaction with Philodina played a role in the cases of K. cochlearis and Filinia is difficult to assess. All three species are filter-feeders on a similar particle size range (<12 microns for Filinia and <15

microns for Philodina, Pourroit 1977). However, Filinia is triptophagous with malleoramate trophi; Philodina and K. cochlearis are polyphagous with ramate and malleate trophi, respectively. In the second association, Polyarthra was negatively correlated with Kellicottia and Synchaeta. All three are phytophagous. Also, Polyarthra and Synchaeta have identical food preferences and food-gathering methods. However, Polyarthra was spatially separated from Kellicottia and Synchaeta. In the third association, Bosmina was negatively correlated with Synchaeta. Both species have a preference for large flagellates, but Synchaeta occurred mainly in the 80 to 120 m interval and Bosmina in the 20 to 80 m interval.

From the above, exploitative competition may have played an important role in Crater Lake's 1986 zooplankton structure. Food availability often is suggested to be a major regulator in zooplankton community structure (Pourroit 1965, as cited by Elliott 1977; Makarewicz and Likens 1975; Radwan 1980; May 1983; Berner-Fankhauser 1987), and this may be the case in Crater Lake. The edible component of the phytoplankton community, i.e., the portion of primary production available to herbivorous zooplankton, was well represented throughout the summer. However, no measures of detritus and bacteria were available during this study. Nonetheless, phytoplankton--in the form of decaying algal cells--and zooplankton

activities--in the form of released exuviae and partially digested food--are important detrital sources (Edmondson 1957). Thus, the plankton, itself, may serve as an index to detritus quantity. Both the polyphagous and triptophagous groups of zooplankton increased in densities throughout the season, even when nannoplankton densities decreased, indicating the availability and use of other food resources (i.e., detritus and bacteria). Also, the increase in the polyphagous and triptophagous groups indicated the detrital component may have been of sufficient quantities in that it supported both generalist and specialist zooplankton species.

Food resources, then, may have been relatively non-limiting, in terms of the coexisting zooplankton community, during summer 1986. This, in addition to a stable environment, may be a key factor in explaining the stability of the zooplankton community. Possible reasons for an apparently adequate food base are threefold. First, the structure of the zooplankton community itself, and its resulting grazing effects, is known to affect phytoplankton community structure. In general terms, large-sized grazers (i.e., daphnids) shift phytoplankton structure towards large, inedible species; small-sized grazers (rotifers, bosminids) shift phytoplankton to small, edible species (Porter 1973, McCauley and Briand 1979, Berquist et al. 1985). Second, the biologically-

induced recycling and regeneration of nutrients for availability to phytoplankton in the hypolimnion may have been enhanced and optimized by the presence of kokanee and high densities of rotifers. Fish excretions can be a major nutrient regeneration source (Hillbricht-Ilkowska 1977, Neill 1984, Threlkeld 1987), and rotifers play a major role in nutrient recycling (Makarewicz and Likens 1979, Bogdan and Gilbert 1982). Third, in addition to decaying plankton particles and their associated bacteria, kokanee may have significantly contributed to the detrital component of the food base as detritus has been observed to increase when fish are present (Neill 1984, Hessen and Nilssen 1986, Threlkeld 1987).

Long-term Perspectives on Community Structure

Structure is a dynamic expression of communities. Although the pelagic zooplankton community structure was highly similar in 1985 and 1986, subtle differences and possible changes could be detected. For example, where K. cochlearis, Filinia, Polyarthra, and Synchaeta densities appeared similar in both years, Bosmina, Kellicottia, and K. quadrata densities appeared to have declined in 1986. Philodina and Daphnia densities appeared to have increased. Colletheca was present only in 1985; Conochilus was present only in 1986. Because differences in sampling intensities occurred during the two years, I

cannot evaluate the importance of these possible changes. Nor can I assess the 1986 zooplankton structure as "normal" or "typical" of the Crater Lake system. Evidence from historical records indicates that Daphnia populations tend to fluctuate, being highly abundant in some years and rare in others. If these extreme density changes are typical to Crater Lake on a cyclic basis, several consequential changes could be possible. However, as Likens (1984) noted, concepts of what is considered "typical" can be understood and defined only within a long-term context.

To explore long-term community structure perspectives, I will use the components and general relationships represented in the conceptual framework presented in Figure 1. The overall framework appears to be applicable to the Crater Lake system for the summer of 1986 in that only one fish species--the zooplanktivorous kokanee--occurred in the pelagia, the zooplankton community consisted of two cladoceran and several rotifer species, and no invertebrate predators existed in the open waters. Lack of consistent, long-term data prevents comparisons of some of the components on a relative basis. For example, although kokanee was collected from 10 to 81 m in the pelagia during summer 1986 (Mark Buktenica, personal communication), comparable data is not available for previous years. In summer 1986, the large cladoceran

(i.e., Daphnia pulicaria) was rare, but the small cladoceran (i.e., Bosmina longirostris) and rotifers were abundant. In the summer of 1969, Daphnia was highly abundant relative to Bosmina; however, quantitative data for rotifers are not available. In summer 1986 the phytoplankton community consisted mainly of nanoplankton, which accounted for 84.7% of phytoplankton densities; however, comparable data are not available for relative comparisons to past years. Chlorophyll a concentrations from the surface to 200 m were higher in 1986 (mean = 112.9 mg/m²) than in 1969 (mean = 34.5 mg/m²) (Larson 1987b). Relative comparisons between nutrient concentrations or recycling rates are not available; however, sediment trap data indicated that, in general, recycling rates in the lake currently are high (Bob Collier, personal communication). Water clarity, based on Secchi disk range values, was low (26 to 33 m) compared to the 1969 range of 33 to 39 m (Larson 1987b).

With comparable data limitations in mind, the 1986 "picture" gives some indication of falling into the left-hand portion of the conceptual framework (Fig. 1). However, evidence exists that for Crater Lake long-term variation can occur within the biotic communities of this framework. Dominant year-class tendencies for fish were noted by Hasler and Farner (1942). Also, kokanee populations characteristically exhibit extreme cyclic

abundances (Scott and Crossman 1973). As noted previously, Daphnia also may express extreme fluctuations in densities. Evidence exists that phytoplankton community structure has not remained constant but also tends to change (for review, see Larson 1986). Hence, the question remains as to how the components within the framework might change on a long-term basis.

The ability of zooplanktivorous fishes to suppress populations of large cladocerans, with consequential changes in both the zooplankton and phytoplankton communities, is well established (for review, see de Bernardi et al. 1987). Perturbations of fish predation throughout a lacustrine food web and the complications of stochastic events (e.g., fluctuations in fish year-class strengths) have been recognized (Carpenter et al. 1985, Mills et al. 1987). In Crater Lake, samples from July 1985 through April 1987 revealed extremely low densities of Daphnia. This depression in numbers may be related to fish predation rather than nutrient or food limitations. Though low in numbers, Daphnia accounted for about 10% of the total density of food items found in kokanee stomach samples in summer 1986 (Mark Buktenica, personal communication). Also, zooplankton abundance trends suggest that an adequate base of suitable foods may have existed in summer 1986. Assuming, then, that kokanee are responsible for the historically-suggested fluctuation

trends in Daphnia populations, what changes might be expected in the Crater Lake pelagic zooplankton community during years when Daphnia is not suppressed by predation?

In communities supporting both rotifers and large cladocerans, a general pattern of zooplankton succession has been observed in field studies: Rotifers are abundant in winter and spring but are rapidly replaced by large cladocerans in summer (Comita 1972, Adalsteinsson 1979, Herzig 1987). Due to their ability to feed efficiently at low food concentrations (Stemberger and Gilbert 1985), rotifers may be able to persist in winter and then quickly respond to spring phytoplankton blooms because of their high reproductive abilities (Gilbert 1985). However, when large cladocerans--with their broader food niches and greater grazing rates--begin to increase, they can quickly monopolize food resources (Kerfoot 1987). Their high exploitation abilities can either reduce phytoplankton abundance or shift phytoplankton composition to larger, inedible species (Porter 1973, McCauley and Briand 1979, Berquist et al. 1985).

The above observations represent a general trend. However, the degree to which daphnids might affect small-sized zooplankton can be compounded by other factors such as lake trophic state, mechanical interference, and relative feeding efficiencies. Rotifers and small

cladocerans may be able to coexist with large cladocerans when food resources are highly abundant (Neill 1984, Gilbert 1985, DeMott and Kerfoot 1982). However, Vanni (1986) suggested that the effects of daphnid competition on small-sized zooplankton might be greater in eutrophic environments because the large cladocerans could reach greater densities, thus creating a greater impact on food resources. In addition to high exploitation abilities, daphnids may depress rotifer populations by mechanical interference (Gilbert and Stemberger 1985, Burns and Gilbert 1986). However, the importance of this factor in Crater Lake is questionable as the interference studies used small forms of K. cochlearis: form typica had a mean total length of 115 microns (Gilbert and Stemberger 1985); form tecta, which is spineless, had a mean size of 88 microns (Burns and Gilbert 1986). Form macranthra, which exists in Crater Lake, is about 300 microns. Threlkeld and Choinski (1987) found that resource exploitation, rather than mechanical interference, was the major mechanism influencing negative cladoceran-rotifer interactions. In oligotrophic habitats, the ability to feed efficiently because of low-food conditions is necessary if a zooplankter is to persist. Because they found feeding efficiency was related to body size, Stemberger and Gilbert (1985) suggested rotifers are well adapted to food-poor environments. DeMott (1982) found

that Bosmina longirostris appeared to feed more efficiently on low-food concentrations than Daphnia rosea. Tillmann and Lampert (1984) found that Daphnia pulicaria had intermediate feeding efficiencies when congenerically compared to a larger-sized and smaller-sized daphnid.

In addition to the above, the unusually stable environment of Crater Lake makes predicting the effect of increased Daphnia numbers on the zooplankton community difficult. The lake's oligotrophic nature may lessen Daphnia's full potential to depress the rotifers and Bosmina; that is, the superior ability of smaller-sized zooplankters to feed efficiently at low-food concentrations may balance Daphnia's ability to overgraze and may allow for coexistence between the two groups. On the other hand, the moderate size of Daphnia pulicaria may allow this species to still be effective, even in oligotrophic waters, in suppressing small-sized zooplankters; some evidence of this existed in 1969 when Daphnia dominated the cladoceran populations (Malick 1971). Daphnia's ability to extensively migrate within the water column, as indicated by Hoffman's work (1969), also may enhance Daphnia's competitive abilities; the ability to use the upper strata waters at night opens up an almost exclusive food niche to Daphnia.

Thus, the degree to which Daphnia might affect the pelagic zooplankton community as fish-predation intensities change is not known at this time. Nonetheless, within the conceptual framework presented in Figure 1, hypothetical influences on water clarity due to changes in Crater Lake's trophic structure can be discussed within two extremes: a rotifer-dominated zooplankton community and a daphnid-dominated zooplankton community (Fig. 18). The major keys to these food web models are nutrient availability and recycling. As noted by Carpenter et al. (1985), potential production levels are determined by nutrient supply; however, the actual, or realized, production depends on the availability of nutrients to the biota and the retention of nutrients within the system. Further, these models view water clarity as a function of primary production. Four levels are represented for Crater Lake's pelagic food web: i) kokanee, ii) zooplankton, which is divided into a Bosmina and rotifer component and a Daphnia component, iii) phytoplankton, which consists of a nanoplankton and edible flagellates component and a net plankton and inedible species component, and iv) detritus/bacteria. Although the relationships among the components are the same in both models, the components vary in densities and concentrations. In the rotifer-dominated model, nutrients tend to be retained within the system. The key factor in

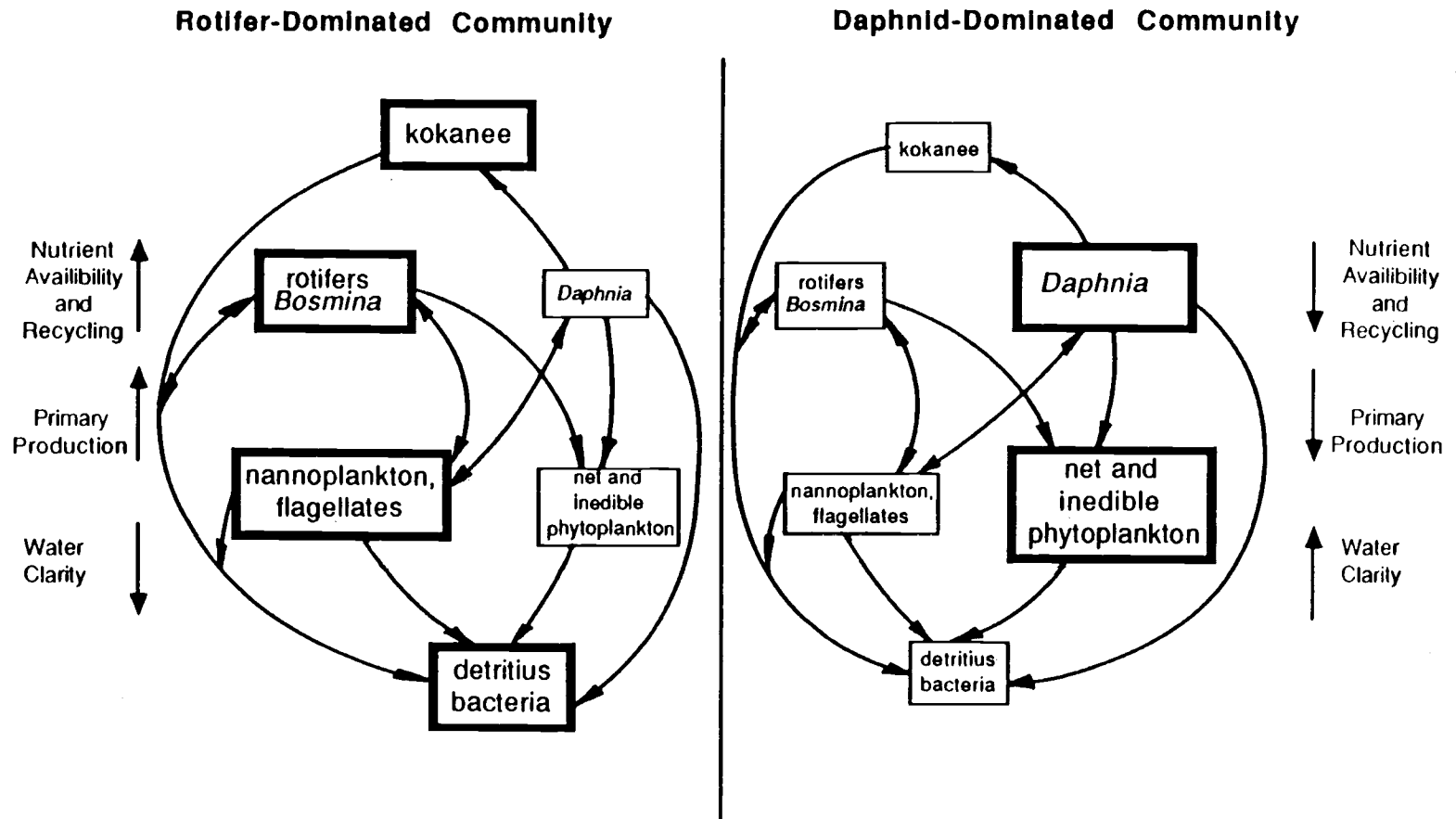


Figure 18. Two hypothetical extremes of the Crater Lake pelagic food web, based on fluctuations between a rotifer-dominated and a daphnid-dominated zooplankton community and their possible effects on water clarity. Size of boxes indicates relative densities within a foodweb; large boxes indicate high densities, and small boxes indicate low densities.

this retention is the fish component: Kokanee preys on Daphnia; its excretions then benefit the smaller zooplankters, who no longer are out-competed by Daphnia, and the phytoplankton component, which is no longer over-grazed by daphnids. The resulting increase in primary production may be due to i) increased availability of nutrients within the food web system, ii) a shift in phytoplankton composition to smaller, more productive species, and iii) intermediate grazing pressure, which tends to maximize production (Larson 1980, Carpenter and Kitchell 1984, Berquist et al. 1985). When primary production is high, water clarity is low. In the daphnid-dominated model, kokanee--which had a positive effect on nutrient availability and on the detritus/bacteria component--is scarce or lacking. Although daphnid excretions can play a major role in nutrient recycling, nutrient availability is less relative to the rotifer-dominated community. Without fish to prey on them, Daphnia may represent a nutritional "dead end"; that is, upon death, these nutrient "packages" may sink out of the system. Primary production may decline due to i) decreased nutrient availability, ii) a shift in phytoplankton composition to larger, less productive species, and iii) intensive grazing which may depress production.

This discussion thus far has taken a "top-down" view of food web influences; that is, kokanee have been assumed to be the driving factor in trophic perturbations and resulting water clarity changes. External nutrient loading into the system, however, could create a pattern similar to the one presented in Figure 1, assuming that the increase in primary production is available to higher trophic levels. This would be a "bottom-up" effect; that is, primary production increases because of additional nutrients introduced into the system. Kokanee populations deserve serious consideration in the Crater Lake issue, but this does not exclude the possibility that external nutrient loading might be occurring. Examination of primary productivity, a commonly-used indicator of lake trophic condition, and its trends alone could be misleading: Carpenter and Kitchell (1984) noted that, even at a fixed level of nutrient loading, the modeled effects of fish predation through food webs were responsible for up to a hundredfold variation in primary production. Two "tools" are needed to adequately assess this problem. First, an integrated, holistic approach is essential; changes in one trophic level can be understood and interpreted only in relation to the trophic levels above and below (Larson 1980). In this thesis, I have considered interactions among fish, zooplankton, phytoplankton, and nutrients. Second, long-term data are

required to determine if a system is stable (i.e., fluctuations or variations occur around some mean value or factor that remains relatively constant) or undergoing dynamic change (i.e., fluctuations occur around a mean factor that is progressively increasing or decreasing through time). Consistent sampling procedures are necessary to long-term studies so that sampling variation can be separated from resource variation. An example of the value of long-term studies was provided by Pedros-Alio and Brock (1985). They compared two zooplankton data sets--1894 to 1896 and 1976 to 1980--from Lake Mendota, Wisconsin; they found more annual variation within data sets than between and further concluded zooplankton structure was similar for the two time periods.

The problem to be dealt with now is how to interpret zooplankton community information to determine if external nutrient loading, or eutrophication, is occurring in Crater Lake. The problem appears somewhat compounded in that the zooplankton community may alternate between a rotifer-dominated community and a daphnid-dominated community. However, in their study of the zooplankton structure of Lake Constance, West Germany during its course of eutrophication, Walz et al. (1987) determined that increases in rotifer abundances were directly related to eutrophication; structural changes, they found, were due to trophic interactions (i.e., predation and

competition). In a review of Lago di Mergozzo, Italy, Herzig (1987) also noted rotifer numbers, as a whole, increased as the lake underwent eutrophication. An interesting note to the review was that each year was characterized by a few dominant rotifer species, but these dominant species differed from year to year. In reviewing nutrient enrichment studies undertaken in Lake Mitchell, Vermont, Kerfoot (1987) noted that when fish were absent, Daphnia increased three to tenfold over normal levels; when fish were present, however, Daphnia were suppressed and chlorophyll a levels were elevated.

For Crater Lake, then, changes in pelagic zooplankton community structure (i.e., rotifer- to daphnid-dominated structures) most likely relate to trophic factors, such as fish predation and competition. A continual increase, through time, in zooplankton absolute densities in either model would suggest possible eutrophication. However, these factors--structure and abundances--always should be interpreted within a whole-system context and on a long-term basis. In this light, the degree to which pelagic zooplankton--and biotic interactions in general--may influence water clarity can be evaluated along with other factors that also may contribute to changes, or fluctuations, in lake transparency.

BIBLIOGRAPHY

- Adalsteinsson, H. 1979. Zooplankton and its relation to available food in Lake Myvatn. *Oikos* 32:162-194.
- Alveras, R. A. 1970. A comparison of the reproductive rates of zooplankton in East and Paulina Lakes. MS Thesis. Oregon State University, Corvallis, Oregon. 51 pp.
- Banze, K. 1976. Rates of growth, respiration, and photosynthesis of unicellular algae as related to cell size--a review. *J. Phycol.* 12:135-140.
- Berner-Fankhauser, H. 1987. The influence of sampling strategy on the apparent population dynamics of planktonic rotifers. *Hydrobiologia* 147:181-188.
- Berquist, A. M., S. R. Carpenter, and J. C. Latino. 1985. Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages. *Limnology and Oceanography* 30:1037-1045.
- Bogdan, K. G. and J. J. Gilbert. 1982. Seasonal patterns of feeding by natural populations of Keratella, Polyarthra, and Bosmina: clearance rate, selectivities and contributions to community grazing. *Limnology and Oceanography* 27:918-934.
- _____, J. J. Gilbert, and P. L. Starkweather. 1980. In situ clearance rates of planktonic rotifers. *Hydrobiologia* 73:73-77.
- Brandlova, J., Z. Brandl, and C. H. Fernando. 1972. The Cladocera of Ontario with remarks on some species and distribution. *Can. J. Zool.* 50:1373-1403.
- Brode, J. S. 1935. Food habits of Crater Lake fish. *Crater Lake Nature Notes* 8:11-13.
- _____. 1938. The denizens of Crater Lake. *Northwest Science* 12:50-57.
- Brooks, J. L. 1957. The systematics of North American Daphnia. *Mem. Conn. Acad. Arts Sci.* 13:1-180.

- _____, and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150:28-35.
- Burns, C. W. 1968. The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. *Limnology and Oceanography* 13: 675-678.
- _____. 1969. Relationship between filtering rate, temperature, and body size in four species of Daphnia. *Limnology and Oceanography* 14:693-700.
- _____. and F. H. Rigler. 1967. Comparison of filtering rates of Daphnia rosea in lake water and in suspensions of yeast. *Limnology and Oceanography* 12:492-503.
- _____. and J. J. Gilbert. 1986. Effects of daphnid size and density on interference between Daphnia and Keratella cochlearis. *Limnology and Oceanography* 31:848-858.
- Byrne, J. V. 1965. Morphometry of Crater Lake, Oregon. *Limnology and Oceanography* 10:462-465.
- Carlin, B. 1943. Die Planktonrotatorien des Motalastrom. *Medd. Lunds Univ. Limnol. Inst.* 5:256 pp.
- Carpenter, S. R. and J. F. Kitchell. 1984. Plankton community structure and limnetic primary production. *American Naturalist* 124:159-172.
- _____, J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634-639.
- Cassie, R. 1971. Sampling and statistics. In Edmondson, W. T. and G. G. Winberg, eds. *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters*. IBP Handbook No. 17. Oxford: Blackwell. pp. 174-209.
- Comita, G. W. 1972. The seasonal zooplankton cycles, production and transformation of energy in Severson Lake, Minnesota. *Arch. Hydrobiol.* 70: 14-66.

- Cruz-Pizarro, L. 1978. Comparative vertical zonation and diurnal migration among Crustacea and Rotifera in the small mountain lake LaCaldera (Granada, Spain). Verh. Internat. Verein. Limnol. 20:1026-1032.
- de Bernardi, R. 1984. Methods for the estimation of zooplankton abundance. In Downing, J. A. and F. H. Rigler, eds. A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. 2 ed. IBP Handbook 17. Blackwell Scientific Publications: Boston. pp. 59-86.
- _____, R. G. Giussani, and M. Manca. 1987. Cladocera: Predators and prey. Hydrobiologia 145:225-243.
- Deevey, E. S., Jr. and G. B. Deevey. 1971. The American species of Eubosmina Seligo (Crustacea, Cladocera). Limnology and Oceanography 16:201-218.
- DeMott, W. R. 1982. Feeding selectivities and relative ingestion rates of Daphnia and Bosmina. Limnology and Oceanography 27:518-527.
- _____. 1986. The role of taste in food selection by freshwater zooplankton. Oecologia 69:334-340.
- _____, and W. C. Kerfoot. 1982. Competition among cladocerans: nature of the interaction between Bosmina and Daphnia. Ecology 63:1949-1966.
- Dodson, S. I. 1981. Morphological variation of Daphnia pulex Leydig (Crustacea: Cladocera) and related species from North America. Hydrobiologia 83:101-114.
- Downing, J. A., M. Perusse, and Y. Frenette. 1987. Effect of interreplicate variance on zooplankton sampling design and data analysis. Limnology and Oceanography 32:673-679.
- Dumont, H. J. 1977. Biotic factors in the population dynamics of rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8:98-122.
- Edmondson, W. T. 1957. Trophic relations of the zooplankton. American Microscopical Society 76: 225-245.

- _____. 1965. Reproductive rate of planktonic rotifers as related to food and temperature. *Ecological Monographs* 35:61-111.
- _____. 1980. Secchi disk and chlorophyll. *Limnology and Oceanography* 25:378-379.
- Ej-smont-Karabin, J. 1983. Ammonia nitrogen and inorganic phosphorus excretion by the planktonic rotifers. *Hydrobiologia* 104:231-236.
- Elliott, E. T. and L. G. Castanares, D. Perlmutter, and K. G. Porter. 1983. Trophic-level control of productions and nutrient dynamics in an experimental planktonic community. *Oikos* 41:7-16.
- Elliott, J. I. 1977. Seasonal changes in the abundance and distribution of planktonic rotifers in Grasmere (English Lake District). *Freshwater Biology* 7:147-166.
- Evermann, B. W. 1897. United States Fish Commission Investigations at Crater Lake. *Mazama* 1:230-238.
- Forbes, S. A. 1893. A preliminary report on the aquatic invertebrate fauna of the Yellowstone National Park, Wyoming, and of the Flathead Region of Montana. *U. S. Fish. Comm. Bull.* 11:207-256.
- Fryxell, R. 1965. Mazama and Glacier Peak volcanic ash layers: relative ages. *Science* 147:1288-1290.
- Gehringer, J. W. and W. Aron. 1968. Field techniques. In D. J. Tranter, ed. *Zooplankton Sampling*. UNESCO. pp. 87-104.
- George, M. G. and C. H. Fernando. 1970. Diurnal migration in three species of rotifers in Sunfish Lake, Ontario. *Limnology and Oceanography* 15: 218-223.
- Gilbert, J. J. 1985. Competition between rotifers and Daphnia. *Ecology* 66:1943-1950.
- _____, and K. G. Bogdan. 1981. Selectivity of Polyarthra and Keratella for flagellate and aflagellate cells. *Verh. Internat. Verein. Limnol.* 21:1515-1521.

- _____, and R. S. Stemberger. 1985. Control of Keratella populations by interference competition from Daphnia. *Limnology and Oceanography* 30:180-188.
- Green, J. 1977. Sampling rotifers. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8:9-12.
- Goulden, C. E. and D. G. Frey. 1963. The occurrence and significance of lateral head pores in the Genus Bosmina (Cladocera). *Int. Revue ges. Hydrobiol.* 48: 513-522.
- Gutelmacher, B. L. 1975. Relative significance of some species of algae in plankton primary productivity. *Arch. Hydrobiol.* 75:318-328.
- Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnology and Oceanography* 15:839-928.
- Hasler, A. D. 1938. Fish biology and limnology of Crater Lake, Oregon. *Journal of Wildlife Management* 2:94-103.
- _____, and D. S. Farner. 1942. Fisheries investigations in Crater Lake, Oregon, 1937-1940. *Journal of Wildlife Management* 6:319-327.
- Heisey, D. and K. G. Porter. 1977. The effect of ambient oxygen concentration on filtering and respiration rates of Daphnia galeata mendotae and Daphnia magna. *Limnology and Oceanography* 22: 839-845.
- Hendrikson, L., H. G. Nyman, H. G. Oscarson, and J. A. Stenson. 1980. Trophic changes, without changes in the external nutrient loading. *Hydrobiologia* 63: 257-263.
- Herzig, A. 1987. The analysis of planktonic rotifer populations: A plea for long-term investigations. *Hydrobiologia* 147:163-180.
- Hessen, D. O. and J. P. Nilssen. 1986. From phytoplankton to detritus and bacteria: effects of short-term nutrient and fish perturbations in a eutrophic lake. *Arch. Hydrobiol.* 105:273-284.

- Hillbricht-Ilkowska, A. 1977. Trophic relations and energy relations in pelagic plankton. Pol. Ecol. Stud. 3:3-98.
- Hoffman, F. O. 1969. The horizontal distribution and vertical migrations of the limnetic zooplankton in Crater Lake, Oregon. MS Thesis. Oregon State University, Corvallis, Oregon. 60 pp.
- Hofmann, W. 1977. The influence of abiotic environmental factors on population dynamics in planktonic rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8:77-83.
- Hutchison, G. E. 1967. A Treatise on Limnology. Volume 2. Wiley: New York. 1115 pp.
- Hrbáček, J. 1959. Über die angebliche Variabilität von Daphnia pulex L. Zool. Anz. 162:116-126.
- _____, M. Dvořáková, V. Kořínek, and L. Procházková. 1961. Demonstration of the effect of the fish stock on species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verh. Internat. Verein. Limnol. 14:192-195.
- _____, and M. Hrbáčková-Esslová. 1966. The taxonomy of the Genus Daphnia and the problem of "biological indication." Verh. Int. Ver. Limnol. 16:1661-1667.
- Hrbáčková-Esslová, M. 1963. The development of three species of Daphnia in the surface water of the Slapy Reservoir. Int. Revue. ges. Hydrobiol. 48:325-333.
- Johnson, R. A. and D. W. Wischern. 1982. Applied Multivariate Statistical Analysis. Prentice-Hall, Inc.: New Jersey. 594 pp.
- Kalff, J. 1972. Net plankton and nanoplankton production and biomass in a north temperate zone lake. Limnology and Oceanography 17:712-720.
- Kemmerer, G., J. F. Bovard, and W. R. Boorman. 1924. Northwestern lakes of the United States: Biological and chemical studies with reference to possibilities in production of fish. Bulletin of the United States Bureau of Fisheries 39:51-140.

- Kerfoot, W. C. 1987. Cascading effects and indirect pathways. In Kerfoot, W. C. and A. Sih, editors. Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England: Hanover and London. pp. 57-70.
- Kibby, H. V. 1971. Effect of temperature on the feeding behavior of Daphnia rosea. Limnology and Oceanography 16:580-581.
- Lampert, W. 1978. Climatic conditions and planktonic interactions as factors controlling the regular succession of spring algal bloom and extremely clear water in Lake Constance. Verh. Internat. Verein. Limnol. 20:969-974.
- _____, and U. Schober. 1978. The regular pattern of spring algal bloom and extremely clear water in Lake Constance as a result of climatic conditions and planktonic interactions. Arch. Hydrobiol. 82: 364-386.
- Larson, D. W. 1984. The Crater Lake study: Detection of possible optical deterioration of a rare, unusually deep caldera lake in Oregon, USA. Verh. Internat. Verein. Limnol. 22:513-517.
- Larson, G. L. 1980. Interpreting dynamics of aquatic resources: A perspective for resource managers. Environmental Management 4(2):105-110.
- _____. 1986. Crater Lake Limnological Program. 1985 Annual Report. National Park Service Cooperative Studies Unit, Oregon State University.
- _____. 1987a. A review of the Crater Lake limnological programs. In T. P. Boyle, ed. New Approaches to Monitoring Aquatic Ecosystems. American Society for Testing and Materials: Philadelphia. pp. 58-69.
- _____. 1987b. Crater Lake limnological Program. 1986 Annual Report. National Park Service Cooperative Studies Unit, Oregon State University.
- Laxhuber, R. 1987. Abundance and distribution of pelagic rotifers in a cold, deep oligotrophic alpine lake (Konigssee). Hydrobiologia 147:189-196.

- Lehman, J. T. 1980. Nutrient recycling as an interface between algae and grazers in freshwater communities. In W. C. Kerfoot, ed. Evolution and Ecology of Zooplankton Communities. University Press of New England: Hanover, New Hampshire. pp. 251-263.
- Likens, G. E. 1984. Beyond the shoreline: a watershed ecosystem approach. Verh. Int. Ver. Limnol. 22:1-22.
- . and J. J. Gilbert. 1970. Notes on quantitative sampling of natural populations of planktonic rotifers. Limnology and Oceanography 15:816-820.
- Lund, J. W., C. Kipling, and E. D. LeCren. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimation by counting. Hydrobiologia 11:143-170.
- Makarewicz, J. C. and G. E. Likens. 1975. Niche analysis of a zooplankton community. Science 190:1000-1003.
- . and G. E. Likens. 1979. Structure and function of the zooplankton community of Mirror Lake, New Hampshire. Ecological Monographs 49(1):109-127.
- Malick, J. G. 1971. Population dynamics of selected zooplankton in three oligotrophic Oregon lakes. MS Thesis. Oregon State University, Corvallis, Oregon. 112 pp.
- Malone, T. C. 1971. The relative importance of nanoplankton and net plankton as primary producers in tropical oceanic and neritic phytoplankton communities. Limnology and Oceanography 16:633-639.
- May, L. 1983. Rotifer occurrence in relation to water temperature in Loch Leven, Scotland. Hydrobiologia 104:311-315.
- McCauley, E. 1984. The estimation of the abundances and biomass of zooplankton in samples. In Downing, J. A. and F. H. Rigler, eds. A Manual on Methods for the Secondary Productivity in Fresh Waters. 2 ed. IBP Handbood 17. Blackwell Scientific Publications: Boston. pp. 228-265.

- _____, and F. Briand. 1979. Zooplankton grazing and phytoplankton species richness: Field tests of the predation hypothesis. *Limnology and Oceanography* 24:243-252.
- Mills, E. L. and A. Schiavone, Jr. 1982. Evaluation of fish communities through assessment of zooplankton populations and measures of lake productivity. *North Amer. Jour. of Fish. Mgt.* 2:14-27.
- _____, J. L. Forney, and K. J. Wagner. 1987. Fish predation and its cascading effect on Oneida Lake food chain. In Kerfoot, W. C. and A. Sih, editors. *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England: Hanover and London. pp. 118-131.
- Miracle, M. R. 1977a. Migration, patchiness, and distribution in time and space of planktonic rotifers. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8:19-37.
- _____. 1977b. Epidemiology in rotifers. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8:138-141.
- Neill, W. E. 1984. Regulation of rotifer densities by crustacean zooplankton in an oligotrophic montane lake in British Columbia. *Oecologia* 61:175-181.
- Nelson, C. H. 1967. Sediments of Crater Lake, Oregon. *Geological Society of American Bulletin.* 78:833-848.
- Orcutt, J. D., Jr. and K. G. Porter. 1984. The synergistic effects of temperature and food concentration on life history parameters of Daphnia. *Oecologia* 63:300-306.
- Overton, W. S., B. G. Smith, and C. D. McIntire. 1987. AID Programs (Analysis of Information and Diversity). Oregon State University.
- Pedros-Alio, C. and T. D. Brock. 1985. Zooplankton dynamics in Lake Mendota: short-term versus long-term changes. *Freshwater Biology* 15:89-94.
- Peters, R. H. and J. A. Downing. 1984. Empirical analysis of zooplankton filtering and feeding rates. *Limnology and Oceanography* 29: 763-784.

- Porter, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. *Nature* 244:179-180.
- _____. 1977. The plant-animal interface in freshwater ecosystems. *American Scientist* 65:159-170.
- Pourriot, R. 1965. Recherches sur l'écologie des Rotifères. *Vie Milieu*. 21:1-224.
- _____. 1977. Food and feeding habits of Rotifera. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8:243-260.
- Prepas, E. E. 1984. Some statistical methods for the design of experiments and analysis of samples. In Downing, J. A. and F. H. Rigler. *A Manual on Methods for the Secondary Productivity in Fresh Waters*. 2 ed. IBP Handbook 17. Blackwell Scientific Publications: Boston. pp. 266-335.
- Radwan, S. 1980. The effect of some biotic and abiotic factors on the fertility of planktonic rotifer species. *Hydrobiologia* 73:59-62.
- _____. 1984. The influence of some abiotic factors on the occurrence of rotifers of Leczna and Wlodawa Lake District. *Hydrobiologia* 112:117-124.
- Ruttner-Kolisko, A. 1974. *Plankton Rotifers: Biology and Taxonomy*. E. Schweizerbart'sche Verlagsbuchhandlung. 146 pp.
- _____. 1977a. Comparison of various sampling techniques, and results of repeated sampling of planktonic rotifers. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8:13-18.
- _____. 1977b. The effect of the microsporid Plistophora asperospora on Conochilus unicornis in Lunzer Untersee. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8:135-137.
- _____. 1980. The abundance and distribution of Filinia terminalis in various types of lakes as related to temperature, oxygen, and food. *Hydrobiologia* 73: 169-175.

- Schwartz, S. S., D. J. Innes, and P. D. N. Hebert. 1985. Morphological separation of Daphnia pulex and Daphnia obtusa in North America. *Limnology and Oceanography* 30:189-197.
- Scott, W. B. and E. J. Crossman. 1973. *Freshwater Fishes of Canada*. Fisheries Research Board of Canada, Bulletin 184. 966 pp.
- Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: an ecosystem approach to lake restoration. In P. L. Brezonik and J. L. Fox, eds. *Water Quality Management Through Biological Control*. Proc. Symp. Univ. Florida. Dept. of Environmental Engineering. pp. 85-96.
- _____, and D. J. Wright. 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. *Freshwater Biology* 14:371-383.
- Smith, B. G. 1987. CLUSB, Version 3: Recoding for microcomputer and manual revision. Oregon State University.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*, 2 ed. W. H. Freeman and Company: San Francisco. 859 pp.
- Starkweather, P. L. and K. G. Bogdan. 1980. Detrital feeding in natural zooplankton communities: discrimination between live and dead algal foods. *Hydrobiologia* 73:83-85.
- Stemberger, R. S. and J. J. Gilbert. 1985. Body size, food concentration, and population growth in planktonic rotifers. *Ecology* 66:1151-1159.
- Stenson, J. A. E. 1982. Fish impact on rotifer community structure. *Hydrobiologia* 87:57-64.
- Stich, H.-B. and W. Lampert. 1984. Growth and reproduction of migrating and non-migrating Daphnia under simulated food and temperature conditions of diurnal vertical migration. *Oecologia* 61:192-196.
- Straškraba, M. 1965. The effect of fish on the number of invertebrates in ponds and streams. *Mitt. Internat. Verein. Limnol.* 13:106-127.

- Tillmann, U. and W. Lampert. 1984. Competitive ability of differently sized Daphnia species: an experimental test. *Journal of Freshwater Ecology* 2:311-323.
- Threlkeld, S. T. 1987. Experimental evaluation of trophic-cascade and nutrient-mediated effects of planktivorous fish on plankton community structure. In Kerfoot, W. C. and A. Sih, editors. *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England: Hanover and London. pp. 161-173.
- _____, and E. M. Choinski. 1987. Rotifers, cladocerans and planktivorous fish: What are the major interactions? *Hydrobiologia* 147:239-243.
- Vanni, M. J. 1986. Competition in zooplankton communities: Suppression of small species by Daphnia pulex. *Limnology and Oceanography* 31:1039-1056.
- _____. 1977. Indirect effect of predators on age-structured prey populations: planktivorous fish and zooplankton. In Kerfoot, W. C. and A. Sih, editors. *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England: Hanover and London. pp. 149-160.
- Walz, N., H. Elster, and M. Mezger. 1987. The development of the rotifer community structure in Lake Constance during its eutrophication. *Arch. Hydrobiol. Monogr. Beitr.* 4:452-487.
- Wetzel, R. G. 1983. *Limnology*. 2 ed. Saunders College Publishing: Philadelphia. 767 pp.
- Williamson, C. E. 1983. Invertebrate predation on planktonic rotifers. *Hydrobiologia* 104:385-396.

APPENDICES

Appendix I. Classification listing for each phytoplankton species occurring between 0 and 200 m at station 13, Crater Lake, from 25 June to 17 September 1986. Classification is based on size and potential use as a food source to zooplankton (i.e. edible vs inedible). Key for Division category is: CHR = Chrysophyceae, BAC = Bacillariophyceae, XAN = Xanthophyceae, CHL = Chlorophyta, CYA = Cyanophyta, PYR = Pyrrophyta, and CRY = Cryptophyta. "F" indicates species is flagellated.

Edible 1-10 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
CHR		<u>Chrysophyta, unidentified</u>
BAC		<u>Stephanodiscus hantzchii</u>
CHR	F	<u>Chromulina sp</u>
CHR	F	<u>Chromulina-like spp (2)</u>
CHR	F	<u>Ochromonas spp (4)</u>
CHR	F	<u>Ochromonas-like sp</u>
CHR		<u>Diplomitella socialis</u>
CHR	F	<u>Chrysochromulina sp</u>
CHL		<u>Chlorophyta, unidentified spp (9)</u>
CHL		<u>Oocystis pusilla</u>
CHL		<u>Kirchneriella contorta</u>
CHL		<u>Planktosphaeria gelatinosa</u>
CHL		<u>Scenedesmus bijuga</u>
CHL		<u>Selenastrum minuta</u>
CRY	F	<u>Rhodomonas minuta</u> var. <u>nannoplantica</u>
CRY	F	<u>Rhodomonas sp</u>
PYR	F	<u>Amphidinium lutem</u>
CHR		<u>Chrysocapsa planctonica</u>
CHR	F	<u>Ochromonas miniscula</u>
BAC		<u>Nitzschia dissipata</u>
BAC		<u>Nitzschia sp</u>
CHR	F	<u>Pseudochromulina asymmetrica</u>
CHR	F	<u>Ochromonas verrucosa</u>
CHR	F	<u>Chromulina spectabilis</u>
CYA		<u>Spirulina major</u>
CHL		<u>Crucigenia quadrata</u>
BAC		Colonial diatom
BAC		<u>Navicula seminulum</u>
CHR	F	<u>Chromulina minor</u>

Inedible 1-10 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
CYA		<u>Anabaena</u>
CYA		<u>Cyanophyta</u>
CHR	F	<u>Kephyrion</u> sp
CHR	F	<u>Kephyrion asper</u>
CHR	F	<u>Chrysolykos planctonicus</u>
CHR	F	<u>Pseudokephyrion</u> spp (5)
CHR		Chrysophyte statospore (5)
CHR	F	<u>Kephyrion spirale</u>
CHR	F	<u>Pseudokephyrion conicum</u>
BAC		<u>Fragilaria construens</u> var. <u>veneta</u>
CHR		<u>Bicoeca petiolatum</u>
CHR		Chrysophyte endocyst
CHR	F	<u>Kephyrion cupriloforme</u>

Edible 11-20 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
BAC		<u>Fragilaria construens</u>
BAC		<u>Navicula</u> sp
BAC		<u>Nitzschia</u> spp (2)
CHR	F	<u>Pseudopedinella</u> sp
CHR	F	<u>Dinobryon sertularia</u>
CHL		<u>Ankistrodesmus falcatus</u> var. <u>acicularis</u>
CHL		<u>Ankistrodesmus spiralis</u>
CRY	F	<u>Rhodomonas minuta</u>
CRY	F	<u>Rhodomonas lacustris</u>
BAC		<u>Cyclotella kutzingiana</u>
CHR	F	<u>Dinobryon bavaricum</u>
CHR	F	<u>Dinobryon sociale</u>
CHR	F	<u>Chrysophyta</u> sp, unidentified
CHR	F	<u>Chromulina grandis</u>
BAC		<u>Fragilaria pinnata</u>
CHR	F	<u>Ochromonas granulosa</u>
BAC		unknown
CHR	F	<u>Pseudopedinella</u> sp

Inedible 11-20 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
CHR	F	<u>Calycomonas</u>
PYR		<u>Cryptochrysis polychrysis</u>
CHR	F	<u>Calycomonas</u> sp

Edible 21-50 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
BAC		<u>Nitzschia perminuta</u>
BAC		<u>Nitzschia frustulum</u>
PYR	F	<u>Gymnodinium inversum</u>
BAC		<u>Nitzschia innominata</u>
BAC		<u>Nitzschia fonticola</u>

Inedible 21-50 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
BAC		<u>Synedra mazamaensis</u>
BAC		<u>Achnanthes minutissima</u>
BAC		<u>Navicula cryptocephala</u>
BAC		<u>Gomphonema olivaceum</u> var. <u>calcareum</u>
BAC		<u>Fragilaria vaucheriae</u>
BAC		<u>Gomphonema heidinii</u>
PYR	F	<u>Peridinium inconspicuum</u>
PYR	F	<u>Peridinium aciculiferum</u>
BAC		<u>Fragilaria leptostauron</u>
BAC		<u>Achnanthe lanceolata</u>
PYR	F	Pyrrophyte statospore
PYR		Pyrrophyte, unidentified
BAC		<u>Gomphonema paravulum</u>
PYR		Pyrrophyte statospore
BAC		<u>Achnanthes lanceolata</u> var. <u>dubia</u>
CHR		<u>Dinobryon sertularia</u> statospore

Edible 51-70 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
XAN		<u>Tribonema</u> sp

Inedible 51-70 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
BAC		<u>Fragilaria vaucheriae</u> var. <u>capitellata</u>
BAC		<u>Synedra rumpens</u>
PYR		Pyrrophyta, unidentified
PYR	F	<u>Gymnodinium fuscum</u>
BAC		<u>Nitzschia acicularis</u>
BAC		<u>Cocconeis rugosa</u>

Edible 71-90 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
BAC		<u>Nitzschia gracilis</u>
CHL		<u>Ankistrodesmus falcatus</u>

Inedible 71-90 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
XAN		<u>Tribonema affine</u>
BAC		<u>Synedra rumpens</u> var. <u>familiaris</u>
BAC		<u>Nitzschia palea</u>
BAC		<u>Nitzschia bacata</u>
BAC		<u>Nitzschia closterium</u>
BAC		<u>Rhoicosphenia curvata</u>

Inedible 91-150 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
BAC		<u>Synedra radians</u>
BAC		<u>Nitzschia serpenticula</u>
BAC		<u>Fragilaria crotonensis</u> var. <u>oregona</u>
BAC		<u>Synedra tenera</u>
BAC		<u>Nitzschia acuta</u>
BAC		<u>Cymbella turqida</u>

Edible >150 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
CHL		<u>Mougeotia</u> sp

Inedible >150 microns

<u>Divs</u>	<u>F</u>	<u>Species</u>
BAC		<u>Asterionella formosa</u>
BAC		<u>Synedra acus</u>
BAC		<u>Synedra delicatissima</u>
BAC		<u>Nitzschia linearis</u>
BAC		<u>Nitzschia vermicularis</u>
BAC		<u>Nitzschia tryblionella</u>
BAC		<u>Epithemia sorex</u>

Appendix II. Estimated numbers of zooplankton per cubic meter of water sampled from Crater Lake in 1985 and 1986 while using the 0.75 m net. Corrected numbers reflect adjustment of the net filtration factor to account for extraneous flowmeter readings. Tows from each interval on 14 August 1985 were duplicated; tows from the 20-80, 80-120, and 120-200 m intervals in all 1986 samples were triplicated; all other tows were single. Values presented represent the mean of any replicated tows. Key to "Lake condition" category is: C = calm, I = intermediate, and R = rough.

Date	Station	Depth interval(m)	Numbers/m ³		Percent bias	Lake condition
			Uncorrected	Corrected		
7/23/85	13	0- 20	+	+	---	R
		20- 40	2,050	2,334	12.2	R
		40- 80	29,101	35,482	18.0	R
		80-120	117,541	165,676	29.0	R
		120-160	25,638	29,841	14.1	R
		160-200	6,130	5,788	5.6	R
		200-300	362	690	47.5	R
		300-400	65	116	44.0	R
8/14/85	13	0- 20	939	1,190	21.1	C
		20- 40	26,741	37,714	29.0	R
		40- 80	34,913	51,773	32.6	R
		80-120	114,279	161,720	29.3	R
		120-160	31,512	55,468	43.2	R
		160-200	1,121	1,985	43.5	R
		200-300	218	239	8.8	C
		300-400	40	44	9.1	C
		400-500	23	24	4.2	C
6/24/86	13	0- 40	5,080	5,825	12.8	C
		20- 80	56,909	62,048	8.3	C
		80-120	120,636	141,801	14.9	C
		120-200	16,437	18,249	9.9	C
		200-500	885	708	20.0	C
7/2/86	13	20- 80	67,201	79,205	15.2	R
		80-120	123,440	177,354	30.4	R
		120-200	17,376	22,191	21.7	R
	23	20- 80	75,840	91,764	17.3	R
		80-120	102,633	119,360	14.0	R
		120-200	15,849	20,255	21.7	R

Appendix II. Continued

Date	Station	Depth interval(m)	Numbers/m ³		Percent bias	Lake Condition
			Uncorrected	Corrected		
7/22/86	13	0- 40	56,915	67,203	15.3	C
		20- 80	82,586	90,116	8.4	C
		80-120	134,859	144,708	6.8	C
		120-200	15,766	19,963	21.0	R
		200-500	830	956	13.2	R
8/4/86	13	20- 80	67,435	87,036	22.5	R
		80-120	162,937	199,299	18.2	C
		120-200	23,179	22,991	8.1	C
	23	20- 80	44,698	49,878	10.4	C
		80-120	174,197	191,241	8.9	C
		120-200	12,048	15,290	21.2	R
8/19/86	13	0- 40	22,040	25,600	13.9	C
		20- 80	44,595	48,832	8.7	C
		80-120	184,594	222,936	17.2	C
		120-200	22,268	19,765	11.2	I
		200-500	891	501	43.8	I
9/2/86	13	0- 40	22,158	23,796	6.9	C
		20- 80	64,637	77,021	16.1	C
		80-120	131,515	149,476	12.0	C
		120-200	13,667	13,558	0.8	C
		200-500	476	483	1.4	C
	23	0- 40	35,534	41,958	15.3	C
		20- 80	75,835	85,356	11.1	C
		80-120	240,234	288,058	16.6	C
		120-200	21,325	21,931	3.8	C
		9/16/87	13	0- 40	23,529	40,672
20- 80	111,833			114,802	2.6	R
80-120	97,701			141,842	31.1	R
120-200	10,272			12,725	19.3	R
200-500	401			573	30.0	R

Appendix III. Number of organisms per cubic meter of water sampled from 20 to 200 m at station 13, Crater Lake, from 24 June to 16 September 1986.

Species	Sampling dates							Totals
	24 Jun	2 Jul	22 Jul	4 Aug	19 Aug	2 Sep	16 Sep	
<u>Keratella cochlearis</u>	43,406	51,966	44,696	57,375	56,046	46,836	58,170	358,495
<u>Polyarthra</u>	7,629	11,870	16,226	14,005	5,586	6,402	7,581 ^a	69,299
<u>Philodina</u>	2,341	3,021	3,376	4,461	5,730	4,686	6,249	29,864
<u>Filinia</u>	1,155	2,300	2,023	3,052	3,211	3,831	3,887	19,459
<u>Bosmina</u>	1,815	1,585	1,761	2,007	1,398	1,072	973	10,611
<u>Synchaeta</u>	1,259	1,551	972	933	1,047	1,029	1,866	8,657
<u>Kellicottia</u>	1,030	1,466	1,197	1,172	1,405	906	1,396	8,572
<u>Keratella quadrata</u>	1,725	1,916	810	502	155	127	80	5,315
<u>Daphnia</u>	0	2	7	11	23	9	22	74
<u>Conochilus</u>	0	0	0	0	0	0	13	13
Totals	60,360	75,677	71,068	83,518	74,601	64,898	80,237	510,359

^aEstimate includes organisms present in 0 to 20 m interval.

Appendix IV. Body Length Measurements

The purpose of this section is to document body length measurements taken from Crater Lake cladocerans (Table 35). Body length information is useful, not only for species identification, but also for indicating the relative abundances of age classes within a population at a given time. Such information, on a seasonal basis, provides a general juvenile/adult ratio. On a long term basis, changes in mean body length may correspond with changes in coexisting predator populations due to preferred age class predation (e.g., see Vanni 1987).

Most of the measurements were taken from bosminid specimens from 1986 and winter 1987 samples. Measurements of Bosmina also were taken from August 1968 and August 1969 samples. Daphnid measurements were taken from August 1968, August 1969, September 1986, and January 1987 samples. Preserved specimens were measured as they were encountered in a subsample. Sample size was based on a 95% confidence interval level and either a 10% or 20% allowable error (Prepas 1984, p. 273). One exception--a 30% allowable error for Bosmina taken from a 1969 sample--occurred because few specimens were available. Total length of a specimen was measured (i.e., from the top of the head to the point of tail insertion.

Table 35. Body length measurements of Crater Lake cladocerans. All samples were taken from station 13 with the exception of the 8/5/69 samples, which were taken from station 18. All samples were obtained from vertical tows with the exception of the 8/29/68 samples, which were obtained from horizontal tows.

Species	Sampling date	Depth interval (m)	Sample size	Allowable error (%) (mm)	Mean length (mm)	Range of length
<u>Daphnia</u>	8/29/68	25-125	181	20	1.03	0.55-2.25
<u>pulicaria</u>	8/05/69	0-100	40	20	1.05	0.58-2.00
	8/31/69	0-200	43	20	1.14	0.53-2.20
	9/02/86	20-200	46	20	1.19	0.60-2.00
	1/19/87	0-100	27	20	1.02	0.53-1.88
<u>Bosmina</u>	8/29/68	25-125	181	10	0.39	0.25-0.60
<u>longirostris</u>	8/05/69	0-100	5	30	0.41	0.38-0.50
	3/05/86	0-100	30	10	0.43	0.28-0.60
	5/29/86	0-100	30	10	0.42	0.28-0.58
	6/24/86	20-120	130	10	0.41	0.23-0.63
	7/02/86	20- 80	50	10	0.40	0.23-0.60
	7/22/86	20-120	130	10	0.37	0.23-0.60
	8/04/86	20-120	130	10	0.40	0.25-0.60
	8/19/86	20-120	130	10	0.42	0.25-0.63
	9/02/86	20- 80	50	10	0.40	0.25-0.60
	9/16/86	0-120	180	10	0.35	0.25-0.63
	1/19/87	0-100	30	10	0.38	0.28-0.58
	4/14/87	0-100	30	10	0.46	0.33-0.48

Appendix V. Bosmina Egg Ratios

The ratio of eggs to female adults often is used as a population reproductive index in major zooplankton groups such as Cladocera, Rotifera, and Copepoda. The purpose of this section is to document egg ratios calculated for Bosmina longirostris from samples taken during winter and summer 1986 and winter 1987 (Table 36).

To obtain egg ratio values, I counted the number of eggs contained within the brood pouches of the first 100 mature bosminids encountered in a subsample. Three subsamples were taken from each sample in which an egg ratio was determined. The mean egg ratio was then calculated for the 3 subsamples. "Mature" was defined as the minimum specimen size in which eggs first appeared.

From the 1986 through winter 1987 egg ratio computations, I found that the highest egg ratios occurred in March 1986 and April 1987 (Table 36). During the summer of 1986, the lowest egg ratio coincided with the highest density value (Fig. 19).

Table 36. Egg ratio values for Bosmina sampled at station 13, Crater Lake from winter 1986 through winter 1987.

Sampling date	Depth interval (m)	Eggs/female
3/ 5/86	0 - 100	0.46
5/29/86	0 - 100	0.93
6/24/86	20 - 80	0.32
	80 - 120	0.48
	120 - 200	0.26
7/ 2/86	20 - 80	0.35
	80 - 120	0.22
	120 - 200	0.15
7/22/86	20 - 80	0.11
	80 - 120	0.13
	120 - 200	0.10
8/ 4/86	20 - 80	0.10
	80 - 120	0.03
	120 - 200	0.03
8/19/86	20 - 80	0.21
	80 - 120	0.15
	120 - 200	0.06
9/ 4/86	20 - 80	0.46
	80 - 120	0.14
	120 - 200	0.02
9/16/86	0 - 40	0.35
	20 - 80	0.47
	80 - 120	0.07
	120 - 200	0.06
1/19/87	0 - 100	0.15
4/14/87	0 - 100	0.92

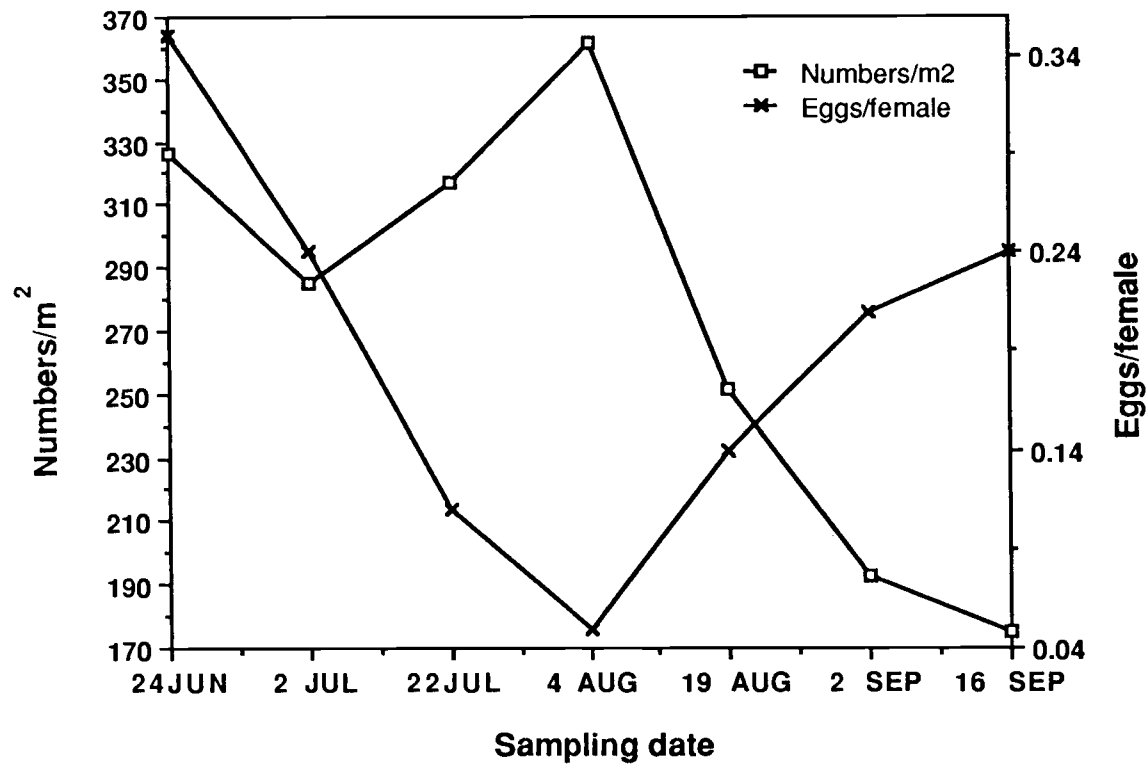


Figure 19. Comparison of numbers of *Bosmina* per square meter of water sampled and number of eggs per adult female *Bosmina*. Data are from 20 to 20 m, at station 13, Crater Lake, during summer 1986.