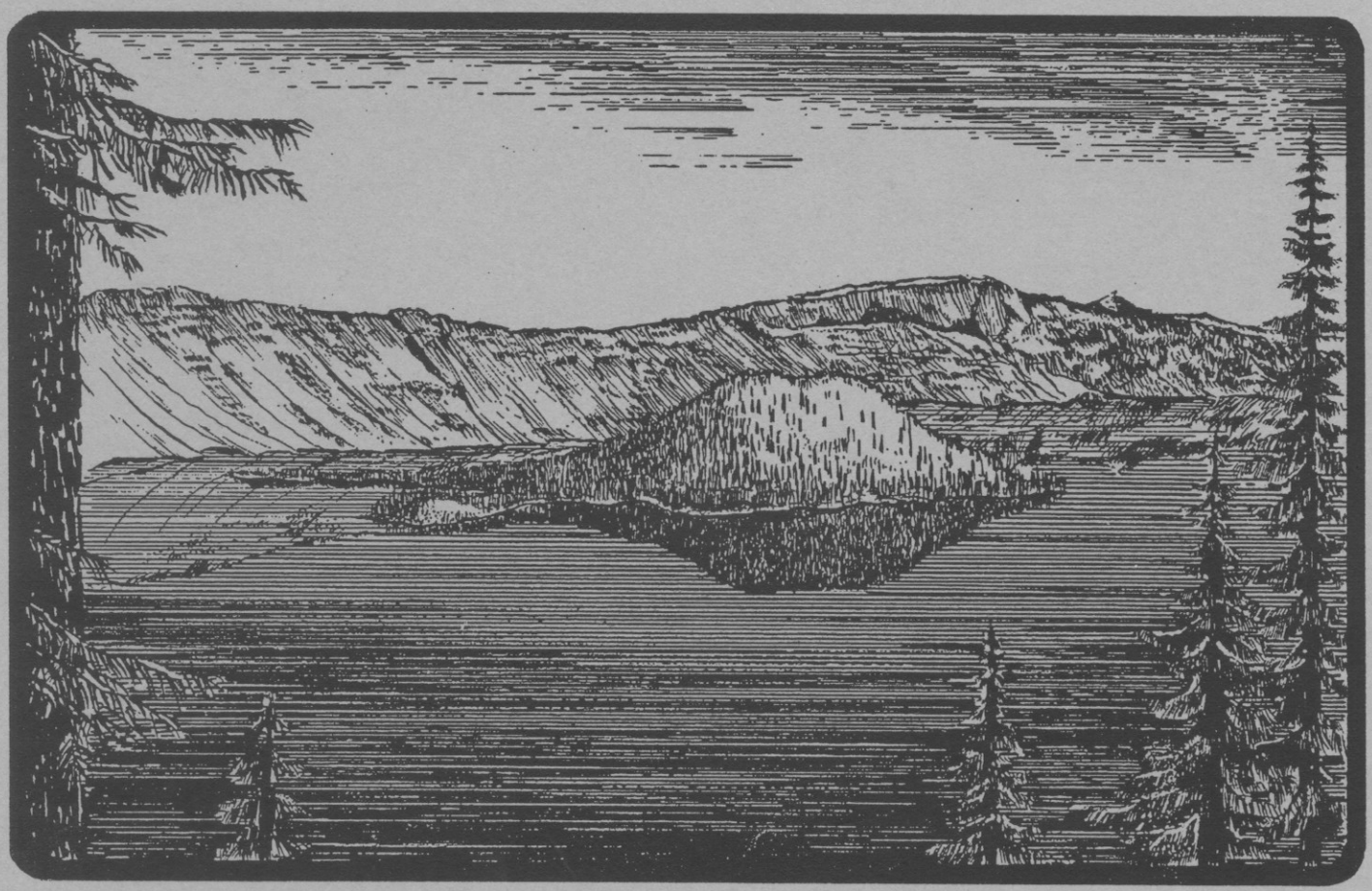
Crater Lake Limnological Studies

Draft Final

Crater Lake National Park

December 1992



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CRATER LAKE LIMNOLOGICAL STUDIES
DRAFT FINAL REPORT

Edited by

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December 1992

Technical Report NPS/PNROUS/NRTR-

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Executive Summary

Limnological studies of Crater Lake were initiated by the National Park Service in 1982 in response to an apparent decline in lake clarity and changes in the characteristics of the algal community. In the fall of 1982, Congress passed Public Law 97-250 which mandated the Secretary of the Interior to conduct a 10-year study of the lake. The broad goals of the study included: (1) development of a limnological data base to be used for comparisons of future conditions; (2) development of a better understanding among physical, chemical and biological components of the lake system; and (3) development of a long-term monitoring program. An important aspect of the program was to determine if the lake had experienced recent changes, and if changes were present and human related, identify the cause(s) and recommend ways of mitigating the change(s).

An ecosystem approach was used to develop the program. Conceptual models of the lake ecosystem were developed and used to guide research and analyses. Studies included quantity and chemistry of precipitation, lake-level fluctuations, solar radiation, chemistry of intra-caldera springs, lake clarity, lake color, lake chemistry, particle flux, chlorophyll, primary production, phytoplankton, zooplankton, bottom fauna and flora, and fish. An extensive data base was assembled for each aspect of the study.

Comparisons of older limnological data collected from Crater Lake, though sparse, indicated that there have been no major changes in the near-surface water quality of the lake. Hydrothermal inputs are responsible for the stable water quality through time. Although the analysis of Secchi disk records collected between 1896 and 1969 and 1978 and 1991 suggests that the data sets are fairly comparable, this result does not

imply that Crater Lake has not changed through the years. Changes in nutrient input from the atmosphere and potential local sources of nutrients may have some long-term roles to play in the productivity and clarity of Crater Lake. The extent that Crater Lake may have changed is not known because it is difficult to assess the natural variability of the disk readings relative to any changes caused by human-related activities. Secchi disk readings in the range of 39-40 m recorded in August of 1973 and 1969 were not observed between 1978 and 1991. The absence of extremely deep Secchi disk readings during this study may be a sign of change, but a 33.5 m reading in August 1954, the only bona fide August Secchi disk reading between 1937 and the late 1960's, illustrates the problem of separating the natural dynamics of lake clarity from any long-term decreases in clarity. Fluctuations in the surface elevation of the lake between 1982 and 1992 were similar to those observed since 1900. The cyclic nature of the largest crustacean zooplankton species was consistent with the results from studies conducted in the late 1960's. Population fluctuations of kokanee salmon were consistent with general observations made at the lake for the last 25 - 30 years.

Lake sampling was conducted between June and September when the lake was accessible by a trail at Cleetwood Cove. A boathouse was constructed on Wizard Island, the largest island on Crater Lake, in the summer of 1985. Winter and spring sampling began in 1986.

Crater Lake was found to be a complex and dynamic oligotrophic (nutrient-poor) system. The volume of the lake responded quickly to changes in precipitation because the closed basin (no surface outlet) functioned like a leaky rain gauge and evaporation pan. Although the lake level fluctuates about 0.5 m annually, the lake surface dropped about 3 m in elevation between 1984 and 1992. The lake was relatively high in dissolved

salts, total alkalinity, and conductivity; pH ranged between 7 and 8. Hydrothermal fluids from the lake bottom contributed to the relatively high salt content of the lake. Phosphorus and nitrate were low in concentration, although the concentration of the latter increased substantially below a depth of 200 m. On an annual basis, atmospheric bulk deposition accounted for about 70% of the nitrogen and 30% of the phosphorus input to the lake. Internal recycling of nutrients was important to the nutrient budget of the lake.

In winter and spring the lake circulated to a depth of about 200 m by wind. Some deep-water mixing was indicated by high concentrations of dissolved oxygen at the lake bottom. The lake was thermally stratified in summer and fall. The interface between the warmed surface waters and the cold waters of the deep lake was at a depth of about 80 m.

Secchi disk clarity generally was in the high 20 m to mid-30 m range. The depth of 1% of the incident surface light generally was between 80 and 100 m. Seasonal and long-term changes of Secchi disk readings and the depth of 1% incident light were observed. In summer, a layer of near-surface turbidity was associated with changes in Secchi disk clarity. Lake color measurements indicated that the near-surface water was very blue.

Water chemistry of caldera springs exhibited a wide range of chemical concentrations and total ionic compositions over short distances around the perimeter of the lake. Calcium, magnesium, and sodium were the major cations, and bicarbonate was the major anion. Three springs along the south wall of the caldera were relatively high in nitrate. Although the origin of the nitrate could not be confirmed, patterns of nitrate concentrations were influenced strongly by stream discharge.

In winter and spring, chlorophyll, phytoplankton, and zooplankton were uniformly distributed from the lake surface to the depth of mixing (maximum depth about 200 m). Maximum primary production occurred between 40 and 60 m. In summer and fall, a deep-water chlorophyll maximum developed between 100 and 140 m. Maximum primary production typically occurred between 40 and 80 m. About 96% of total primary production was associated with nutrients recycled in the euphotic zone. A sparse but complex phytoplankton community partitioned the water column to a depth of 200 m. A high density of phytoplankton typically developed in the warm near-surface waters. Long-term fluctuations in chlorophyll, primary production, and phytoplankton density were observed. Periods of upwelling of nutrient rich waters from the deep lake were thought to influence the productivity of the lake. In summer and fall, the zooplankton community, comprised of eight rotifer species and two species of crustaceans, partitioned the water column to a depth of 200 m. Zooplankton abundance in the upper 20 m of the water column was very low. The highest densities of zooplankton were located in the 80 to 180 m depth interval. Closely related or competing species were found in different portions of the water column. The largest crustacean species was cyclic in abundance. Its abundance was related to lake productivity and fish predation, and when abundant, rotifer abundances declined and changes in the distribution of the other crustacean species were observed.

Two species of fish, rainbow trout and kokanee salmon, exist in the lake. Both species were stocked many years ago and reproduce in the lake. Kokanee salmon mostly were pelagic and fed primarily on crustacean zooplankton and small-bodied bottom fauna. Abundances of kokanee were cyclic owing to the numerical dominance of one year class. Rainbow trout were found along the littoral zone of the lake and fed on

terrestrial insects at the lake surface, large-bodied bottom fauna, and kokanee. Introduced fish present long-term implications to lake ecology.

Benthic macroinvertebrate richness was moderate in Crater Lake and comparable to the richness found in other large, cold oligotrophic lakes in the northern hemisphere. Densities of epibenthic macroinvertebrates on rocky substrates in the littoral zone were relatively high. Most taxa in the littoral zone were types common to streams and rivers in montane areas of western North America. Snails were common to a depth of 100 m. Oligocheata worms and chironomid midges were common in the deep lake.

A new species of aquatic mite, *Algophagopsis* sp., was found in the lake. This is the only known local for this species. The mite was abundant on rock surfaces in association with aquatic lichen and *Nostoc* in the main lake, on filamentous algae in Emerald pool located on Wizard Island, and on the aquatic moss, *Drepanocladus aduncus*, with the deepest collection from 118 m.

Beds of macrophytes were found on some of the sand-gravel benches around the perimeter of the lake. *Drepanocladus* was present in dense beds in the lake in the 30 to 120 m depth interval. Several species of diatoms were associated with the moss. Periphyton was collected from many sites around the margin of the lake, as well as from depths as great as 120 m.

Introduction to the 10-Year Study

Gary L. Larson, C. David McIntire, and Mark Buktenica

Crater Lake is a primary resource of Crater Lake National Park in southern Oregon. The lake is well-known for its deep blue color, optical properties (Pettit 1936, Smith et al. 1973), and extreme water clarity. These characteristics exist for many reasons, but some important ones are the lake's great mean depth, a very small watershed to lake surface area ratio (0.27), a lack of influences from inflowing streams, a small watershed, and its national park status, which protects the lake from within basin anthropogenic impacts (Larson 1987). Considerable concern was voiced, therefore, by park management, scientists, and the public when limnological studies conducted from 1978 to 1981 (Larson 1984) suggested that lake clarity had declined, and that the species composition of the phytoplankton community had changed.

In early 1982, the National Park Service convened a panel of limnologists to evaluate the available limnological data. This panel concluded that the data were insufficient to determine if the clarity had changed. On their recommendation, the National Park Service sponsored a limnological study of the lake, which was initiated in the summer of 1982. In the fall of 1982, Congress passed Public Law 97-250, which mandated that the Secretary of the Interior conduct a 10-year limnological study of Crater Lake. Broad goals of the 10-year study were to: (1) develop reliable baseline data for use in the future; (2) develop a better understanding of physical, chemical, and biological characteristics and processes of the lake; and (3) establish a long-term monitoring program to examine limnological characteristics of the lake through time. This applied limnological study was designed to investigate the possibility of long-term

changes in lake conditions, and if such changes were found, to develop studies to identify causal factors. If any changes were determined to be anthropogenic, mitigation measures were to be recommended.

The 10-year study of Crater Lake began in the summer of 1983 with emphasis on establishment of a monitoring program (Larson 1990). By 1985, much of the preliminary work was done, and two conceptual models were developed to guide additional monitoring and research (Figures 1 and 2). The first model (Fig. 1) identified the various components involved in the functioning of the Crater Lake ecosystem and their interrelationships, whereas the second model (Fig. 2) focused on ecosystem components within the lake. Based on these models, a set of working objectives was developed, and a format for the monitoring program was completed (Tables 1 and 2). The working objectives were divided into three subdivisions: (1) baseline; (2) lake structure and organization; and (3) examination of changing lake conditions through analysis of baseline data, lake color, optical properties and paleolimnology. All components listed in Table 1 were addressed in the program. The optical study by Smith et al. (1973) was repeated, and lake cores were obtained to evaluate historic lake conditions from the physical, chemical, and diatom fossil records in the sediments. However, analyses of these data have not yet been completed in time to include the results in the writing of this report.

Studies of the lake were conducted from late June through September from 1983 to 1985. During this period, the lake was inaccessible in the winter and spring. In 1985 a boathouse was constructed on Wizard Island, the largest island in the lake (Fig. 3), and this facility permitted sampling of the lake in winter and spring. In summer, research staff reached the lake via a 1.6-km trail on the northside of the caldera (Fig. 3). A four-

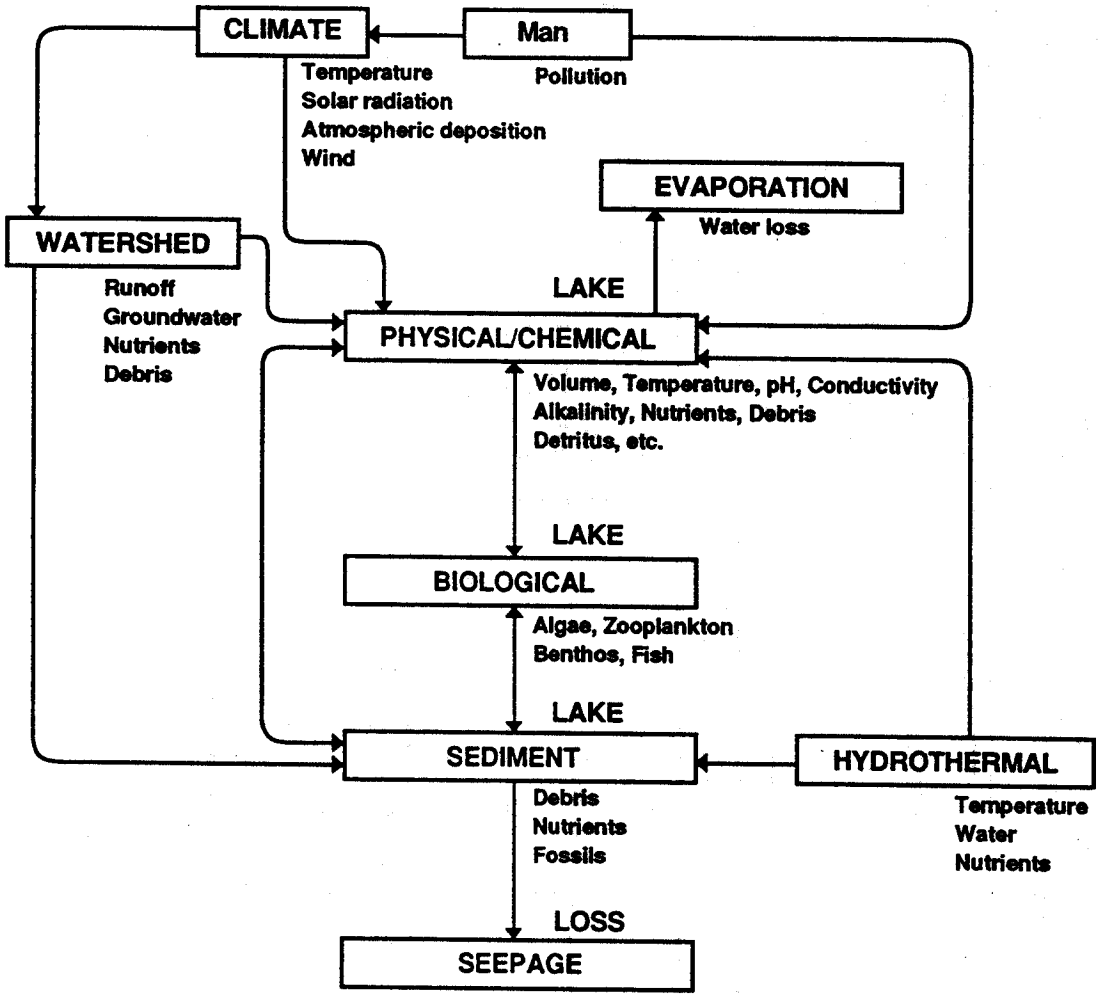


Figure 1. Conceptual model of the Crater Lake ecoystem (after Larson 1990).

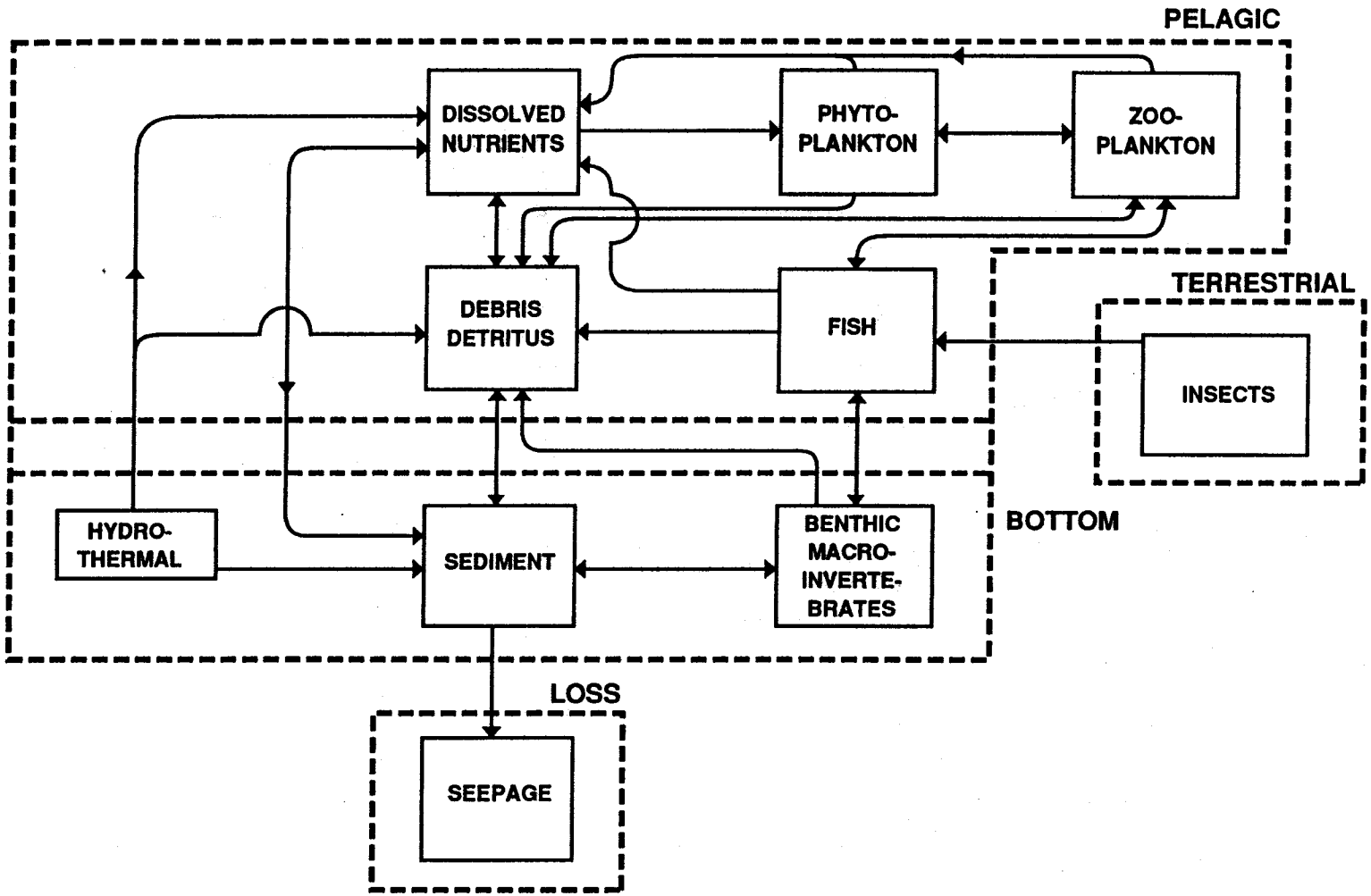


Figure 2. Details of the lake aspects of the conceptual model shown in Figure 1 (after Larson 1990).

Table 1. Working objectives of the Crater Lake limnological studies (after Larson 1990).

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1. Baseline data base.

   A. Describe the general physical, chemical, and biological characteristics of the lake for the period 1983-1992.

      1. Determine the amount of seasonal and annual variation of each variable.

      2. Determine how each variable varies with depth.

      3. Determine the amount of spatial (horizontal) variation of each variable.

      4. Evaluate the lake clarity data relative to the physical, chemical, and biological conditions of the lake.

2. Lake organization and structure.

   A. Lake volume, stratification and circulation.

      1. Estimate water input into the caldera.

      2. Document relationships between input and changing lake levels.

      3. Evaluate conditions necessary for the development of thermal stratification.

      4. Describe the circulation patterns and processes of the lake.

   B. Nutrients.

      1. Estimate nutrient loading of the lake from atmospheric sources and caldera springs.

      2. Estimate loss of nutrients by sedimentation.

      3. Evaluate nutrient concentrations in the lake through time relative to inputs, losses, and recycling.

Table 1. (continued)

C. Biological features.

1. Describe the relationships of phytoplankton species, abundance biovolume, distribution, and production relative to physical and chemical lake features and zooplankton.

2. Describe the relationships of zooplankton species, abundance, biomass, and distribution relative to physical and chemical lake features, phytoplankton, and fish.

3. Describe the relationships of benthic macro-invertebrate species, distribution, and abundance relative to physical and chemical lake features.

4. Describe the relationships of fish species, abundance, biomass, and distribution relative to physical and chemical lake features and zooplankton, benthic macro-invertebrates and terrestrial insects.

3. Optical characteristics, lake color, and paleolimnology.

A. Color and optical properties.

1. Determine color, and optical properties of the lake as measured by Secchi disk, photometer, and transmissometer.

a. Compare data with Pettit's 1935 lake color study.
b. Compare data with Smith et al., 1969 optical study.
c. Compare data with pre-1983 Secchi disk data.
d. Compare data with pre-1983 photometer data.
e. Compare Secchi disk data with photometer and transmissometer data.

2. If changes are observed, (3.A1), interpret these relative to modern lake clarity conditions (1.A4).

B. Paleolimnology.

1. Evaluate historic lake conditions from analyses of sediment cores from the lake.

a. Determine how selected physical characteristics changed through time.

Table 1. (continued)

	b.	Determine how selected chemical characteristics changed through time.
	c.	Examine the fossil record through time.
2.		Determine relationships between the characteristics of surface sediments and settling materials.
4.		Evaluate long-term system dynamics (from 1, 2, and 3).
A.		Determine if any variable under study shows signs of change that are greater than would be expected from modern annual variations.
B.		Determine if any detected changes were related to a loss of lake clarity.
C.		To the extent necessary, identify and conduct special studies to evaluate factors that may be impacting lake water quality.

Table 2. Baseline limnological monitoring of Crater Lake and at intra-caldera springs (after Larson 1990).

1.		Lake Program.
A.		Temperature.
	1.	Temperature profiles to 250 m (maximum length of thermistor cable) at: 1-m intervals from 0 to 20 m 5-m intervals from 20 to 100 m 20-m intervals from 100 to 200 m, and 25-m intervals from 200 to 250 m
	2.	Conductivity, temperature and depth probe (CTD) to 550 m.
B.		Optical properties.
	1.	20-cm Secchi disk
	2.	Photometer (to 150 m)
	3.	Transmissometer (to 550 m)

Table 2 (continued)

C. Chemical properties.

Total alkalinity, pH, specific conductance, and the concentrations of dissolved oxygen, total phosphorus, orthophosphate, nitrate-nitrogen, total Kjeldahl-nitrogen, ammonia-nitrogen, silica, and trace elements at all or selected depths from the following depth sequence: 0, 5, 10, 20, 60, 100, 200, 300, 400, 500, and 550 m.

D. Biological properties.

1. Chlorophyll *a*.

In vitro chlorophyll concentration according to the following depth sequence:

5-m intervals from 0 to 10 m.
20-m intervals from 20 to 200 m.
25-m intervals from 200 to 300 m.

2. Primary production (carbon-14 light/dark bottle).

C-14 Primary production at the chlorophyll sampling depths to 180 m.

3. Phytoplankton.

Species, density, and biovolumes at all chlorophyll sampling depths.

4. Zooplankton.

Species, density, and biomass in samples obtained by a vertical tow of a .5 m diameter, number 25 closing net.

5. Fish.

Species, abundance, and biomass, spatial distribution, age, sex, growth and food habits. Samples collected with gill nets, hook and line, and down rigger. Pelagic distributions estimated using an echo-sounder.

Table 2. (continued)

2.	Springs.	
	A.	Location.
		Each spring identified by a numbered tag.
	B.	Physical and chemical water quality and bacteria.
		Record temperature and take samples for pH, conductivity, alkalinity, nutrients, trace elements, and bacteria (total coliforms, fecal coliforms, and fecal streptococcus).

wheel-drive tract tractor was used to transport equipment and supplies. In winter, they were helicoptered in or walked down the caldera wall. Monitoring occurred in the deepest basin of the lake at a site designated as Station 13 (Fig. 3) because much of the historical data were collected at this site and because limnological conditions in the deep basin were similar to conditions at station 23, a site located in the south basin (Larson 1985).

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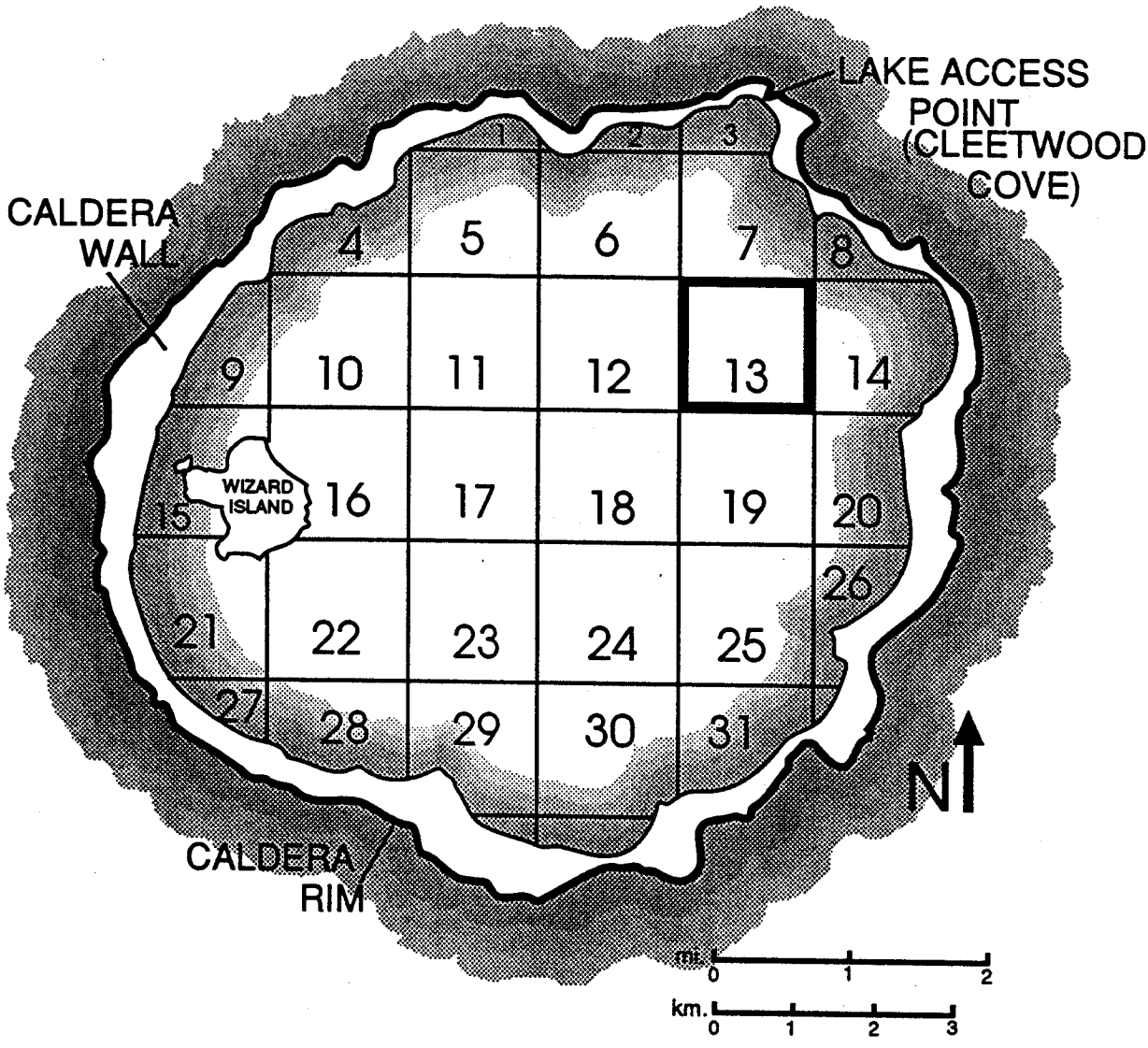


Figure 3. Grid system of Crater Lake stations established by Hoffman (1969). The main monitoring station (13) is 589 m deep.

Study Area and Facilities

Gary L. Larson, C. David McIntire, and Mark Buktenica

Study Area

Crater Lake is within Crater Lake National Park in the Cascade Mountain Range. This southern Oregon lake basin (caldera) was formed by catastrophic collapse of the sides of Mount Mazama following a violent eruption about 6,850 years ago (Bacon and Lanphere 1990). Walls of the caldera have been enlarged by caving and sliding to form a scalloped outline between 8 and 10 km in diameter. Postcaldera volcanism inside the caldera formed the central platform, Merrium Cone, and Wizard Island (Fig. 1). The lake was filled to nearly its present level before the end of andesitic postcaldera volcanism, about 6,000 years ago. A small rhyodacite dome east of Wizard Island was extruded about 4,000 years ago (Bacon and Lanphere 1990). The rim of the caldera averages about 2,100 m in elevation, with some peaks reaching about 2,500 m.

Crater Lake occupies 79% of the caldera of Mount Mazama. The lake has a surface area of 48 km^2, maximum depth of 589 m, a mean depth of 325 m, and shoreline length of 31 km (Fig. 1, Byrne 1965). The average elevation of the lake surface is 1,882 m. There is no surface outlet, but over 40 permanent and ephemeral inlet streams (also referred to as springs) occur in the caldera.

Facilities

The limnological studies of Crater Lake were conducted from a 5.5-m-long Boston Whaler and an 8-m-long double-pontoon vessel with a flat deck and open center well. The Boston Whaler was usually reserved for winter and fall sampling. Water samples

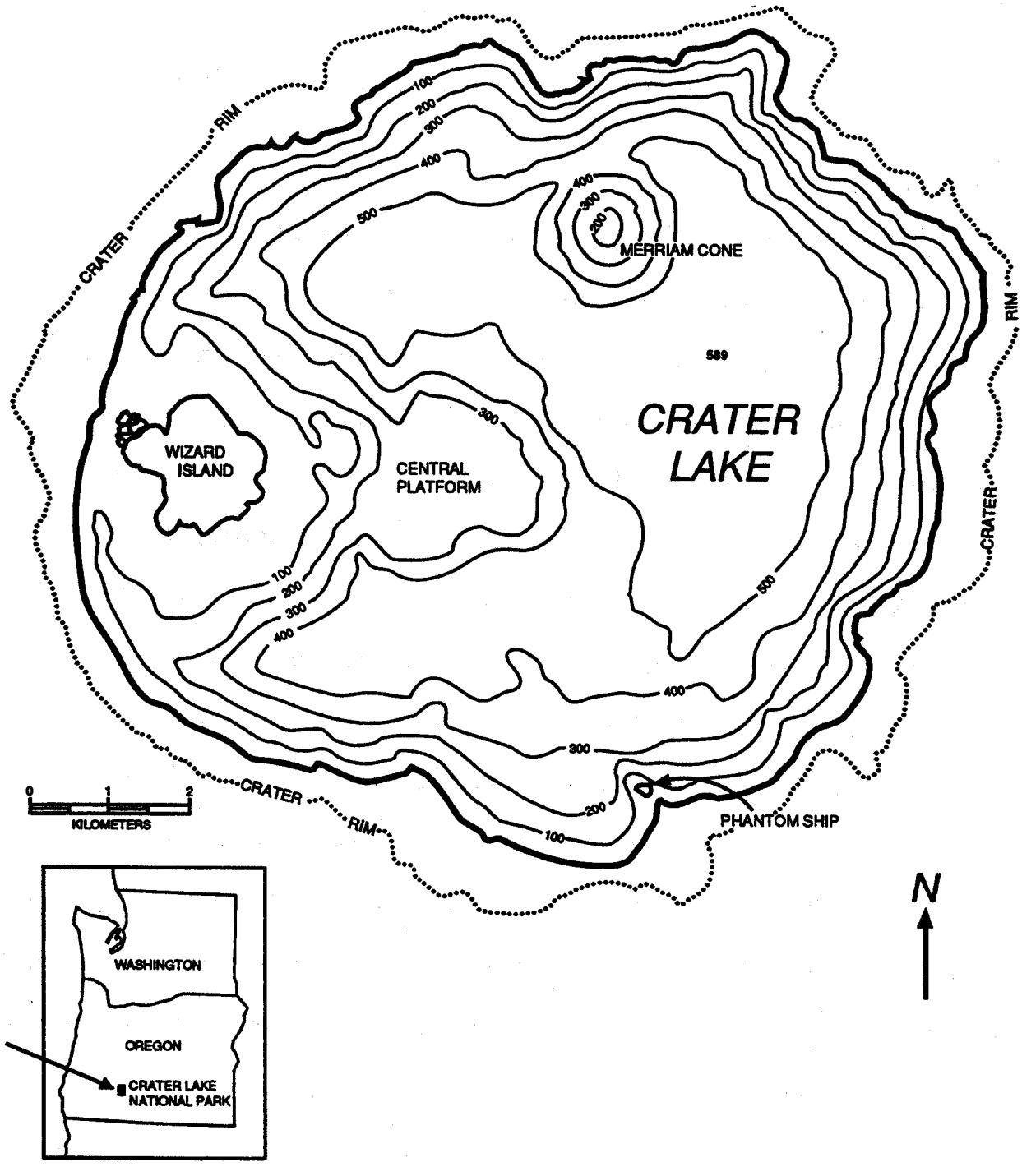


Figure 1. Bathymetry and important morphological features of Crater Lake (after Barber and Nelson 1990)

were collected to a depth of 300 m from the Boston Whaler using a hand-cranked winch with a meter wheel. The pontoon boat was covered by a canopy and equipped with a gasoline-powered winch. A meter wheel was used on the pontoon boat to determine sampling depths from 0 to 550 m. Both boats were powered by gasoline outboard engines.

Limnological sampling of the lake prior to 1986 was restricted to summer months because there were no facilities for boat storage in the caldera during other seasons of the year. Research vessels were flown to the lake by helicopter or winched down the side of the caldera in the early summer and removed from the lake by helicopter in the fall. In 1985 a boat house, with storage space and living quarters, was constructed on Wizard Island. Research vessels were brought in and out of the boat house on a dolly-rail system. After 1985, sampling during the spring and winter months was possible. However, research personnel, sampling equipment, and support equipment still required helicopter assistance or winching to get to and from the lake.

Dissolved oxygen analyses, water filtering, and processing of biological samples were conducted in a laboratory at Crater Lake National Park. For information about other analyses of the water samples, see the section - Procedures of the Cooperative Chemical Analytical Laboratory. From 1982 to 1986 the processing and analyses in the park were done in a small make-shift laboratory. In 1987 a room in a park building was converted into a chemistry laboratory and equipped with acid-proof bench tops, storage cabinets, and a fume hood. Analytical procedures used at the park's chemistry laboratory were outlined in a handbook of standard operating procedures for the Crater Lake program (Salinas 1992).

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Quality Assurance Program of the Cooperative Chemical Analytical Laboratory

Cameron Jones

The Oregon State University Pacific Northwest Cooperative Chemical Analytical Laboratory (CCAL) handled the analysis of the water samples collected from Crater Lake during the 10-year study except for a limited number of analyses performed at Crater Lake National Park (see Study Area and Facilities section). The CCAL has a rigorous quality assurance (QA) program to monitor work conducted in the laboratory. The seven elements of the program are as follows:

1. Provide sample information concerning arrival date and analysis date.
2. Provide sample data with calibration summaries in a data report.
3. Perform and monitor QA procedures and criteria for each analysis method:
    a. Derive standard curves.
    b. Monitor precision/accuracy within each analysis batch.
    c. Derive level of detection for each analysis.
    d. Compare new standard solutions to old standard solutions.
4. Compare duplicate analyses within analytical batches.
5. Analyze duplicate samples submitted by investigators.
6. Compare current results with historical data.
7. Provide a report delineating precision and accuracy of standards, blanks, and duplicates two to three times per year.

Detailed descriptions of the procedures carried out under this QA program follow.

Reporting Sample Arrival and Analysis Dates

A log sheet documenting arrival date and correlating investigator sample identification with laboratory sample numbers accompanies each data report. Analysis run dates for each analysis are provided on sample data reports in the calibration summary section.

Sample Data Reports

The data report contains calibration summaries for all samples analyzed. This includes the standard concentrations and response (i.e., absorbance and chart units) used to create the standard curve for that analytical batch. For TKN, TP, OP, NO_3-N, NH_3-N, and Si, (see Appendix 1 for definition of acronyms) linear regression information from the standard curve is listed. This includes r^2, intercept, and slope. Instrument response for the reagent blank is listed. For TKN the average digest blank is listed. Individual laboratory numbers for samples analyzed with that standard curve are listed.

QA Procedures Used to Evaluate Sample Data

Derivation of Standard Curves

For each analysis, a standard curve is generated using standard solutions that have been diluted from a precisely prepared stock solution of known concentration. Anhydrous chemicals used for preparation of stock solutions are oven dried for at least 24 hours and then stored in a desiccator immediately prior to use. Hydrated chemicals are dried in a desiccator for at least 48 hours immediately prior to use. All chemicals used to prepare stock solutions are weighed to a tenth of a mg. Dilutions are prepared using class "A" volumetric glassware or are measured by weight to the nearest mg. Dilutions are made to a concentration level appropriate for the range of samples

regularly analyzed by the laboratory and that give a reasonable response from the instrument detector. A reasonable response is one that is well above any signal or noise generated by a reagent blank solution. Samples are then analyzed and compared to the standard curve, and results calculated from the comparison. For most analyses, at least three concentration levels plus a reagent blank are used to generate a standard curve. The exceptions are conductivity (1 standard + deionized water (DIW)) and alkalinity (2 standards + 2 DIW).

Standard solutions are analyzed with each analysis batch and the results are examined and evaluated for linearity. Each analysis has specific criteria for evaluation that are explained below. Additionally, the detection response (i.e., absorbance) is examined for comparability with previous standards of the same concentration. Any significant deviation from historical values for these standards is cause for close examination of the entire analysis.

For some analyses (TKN, TP, and OP), a computer calculated "r" value that relates degree of correlation is automatically generated from the analytical instrument giving the analyst precise information regarding linearity. The lab strives for r^2 values of 1.000 for each analysis, and r^2 values are expected to meet or exceed 0.9990, but r^2 values down to 0.9900 are acceptable, especially if no repeat analysis is feasible. If non-linearity is in evidence (<0.9900 r^2 value), or poor linearity is in evidence (<0.9990 r^2 value), the standard curve is examined for procedural errors (e.g., incorrectly entered standard information, reagents not prepared correctly, or reagents not added). Procedural errors, if found, are corrected and the standard curve is reevaluated. If non-linearity is still in evidence, the samples for that run are designated questionable and are repeated with a new standard set if sufficient sample volume remains. Sample

results are not reported from questionable standard sets that have had valid repeat analysis.

- If insufficient sample remains to repeat the analysis, the data are carefully scrutinized and evaluated on other factors within the analysis run for validity (e.g., duplicate samples, duplicate analyses, digest blanks, digest standards, quality control check sample, and recalculation of standard curve after eliminating outlier standard values). These results, if acceptable, are reported to the investigator as valid, but with a hand-written note on the data report alerting investigators to the possibly anomalous values. If the results do not meet the secondary criteria for non-standard validity, then the data are reported as questionable on the data report. This is denoted by a lower-case letter "q" next to the questionable value. No values are reported in extreme cases where meaningful data has not been produced.

In instances where the analysis is not affected by time constraints (digest time, color development), the standards are again prepared before any samples are analyzed until a linear calibration is achieved.

Other analyses (NO^3-N, NH^3-N, and Si) are evaluated visually for linearity during sample analysis. Once the analysis is complete, a hand calculated regression curve using the standard solution data is evaluated for linearity using the criteria stated above. When the data has met all criteria, it is digitized and entered into the laboratory data management program. This program produces a regression equation that is evaluated using the criteria from above and is then compared to the hand calculated regression equation. Anomalies between the hand calculated and data program regression equations are resolved before the data report is sent to the investigator.

When the standard curve has an intercept other than zero, and sample results fall within the range between zero and the first standard, sample values are calculated using a two-point regression using the first standard and zero. This is dependent upon the reagent blank representing zero concentration, or the reagent blank being subtracted from the raw sample result before calculation. Analyses producing data values derived from a two-point regression equation are noted in the calibration summary on the data report. Any single data value falling between zero and the detection level but having a detectable response is listed on the final data report with an asterisk denoting that the value is below the level of detection.

Each analysis has a standard operating procedure for generating a standard curve that is documented in the CCAL Chemical Analysis Procedure Manual. The following are brief descriptions of solutions analyzed to produce standard curves for these procedures and the instrumentation used for analysis.

Alkalinity. Two dilute standard solutions per analysis batch are analyzed to verify titrant concentration and proper operating conditions of the auto-titrator. Two deionized water (DIW) blanks are analyzed for use in calculating titrant concentration and to evaluate precision. The standard stock solution is 0.02 N sodium carbonate. Instrumentation is a Radiometer type TTT 1c auto-titrator using a glass pH electrode with a calomel reference electrode and a temperature compensator electrode. Samples are titrated to pH 4.5.

Ammonia-Nitrogen. Concentrations of 0.050 mg/l, 0.100 mg/l, and 0.200 mg/l are used. Standard stock solution is 1000 mg/l NH_3-N made from ammonium chloride. Instrumentation is a Technicon Auto-Analyzer II.

Nitrate-Nitrogen. Concentrations of 0.025 mg/l, 0.050 mg/l, and 0.100 mg/l are used. Standard stock solution is 1000 mg/l NO_3-N made from potassium nitrate. Instrumentation is a Technicon Auto-Analyzer II.

Ortho-Phosphate. Concentrations of 0.050 mg/l, 0.100 mg/l, and 0.200 mg/l, and a reagent blank are used. The spectrophotometer provides calibration slope, intercept, and correlation information for immediate evaluation before preceding with sample analysis. For samples high in phosphate, a 0.300 mg/l standard is also analyzed. Standard stock solution is 50 mg/l PO_4-P made from monobasic potassium phosphate. Instrumentation since March 1989 is a Milton-Roy 601 spectrophotometer with a 10 cm path length. Analysis occurs at 880 nm. Instrumentation prior to March 1989 is a Klett Summerson colorimeter, model 900-3 with a 1.5 cm path length cell. Analysis occurred at 660 nm with a red filter.

pH. Three buffer solutions of 7.0, 4.0, and 10.0 are used. Instrumentation is a Radiometer type TTT 1c auto-titrator pH meter using a glass pH electrode with a calomel reference electrode and a temperature compensator electrode.

Silica. Concentrations of 5.0 mg/l, 15.0 mg/l, 25.0 mg/l as SiO_2 are used. Data are converted to Si by calculation. Standard stock solution is a purchased prepared 1000 mg/l SiO_2. Instrumentation is a Technicon Auto-Analyzer II.

Specific Conductance. A standard solution of 0.01 N potassium chloride is analyzed at the beginning of each analysis batch. A DIW blank is also analyzed. Instrumentation is a YSI model 31 conductivity bridge.

Total Kjeldahl Nitrogen. Concentrations of 0.20 mg/l, 0.40 mg/l, 0.80 mg/l, 1.00 mg/l, 1.50 mg/l, and a reagent blank are used. The spectrophotometer provides calibration slope, intercept, and correlation information for immediate evaluation before

preceding with sample analysis. For samples high in TKN, a 2.00 mg/l standard is also analyzed. Two digested reagent blanks and at least one digested standard solution are included with each analysis batch. Digest standards are ammonium chloride solutions of the same concentration range as those used to generate the standard curve. A single concentration is analyzed (one per rack) on all 12 burner/distillation positions before rotating to the next concentration range. This assures that each burner/distillation position is checked at each concentration level. Standard stock solution is 1000 mg/l NH_3-N made from ammonium chloride. Recovery for ammonium chloride digest standards must be 85% or better to validate the analysis. Lower recoveries indicate questionable data. Analysis batches producing low-recovery data may still have to be used due to the large sample volume requirement for TKN (500 mls). Organic nitrogen digestion efficiency is checked with a 50 mg/l cystine standard solution. Recovery must be at least 85%, and for the cystine standard, recoveries are expected to exceed 90%. Certified National Bureau of Standards reference material cystine is used. Instrumentation since December 1986 is a Milton-Roy 601 spectrophotometer with a 2.54-cm path-length cell. Analysis occurs at 425 nm. Instrumentation prior to December 1986 is a Fisher Electro spectrophotometer, model 81 with a 2.54-cm path-length cell. Analysis occurred at 425 nm with a blue filter.

Total Phosphorous. Concentrations of 0.050 mg/l, 0.100 mg/l, 0.200 mg/l and a blank are analyzed. The spectrophotometer provides calibration slope, intercept, and correlation information for immediate evaluation before preceding with sample analysis. All standards are digested with the sample set. Standard stock solution is 50 mg/l PO_4-P made from monobasic potassium phosphate. Instrumentation since April 1989 is a Milton-Roy 601 spectrophotometer with a 10 cm path length. Analysis occurs at 880 nm.

Instrumentation prior to April 1989 is a Klett Summerson colorimeter, model 900-3 with a 1.5 cm path length cell. Analysis occurred at 660 nm with a red filter.

Precision and Accuracy of Analyses

Accuracy is evaluated with each analysis batch by comparing instrument response measurements of the standard solutions used for that run with historical values generated by standard solutions for that analysis. With large-batch sample sets (>20 samples), standard solutions are analyzed within the run at regular intervals to check for continued validity of results. These check standards are evaluated as they are analyzed, and the continuation of the analysis of further samples is dependent upon good correlation (+/-10%) of the theoretical value of the check standard with the measured response. If response is low, then action is taken to uncover the cause and correct it before analyzing samples. Sample results from low-response analysis batches are inspected for validity and are repeated when necessary if there is sufficient sample remaining. Analyses using check standards are: NO_3-N, NH_3-N, and Si.

An overall assessment of analytical accuracy is made by analyzing blind QA samples from the U.S. Geological Survey Standard Reference Water Survey Program twice a year. Depending upon the selection of check samples available, one, two, three, or four samples are analyzed during each check period. Concentration ranges vary from dilute (precipitation) to relatively high concentration samples (2500uS/cm). These blind standards allow the laboratory to compare results with other participating laboratories to gauge analytic accuracy. The U.S. Geological Survey reports the results to the laboratory as variation from the mean of all laboratories analyzing that sample, with extreme outlier values disregarded in calculating a mean value for any particular parameter. These

check samples test for the following nutrients and/or physical properties: total phosphorous, ortho-phosphate, ammonia-nitrogen, nitrate + nitrite-nitrogen, organic nitrogen (Kjeldahl), silica, pH, alkalinity, and specific conductance.

Once a year EPA Water Pollution Quality Control Samples are analyzed. These standards come as sealed ampuls that are diluted according to directions. The analyzed values can then be checked against the nominal values supplied with the check standard. The following nutrients are analyzed using this standard: total Kjeldahl nitrogen, ortho-phosphate, total phosphorous, nitrate, and ammonia. Between the two check standard programs all analyses are validated at least once a year by outside programs.

Precision is evaluated for each analysis batch by analyzing duplicate samples and comparing the raw and calculated values generated from the analysis. Each analysis has duplicate samples set-up as a precision check (with the exception of TKN where digest blanks are duplicated with each run). Duplicate samples are chosen randomly. If duplicate analyses do not produce acceptable results within the precision limits established for that particular analysis (Table 1), the sample is repeated for further comparison. In such instances the entire analysis batch is examined for validity and possible error sources (e.g., instrument malfunction, analyst error, inhomogeneous sample, unfiltered analyses, or contaminated glassware).

If conforming results are produced by additional in-batch replication, then the entire analysis batch is evaluated for obvious outlier sample results. Samples with outlier results are repeated when sufficient sample remains. All other sample data in such sets is closely examined and evaluated for validity.

If anomalous duplicate data are present and replication produces additional nonconforming data, then the entire analysis batch is repeated when sufficient sample

Table 1. Analytical detection levels and precision limits of the Cooperative Chemical Analytical Laboratory.

Analysis	Level of Detection	Precision
Alkalinity	0.2 mg/1	+/- 0.02 mg/1[1]
Ammonia-nitrogen*	0.010 mg/1	+/- 0.002 mg/1[4]
Chloride	0.10 mg/1[c]	+/- 0.06 mg/1 @ 0.25 mg/1 +/- 0.03 mg/1 @ 5.00 mg/1
	0.02 mg/1[b]	not available
	0.20 mg/1[a]	not available
Nitrate-nitrogen	0.001 mg/1	+/- 0.001 mg/1[4]
Phosphate, ortho	0.001 mg/1[e]	+/- 0.001 mg/1[6]
	0.002 mg/1[d]	+/- 0.001 mg/1[6]
pH	0-14 pH units	+/- 0.1 pH unit[2]
Silica	0.20 mg/1	+/- 0.05 mg/1[4]
Specific conductance	0.4 us/cm	+/- 2%[3]
Sulfate	0.10 mg/1[c]	+/- 0.005 mg/1 @ 0.10 mg/1 +/- 0.2 mg/1 @ 1.00 mg/1
	0.01 mg/1[b]	not available
	0.20 mg/1[a]	not available
Nitrogen, total	0.010 mg/1	+/- 0.006 mg/1[5]
Kjeldahl	0.010 mg/1	+/- 0.007 mg/1[5]
Total phosphorus	0.001 mg/1[g]	+/- 0.002 mg/1[6]
	0.004 mg/1[f]	+/- 0.002 mg/1[6]

[1]Evaluation of titration precision and accuracy by comparison with Gran titration results.
[2]Limitation of analog instrument currently in use.
[3]Limitation of instrument scale on instrument currently in use.
[4]Method specified detection level as yet unconfirmed, but evaluated as reasonable by monitoring sample response at this concentration level.
[5]Estimate based on low concentration standards analyzed on a continuing basis.
[6]Evaluated by low concentration detection level analysis.

[a] $\leq$ sample number 1072 (except sample number 1052).
[b] sample numbers 1052, 1073 - 1080.
[c] $\geq$ sample number 1083.
[d] 1983 - February 1989
[e] March 1989 - 1991
[f] 1983 - March 1989
[g] April 1989 - 1991

* For ammonia-nitrogen, the laboratory has been able to produce data with the same precision as stated above at a DL of 0.005 mg/l.

remains. Repeating the entire analysis batch occurs only if there is more than one questionable circumstance associated with that particular analysis batch. Samples with insufficient volume for repeat analysis are examined and reported above in the section Derivation of Standard Curves.

For some analyses, standard solutions that are analyzed as an accuracy check are also evaluated for repeatability to establish within-batch precision. Precision has been evaluated at low concentrations for those analyses for which detection levels have been determined.

Whenever the laboratory changes analytical methods and/or instrumentation, investigators will be informed of the resulting new precision and accuracy for that analysis. A hand-written note on data reports will alert investigators to changes in methods/instrumentation and a formal notification will accompany the data. Comparability between methods is evaluated by analyzing standard solutions and quantifying any differences.

Quality control check standards (QCCS) are used to monitor batch to batch accuracy and precision. QCCS are selected and prepared to be within the actual concentration range of submitted samples. A large volume of naturally occurring surface water is collected and brought to the laboratory. It is filtered through a GF/F filter (0.7 um retention) and allowed to stabilize for a period of time ranging from 1 to 20 weeks. The sample is selected for specific target analyses dependent on expected nutrient concentration. Water from Crater Lake, Oregon is used as a QCCS for all phosphorous analyses. Water from Mack Creek, a stream located in the H.J. Andrews Experimental Forest in western Oregon, is used for Kjeldahl-nitrogen analyses. After allowing a sample to stabilize, the QCCS is analyzed repeatedly to develop a mean concentration

value and standard error range. For phosphorous QCCS, a minimum of 30 replicates are analyzed to characterize the water. For Kjeldahl-nitrogen QCCS, a minimum of 16 replicates are analyzed to characterize the water. All accuracy and precision criteria are applied to the QCCS characterization analyses. Error ranges of plus or minus one, two and three standard deviations are developed from a statistical analysis of the replicate analyses. QCCS characterization data must conform with expected QA population distribution before it is accepted (68.3% ± 1 SD, 95.5% ± 2SD, and 99.7% ± 3SD). Once a QCCS has been characterized and is accepted, it is analyzed with each batch of samples for the phosphorous analyses. Due to the time and labor intensive nature of the Kjeldahl nitrogen analysis, the QCCS is analyzed once for every six batches of analyses. QCCS data from individual analysis batches must fall within the expected concentration range developed from the characterization analyses. If QCCS data do not fall within the expected concentration range, then the entire analysis is examined for analytical problems.

QCCS are closely monitored for degradation. When QCCS degradation becomes evident, a new QCCS is characterized and established before sufficient degradation occurs to the previous QCCS that would produce results varying greater than the ± 3SD error range initially established.

QCCS have been attempted to be developed for the ammonia-nitrogen and nitrate-nitrogen analyses but have proved to degrade too quickly to be of any use as a QA check. Eventually the laboratory will either develop artificial QCCS for these analyses or will purchase QCCS for these analyses from an outside source.

Level of Detection

Detection level (DL) of analysis has been determined methodologically for ortho-phosphate and total phosphorous. For these analyses, low-concentration standard solutions were analyzed along with reagent blanks to determine what concentration level produces a quantifiable instrument response. A detection level is set at the concentration level that produces a repeatable response with a demonstrated degree of accuracy. The degree of accuracy at low concentration levels can vary widely on a percent recovery basis, and precision must be very good at those levels before qualifying as a legitimate detection level. Once a detection level has been determined, no regular detection level standard is analyzed on a batch by batch basis. Instead, operating conditions are monitored closely in conjunction with the range of samples being analyzed.

For the remainder of analyses, the detection levels have been assigned as those specified by the standard method from which the analysis is derived. Assigned DL's are evaluated for each analysis by examining instrument response from sample data that approach the DL. For all analyses, the proscribed DL has been met or improved.

Comparison of Standard Solutions

Whenever a new stock standard solution (the solution from which further serial dilutions are prepared) is prepared, it is compared to the old stock solution before the new stock solution is used for calibration standards in an analysis. Serial dilutions of the new solution are compared directly to serial dilutions of the old solution. There must be good correlation (>95%) between standards before the new calibration standards are used in analysis. The only exception to this comparison method is for stock solutions

that tend to degrade over time. For this situation a comparison is still made, with a greater concentration value expected for the new stock standards in comparison to the old. Low concentration standard solutions of ammonia are most prone to this tendency. Great care is taken to make stock solutions and calibration standards for ammonia well before any degradation occurs, but experience has shown that some degradation occurs regardless. The above procedure also checks comparability for intermediate working solutions (solutions made on an as needed basis from the stock solution that facilitate the preparation of calibration standards). Calibration standards are subjected to comparison as part of either the stock or working solution comparisons.

New stock solutions are prepared at least once a year regardless of the continued validity of calibration standards made from the solution. Comparisons are also made of prepared stock solutions purchased from chemical suppliers. Reagent preparation is documented by date, technician preparing the solution, and chemical lot number for all analyses. Preparation date appears both on the reagent bottle and on a reagent tracking chart. Notation is made on data sheets whenever new reagent solutions are used.

Duplicate Analyses

Duplicate laboratory analyses are reported on the data reports and are designated by a "D" following the laboratory sample number. These duplicates are used to monitor precision on a within-batch basis. No statistical information regarding duplicate laboratory analyses is currently provided in the final data report. Duplicate values are checked for acceptable correlation before data is sent to the investigator. If duplicate correlation does not conform to expected precision levels, the data are reported according to the guidelines outlined in Derivation of Standard Curves.

Field Duplicates

Statistical information concerning field duplicate sample results (co-submitted split samples) is not provided. The laboratory will perform analyses on field duplicate samples -- termed analytical duplicates -- at no additional charge (1 duplicate for every 10 samples submitted). To receive the blind duplicate sample analyses at no charge investigators must identify the blind duplicates after receiving the data report. Blind duplicates cannot be positively identified prior to data reporting thus preventing any statistical comparison. Known duplicate samples are examined for precision as part of the data quality check before data are sent to the investigator.

The laboratory encourages all investigators to evaluate collection variation by submitting field blanks and field replicate samples for analysis. However, information of this nature goes beyond assessing conditions controllable by the laboratory because sample splitting is essentially limited by field procedures.

Comparison of Current Data with Historic Data

Comparison of current laboratory results to results of historically analyzed samples from the same site is done on a rudimentary level. If the laboratory has analyzed enough samples to give an indication of expected results, the current data are evaluated in a broad sense by confirming that the samples fall within the same general concentration range. However, the validity of analysis results are based solely on analytical criteria for calibration, accuracy, and precision and not on producing a result that fits the study plan or conforms to historical norms. Historical comparisons of this type can lead to a bias of dynamic sample monitoring.

QA Report

The laboratory compiles all data from individual analysis batches to statistically evaluate the data. The data have been gathered and filed since 1983. The compiled information includes: reagent blank values, calibration standard values, standard curve information, check standard values, digest standard values, and digest blank values. These data have been monitored and evaluated on a batch-by-batch basis as they have been collected. This has lead to a generalized overview for expected ranges and deviations for each analytical parameter. No summary report has been issued or compiled to date.

Appendix 1. Definition of acronyms and abbreviations used in this section.

CCAL	-	Cooperative Chemical Analytical Laboratory
DIW	-	Deionized Water
DL	-	Detection Level
EPA	-	U.S. Environmental Protection Agency
mg/l	-	Milligrams per Liter
NH_3-N	-	Ammonia Nitrogen
NO_3-N	-	Nitrate + Nitrite Nitrogen
OP	-	Ortho Phosphate
OSU	-	Oregon State University
PNW	-	USDA Forest Service Pacific Northwest Forestry Science Laboratory
PO_4-P	-	Phosphate Phosphorous
QA	-	Quality Assurance
QC	-	Quality Control
QCCS	-	Quality Control Check Sample
Si	-	Silica
TKN	-	Total Kjeldahl Nitrogen
TP	-	Total Phosphorous
USGS	-	U.S. Geological Survey

Appendix 2. Analytical methodology of the Cooperative Chemical Analytical Laboratory.

Analysis	*Method # with Specifications and Modifications
Alkalinity	403, procedure 4c, titrate to pH 4.5. Modifications: Use 0.02N N $a_2CO_3$and 0.02N H_2SO_4
Ammonia	417F.
Chloride	Technicon industrial method 99-70W.[a] 4110B.[b]
Specific Conductance	205; Wheatstone bridge.
Metals-Trace	USEPA 200.7; Induction coupled plasma emission spectroscopy.
Nitrate	418F. Technicon industrial method 100-70W; different formulations for color and ammonium chloride reagents.
Nitrogen, Total Kjeldahl	Kjeldahl digestion: H_2SO_4, $CuSO_4$/KCl, Nessler finish.
pH	423; Calomel reference electrode, glass pH electrode, temperature compensator.
Phosphate-Ortho	424F. Modifications: Ascorbic acid reagent 2g/100 ml.
Phosphorous-Total	424C, 424F. Modifications: microwave digestion 60 minutes, 50 ml analysis volume, ascorbic acid reagent 2g/100 ml.
Silica	Technicon industrial method 105-71W/B.
Sulfate	Technicon industrial method 105-72W.[a] 4110B.[b]

* Method numbers refer to Standard Methods For the Examination of Water and Wastewater 15th Edition, 1980, except sulfate and chloride Standard Methods For the Examination of Water and Wastewater 17th Edition, 1989.

[a] $\leq$ sample number 1072 (except sample number 1052)
[b] sample numbers 1052, $\geq$ 1073

Appendix 3. Analytical Instrumentation used by the Cooperative Chemical Analytical Laboratory.

Analysis	Instrumentation
Alkalinity	Radiometer type TTT 1c auto-titrator with glass pH electrode, calomel reference electrode and temperature compensator electrode.
Ammonia	Technicon Auto-Analyzer II.
Chloride	Technicon Auto-Analyzer II.[a] Dionex 4000i Ion Chromatograph.[b]
Specific Conductance	YSI model 31 conductivity bridge.
Metals-Trace	Bausch and Lomb Model 3580 ICPAES
Nitrate	Technicon Auto-Analyzer II.
Nitrogen, Total Kjeldahl	Milton-Roy 601 spectrophotometer with 2.54-cm-path-length cell. Analyze at 425 nm.[d] Fisher Electro spectrophotometer, model 81 with 2.54-cm-path-length cell. Analyze at 425 nm with a blue filter.[c]
pH	Radiometer type TTT 1c auto-titrator with glass pH electrode, calomel reference electrode and temperature compensator electrode.
Phosphate-Ortho	Milton-Roy 601 spectrophotometer with 10-cm-path length.[f] Klett Summerson colorimeter, model 900-3 with 1.5-cm-path-length cell. Analyze at 660 nm with a red filter.[e]
Phosphorous-Total	Milton-Roy 601 spectrophotometer with 10-cm-path length.[h] Klett Summerson colorimeter, model 900-3 with 1.5-cm-path-length cell. Analyze at 660 nm with a red filter.[g]
Silica	Technicon Auto-Analyzer II.
Sulfate	Technicon Auto-Analyzer II.[a] Dionex 4000i Ion Chromatograph.[b]

[a] $\leq$ sample number 1072 (except sample number 1052)
[b] sample numbers 1052, $\geq$ 1073
[c] 1983 - November 1986
[d] December 1986 - 1991
[e] 1983 - February 1989
[f] March 1989 - 1991
[g] 1983 - March 1989
[h] April 1989 - 1991

Climate Variability at Crater Lake National Park and its Effect on Water Level

Kelly Redmond

Knowledge of climate variations in Crater Lake National Park is essential for understanding the behavior of the natural physical and biological systems in the park. Such knowledge is also needed for practical applications in planning and maintaining facilities and services for the visiting public. Studies of climate and effects of climate on lake levels were initially motivated by a desire to explain the substantial changes in lake level over this century (Fig. 1). The most notable feature of the record of lake levels was a rapid decrease in lake elevation in the 1920s, which culminated in a decade (1931-1942) of low water levels 4-5 m below those recorded before or since. An understanding of these and other lake-level variations in turn required knowledge of variations in components of the lake's water budget.

The lake's water budget was first considered by Diller (1902). Harding (MS, 1953) later re-examined these figures. Phillips (1968) investigated the hydrology of Crater Lake and two other lakes in Oregon. Simpson (1970) performed another analysis of the water budget of Crater Lake to understand the mixing of tritium from atmospheric testing to depths in the lake. Nathansen (1992) investigated aspects of the water budget for the purpose of interpreting data pertinent to fluxes of dissolved constituents in the lake. The objectives of the present study were to:

1) describe important features of the long-term climate of Crater Lake, and assemble this information for use by other researchers,

2) describe variations of principal climate elements about their long-term mean values,

3) explain the observed variation in lake level during this century.

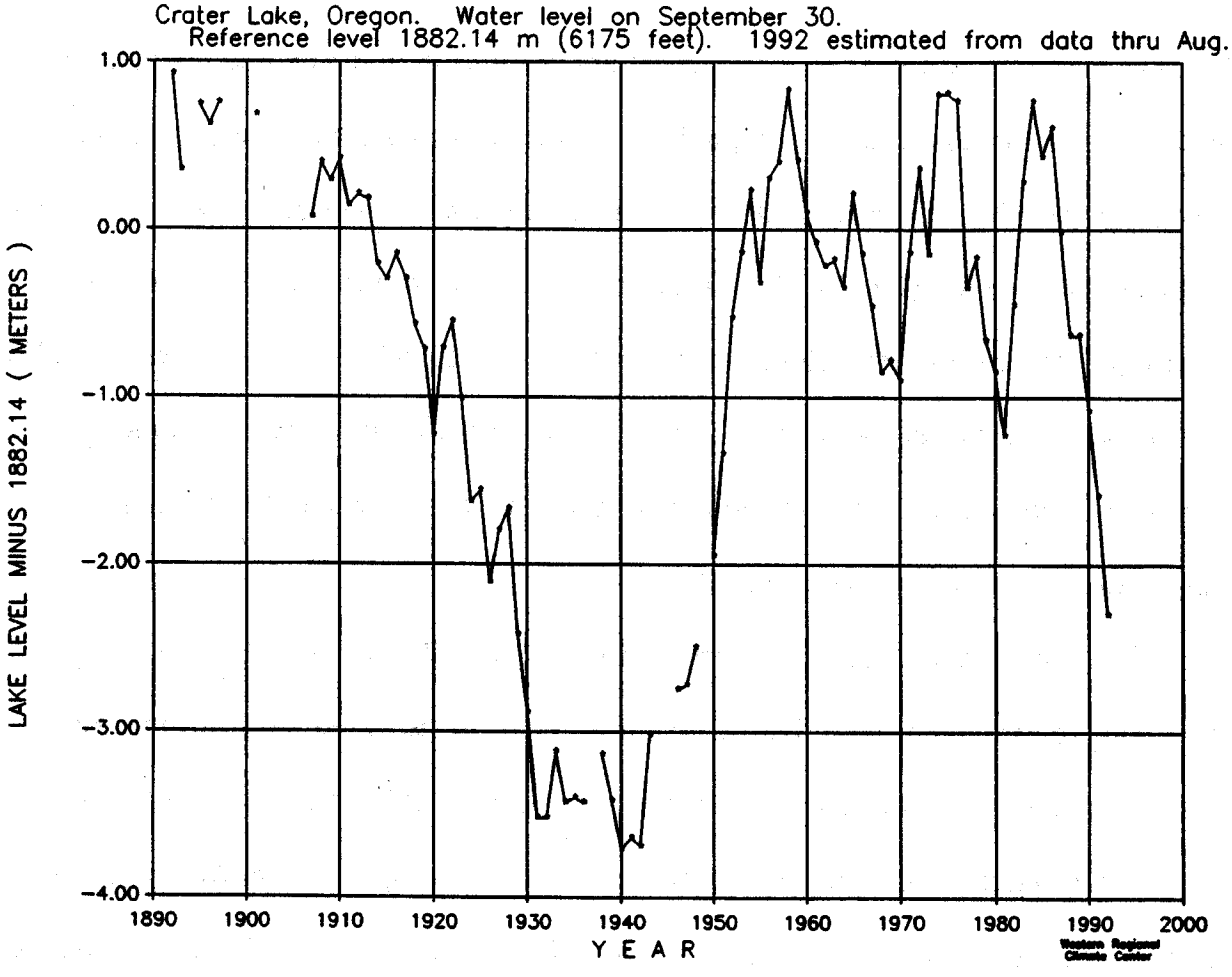


Figure 1. Observed elevation of the lake surface this century, expressed as a departure from the nominal elevation of 1,882.14 m (6,175 ft). The 1992 value is based on an observation on Aug. 28 plus normal decline to Sept. 30.

4) develop estimates of annual values of the principal elements of the water budget of Crater Lake,

5) begin the development of methods to model daily variations in the level of Crater Lake, and

6) describe the relation of climate in Crater Lake National Park to global scale climate, particularly the El Niño/Southern Oscillation (ENSO).

The Physical Setting

Several aspects of the physical setting (see Study Area and Facilities section) are relevant to the water budget of the lake. The water surface, itself about 300 m below the caldera rim, has a mean elevation of 1,882 m, which is considerably above the surrounding landscape. The mean annual temperature at the weather station at park headquarters (1,973 m) is about 3°C. Thus, the water in the lake is quite cold but not as cold as the air. Except for a brief period in mid-summer, the mean daily air temperature is lower than the water temperature (Redmond 1990). Prevailing south to west winds during winter months are forced to rise and deposit heavy precipitation near the Cascade crest. Crater Lake straddles a sharp east-west gradient in annual precipitation. The southwest rim receives approximately twice the precipitation (about 200 cm) that falls on the northeast rim, (about 100 cm), although these two locations are only 10 km apart. The lake occupies about 78 percent of its own drainage basin, which has steep, nearly cliff-like sides. A substantial part of the water budget, therefore, consists of vertical fluxes directly onto or away from the lake surface. Most of the copious annual precipitation falls in winter as snow, and in the small part of the basin that is land surface, snow melt does not occur until spring or early summer. This delayed runoff keeps the lake high well into early summer even when precipitation is low (Redmond

1990). In mid- to late summer the level of the lake begins to fall because diminishing snowmelt and ground water runoff cannot compensate for lack of precipitation. On average the lake drops about 0.5 m during summer. Water level begins to rise in late October with the onset of the next precipitation season. Thus, the lake appears to evaporate at the highest rate in summer. However, winter evaporation may be substantial but hidden by effects of abundant precipitation.

Methods

The general approach of this study was to assemble and use historical climate information from standard sources, supplemented by additional available data. Much of the historical climate data were maintained as part of the archives of the Oregon Office of State Climatologist. These data were available at the Western Regional Climate Center of the Desert Research Institute in Reno.

Statistical relations were developed between data sets expected to possess physical linkages. As much advantage as possible was made of the availability of relatively long, systematic and regular observations. For example, through the end of 1991, 22,280 daily measurements of precipitation had been recorded at park headquarters. For other portions of the work, stratified samples were utilized (such as for studies of daily evaporation and the relation to ENSO). Procedures were developed to adjust non-concurrent measurements to either standard time intervals or dates.

Climate measurements have been made at a consistent location at park headquarters since 1931. This site is about 2 km to the southwest of Rim Village and 200 m below the village. These readings include daily maximum and minimum temperature, precipitation, snowfall, and snow depth. Lake elevation has been measured

daily with a resolution of 0.01 foot (3 mm) at a USGS gaging station at Cleetwood Cove since 1961. These readings were reasonably continuous with occasional gaps of a few months. Seasonal precipitation totals were measured using a storage gage on the rim above Cleetwood Cove since October 1964. Storage gages were placed on Wizard Island in 1987 and on the southwest rim near Rim Village in 1986.

In the summer of 1991, a floating weather station was anchored at Station 13, south of Cleetwood Cove. This device measures hourly temperature, humidity, wind speed and direction and near-surface water temperature. A chain of thermistors below the water surface measures changes in the vertical water temperature profile. Another station was installed on the rim a few hundred meters northwest of Rim Village, also with the capability to measure temperature, humidity, and wind at hourly intervals. Data from neither platform were available for this report, but in the future these will be valuable sources of information.

Results and Discussion

Climate

The park experienced a wide range of climatic conditions during the course of the 10-year study. Successive wet winters occurred in the early 1980s, followed by a succession of very dry winters in the later 1980s and early 1990s (Fig. 2 and Appendix I). Despite such extreme variability, precipitation for the decade was about average for the period 1931-1990. At this writing, the Crater Lake region is experiencing one of the most significant droughts in its recorded history. The sum of the past three water years (October-September) is the lowest three-year sum since records began at Park Headquarters in 1931.

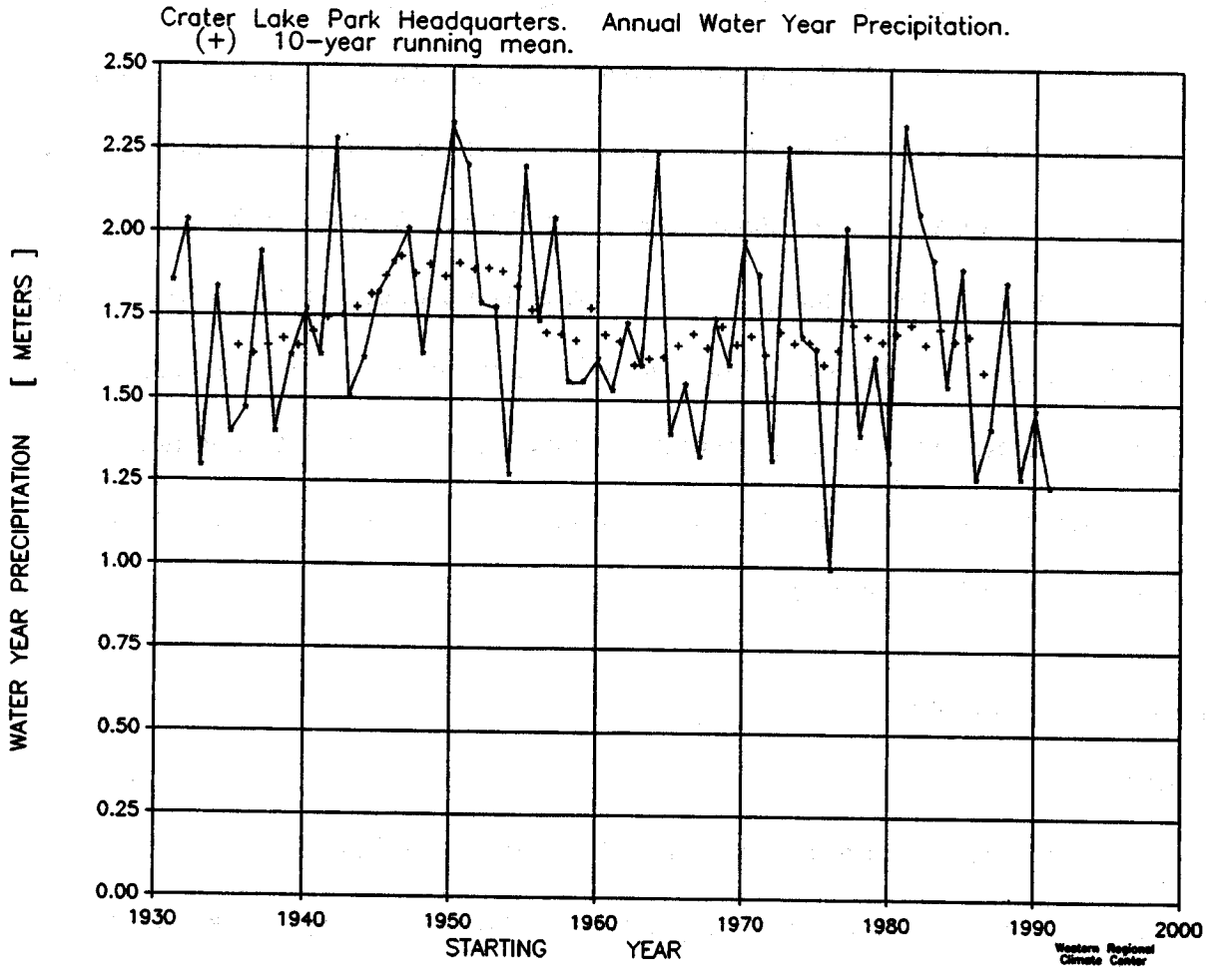


Figure 2. Annual precipitation for the water year (October through September) at Park Headquarters, plotted in the starting year, expressed in meters. Some values during 1943-46 are estimated. (+) is a 10-year running mean.

Data from the park weather station has been collected at 8 am since January 1, 1982. Observation time affects the reported mean temperature. Cool years in the early 1980's have given way to warmer years. The water year just ended, 1991-1992, was by far the warmest in recent decades (Fig. 3 and Appendix I). Through August 1992, Crater Lake has experienced 14 consecutive warmer-than-average months. Because of its high altitude and similarity to free-air conditions, there is no particular reason for temperature fluctuations at Crater Lake to mimic those at lower elevations to the west or east. Indeed, the correlation between annual mean air temperature at Medford and Sexton Summit (a good analog to Crater Lake) over several decades is only 0.57. Data from the Crater Lake station shows no sign of long-term warming.

Water Budget Elements

Four principal factors affect the water budget. The lake gains water from precipitation and from immediate and delayed runoff from the caldera sides. The lake loses water upward by evaporation and downward by seepage from the bottom (Fig. 4) In an interesting departure from the usual situation in hydrology, the easiest of these four quantities to measure appears to be seepage.

The surface of Crater Lake almost never freezes entirely across. The surface was solidly frozen in 1949, and then not again until during the study period-once in January and again in December, 1985. In both instances, another rare event occurred simultaneously - an extended winter period with almost no precipitation. During these situations, with evaporation effectively shut off by a lid of ice and runoff at a minimum because of the cold, the lake level continued to fall at a steady rate through seepage over about 40 days, at an average rate of 3.47 mm/day.

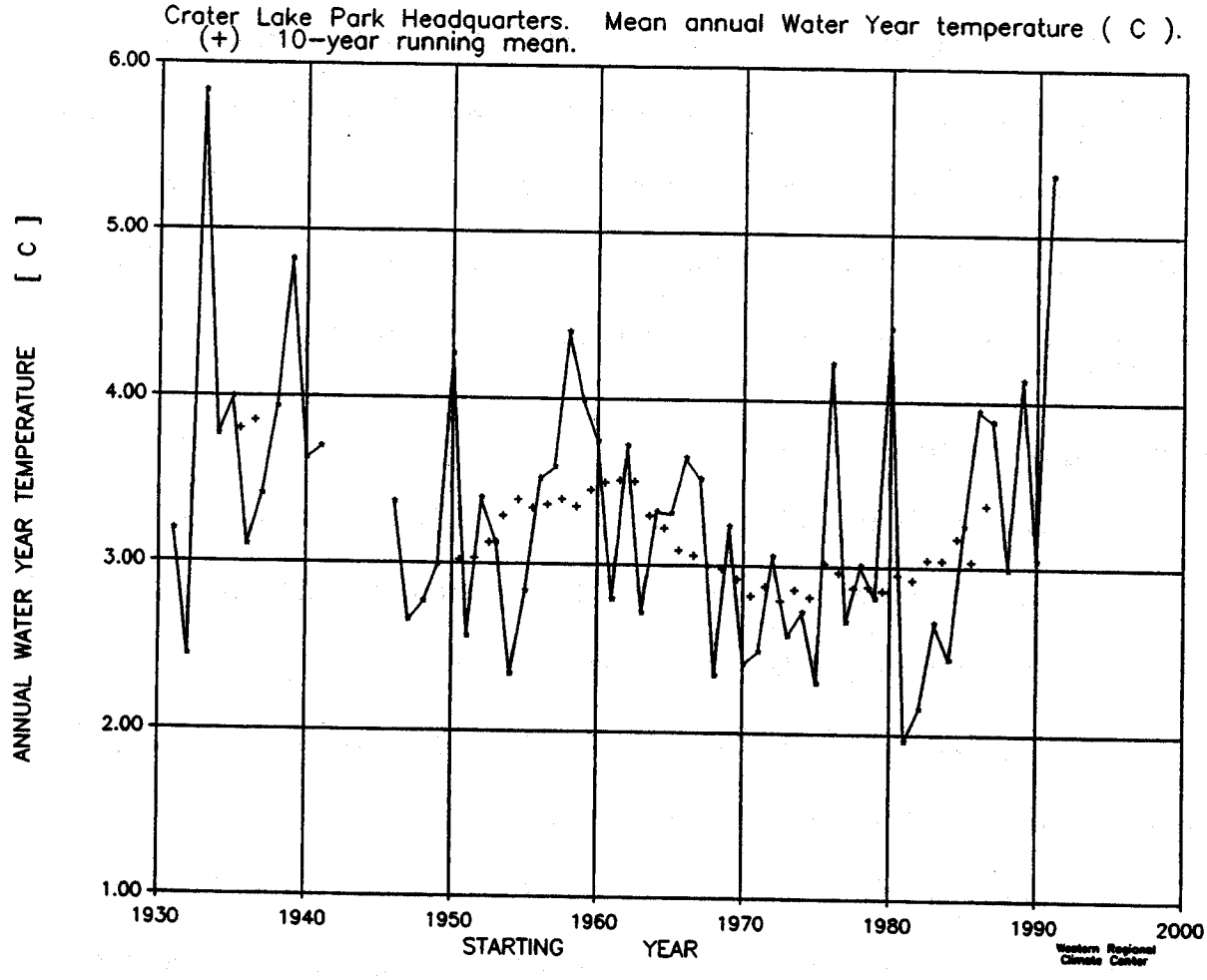


Figure 3. Annual mean temperature for the water year (October-March) at Park Headquarters, plotted in the starting year, expressed in degrees C. (+) is a 10-year running mean.

Average precipitation for the basin is not known well enough to establish its relation to the time rate of change of lake volume with high accuracy. It is well established that in this region there is significant spatial correlation of annual and monthly precipitation. Thus, basin-average precipitation should be proportional to that at any nearby upwind site, in particular park headquarters. As evidence of this, the 1964-1988 correlation of July-June precipitation at Cleetwood Cove to that at park headquarters is 0.90 even though Cleetwood receives only 72% as much precipitation as park headquarters. However, the mean ratio of 0.715 had a standard deviation of 0.074 over these 24 years, and varied from 0.62 to 0.92. The relation between the two sites is

$$P_{CC} = -1.9 + 0.730\, P_{HQ} \quad (cm),$$

where P_{CC} is precipitation at Cleetwood Cove and P_{HQ} is precipitation at park headquarters.

The relation between water year (October through September) precipitation and lake level change was established using data from park headquarters. The relationship from 1961 - 1988 was:

$$LLC = -246.5 + 1.457\, P_{HQ} \quad (cm)\,,$$

($r = .96$), where P_{HQ} is the precipitation at park headquarters. Nathenson (1992) observed that use of multiple gages generally improves the reliability of regressions. The use of combined Cleetwood and headquarters precipitation data changes the constant to about -210 to -220. An increase in the value of this constant implies that evaporation is reduced (see below). For this study, park headquarters precipitation was used because the record there extends back to 1931. This period of records is much larger than the period of records collected at Cleetwood Cove and, therefore, is more useful for reconstruction purposes. Missing precipitation values for winter months during 1943-46

were estimated from data collected at a nearby climate station at Prospect, Oregon. These estimates of the missing data points are better than previous estimates based on observations at Roseburg, Oregon.

The relation since 1961 between precipitation at park headquarters and lake level change can be used to reconstruct the annual lake level changes back to 1931. The reconstruction can be extended further back in time by estimating precipitation, at park headquarters using data from two towns within 120 km of the lake, Grants Pass and Roseburg, Oregon. These reconstructions indicate that a precipitation minimum in the 1910s and 1920s led to a lower lake until a period of high precipitation rapidly raised the lake around 1950 (Fig. 4). An improved estimate of Crater lake precipitation during World War II has modified this reconstruction from those published earlier. In summary, precipitation variations in large measure account for fluctuations in lake level, and variations in evaporation or seepage are less influential. An analysis in Redmond (1990) showed that seepage did not appear to be a function of stage.

During colder portions of the year when runoff is low, variations in the day-to-day change of lake level are primarily controlled by precipitation and evaporation directly over the lake. An analysis of daily lake-level changes can provide a number of insights into the evaporation process at the lake.

The constants in the expressions relating annual lake-level change to annual precipitation contain information about the rate of water loss. Seepage was determined to be 3.47 mm/day, or 127 cm per year. This relatively direct determination compared with values of 149 cm per year by Phillips (1968) and 139 cm per year by Simpson

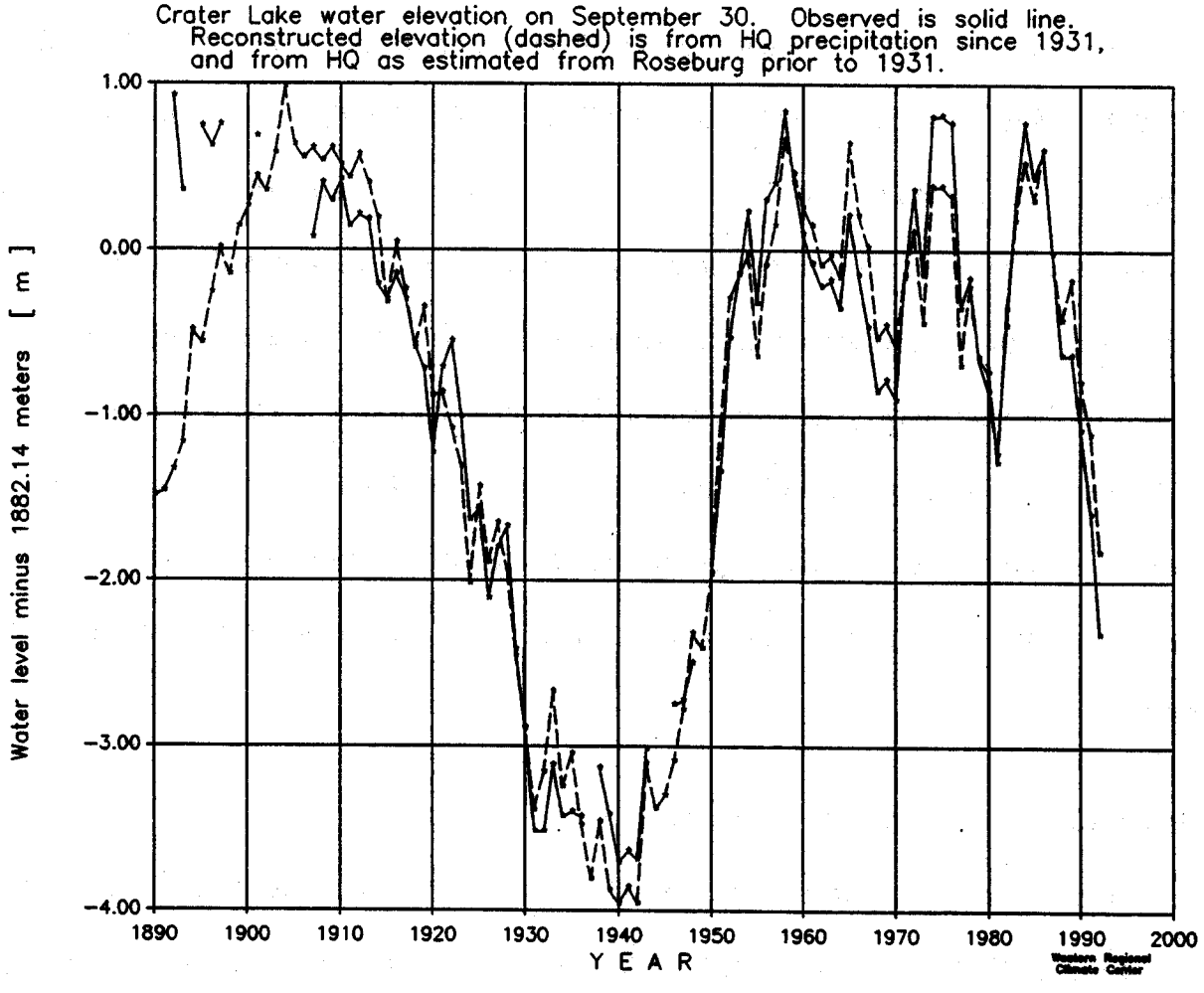


Figure 4. Lake level as reconstructed from park headquarters precipitation. Using Grants Pass precipitation data for years before 1931.

(1970), who used means more indirect than those used in this study. The difference between annual seepage and the constant term can be ascribed to evaporation. Depending on the combination of gages used and the particular 12-month period used, values for this constant range from -190 to -246 cm, resulting in implied evaporation of 63 to 119 cm per year. Earlier work by Redmond (1990) tended toward the higher value for evaporation (120 cm), compared with values of 86 cm by Meyers (1962), 58 cm by Phillips (1968), and 69 cm by Simpson (1970). Meyers, Phillips, and Simpson felt that the warm season accounted for most of the evaporation. Simpson (1970) concluded that the absence of seasonal variation in loss rate implied that seepage was the dominant loss mechanism. However, as with other unfrozen lakes under cold air, evaporation in other portions of the year may be as significant as summer evaporation. There is clear evidence that the highest rates of evaporation from Crater Lake occur on the coldest winter days. For those reasons, it appears that annual evaporation may exceed the previous estimates, but considerable uncertainty remains regarding the magnitude of this term.

Relation to El Niño/Southern Oscillation

Interest has greatly increased in El Niño and its effects on global climate change since the large El Niño event of 1982-1983. Although the term is often used rather carelessly (Aceituno 1992), El Niño refers to the anomalous warming of the ocean to the west of Peru along the equator. El Niño is just one phase of a phenomenon having a longer time scale (usually four to nine years) known as the Southern Oscillation. A cold phase (sometimes called "anti-El Niño" or "La Niña") of the same oscillation is often overlooked. The relation between the phases of the Southern Oscillation, and El Niño in particular, and regional climate around the globe, have been the subject of a number

of studies. The western United States was the focus of a recent study by Redmond and Koch (1991), who showed that El Niño is associated with dry and warm winters in the Pacific Northwest and wet and somewhat cool winters in the southwestern United States. They showed that the highest correlations were found when the six-month average Southern Oscillation Index (SOI) leads the six-month average climate variable by about four months. The SOI is a standardized index that consists of the monthly sea-level pressure at Tahiti minus the monthly sea-level pressure at Darwin, Australia, expressed as a departure in standard deviations from the average difference. A negative SOI is associated with El Niño, and positive SOI is associated with the cool ocean water in the equatorial Pacific.

Crater Lake shows the same relationship to the Southern Oscillation as the rest of the Pacific Northwest. Scatter plots of June-November SOI versus the subsequent October-March precipitation and snowfall at Crater Lake are shown in Figs. 5 and 6. Although the overall correlation coefficient is modest, the extreme cases (with absolute value of the SOI of 0.50 or greater) separate clearly into two groups. The total October-March snowfall in years with SOI of +0.50 or greater (12 cases, with an average six-month total of 13.22 m) is 2.78 m heavier than in years with SOI of -0.50 or less (16 cases, with an average six-month total of 10.44 m, over the past 60 years. The difference is significant at the 5 percent level. For years with SOI below -0.50, 11 of 16 such years are less snowy than average, and for years with SOI above +0.50, 11 of 12 such years are snowier than average.

As fall of 1991 approached, with low SOI values all summer, it became very apparent that the winter of 1991-1992 at Crater Lake would likely be a dry and warm winter. October through March precipitation totaled 84 cm and was second only to

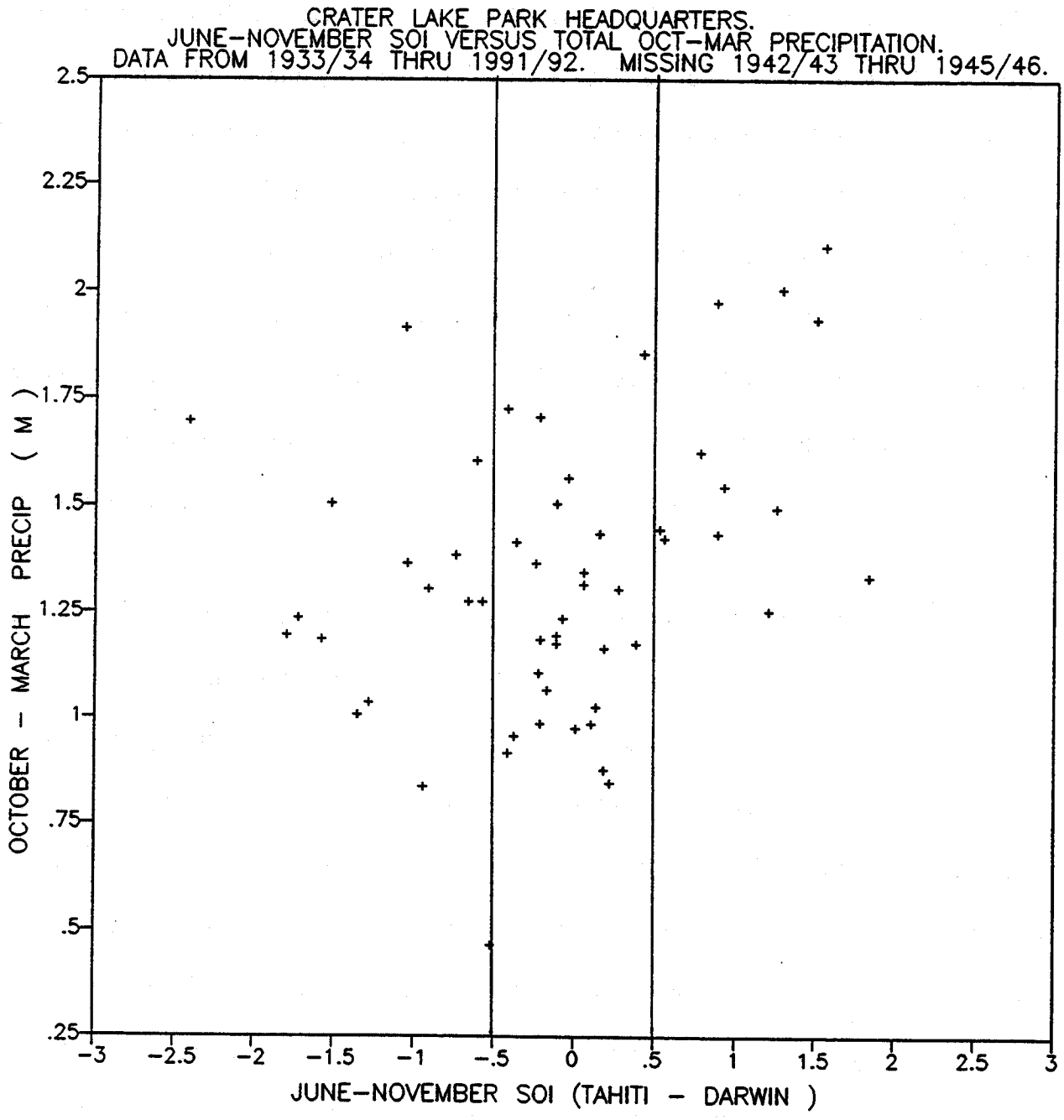


Figure 5. Scatter plot of June through November Southern Oscillation Index (SOI) and the total precipitation for the following October through March. Based on winters from 1933/34 through 1991/92. Vertical lines denote SOI values of -0.50 and +0.50. Years with absolute values greater than 0.5 appear to belong to different populations.

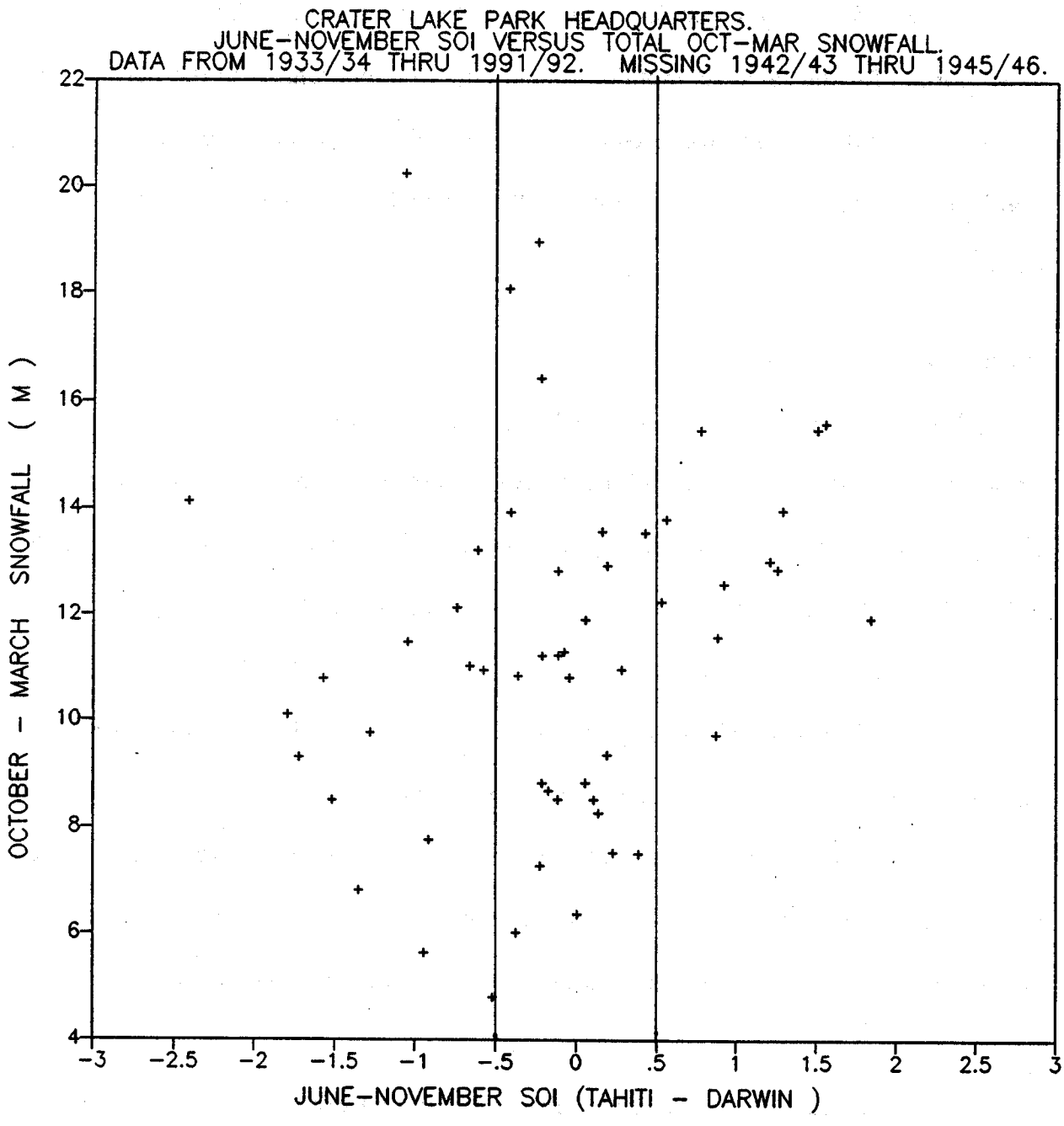


Figure 6. Scatter plot of June through November Southern Oscillation Index (SOI) and the total snowfall for the following October through March. Based on winters from 1933/34 through 1991/92. Vertical lines denote SOI values of -0.50 and +0.50. Years with absolute values greater than 0.5 appear to belong to different populations.

1976-77 levels when only 47 cm fell. Similarly, 1991-92 temperature averaged 2.2°C above normal for the same six months, second only to temperatures in the period 1933-34. Because of the dry and warm conditions, only 5.67 m of snow fell during the 6 months from October 1991 through March 1992, second only to October-March 1976-77 when 4.83 m fell.

Conclusions

The data records from the Crater Lake area are of modest length by climatological standards (30-60% of a century) but are relatively long in comparison with many geophysical, chemical, and biological records. The combination of these records and the unusual physical circumstances at the lake provide many interesting and unique possibilities for additional studies.

During the course of this project it was shown that the observed lake-level variations this century can be explained primarily by precipitation, with the effects of fluctuations in evaporation of secondary importance. The ability to directly determine a value for seepage as the result of a fortuitous congruence of unusual combinations of climatic conditions, the physical setting, and a long-term monitoring program is certainly unique.

The daily climate and lake-level records at Crater Lake constitute a potentially rich source of information about evaporation and the water budget. The ability to use direct measurements and employ the lake itself either as a precipitation gage or as an evaporation "pan" provides the prospect for novel ways of studying components of the water balance. For example, on winter days with no precipitation, the lake often falls more than on dry summer days. On dry winter days, more evaporation occurs on cold

days than on warm days. The lake also appears to fall more on days with just a little rain than on days with no rain, a physically plausible situation. Because of the altitude, humidity is usually low (even with frequent precipitation), wind speeds are often high, and the exchange coefficient is kept high because the water is warmer than the air.

The recent installation of automated weather instruments on the lake and rim will offer alternative ways of independently verifying conclusions derived using other types of data. Evaporation can be calculated from the hourly weather data. The influence of wind on the underwater temperature stratification can be more easily assessed than before. The representativeness of shore-based measurements as a way of inferring lake surface conditions can be better established.

The value of time series of geophysical data increases at a rate faster than the linear rate at which the information is recorded. That is, a time series of 20 years can provide more than just twice the information of a 10-year time series. In addition many interesting phenomena will be recorded "by accident" and not recognized as such except retrospectively. Therefore, once measurement programs have been running for a few years, a concerted effort should be made to sustain them.

The lake level fell substantially over the dry winter of 1992. When the gaging station was visited on August 28, 1992, the elevation stood at 1,880.061 m above sea level, a decrease of 68 cm from the elevation on August 28, 1991. The water year total of 120.8 cm of precipitation at park headquarters through September 1992 would be expected to produce a drop of 71 cm from September 30, 1991 to September 30, 1992. This was the sixth successive year of decline, for a total drop of 292 cm from the value of September 30, 1986. The lake has now returned a substantial fraction of the way toward the historically low values observed in the 1930s.

Acknowledgements

At various times over the course of this project, several individuals have provided data, commentary, lodging, field trips, good Italian food, and other helpful services. Among these are Gary Larson, Mark Buktenica, Tom McDonaugh, Jim Moffet, Larry Hubbard, and Bob Collier. The assistance of these and others is gratefully acknowledged.

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Appendix I. Monthly statistics at Park Headquarters during the period since 1980.

Part A. Mean monthly and annual temperature at Park Headquarters, expressed as departure from 1961-1990 average ("Ave"), in degrees C.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Ann
1980	-0.7	+1.3	-1.2	+0.6	-0.6	-3.3	+0.4	-1.2	-0.1	+1.5	+1.5	+3.3	+0.1
1981	+3.8	+1.1	+1.0	+0.8	-0.1	+0.2	+0.4	+2.2	+1.1	-1.7	+0.4	+0.2	+0.8
1982	-1.9	-1.2	-1.4	-2.9	+0.1	-0.9	-1.2	-0.4	-2.1	-1.8	-1.6	-0.1	-1.3
1983	+1.3	-0.4	+0.6	+0.1	-0.6	-2.2	-4.8	-0.5	-0.8	+0.6	-1.6	-1.4	-0.8
1984	+1.8	+0.8	+1.2	-1.9	-0.8	-2.0	+0.5	-0.3	-1.4	-3.8	-2.8	-2.3	-0.9
1985	+2.3	-1.0	-1.0	+3.2	-0.4	+0.9	+3.0	-1.5	-3.6	-1.7	-3.8	+3.3	-0.0
1986	+2.1	+1.2	+2.7	+0.1	-0.3	+1.9	-1.6	+2.6	-3.8	+0.6	+0.8	+1.2	+0.6
1987	-0.5	+0.3	-0.3	+3.1	+2.2	+2.2	-1.7	+0.4	+2.7	+5.0	+0.9	-1.9	+1.0
1988	-1.1	+2.7	+0.7	+1.8	-1.3	-0.4	+1.7	+1.0	+1.1	+5.2	-1.4	+0.7	+0.9
1989	+0.2	-4.3	-0.4	+2.8	-0.8	+0.5	-0.8	-2.1	+0.2	-1.2	+2.1	+4.1	-0.0
1990	+0.2	-1.8	+2.1	+3.9	-0.3	-0.1	+1.7	+0.3	+2.1	-0.6	+0.2	-2.9	+0.4
1991	+1.3	+3.8	-1.9	-1.2	-1.7	-2.8	+1.3	+0.8	+3.8	+2.4	+1.4	+1.5	+0.7
1992	+1.3	+2.3	+4.3	+2.8	+5.7	+3.0	+0.1	+2.6	+0.8				
Ave	-3.3	-3.0	-2.6	-0.3	3.4	7.8	11.9	12.4	9.2	4.9	-0.8	-3.2	3.0

Part B. Monthly and annual precipitation at Park Headquarters, expressed as departure from 1961-1990 average ("Ave"), in mm. July-June total is for the 12 months ending in June of the year shown.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Ann	Jul-Jun
1980	+ 36	+ 4	- 16	+ 28	- 21	+ 20	- 17	- 33	- 20	- 53	- 45	- 38	-155	+ 40
1981	-148	- 8	- 61	- 37	+ 42	+ 17	- 1	- 33	+ 18	+ 69	+ 69	+326	+253	-401
1982	+ 21	+ 77	- 16	+ 93	- 73	+ 44	+ 6	- 14	+ 59	+ 46	- 47	+119	+315	+594
1983	- 20	+146	+151	- 19	- 17	+ 8	+ 36	+ 44	- 51	- 59	+157	+198	+574	+452
1984	-160	+ 15	+ 51	+ 48	+ 55	+ 20	- 17	- 18	- 33	+ 83	+192	-115	+130	+354
1985	-229	- 45	- 3	- 29	- 26	- 26	+ 24	- 4	+ 59	+ 39	- 52	-155	-447	-266
1986	+ 32	+246	- 3	+ 2	+ 17	- 33	+ 5	- 29	+162	- 30	- 77	-167	+125	+172
1987	- 18	+ 4	- 29	- 78	+ 3	- 12	+ 87	- 20	- 60	-120	- 96	+ 76	-263	-266
1988	+ 16	-147	- 28	+ 6	+ 74	+ 44	- 17	- 33	- 20	-105	+305	- 88	+147	-168
1989	- 25	- 77	+181	+ 29	+ 31	- 24	- 16	- 6	- 15	- 10	-149	-237	-318	+157
1990	+ 27	+ 9	-100	- 2	+ 93	- 12	- 7	+ 30	- 38	+ 13	- 79	-158	-224	-418
1991	- 36	- 31	+ 91	+ 41	+ 32	- 25	+ 25	- 5	- 57	- 16	+ 50	-124	- 55	-167
1992	-127	- 71	-180	+ 93	- 58	+ 57	+ 12	- 32	- 24					-413
Ave	245	198	202	117	77	50	17	33	60	121	268	275		1664

Part C. Monthly and seasonal snowfall at Park Headquarters, expressed as departure from 1961-1990 average ("Ave"), in cm. Seasonal total for July-June is the 12-month total ending in June of the year shown.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jul-Jun
1980	- 73	- 46	- 24	+ 15	+ 9	+ 1	- 1	- 1	- 10	- 7	- 81	- 95	-163
1981	-119	- 82	- 76	- 51	- 8	0	+ 1	- 1	- 10	+ 22	+ 14	+159	-531
1982	+174	- 69	- 6	+103	- 49	+ 3	+ 4	- 1	+ 11	+ 9	+ 5	+ 89	+341
1983	- 50	+142	+157	- 8	+ 20	- 1	- 1	- 1	- 10	- 53	+ 96	+150	+377
1984	-166	+ 50	- 16	+ 43	- 3	+ 28	- 1	- 1	- 9	+ 68	+223	- 39	+117
1985	-194	- 48	+ 50	- 88	+ 40	- 10	- 1	- 1	+ 7	- 6	+ 76	-104	- 9
1986	- 20	+175	-100	- 28	+ 20	- 8	+ 3	- 1	+132	- 11	- 23	- 99	+ 10
1987	- 11	+ 10	- 44	- 89	- 19	- 8	+ 1	- 1	- 10	- 54	-102	+ 18	-160
1988	+ 25	-168	-100	- 5	+ 56	+ 30	- 1	- 1	- 10	- 54	+203	+ 15	-310
1989	+ 75	- 39	+ 25	+ 48	+ 9	- 8	- 1	0	- 10	+ 14	- 74	-194	+262
1990	- 16	+ 58	- 98	- 97	+ 2	- 10	+ 8	- 1	- 10	- 44	- 38	-114	-413
1991	-140	- 87	+ 88	+ 41	+ 35	- 10	- 1	- 1	- 10	+ 30	- 56	-116	-272
1992	-106	- 56	-194	- 64	- 49	- 5	- 1	- 1	- 9				-628
Ave	217	186	219	109	49	10	1	1	10	54	176	213	1245

Lake Circulation

James McManus, Robert Collier, and Jack Dymond

An understanding of the physical processes that redistribute heat and salt in Crater Lake is essential to modeling the biogeochemical cycling of elements in the lake. There are only a few studies of Crater Lake's physical limnology. Kibby et al. (1968) reported surface current observations as well as the vertical and horizontal distribution of temperature in the upper water column. Radioisotope data from Simpson (1970 a, b) and Volchok et al. (1970) indicate that the characteristic time-scale of deep-lake ventilation is approximately one year. Neal et al. (1971, 1972) provided temperature microstructure measurements that demonstrate the hyperadiabatic nature of the thermal gradient in the deep lake. The term "hyperadiabatic" derives from the fact that the thermal gradient below 350 m in the deep lake is at least two orders of magnitude greater than the adiabatic gradient (Fig. 1). Williams and Von Herzen (1983) identified two areas of high heat flow along the lake floor; one in the north basin near Merriam Cone, and a second in the south basin where their highest heat flow measurements were recorded. Assuming a homogeneous salinity distribution, they discussed the apparent vertical instabilities and convection that would accompany the observed temperature distribution. Although the work of Williams and Von Herzen (1983) served as a catalyst for our work, a lack of high precision salt determinations limited their ability to interpret the temperature microstructure of the hypolimnion in Crater Lake. Our research has provided both the high precision temperature and salinity data that are necessary for the accurate determination of the physical properties and the mixing dynamics of the lake (McManus et al. 1992).

Although, to a first approximation, Crater Lake is well mixed with respect to major ions (Collier et al. 1990a, Nathenson 1990, Thompson et al. 1990, Nathenson and Thompson 1990, McManus et al. 1992), our measurements document a salinity gradient below 200 m at all times (Fig. 1) (McManus et al. 1992). Because of the active input of hydrothermal fluid and the transport of this fluid throughout the deep lake, both the salinity and temperature gradients of the deep-water column exhibit spatial and temporal variability. The primary source of the

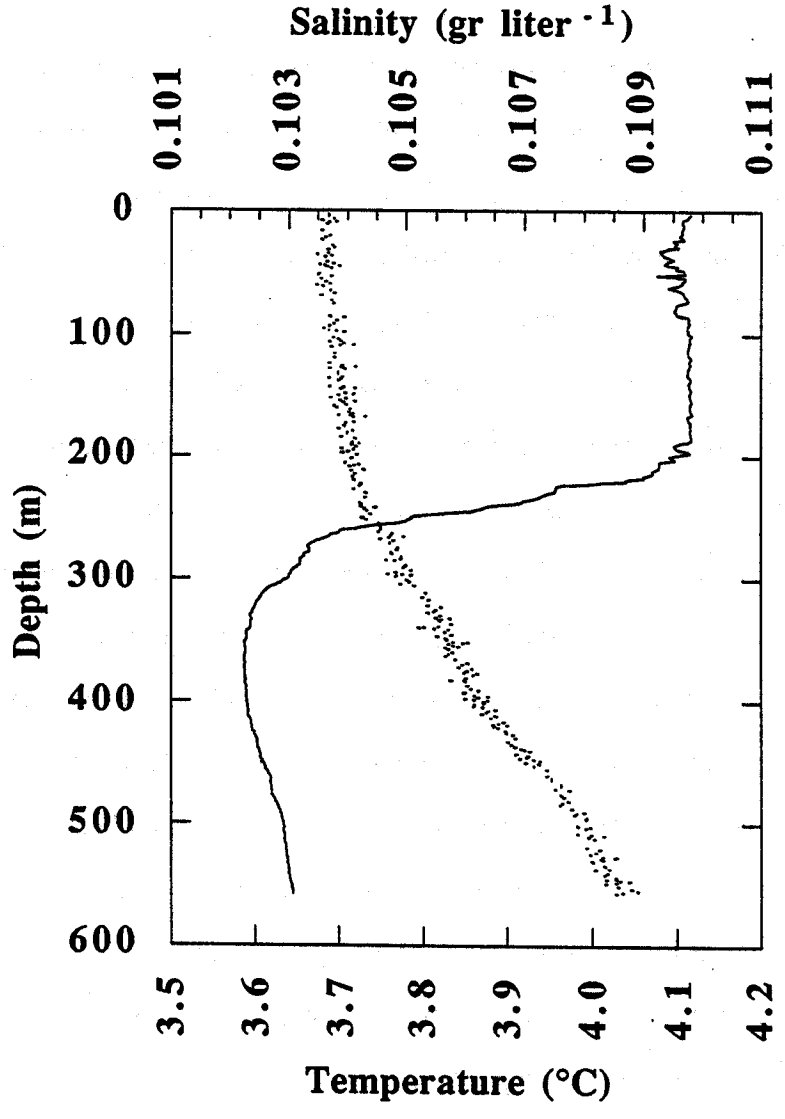


Figure 1. Salinity (g liter^{-1}) and temperature (°C) as a function of depth. Data was taken from the north basin on 19 January 1990. Note the near-uniform salinity of the upper 200 m interval and the increase in temperature and salinity with depths below ~350 m.

hydrothermally enriched fluids appears to be deep within the south basin (Williams and Von Herzen 1983, Dymond et al. 1989, Collier et al. 1990, McManus et al. 1992). Variability in the vertical and horizontal temperature and salinity distribution occurs over time scales of weeks, suggesting that the hydrothermal fluid mixes rapidly throughout the deep lake.

The objective of this section is to define the magnitude of the hydrothermally derived heat and salt fluxes to the deep lake through a time-series of temperature and salinity measurements. In addition, we will discuss how this heat and salt mix throughout the deep lake. We will first examine mixing processes in the upper lake during seasonal changes in stratification. We will then estimate the degree to which water mixes from the surface layer to the deep lake during periods of minimum surface stratification, and we will present data that demonstrates the mechanism for deep lake ventilation. Finally, we will discuss how the hydrothermally enriched waters mix through the deep lake during periods of maximum surface stratification.

Methods

Temperature, pressure, conductivity, and light transmission were measured using a CTD ("conductivity, temperature, depth" recording instrument, SEACAT® model SBE19, Sea-Bird Electronics Inc.) modified for low-conductivity waters and equipped with a 25-cm-path-length light-beam transmissometer (Sea Tech. Inc.). The CTD records all data internally at 2 scans per second. Temperature resolution is ±0.0005 °C and, based on laboratory triple point calibrations of the temperature sensor, the absolute accuracy of the temperature sensor is ~0.001°C from 1987 to 1989. Laboratory calibration of the conductivity sensor using Crater Lake water and subsequent chemical analysis of this water provided us with sufficient salinity, conductivity, and temperature data to obtain an expression for salinity as a function of *in situ* conductivity and temperature (McManus et al. 1992). Salinities calculated from our expression are ~25% greater than would be predicted from strong electrolytes alone. This is because silicic acid accounts for approximately 25% of the total dissolved solids in the lake. The details of the experiments and further explanation of the affects of silicic acid on the density of Crater Lake water are presented in McManus et al. (1992).

The CTD was deployed on a hydrographic wire lowered from the NPS research boat. The time series hydrographic data presented in this section was collected in the northeastern portion of the north basin (National Park Service [NPS] Station 13), the south basin, NPS Station 23, and in the northwestern portion of the lake, NPS Station 11 (Fig. 2). Time-series temperature data were also collected using two moored thermistor chains deployed in the south basin from 3 September 1989 until July 1990. One chain (TC1084) was located at 50-150 m depth, and the other (TC8) extended from 350 m to the bottom (450 m). The chains were equipped with 11 thermistors spaced at 10-m intervals. The thermistors recorded a temperature every three hours throughout deployment. We calibrated the thermistors at the OSU calibration facility both before and after deployment. The absolute accuracy of the thermistors is ±0.010 °C, and the in-field precision, based on daily temperature measurements from the deep lake, is ±0.005 °C.

Dissolved oxygen contents of water samples were determined using a whole-flask Winkler titration method with the modifications of Carpenter (1965 a, b). The overall precision of the oxygen measurement is based on the percent difference between duplicate sample analysis and is better than 0.5%. We employed the equations presented in Benson and Krause (1984) to determine the solubility of dissolved oxygen in Crater Lake. The mean atmospheric pressure at the lake surface was calculated from the altitude-dependent equation given by Mortimer (1981).

Results and Discussion

Heat and Salt Flux into the Deep Lake

A time-series of CTD data and data from a thermistor chain mooring indicate that there is a consistent input of heat and salt into the deep hypolimnion of Crater Lake. The input of heat is demonstrated in the deep lake by the gradual increase in temperature over time observed during periods of surface stratification (Fig. 3).

Integrated values for the flux of heat and salt are calculated from the time-series of CTD data. This is accomplished by integrating the area under a vertical profile (either salinity or temperature) and subtracting the area under a profile taken at the same location at an earlier time. For instance, the integrated temperature change between 17 July and 17 August below 350 m

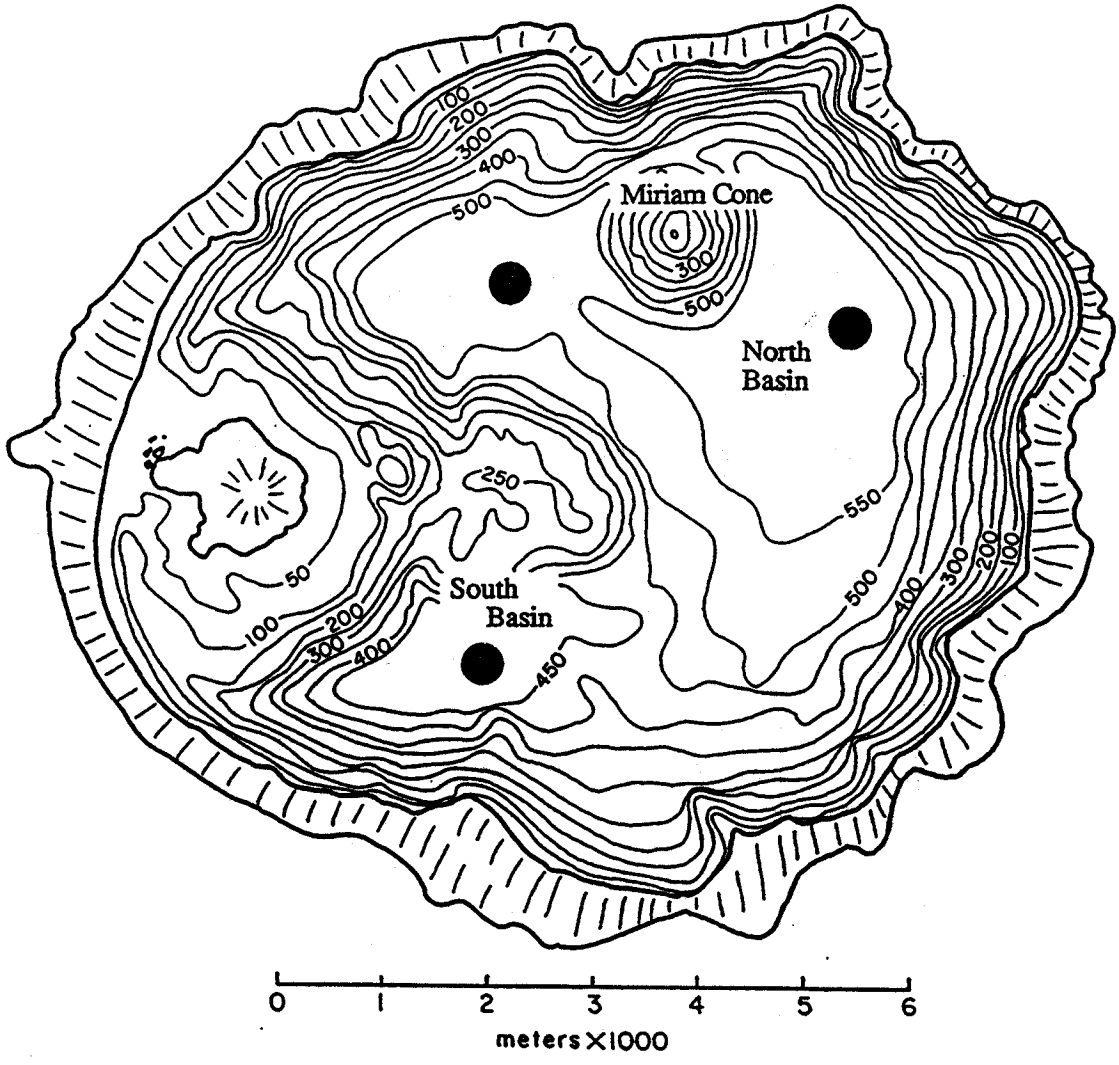


Figure 2. Bathymetric map of Crater Lake with geologic features. Large dots represent approximate locations of time series monitoring stations: Station 23 located in the south basin, Station 13 located in the north basin, and Station 11 located in the northwest portion of the lake. The bathymetry is taken from Byrne (1965).

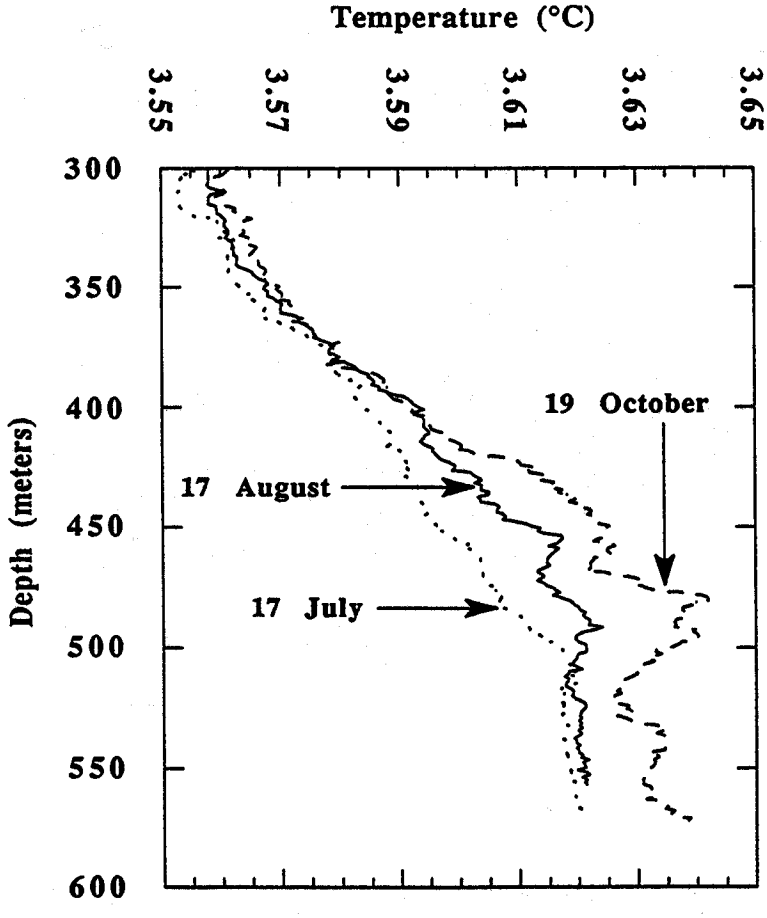


Figure 3. Temperature as a function of depth in time series. This CTD data was taken from the north basin. The data demonstrates the accumulation of heat in the hypolimnion throughout the summer months.

(Fig. 3) is converted to a net heat flux. Each flux calculation represents a volume-weighted average of CTD data from the three monitoring stations (Fig. 2). Basin volumes were determined from the hypsographic curve presented in Byrne (1965).

The rate of deep-lake warming can also be estimated using deep-lake temperature data from the thermistor chain moored within the south basin. This is accomplished in a manner similar to the treatment of the CTD data by calculating the change in temperature between 440 and 350 m during periods of surface stratification. To demonstrate the warming of the deep lake, we show an expanded-scale plot of temperature versus time for the thermistor deployed at 410 m (Fig. 4). The arrows indicate deep-lake warming during periods of upper-water-column stability (fall and late spring/early summer). During winter there is some cooling of the deep waters, which is associated with deep-lake ventilation.

Table 1 presents the results of the calculations for heat and salt flux. The heat and salt flux values are for discrete time intervals during a given year, and the flux values represent differences between two profiles separated in time by at least several weeks. Our method of calculating the net heat flux yields results that agree with those of Williams and Von Herzen (1983) who reported values between 0.7 and 1.4 W m^{-2}.

Fluid flow (Table 1) is estimated directly from the salt flux values. In calculating the fluid flow, we have assumed that the salinity of the hydrothermal fluid is 0.6 gr kg^{-1} as it enters the south basin. This salinity value is based on pore-water chemistry data (Wheat, unpublished) and the chemical composition of brines, which are found at the source of the thermal inputs in the south basin (Collier et al. 1990b). The estimates of fluid flow are consistent with other values suggested by Nathenson (1990), 80-1900 liters sec^{-1}. Because there may be variations in the end-member composition, the estimated flow rates are only rough estimates of the net fluid flow associated with these inputs.

Although the annual fluid input due to hydrothermal activity is small compared to the lake volume (17.3 km^3), the fluid flow rate given in Table 1 (~0.2 m^3 sec^{-1}) is large (~5%) compared

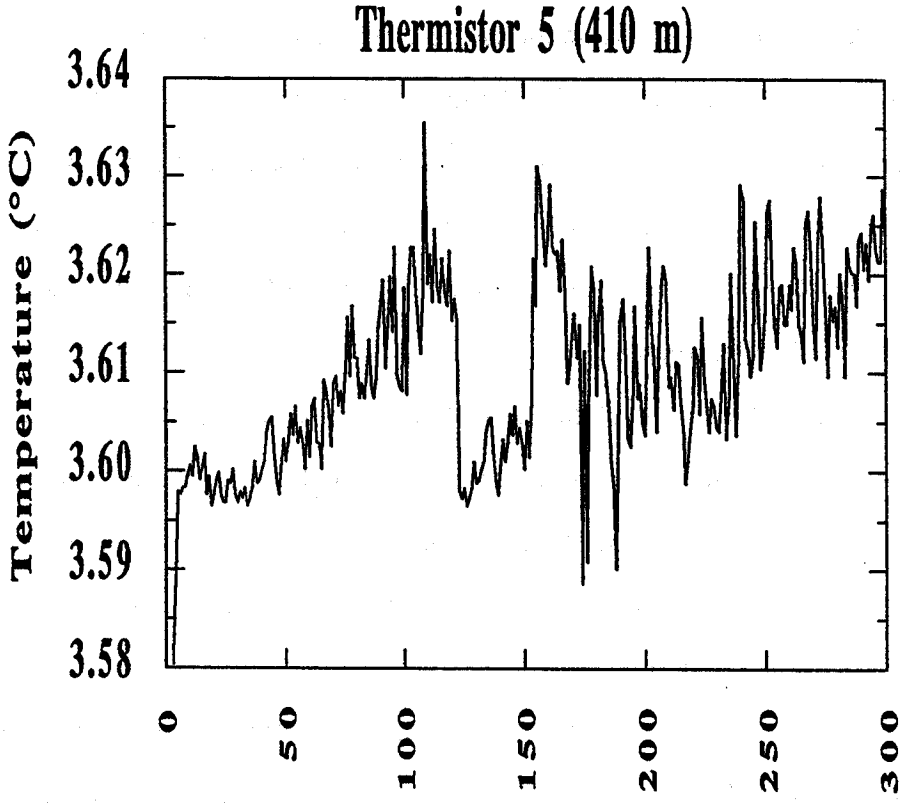


Figure 4. Temperature as a function of time from the thermistor at a depth of 410 m in the south basin from September 1989 to July 1990. The figure demonstrates the warming due to the constant input of heat from hydrothermal activity and the cooling due to winter mixing. The absence of data apparent in the figure marks a period of time of recorder malfunction.

Table 1. Heat flux, salt flux, and fluid flow.*

Year/ season	Method	Heat Flux ($W\ m^{-2}$)	Salt Flux ($mg\ m^{-2}\cdot sec$)	Estimated Fluid flow ($liters\ sec^{-1}$)
1989/S	CTD	0.9 ± 0.5	4.2 ± 2.5	141±84
1989/F	Thermistor	1.0 ± 0.3	N/A	N/A
1990/Sp	Thermistor	1.2 ± 0.6	N/A	N/A
1990/ES	CTD	0.9 ± 0.2	5.2 ± 3.0	254±146
1990/LS	CTD	1.0 ± 0.4	5.7 ± 3.0	278±146

*S, F, and Sp represent summer, fall, and spring, respectively where E and L are early and late, respectively. The surface area of the lake over which the integration was calculated was 22.9 km^2 for 1989 and 20.2 km^2 for 1990.

to the annual input of water due to precipitation (~4.2 $m^3\ sec^{-1}$, Redmond 1990). Because the hydrothermal fluid is rich in salt relative to precipitation, the input of this high-salinity fluid will have a dominant effect on the salt budget. A more detailed treatment of the geochemical budgets are presented in Collier et al. (1991). It is sufficient for the purposes of this section to point out that hydrothermal activity is the dominant source of salt to Crater Lake.

The data presented here represent the first direct observations of the accumulation of heat and salt over time in the deep water column of Crater Lake. Despite the uncertainties in the calculations, the method for estimating heat flux, salt flux, and fluid flow confirm and refine the previously reported values.

Vertical mixing of heat and salt

During periods of reduced vertical stability of the water column, some deep lake water is mixed with surface water. This mixing results in the exchange of thermally and chemically enriched water from the deep lake with cooler, lower-salinity surface water. Since deep-lake water is rich in biochemically important nutrients, particularly dissolved nitrate, this exchange is critical to new biological productivity in the upper 200 m. Such exchange also carries cooler, oxygen-rich

waters from the surface to the hypolimnion. Therefore, the dissolved oxygen content of the deep lake allows us to estimate the degree to which surface-to-bottom exchange has occurred. For example, if at any period the entire lake was to reach atmospheric saturation with respect to dissolved oxygen, we could then conclude that all of the waters have come into contact with the surface during a single mixing period. In the following sections, we examine three stages of vertical mixing in Crater Lake - the breakdown of the seasonal thermocline, inverse stratification, and the mixing of surface water with deep water that takes place during a minimum in water column vertical stability.

Breakdown of the seasonal thermocline Most temperate lakes undergo three stages of cooling -the breakdown of the seasonal thermocline, isothermal overturn, and inverse stratification (Carmack and Farmer 1982). The breakdown of the thermocline is characterized by a decrease in the surface density gradient and an increase in the depth of the surface mixed layer. In many lakes, continued wind mixing and cold-water convection result in an isothermal water column near the temperature of maximum density. The formation of an isothermal water column is then followed by surface restratification due to continued cooling of the surface water. However, for very deep lakes like Crater Lake, the full water column is rarely isothermal because the temperature of maximum density decreases at a rate of approximately 0.02 °C bar^{-1} (~0.002 °C m^{-1}). Thus, waters near their density maximum at the surface will not be able to undergo free convection to the lake bottom. The maximum depth of complete mixing in deep lakes is, therefore, influenced by the *in situ* physical properties of lake water, which influence the depth of free convection, as well as wind forcing.

The upper water column of Crater Lake begins to undergo destratification in early fall as the density of the surface water increases due to cooling. As the thermocline breaks down, mixing of the surface water with water below causes an initial increase in temperature at depth (i.e. arrows in Fig. 5). This mixing is driven by wind mixing at the surface and convection of the surface water as it cools. The increase in temperature is seen at 90 m by late December (Fig. 6a). By mid-

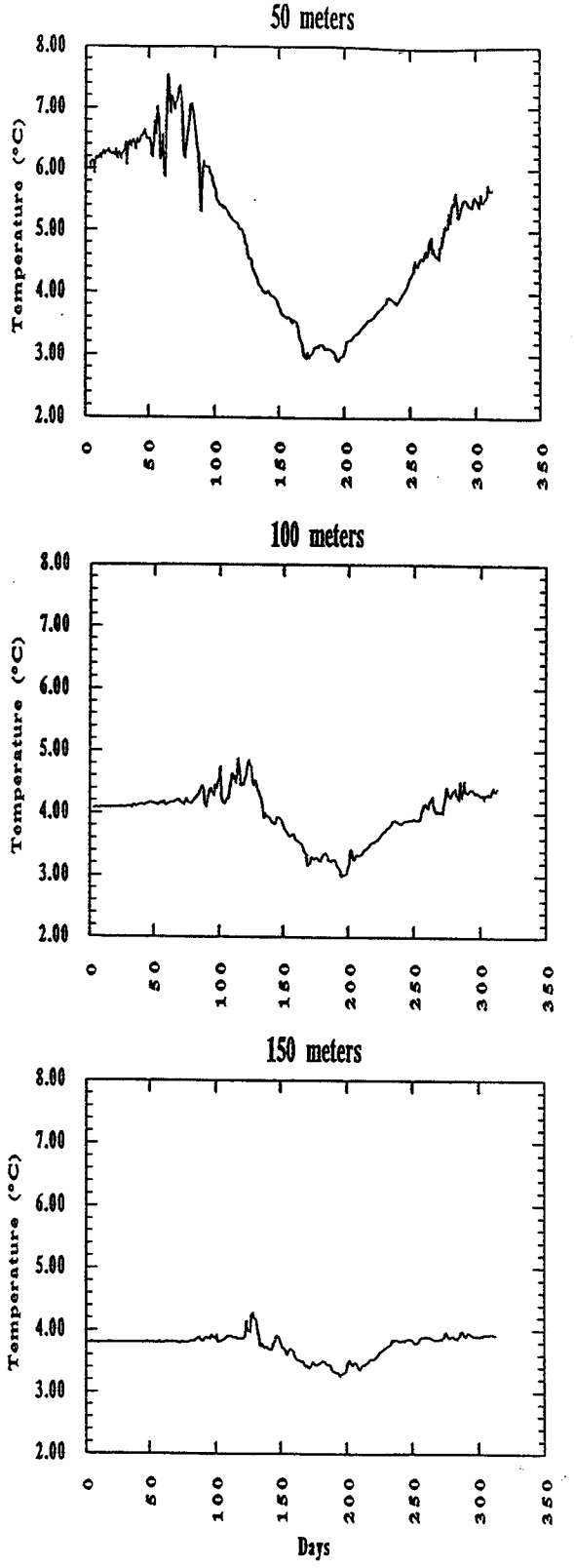


Figure 5. Thermistor data from the upper water column demonstrating the change in temperature over time. Thermistors were spaced at 10-m intervals between 50 m and 150 m. Data from the 50-m, 100-m, and 150-m thermistors are shown as examples. During the breakdown of stratification, warm water from above is mixed with ambient (cooler) water (arrows).

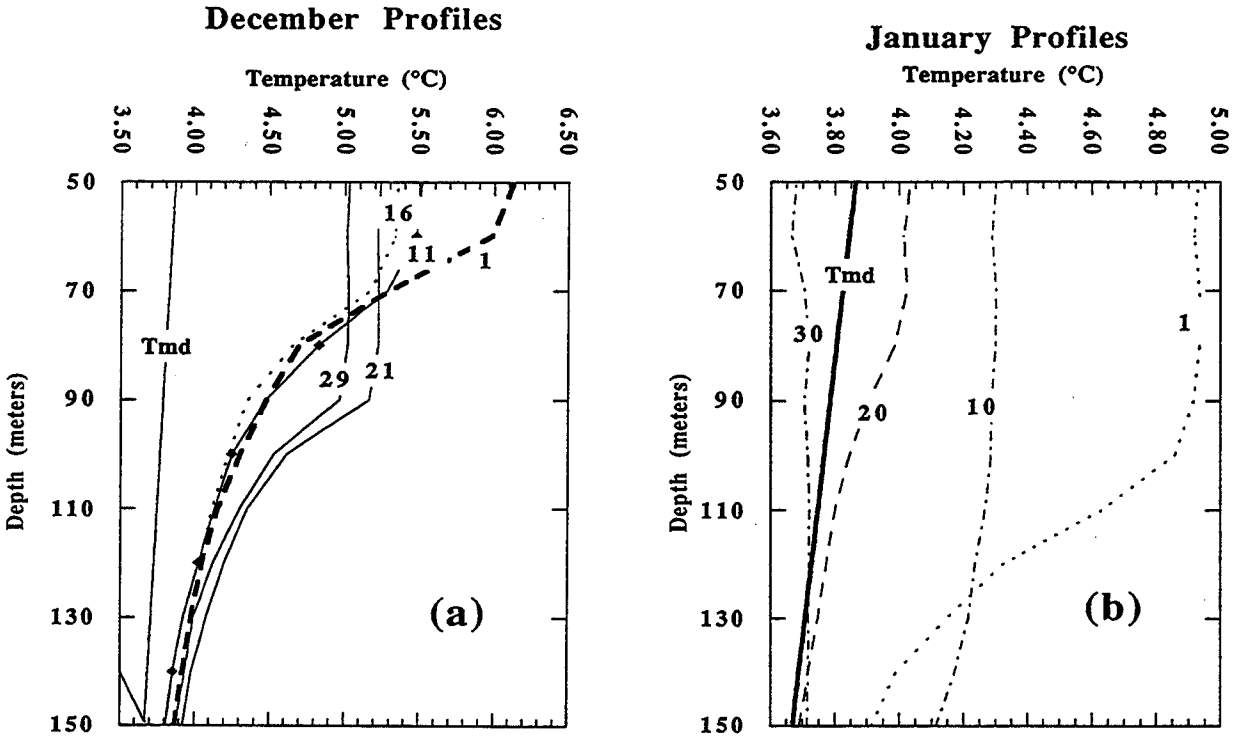


Figure 6. Temperature as a function of depth in the upper part of the water column for (a) December and (b) January. Data are taken from the thermistor chain between 50 m and 150 m and demonstrates the results of the breakdown of thermal stratification in the upper 200 m.

January this warming signal has penetrated to >150 m (Fig. 6b). At this time, at least the entire upper 150 m are isothermal and the mixed layer reaches depths of at least 200 m (Fig. 1).

The rate of penetration of the mixed layer also reflects the stronger stratification initially present in the upper 100 m as compared to the depth range of 100-150 m. Between 50 and 90 m, the base of the mixed layer descends through the water column at a rate of approximately 1 m day^{-1} until it reaches ~90 m (Fig. 5 and 6). The rate of mixed layer deepening from 100 m to 130 m increases to ~8 m day^{-1}. Although the data are inadequate to accurately determine the descent rate below this depth, the rate appears to be between 10 and 20 m day^{-1}. In Babine Lake, Carmack and Farmer (1982) found the mixed layer penetration rate to be ~0.4 m day^{-1} at the surface and found it to increase to rates as high as 20 m day^{-1} during the later stages of mixed layer deepening. It is surprising that the rate of mixed layer formation in Crater Lake, a sheltered near-circular lake with a maximum fetch of 10 km, is similar to that in Babine Lake, which is 150 km in length, 4 km in width, and has a maximum depth of 230 m. The similarities between the two lakes emphasize the importance of convection in the breakdown of the seasonal thermocline and formation of the winter mixed layer in freshwater systems.

Inverse stratification After the initial mixing, which results in an increase in temperature at the deeper levels of the thermocline, continued winter cooling causes a gradual decrease in the temperature of the upper water column. During the winter of 1990, this cooling continued until mid-March (Fig. 5) and by early April, water column warming was occurring at depths greater than 50 m. Once the temperature profile crossed the T_{md} in mid-April, thermocline development began.

Since the surface waters are still colder than the T_{md} in early April, initial warming produces parcels of water of greater density that drive convection. Temperature profiles obtained with the CTD from early May 1989 (Fig. 7) illustrate the results of this process. Heating of the surface waters during the day form convective cells that sink throughout the course of the day (solid line Fig. 7). This continued process warms the entire water column through which convection may occur, leaving a warmer column of near-uniform temperature water at the end of

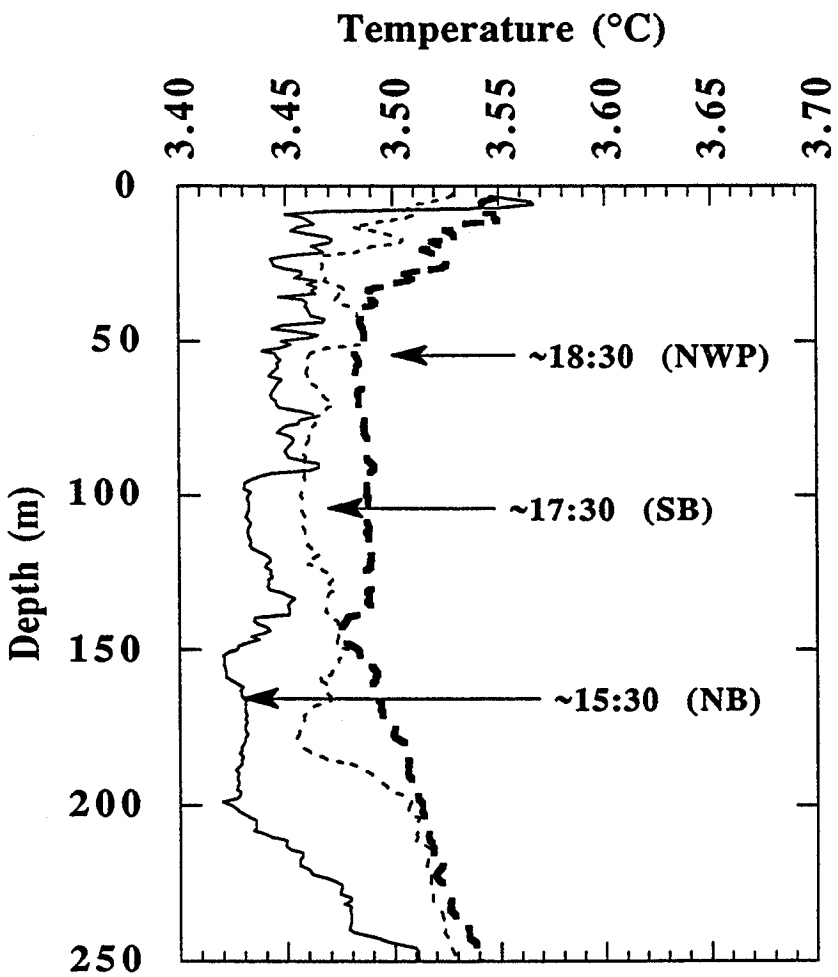


Figure 7. One-day time series of temperature vs. depth for Crater Lake taken in May 1989. The figure demonstrates convective warming in the late afternoon (solid line), the gradual slowing of the convection by early evening (dotted line), and the near-uniform temperature profile by sunset (heavy dashed line). NB represents north basin; SB south basin; and NWP represents the northwest portion of the lake.

the day (dashed line Fig. 7). The three profiles in Fig. 7 are from the three different monitoring stations (Fig. 2) on 11 May and some of the differences are due to horizontal variations in mixing and heating. Therefore, the net warming, which is apparent between the three profiles, can not be used to estimate a one-dimensional heat input into the upper lake.

Spring heating of the water column results in a cycle of warmer temperatures during the day and cooler temperatures at night in the thermistor record of the upper water column (Fig. 8). The maximum daily water temperature, recorded at 50 m during the month of April, occurs at 1,300 and the minimum between 100 m and 500 m. As the temperature of the upper lake approaches the temperature of maximum density at 50 m (~April 20), the upper water column becomes nearly isothermal at about 3.9°C (Fig. 8). After this point (~1 May), rapid warming of the surface water leads to a stratified water column, thereby isolating the deeper water as suggested by the near-constant water temperature at 100 m until approximately 10 May. After approximately 10 May, we observe large variations in the daily water column temperatures. These fluctuations are probably driven by a combination of storms, surface driven convection due to cooling, strong horizontal thermal gradients, and other upper water column mixing processes.

Of particular importance with respect to this work is the relative speed with which the water column undergoes restratification in the spring. Once the upper waters are restratified, mixing between the upper and deep lake can no longer occur. Storms occurring during periods of minimum stability, i.e., while the water column temperature is closest to the T_{md}, as seen on 10 May, may provide the impetus for deep mixing. Climate variability will therefore influence deep mixing in the spring, as well as during the winter.

A more detailed study of the upper water column-atmosphere interactions should include thermistors that extend to the surface as well as detailed meteorological data. In addition, future modeling efforts should accurately represent convection as well as shear-induced wind mixing. For our purposes it is important to point out that the upper 200 m of the water column in Crater Lake are well-mixed twice annually (winter and late spring). During these periods of mixing, both

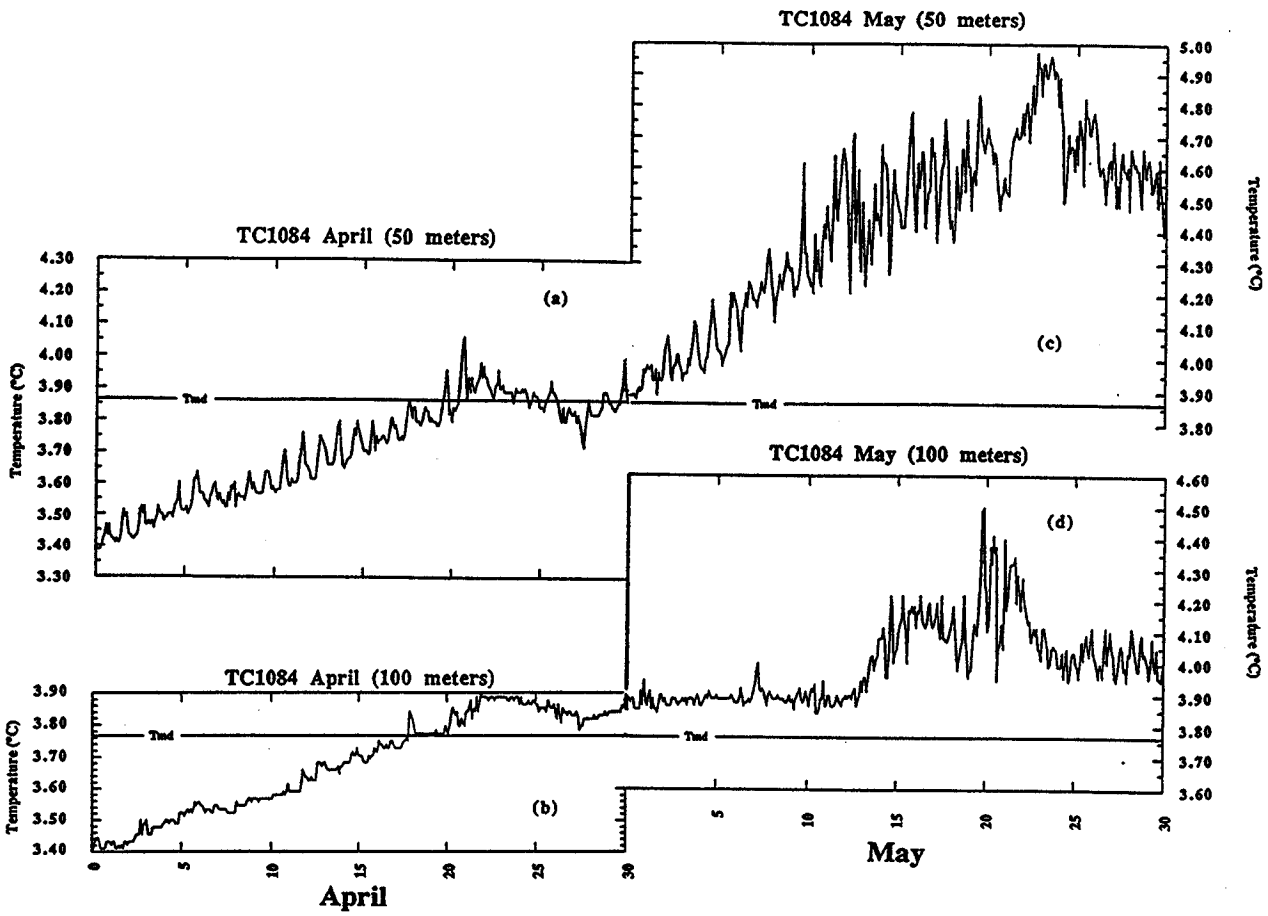


Figure 8. April - May 1990 expanded-scale thermistor chain data (TC1084). Data are from 50 m (top) and 100 m (bottom). The temperature of maximum density (Tmd) was calculated from the equation of state (Chen and Millero 1986).

CTD measurements and our thermistor data indicate that the upper 200 meters of the water column is isothermal.

It is remarkable that the mixed layer in Crater Lake achieves such great depths. The similarities in the rate of mixed-layer deepening for Crater Lake and Babine Lake appear to be a function of convective mixing. In addition, the fact that fresh water has a density maximum that is between 3 and 4 °C in the upper 200 m has an influence on mixing in deep lakes (Weiss et al. 1991).

Mixing of surface water with deep lake water. Time-series dissolved-oxygen data, CTD data, and thermistor chain data all indicate that some exchange of surface water (defined here as water from the upper 200 m) with deep water occurs in Crater Lake at least once a year. The data suggest that this annual mixing process is likely to be incomplete.

Dissolved oxygen is a useful tool for the study of mixing processes in lakes. We discuss the details of the oxygen budget of the deep lake elsewhere; however, it is sufficient for the purposes of this section to point out that deep-oxygen consumption can occur by two processes. Dissolved oxygen is consumed by the decomposition of particulate organic material raining out of the euphotic zone. Also, in Crater Lake, reduced chemical inputs from hydrothermal activity contribute to the depletion of dissolved oxygen in the deep lake.

Convective mixing during the winter and spring tends to saturate the upper water column with dissolved oxygen (e.g., April oxygen profile in Fig. 9). Because annual mixing of deep lake water with well-oxygenated surface water is the only mechanism that will increase the dissolved oxygen contents of the deep lake, changes in deep-lake dissolved oxygen serve as a semi-quantitative measure of the extent of vertical mixing in Crater Lake.

Data collected from September 1988 and April 1989 demonstrate an increase in dissolved oxygen, measured at 550 m, of nearly 10 μmol liter^{-1} (Fig. 9). Likewise, from January 1990 to July 1990 we observe another increase in deep lake dissolved oxygen, indicating that the ventilation process reoccurred during the winter and possibly spring of 1990. This mixing is, however, incomplete, leaving the deep lake undersaturated with respect to atmospheric saturation

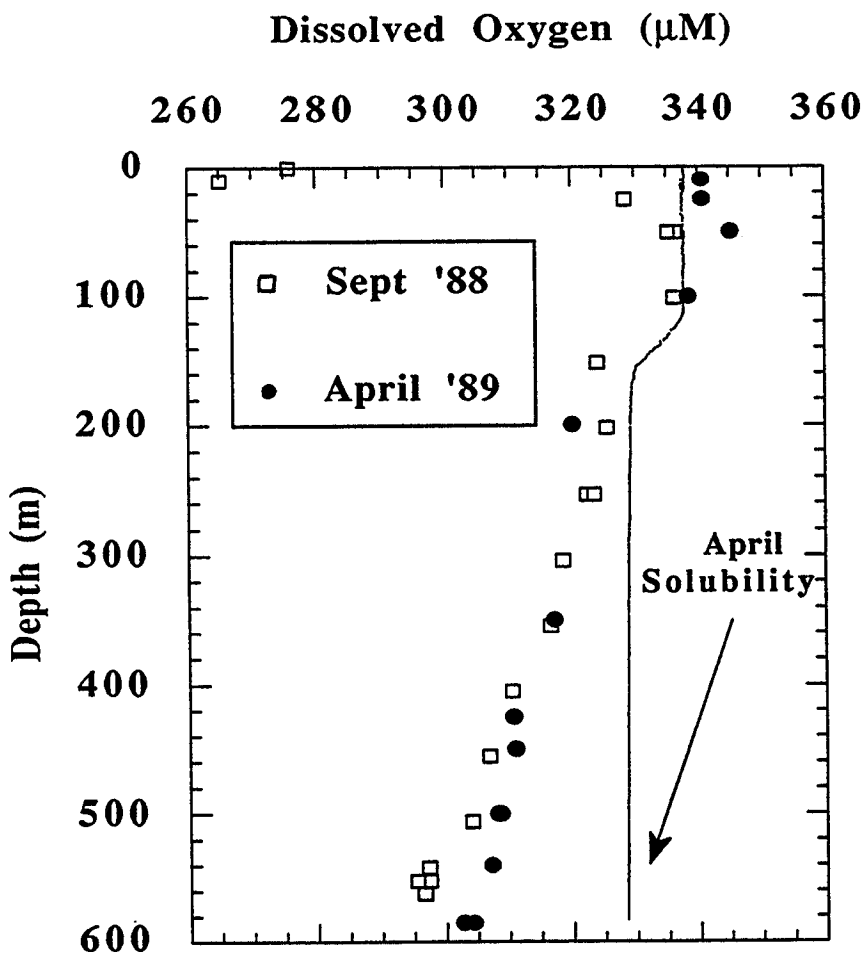


Figure 9. Expanded-scale dissolved oxygen as a function of depth for September 1988 and April 1989. Note that the measured dissolved oxygen is always within ~15% of the saturated value. The figure demonstrates the increase in deep-lake oxygen from fall/winter to spring/summer. The line of oxygen solubility is for April and is calculated from equations presented in Benson and Krause (1984). Solubility is calculated with respect to atmospheric saturation of dissolved oxygen at the *in situ* temperature.

of dissolved oxygen at all times sampled. Mass balance calculations indicate that for the 1988-89 field season 30-45% of deep lake water was exchanged with aerated surface water. This implies a characteristic time scale of deep lake ventilation between 2 and 4 years.

CTD data collected at the same time as the dissolved oxygen data and thermistor chain data also provide evidence for the exchange of surface water with water from the deep hypolimnion. A one dimensional approximation of the heat budget in the deep north basin from January 1990 to July 1990 (Fig. 10) indicates that a net loss of heat (225 kcal m^{-2}) occurred between January 1990 and July 1990 in north basin deep water (> 475 m). This calculation simply represents the difference in the heat contents of the deep north basin between January and July 1990. This loss of heat is due to the transfer of the warmer deep-water upward, providing further evidence for exchange between surface and deep water. Both the dissolved-oxygen data and the CTD data are consistent with the deep-water cooling evident in the thermistor chain data collected from the south basin (Fig. 4).

The deep lake thermistor chain data imply that deep-lake vertical mixing lasted approximately one month during the winter of 1990 (Fig. 4). Most of the thermistors in this chain recorded the maximum in deep-lake temperature in early February. After this time the deep lake underwent cooling until it again began to warm. Water-column cooling occurs during a period of reduced upper water-column stability, which is due to a reduction in stratification as described in the previous sections. During a minimum in water-column stability, cold waters from the upper 200-300 m exchange with the deeper warmer waters.

There are two phases of deep lake mixing which are illustrated in Fig. 11 - a turbulent diffusion phase and a sudden or episodic convective mixing phase. The gradual decrease in temperature between 1 February and 20 February, over the depth interval 350 m to 420 m is a result of mixing the colder water from above with the deeper warm water and can be modeled with a turbulent diffusion model:

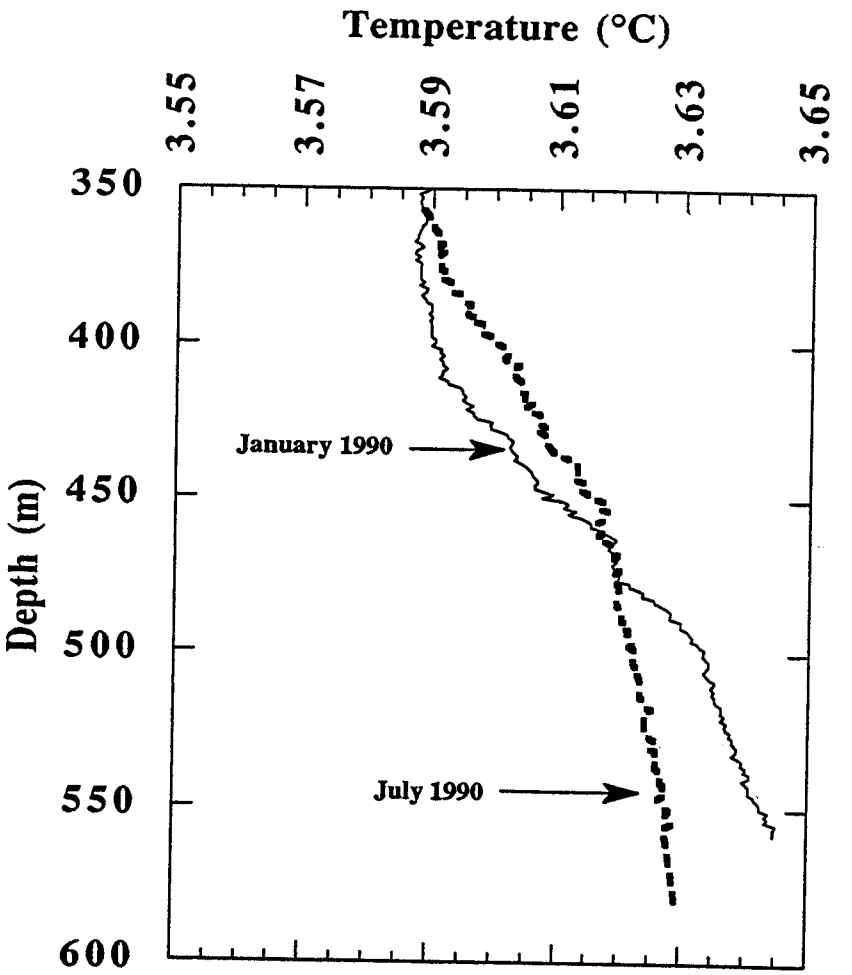


Figure 10. Temperature as a function of depth for January 1990 and July 1990. The cooling of the deep water column due to the exchange of surface water with deep lake water during the winter results in a lower total heat content of the deep water measured in July 1990.

$$F_H(z,t) = \int_0^z rC\,(\partial T[z,t]/\partial t)_z\,dz \qquad (1)$$

and

$$F_H(z,t) = -rC\,K[z,t]\,(\partial T[z,t]/\partial z)_t \qquad (2)$$

In eqn. 1 and 2, F_H is the heat flux, $\partial T/\partial z$ and $\partial T/\partial t$ are the slopes of the temperature versus depth and temperature versus time relationships respectively (Li 1973), and r and C are the density and the specific heat capacity, respectively. The vertical diffusion coefficient (K[z,t]) evaluated from this data is $1.5 - 2 \times 10^{-3}$ m^2 sec^{-1}. This diffusion coefficient is compared to the effective diffusion coefficient calculated for the hypolimnion during periods of upper water surface stratification, later in the text.

We hypothesize that the majority of the exchange between surface and deep water occurs by way of a mechanism that is similar to that proposed by Farmer and Carmack (1981), Carmack and Farmer (1982), Carmack et al. (1989), Carmack and Weiss (1991), and Weiss et al. (1991). This mechanism relies on the effects of pressure on the temperature of maximum density and has, therefore, been termed "thermobaric instability" (Carmack et al. 1989, Carmack and Weiss 1991). Because the temperature of maximum density decreases with increasing pressure, colder water overlying warmer water becomes "conditionally unstable" with respect to water immediately below. Wind forcing and/or internal waves displace a water parcel vertically to a depth where its temperature is closer to the temperature of maximum density than the ambient water at that depth. Once the parcel is displaced, it will continue to descend through the water column, because of its greater density relative to the surrounding water, until it reaches a point of neutral stability.

A requirement for the deep penetration of a water parcel is that DS Dz^{-1} (the vertical salinity gradient) is approximately equal to zero or is negligible compared to the temperature and pressure effects on the density of adjacent water parcels. In Lake Baikal, U.S.S.R., where the results of this process have been clearly shown, this requirement is satisfied (Carmack et al. 1989, Carmack and Weiss 1991,Weiss et al. 1991, Falkner et al. 1991). Surface water descends in Lake Baikal through the water column to near-bottom depths with a well-preserved surface signature in

temperature, dissolved oxygen, and other geochemical tracers (Carmack and Weiss, 1991, Weiss et al. 1991). In Crater Lake between the depths of 200 and 400 m, the approximation of $\Delta S\ \Delta z^{-1} = 0$ may hold; however, the gradual increases in salinity below this depth range will increase the density of the ambient fluid making exchange of the colder, less salty fluids (upper waters) with the warmer, saltier fluids more difficult.

Using estimates of the salinity gradient obtained from January 1990 CTD data and the thermistor data presented in Fig. 11a, we calculate that the density, relative to 400 dbars, of the water above 390 m on 22 February is more dense than the water below 400 m. The temperature profile for the following day shows that there has been some apparent exchange between the colder water from above and the warmer water below, resulting in colder waters now underlying warmer water (Fig. 11b). In the subsequent days there are rapid changes in the vertical temperature distribution in this part of the water column, eventually resulting in a stable density gradient. It is also apparent from the figure that the near-bottom waters have not been mixed to the same degree as the waters above 420 m. The net effect of mixing dense cold waters from above with warm, salty waters from below is that any instability-driven mixing decreases in effectiveness with increasing depth in Crater Lake due to the resisting force of the salinity gradient. In addition, the surface temperature and oxygen signal will simply decrease as it mixes with ambient waters during its decent to the deep lake.

It is reasonable to expect that the magnitude or effectiveness of this type of mixing will vary from year to year. As surface waters cool below the temperature of maximum density, the upper waters become restratified. The rate of cooling and restratification of the upper waters will influence the "completeness" of deep water ventilation. This ventilation is more likely to occur during the winter mixing phase rather than in the spring. Although thermally driven convection will also occur during spring warming, calmer weather at Crater Lake typically dominates during spring. Thus, heating of surface water occurs fairly rapidly, thereby making vertical exchange less likely or less efficient during this period. Year-to-year climate variations will, therefore, affect the extent of annual vertical exchange. This has recently been demonstrated by McCormick (1990)

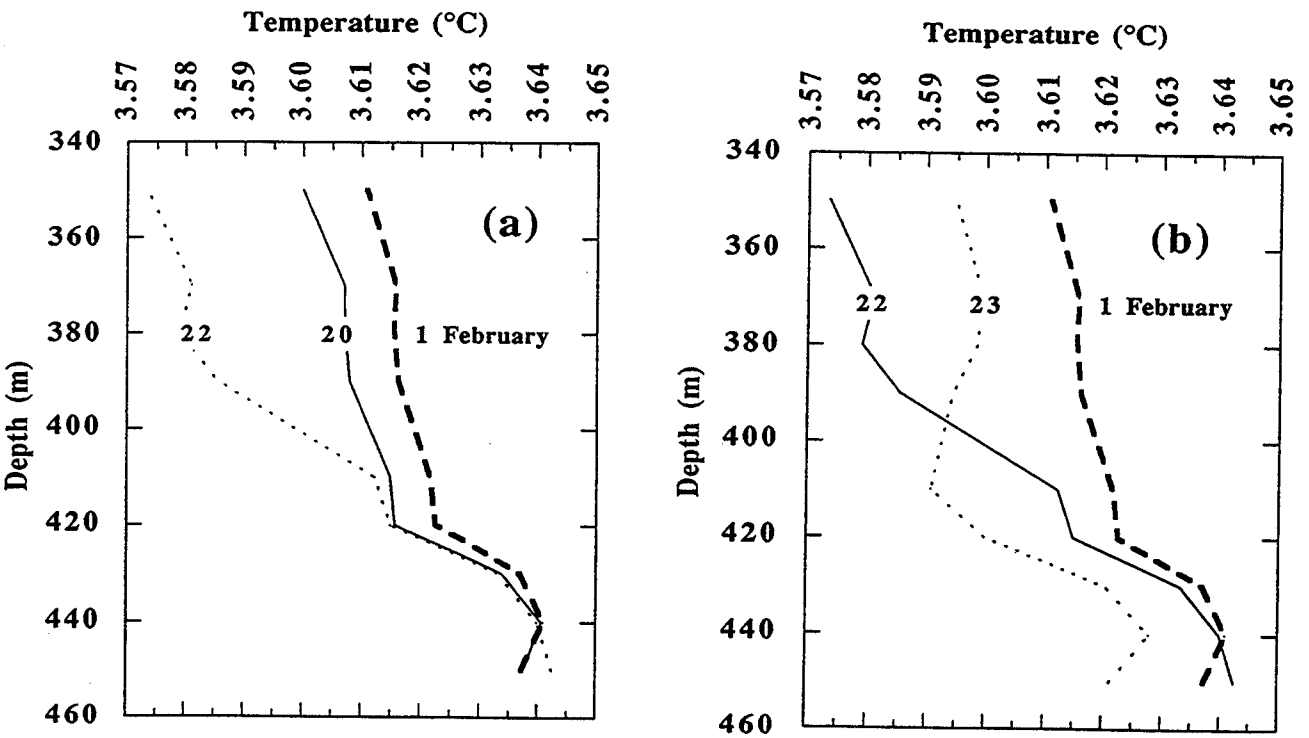


Figure 11. (a) Temperature as a function of depth for 1, 20, and 22 February. (b) Temperature vs depth for 1, 22, and 23 February. In (a) the diffusion of cold water from above dominates the mixing process from 1 February to 20 February. This is followed by the development of an unstable deep water column due to the accelerated (sudden) mixing of cold water from above.

who finds that circulation models coupled with global climate models predict that during warmer years, Lake Michigan may not completely turn over and a permanent thermocline may form in the deep regions of the lake.

The oxygen and temperature data presented here suggest that the annual exchange of surface water with deep water is a critical process for the vertical redistribution of heat and salt in the lake. It is difficult to predict the annual magnitude or extent of this mixing process in the water column without a yearly time series of data. It is likely that a comprehensive model of surface-to-bottom exchange is impossible without detailed meteorological data as well as water column chemistry and temperature data. Pearle et al. (1975) used the appearance of nitrate enrichments in the surface waters to estimate the timing of turnover; unfortunately, we can not apply this approach to the Crater Lake system without frequent collection of nitrate data throughout the year. Crater Lake's inaccessibility makes this method difficult. Some enrichments in surface nitrate have been observed during early April in the upper isothermal layer (Larson 1988); however, it is not clear if these observed surface enrichments are due to upwelling of bottom water, atmospheric inputs, or some combination of the two.

Transport of heat and salt through the deep lake

Deep-lake mixing of hydrothermal fluids during periods of upper water column stratification takes place through a variety of horizontal and vertical mixing processes. Without an understanding of the time scales of this mixing, we can not place confidence in our method for determining the hydrothermal component of the deep lake heat and salt budgets as discussed earlier. This section is, therefore, primarily concerned with understanding the transport of hydrothermal fluids through the deep lake, i.e. deeper than 350 m, during periods of thermal stratification.

Horizontal mixing in the deep lake. During thermal stratification of the upper water column, horizontal basin-to-basin exchange processes dominate deep-lake mixing. This mixing is indicated by changes in the vertical distribution of temperature, salinity, and other geochemical tracers (e.g. dissolved gases and trace elements).

CTD data taken from the north basin in September 1988 show that the vertical temperature and salinity distribution may deviate from the normal near-linear increase with depth (cf. Fig. 1 with Fig. 12). We refer to such variations in the vertical gradients as "microstructure" features. We propose that these features are due to the lateral flow of hydrothermally enriched water from the south basin. As the south basin fills with warm, salty water, it will "spill over" into the deeper portions of the lake because of its greater density relative to non-enriched fluids. The sill depth between these two basins is between a depth of 425 and 450 m. The sill depth corresponds to the depth of the microstructure features observed in the south basin (near the sediment-water interface) and the north basin (mid-water column) (Fig. 12a). The presence of warmer waters in both basins at the same depth (~425 m) supports our hypothesis that the fluids originated in the south basin.

In order to accurately assess the stability of the deep-water column in September 1988, we computed $\sigma_{0.5}$. Where $\sigma_{0.5} = (\rho_{0.5} - 1) \times 1000$ and $\rho_{0.5}$ is the potential density of a fluid at 500 dbars. In deep aquatic systems, σ_θ does not accurately represent the local "stability" of the water column (Fig. 12d). This is due to the effect of pressure on the density of a fluid, where σ_θ is calculated for 1 atm pressure as opposed to a pressure more representative of two deep parcels of water under consideration (i.e. 500 dbars pressure). Most of the water throughout the water column appears to be statically stable with respect to 500 dbars (Fig. 12c); however, stability calculations for some individual points within the water column suggest that there are some unstable parcels of water. These parcels are unstable over vertical distances of 5-10 m. Because changes in the vertical density structure on this scale approach the resolution of our instrument, there is significant uncertainty associated with classifying the "stability" of parcels of water over this depth range. The thermal structure of the deep lake, shown in Fig. 12a, tends to vary over periods of hours. In addition, when we've been able to revisit the lake within weeks of observing these microstructure features, they are no longer present in the water column. These additional observations suggest that these features are indeed unstable and transient.

^{222}Rn and Fe (dissolved and particulate) measurements further illustrate the basin-to-basin exchange process. Water with high ^{222}Rn and Fe contents overlay water of lower ^{222}Rn and Fe

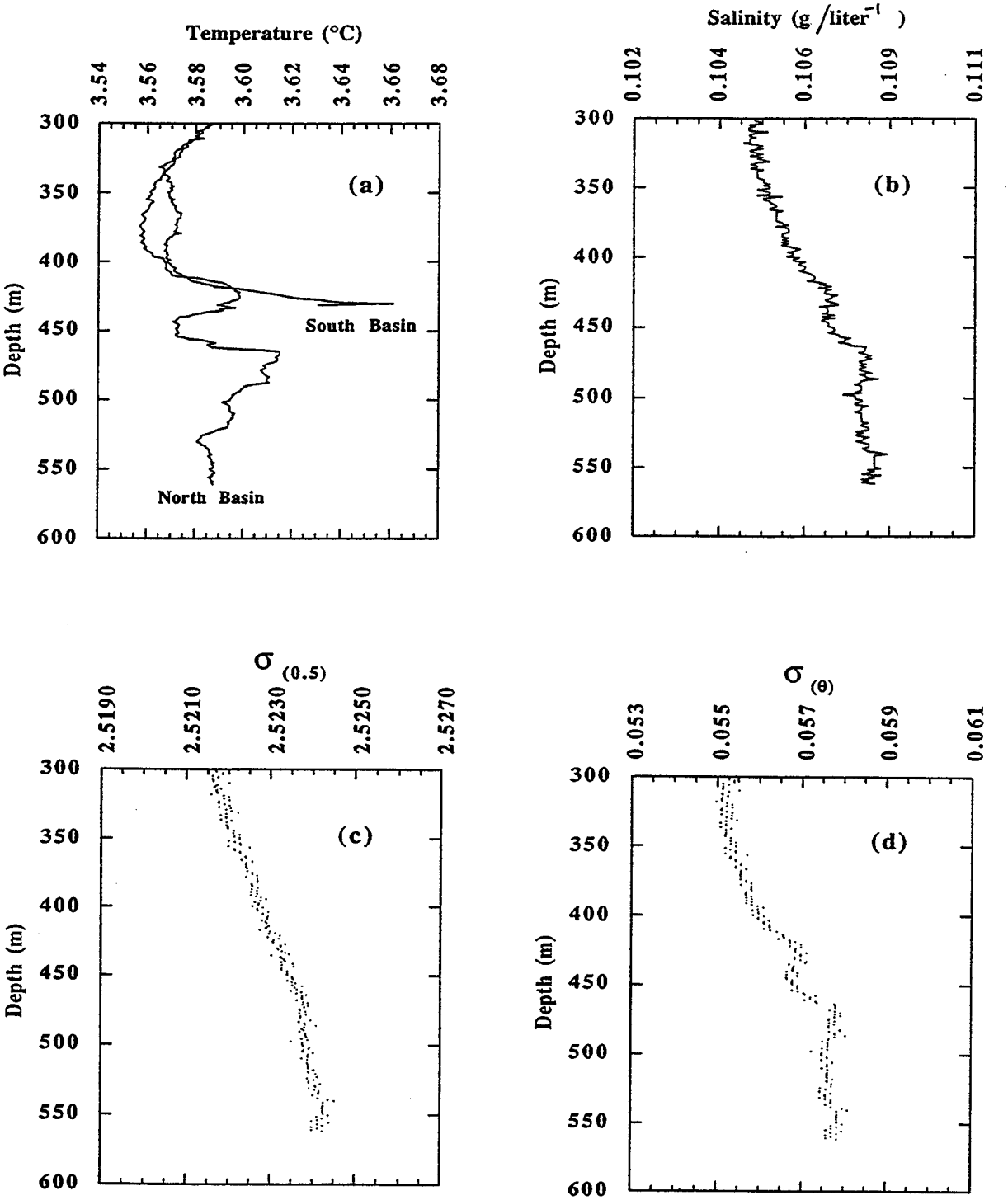


Figure 12. Hydrographic data taken 19 September 1988. (a) Temperature as a function of depth for both the south and the north basins, (b) Salinity as a function of depth for the north basin, (c) $\sigma_{0.5}$ as a function of depth for the north basin, (d) σ_θ as a function of depth for the north basin. Densities are calculated from equations presented in Chen and Millero (1986).

content in the north basin (Fig. 13). These single profiles exhibit the net effect of horizontal exchange. Both ^{222}Rn and Fe are time-dependent tracers of the south basin's hydrothermally enriched water. Iron is highly reactive in well-oxygenated environments and is only found at high concentrations near reduced sediments or hydrothermal vents. Radon is a radioisotope with a half-life of ~3.8 days. It too should only be found near a hydrothermal vent or in the sediments in Crater Lake. The horizontal transport of iron from the south basin leads to a maximum in dissolved and particulate Fe between 450 and 500 m in the north basin (Fig. 13a). ^{222}Rn also exhibits a deep-water maximum at ~475 m in the north basin (Fig. 13b). The net effect of the proposed horizontal movement of waters from the south basin to the north basin is that "younger" (^{222}Rn-enriched) waters overlay the "older" (^{222}Rn-depleted) waters in the north basin.

Although the water column features, indicative of horizontal mixing, have been observed at various times throughout the summer, the most dramatic features are consistently observed in late summer or early fall (September-October). These periods of more-intense horizontal exchange have larger thermal anomalies in the north basin than those typically observed during the summer. Since September and October are periods of thermal stratification, surface disturbances can not supply the necessary forcing for the initiation of this deep lake mixing process.

From our hydrothermal fluid inflow and composition estimates, and the observed near-bottom salinities of south basin waters, we estimate that the south basin could "fill-up" with a mixture of hydrothermal and ambient fluid on the time scale of several weeks to months. The horizontal exchange process proposed here is not necessarily a continuous process. Consequently, the non-steady-state nature of this mixing process in the deep lake results in the relatively large uncertainty (1σ) in the net heat and salt flux estimates, which are based on a few individual vertical profiles (Table 1).

Vertical mixing processes in the deep lake. In addition to horizontal advection playing a large role in the transport of heat and salt through the deep lake, we propose that turbulent diffusion coupled with vertical convection transport heat and salt transport through the hypolimnion. We base this hypothesis on two observations: (1) because the calculated effective

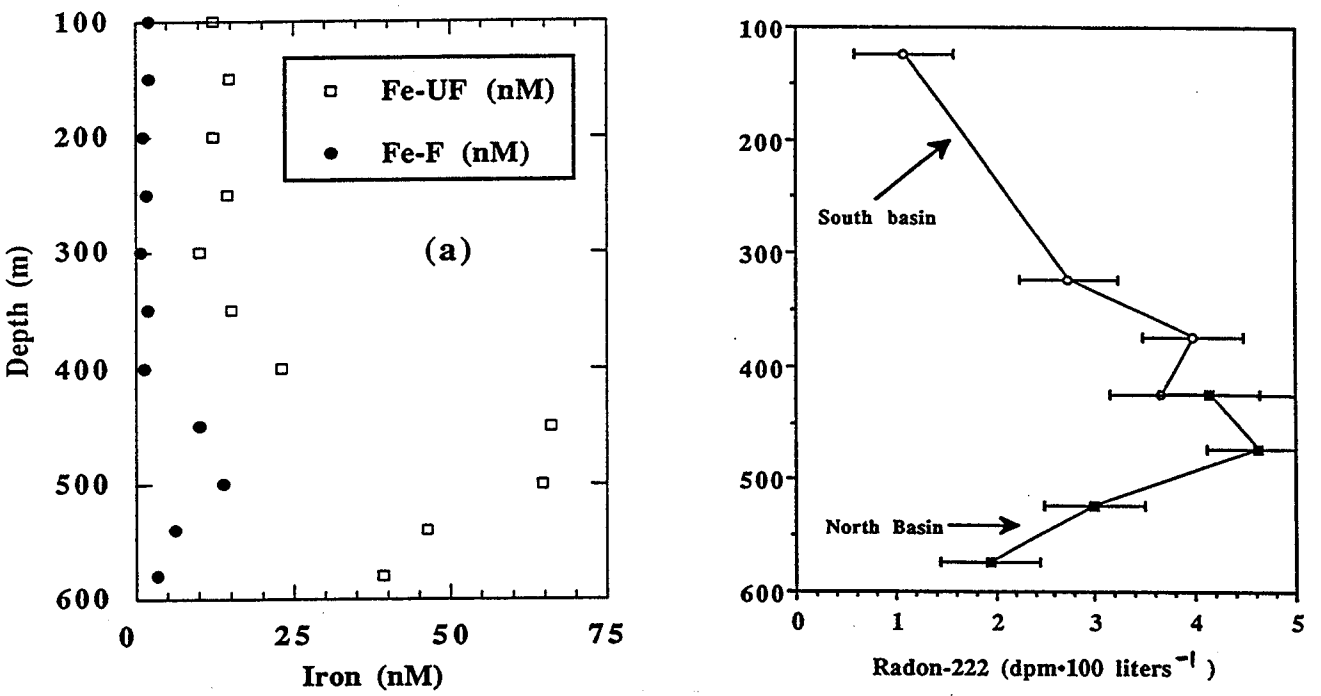


Figure 13. (a) Dissolved and particulate iron as a function of depth from the north basin (data from Collier et al. 1990). (b) ^{222}Rn as a function of depth for the north and south basin. Although not on the graph, the deepest ^{222}Rn value from the particular south basin hydrocast shown on the figure was 35 dpm 100 l^{-1}.

vertical diffusivities for both heat and salt in Crater Lake are the same order of magnitude (10^{-4} m^2 sec^{-1}) and are many orders of magnitude larger than the molecular values (10^{-7}-10^{-9} m^2 sec^{-1} for heat and salt respectively), the mixing process can not be accounted for by molecular diffusion (or double diffusion); (2) there are small-scale vertical thermal instabilities in the water column which do not appear to be due to the horizontal transport of heat and salt described in the previous section.

The effective diffusivities for heat (K_{eT}) and salt (K_{eS}) can be modeled according to a simple diffusion model (see equations 1 and 2 for the development);

$$F_T = K_{eT}\left(\frac{dT}{dz}\right) \qquad (3)$$

and

$$F_S = K_{eS}\left(\frac{dS}{dz}\right) \qquad (4)$$

where F_T and F_S are the measured flux of temperature (°C m s^{-1}) and salt (g m kg^{-1} s^{-1}), respectively. For dimensional simplicity we use F_T as opposed to F_H -- the heat flux. These measurements are again based on time-series CTD measurements (Table 1). Our calculations reveal that the effective diffusivities for heat and salt are approximately 6 to 8 x 10^{-4} m^2 s^{-1}. If molecular diffusion was an important mechanism for the transport of heat and salt through the water column, the calculated effective diffusivity for heat should be two orders of magnitude larger than the effective diffusivity for salt. The effective diffusion coefficient calculated here for the summer-fall period is approximately a factor of two smaller than the diffusion coefficient calculated (earlier in the text) for diffusion during the month of February ~2 x 10^{-3} m^2 sec^{-1}. This observation suggests that the intensity of deep-lake mixing during the winter is slightly greater than during the summer. This is reasonable because the overall stability of the upper water column is greater during the summer than during the winter. However, at all times, turbulent diffusion processes will obviously be smaller in magnitude than the instability-driven convection from the upper lake described earlier in the text.

Observations of small temperature inversions through the mid-water column suggest the presence of small, buoyant "plumes" (Fig. 14). Salinity profiles lack the sensitivity of the temperature profiles and do not show this effect. Therefore we can not accurately calculate the stability of these thermal features. Our data suggest however that they are transient features that occasionally occur in the mid-to-deep lake. These "plumes" could be caused by either of two processes (or some combination of the two). The plumes may be caused by direct inputs of buoyant water into the south basin. Alternatively, they may be generated by conductive heating or double-diffusive development of thermally and chemically enriched waters resting at the sediment-water interface. These processes could eventually lead to instability and formation of thermal convection cells that vertically mix the excess heat and salt.

An alternate convective mechanism for mixing heat and salt through the water column, is suggested as a large temperature anomaly in the middle of the water column (Fig. 15a). We observed this temperature anomaly in the south basin of Crater Lake on 11 September 1987. This anomaly is greater than 0.1°C between 225 and 275 m, relative to the north basin profile. This corresponds to a total heat anomaly of 9600 kcal m^{-2}, which is a factor of five to ten larger than typical near-bottom thermal anomalies measured in the south basin (McManus 1992). Shown with this data (Fig. 15a) are temperature profiles taken from the south basin approximately 6 hours earlier (solid line) and the north basin approximately 3 hours earlier (dotted line). Although the two south basin profiles are from the same general location, they may be separated in space by as much as 500-1,000 meters. T-S diagrams (Fig. 15b-d) of the three hydrocasts (below 100 m) illustrate the dramatic change in the characteristics of the large thermal anomaly. However, the T-S diagrams of all the CTD data show some influence of the warmer, more-saline water, suggesting that the heat and salt seen in SBE028 may be spreading horizontally along a constant density surface.

This large thermal anomaly is hydrostaticly stable with respect to 250 dbars and is buoyant relative to 450 dbars. This suggests that perhaps the water column anomaly represents a "plume" that originated at the sediment-water interface and has risen to neutral buoyancy. Alternatively,

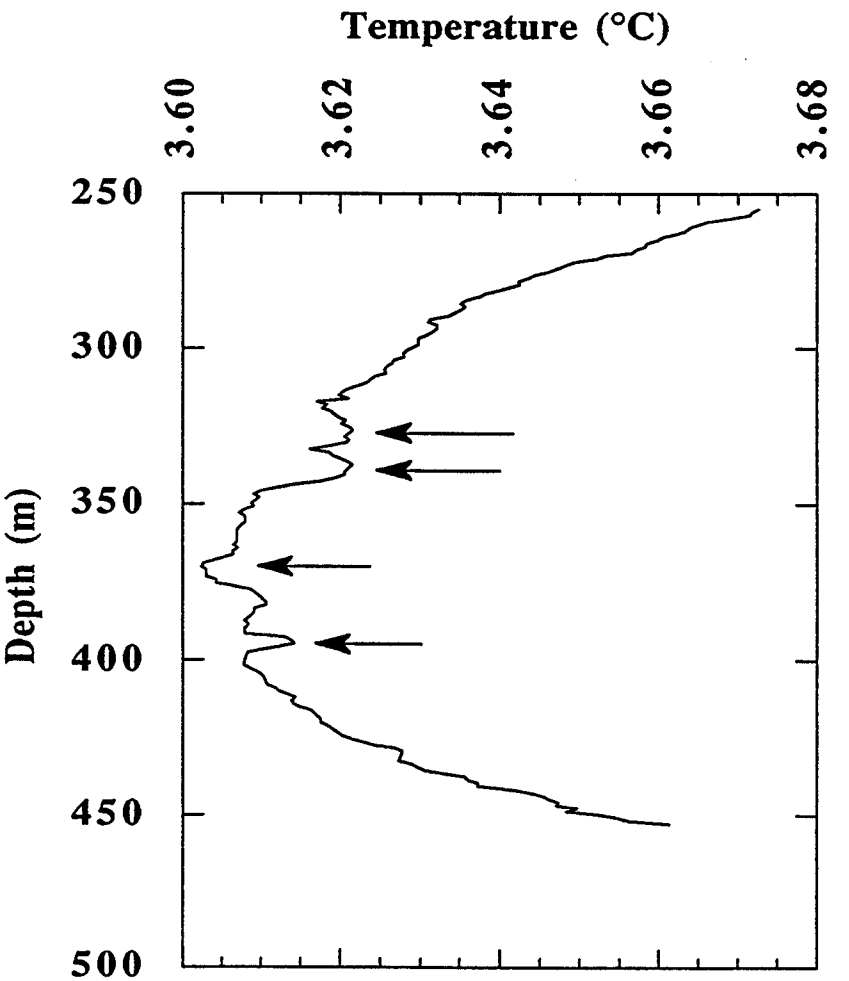


Figure 14. Examples of vertical instabilities (arrows). Data is from 18 September 1990 from the south basin.

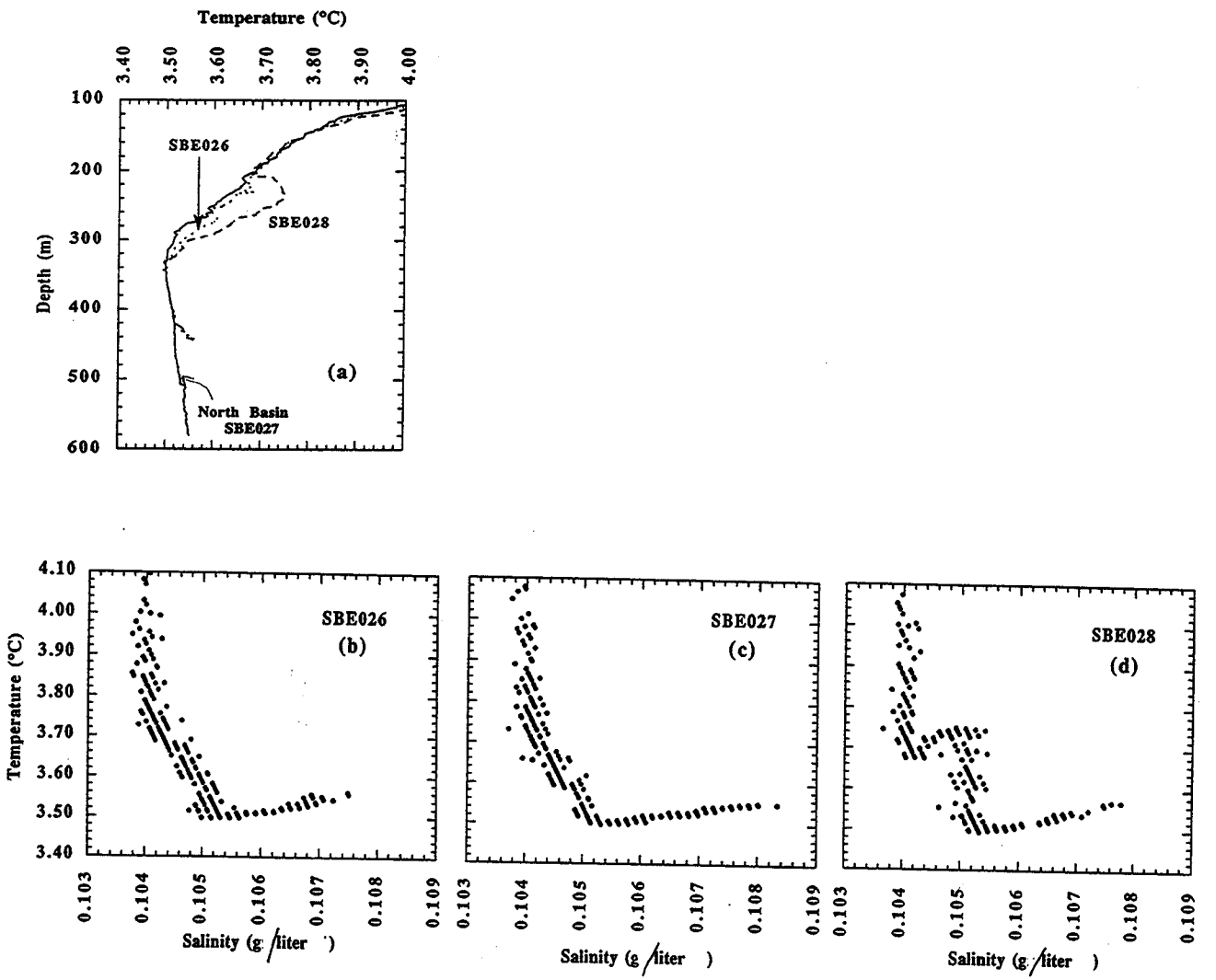


Figure 15. (a) Temperature as a function of depth for SBE026 (solid line, south basin), SBE027 (dotted line, north basin), and SBE027 (dashed line, south basin). (b-d) T-S diagrams for the three hydrocasts. Data shows the T-S anomaly in all three hydrocasts, but is particularly striking for SBE028.

there could be a source of thermally enriched and chemically enriched water along the caldera wall at this depth, which we have not observed to date.

Our calculations suggest that turbulent diffusion rather than by molecular or double diffusion dominates vertical mixing in the deep lake. However, the mechanism that initiates turbulence in Crater Lake is not known. Horizontal advection followed by vertical mixing and vertical convection also play a role in the vertical redistribution of heat and salt through the water column. As would be expected, our calculated diffusion coefficients for the deep lake are larger than values for the region just below the thermocline (50-150 m) in Crater Lake (10^{-5} - 10^{-6} m^2 sec^{-1}). Also, the range in diffusion coefficients calculated for the deep lake (6-20 x 10^{-4} m^2 s^{-1}) compares well with the range for the deep ocean (O[1-100 x 10^{-4} $m^2 s^{-1}$]) as derived from ^{222}Rn-depth profiles (Sarmiento et al. 1976). This comparison illustrates the importance of turbulence in the redistribution of heat and salt in the hypolimnion.

The physical processes described here appear to be directly tied to the active input of thermally and chemically enriched waters and because of these processes the deep lake remains relatively well mixed.

Summary

Our estimates of the deep lake heat budget of Crater Lake are consistent with the previous estimates of Williams and Von Herzen (1983). Because our methods are independent from those of Williams and Von Herzen (1983), who used sediment heat flow measurements, the agreement between the two data sets supports our results. Our data provide the first direct observations of the accumulation of heat and salt in the deep lake and lead to direct estimates of these fluxes.

Dissolved oxygen data, thermistor chain data, and CTD data all indicate that annual vertical mixing is significant in the Crater Lake. Our data also indicate that such ventilation is incomplete, resulting in undersaturation of dissolved oxygen at all times in the hypolimnion. The lack of complete water column mixing in Crater Lake is a consequence of the lake's depth and the vertical density gradient within the deep lake. Incomplete ventilation is a characteristic of deep lakes, and Crater Lake offers a unique environment for the study of deep lake ventilation processes. During

periods of surface stratification, turbulent diffusion and horizontal advection rather than molecular diffusion dominate deep lake mixing, although the forcing mechanism of the turbulence is not known.

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Temperature and Water Quality

Gary L. Larson and C. David McIntire

Introduction

Early studies of the chemical properties and temperature patterns in the water column of Crater Lake were confined to the summer months and were limited in scope (Larson, 1987). However, sufficient data were obtained during these studies to demonstrate the following about the lake: (1) it is thermally stratified in late summer and early fall with a shallow epilimnion; (2) it is slightly basic with a low alkalinity and conductivity; (3) it has very low concentrations of plant nutrients, particularly nitrogen and phosphorus; (4) it has relatively high concentrations of silica and sulfate sulfur; and (5) it is oxygenated throughout the water column. The 10-year study of Crater Lake included an analysis of the chemical properties of the lake at Station 13, with an emphasis on seasonal patterns, and a concurrent evaluation of the most recent data in relation to long-term changes in water quality. In additon, the study was designed to determine if the water column circulated to the lake bottom at any time during the winter or spring months during any year.

Sampling and Analytical Methods

All temperature measurements and water samples for chemical analyses were obtained at Station 13 (see Study Area and Facilities section). Also, some historical temperature data from other studies dating back to 1913 were analyzed along with the more recent data to illustrate long-term trends in the near-surface water of the lake. Samples for nutrient analyses were obtained with 4-l Van Dorn bottles, usually from the depths of 0 m, 5 m, 10 m, 20 m, 60 m, 100 m, 200 m, 300 m, 400 m, 500 m, and 550 m. In general, water quality data presented in this report were collected from 1982 through 1991 in the months of January, March, April, May, June, July, August, September, and October. Not all variables were measured on each sampling date (Tables 1 and 2).

Table 1. A summary of the years and months when measurements of temperature, total alkalinity, dissolved oxygen, pH, and conductivity were made in Crater Lake at station 13 during the 10-year study. Only samples that were included in this analysis are listed.

Time	Temp	Talk	DO	pH	Cond
Year:					
1982	X	X	X	X	
1983	X	X	X	X	
1984	X	X	X	X	
1985	X	X	X	X	
1986	X	X	X	X	X
1987	X	X	X	X	X
1988	X	X	X	X	X
1989	X	X	X	X	X
1990	X	X	X	X	X
1991			X		X
Month:					
Jan	X	X	X	X	X
Mar	X	X	X	X	X
Apr	X	X	X	X	X
May	X	X	X	X	X
Jun	X	X	X	X	X
Jul	X	X	X	X	X
Aug	X	X	X	X	X
Sep	X	X	X	X	X
Oct	X	X	X	X	X

Table 2. A summary of the years and months when measurements of sodium, potassium, magnesium, calcium, sulfate sulfur, silicon, nitrate and ammonium nitrogen, and orthophosphate phosphorus were made in Crater Lake at station 13 during the 10-year study. Only samples that were included in this analysis are listed.

Time	Na	K	Mg	Ca	S	Si	Nit-N	Am-N	Orth-P
Year:									
1983						X	X	X	X
1984						X	X	X	X
1985						X	X	X	X
1986	X	X	X	X	X	X	X	X	X
1987	X	X	X	X	X	X	X	X	X
1988	X	X	X	X	X	X	X	X	X
1989	X	X	X	X	X	X	X	X	X
1990	X	X	X	X	X	X	X	X	X
1991						X	X	X	X
Month:									
Jan	X	X	X	X	X	X	X	X	X
Mar						X	X	X	X
Apr	X	X	X	X	X	X	X	X	X
May	X	X	X	X	X	X	X	X	X
Jun	X	X	X	X	X	X	X	X	X
Jul	X	X	X	X	X	X	X	X	X
Aug	X	X	X	X	X	X	X	X	X
Sep	X	X	X	X	X	X	X	X	X
Oct						X	X	X	X

Temperature was recorded using a Montedoro-Whitney thermister with a 250 m cable between 1982 and 1987; thereafter, measurements were made with a Sea Bird conductivity-temperature depth probe, Model SBE19. The concentration of dissolved oxygen was determined using the modified azide Winkler technique, and percentage saturation, corrected for elevation, was estimated following the method outlined by Wetzel (1975). Total alkalinity was determined colorimetrically (0.018 N H_2SO_4 and brom-cresol green-methyl red) at the Park water laboratory, while nutrient and element analyses were performed by the Cooperative Chemical Analytical Laboratory at Oregon State University using the methods listed in Table 3 (also see Quality Assurance Program of the Cooperative Chemical Analytical Laboratory).

Results

Temperature

Crater Lake was covered by a thin layer of ice and snow for four weeks in January and February of 1985. In 1986, the lake was nearly covered by ice at various times between January and March (Larson 1986, 1987). An ice cover was not observed at any other time during the 10-year study. Historically, ice cover is relatively infrequent.

In the winter and spring the water mass in Crater Lake circulated to a depth of between 200 m and 250 m (see Dissolved Oxygen section), which often resulted in colder water occurring between the surface and a depth of 30 m than between depths of 40 m and 100 m (Fig. 1). In late spring or early summer, the temperature of the lake near the surface increased, and a thermocline formed, usually sometime between July and September. In some years thermal stratification was evident as early as June, while in other years the process was not complete until September (Table 4). In all years of the study, the epilimnion was between 5 m and 20 m in depth, and was deepest in September, presumably because of cooler air temperatures and an increase in mixing generated by storm events in

Table 3. Methods used for the measurement of chemical and physical variables for samples obtained in Crater Lake during the period from 1982 through 1990.

Variable	Chemical/Physical Method
pH	Electrometric glass electrode (Radiometer, Model G202L, reference electrode mercury-mercury chloride half cell K401) with temperature compensation, Radiometer type TTIC
Conducitivity	Wheatstone Bridge, Yellow Springs model 33, temperature corrected to 25 C
Nitrate-N	Technicon Autoanalyzer, automated cadmium reduction
Kjeldahl-N	Nessler's Reagent finish
Ammonia-N	Technicon Autoanalyzer, colormetric automated phenate
Total Phosphorus	Persulfate digestion, ascorbic acid finish
Orthophosphate-P	Reactive phosphate, ascorbic acid finish
Sulfur	Technicon Autoanalyzer, method 105-72W
Silica	Technicon Autoanalyzer, method 105-71W/B
Sodium	Flame atomic absorption
Calcium	Flame atomic absorption
Magnesium	Flame atomic absorption
Potassium	Flame atomic absorption

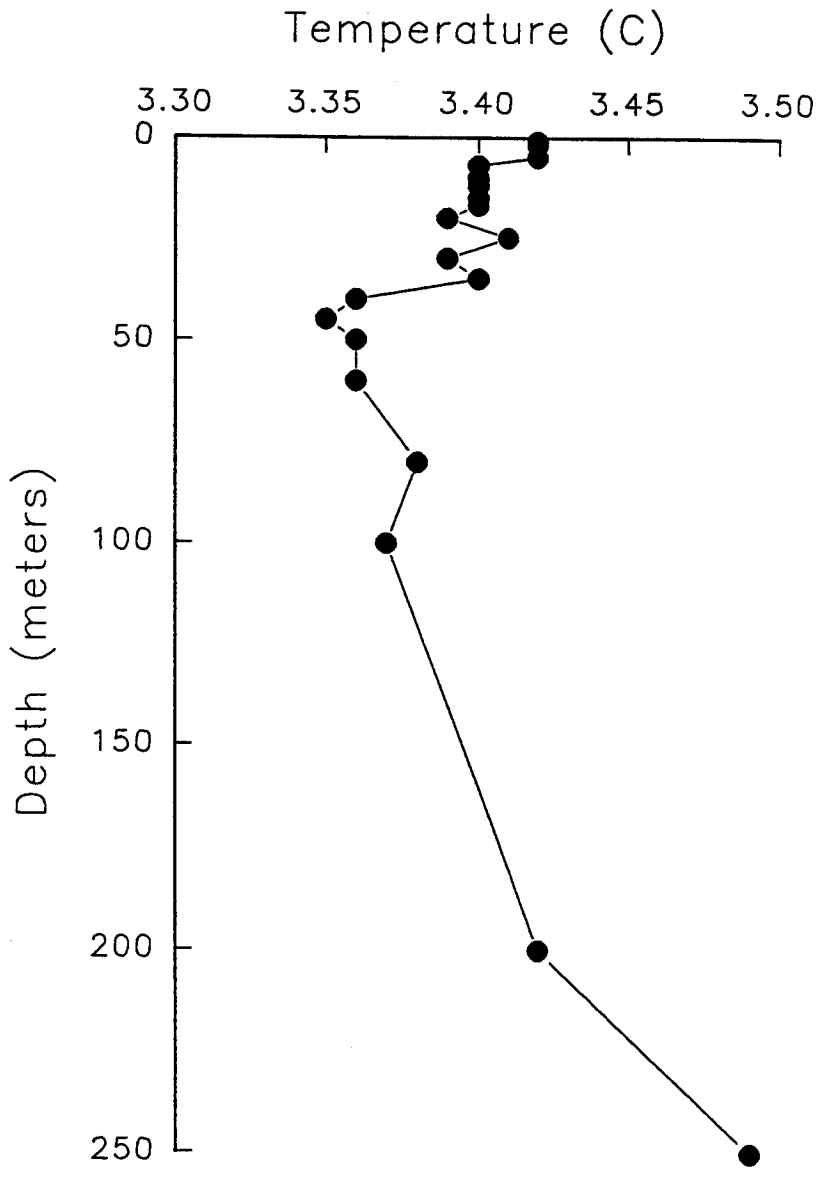


Figure 1. Temperature-depth profile from the water surface to a depth of 250 m at station 13 in April 1987.

Table 4. Approximate depth of the epilimnion during observed periods of thermal stratification in Crater Lake, 1982-1990.

Year	Sample Date	Maximum Depth of Epilimnion (meters)
1982	August 17	9
	September 1	10
	September 7	11
1983	September 2	16
	September 15	9
1984	August 16	8
	August 29	13
	September 12	15
1985	August 20	14
	September 18	20
1986	September 17	20
1987	July 22	10
	September 16	12
1988	July	10
	August	12
	September	16
1989	June	15
	August	10
	September	10
	October	20
1990	June	10
	July	10
	August	12
	September	15

the fall (Table 4). The maximum near-surface water temperature observed in the summer ranged from 14.6 ° C in 1987 and 1989 to 19.2° C in 1982 (Table 5).

The metalimnion in Crater Lake usually extended to a depth of about 80 m (Figs. 2 and 3). Therefore, most of the water volume in the lake during thermal stratification (i.e., water between the depth of 80 m and the bottom) was part of the cold hypolimnion. The minimum temperature in the water column during thermal stratification was located at approximately 250 m below the surface, and owing to adiabatic processes, water temperature increased slightly with depth below this level. The ambient temperature at the bottom of the lake was about 3.5° C (see Dissolved Oxygen section).

Historical data and data obtained during the 10-year study indicated that water temperatures were maximum near the lake surface in August and then decreased in September and October (Fig. 4); temperatures were lowest in the upper 250 m of the water column in March and April (Figs. 4 - 6). At depths of 20 m and 40 m, water temperature gradually increased from May through the month of October, whereas below 40 m, the mean temperature increased slightly in the spring and remained nearly constant in the summer and fall. Because of the unusual pattern of mixing in the deep lake, seasonal variations in water temperature below a depth of 80 m were less than 1° C (Figs. 5 - 6), and only the upper 50 m of the water column exhibited major seasonal changes in temperature. The long-term pattern (between 1896 and 1990) of the near-surface water temperature for the month of August is presented in Figure 7.

pH

The mean pH of all water samples collected at station 13 in Crater Lake between 1982 and 1990 was 7.62. In the upper 20 m of the water column, mean pH ranged from about 7.7 to 7.8 (Fig. 8A), while in January 1987, 1988, and 1990, mean values at the water surface and at a depth of 10 m were slightly lower (Fig. 8B). Below a depth of 20 m, mean pH gradually decreased to a minimum of about 7.4 at a depth of 550 m . The 10-year study

Table 5. Summary of the water quality of Crater Lake, 1982-1990. Data presented as maximum-minimum values for a period from late June or early July to mid-September. Values for pH, total alkalinity, and conductivity are for all samples obtained between the water surface and a depth of 550 m.

Variable	1982*	1983	1984	1985	1986	1987	1988	1989	1990
Temperature (C):									
Surface									
100 m	12.8-19.2	8.8-17.0	12.7-17.7	11.0-16.6	12.4-16.4	9.8-14.6	10.3-17.4	7.9-14.6	9.5-18.0
250 m	3.5-4.2	3.9-4.2	3.9-4.0	4.0-4.3	3.8-4.0	3.9-4.1	4.0-4.2	3.9-4.0	4.2-4.3
	---	3.7	3.6-3.7	3.6-3.7	3.5-3.7	3.5-3.6	3.6-3.7	3.6-3.7***	3.7
pH									
	7.5-7.9	6.9-7.9	7.0-7.9	7.4-8.7	7.4-7.9	7.4-7.9	7.3-8.0	7.1-7.9	7.4-7.9
Total Alkalinity (mg/l):									
	28.8-30.6	29.9-30.7	27.1-30.5	26.5-29.1	25.7-27.5	26.0-29.1	26.8-29.2	26.5-28.5	24.3-31.1
Conductivity (μmhos/cm):									
	---	80-122	100-125**	107-120	112-120	111-119	111-119	110-121	109-120
Dissolved Oxygen (mg/l):									
Surface									
110m									
550m	9.3-12.1	8.5-11.3	8.2-9.5	8.5-9.4	7.8-9.9	7.8-10.1	7.4-9.2	8.3-9.6	7.9-9.6
	11.8-14.4	9.3-11.0	10.4-11.0	9.5-11.4	10.5-12.8	9.4-10.2	9.7-10.3	10.1-10.4	10.1-10.4
	---	---	---	10.0-10.4	9.2-10.0	9.0-9.5	9.1-9.2	9.2-9.4	9.3-9.5

* 0-300 m, except for temperature
** One surface sample of 166 omitted because of suspected contamination
*** 200m

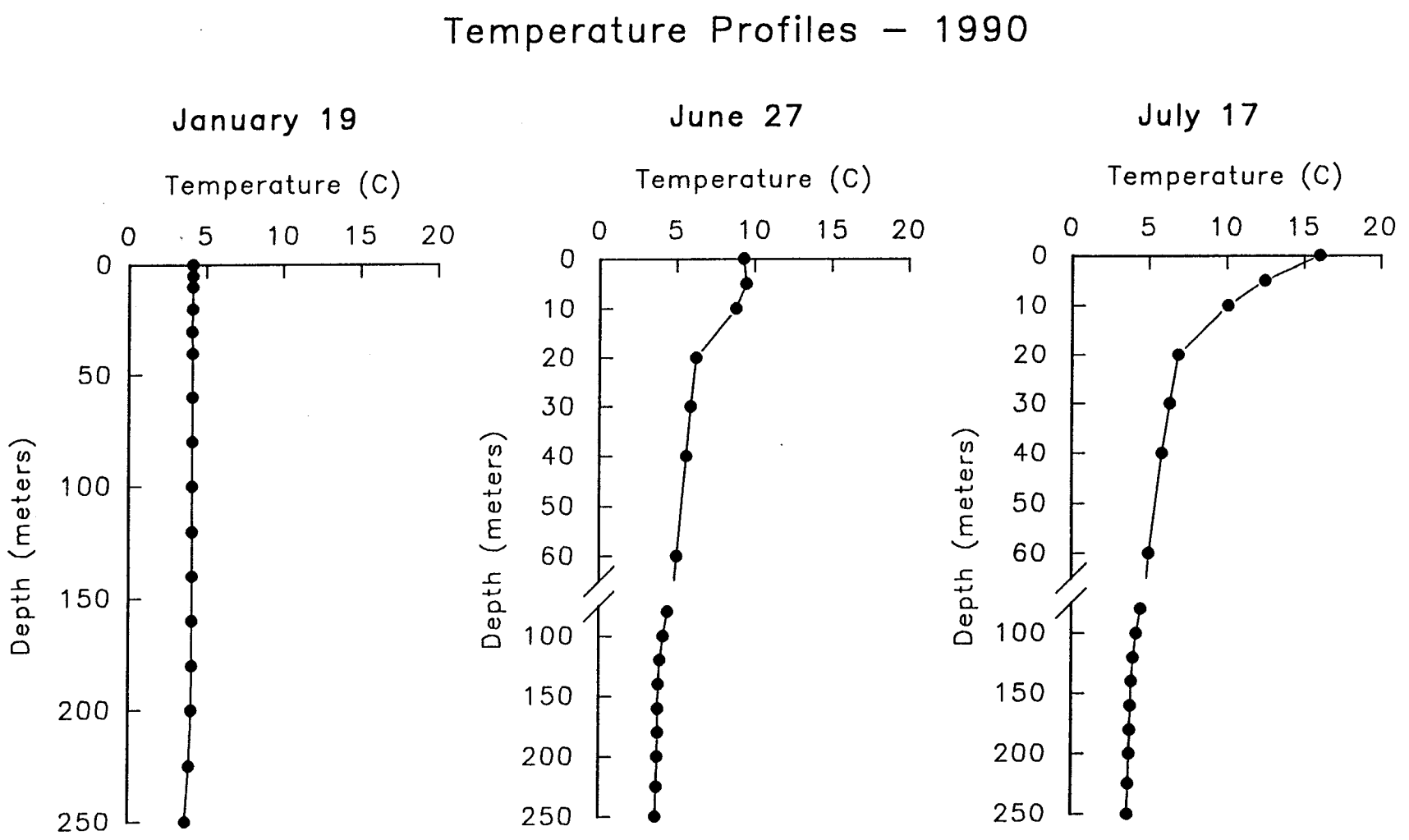


Figure 2. Temperature-depth profiles from the water surface to a depth of 250 m at Station 13 in January, June and July 1990.

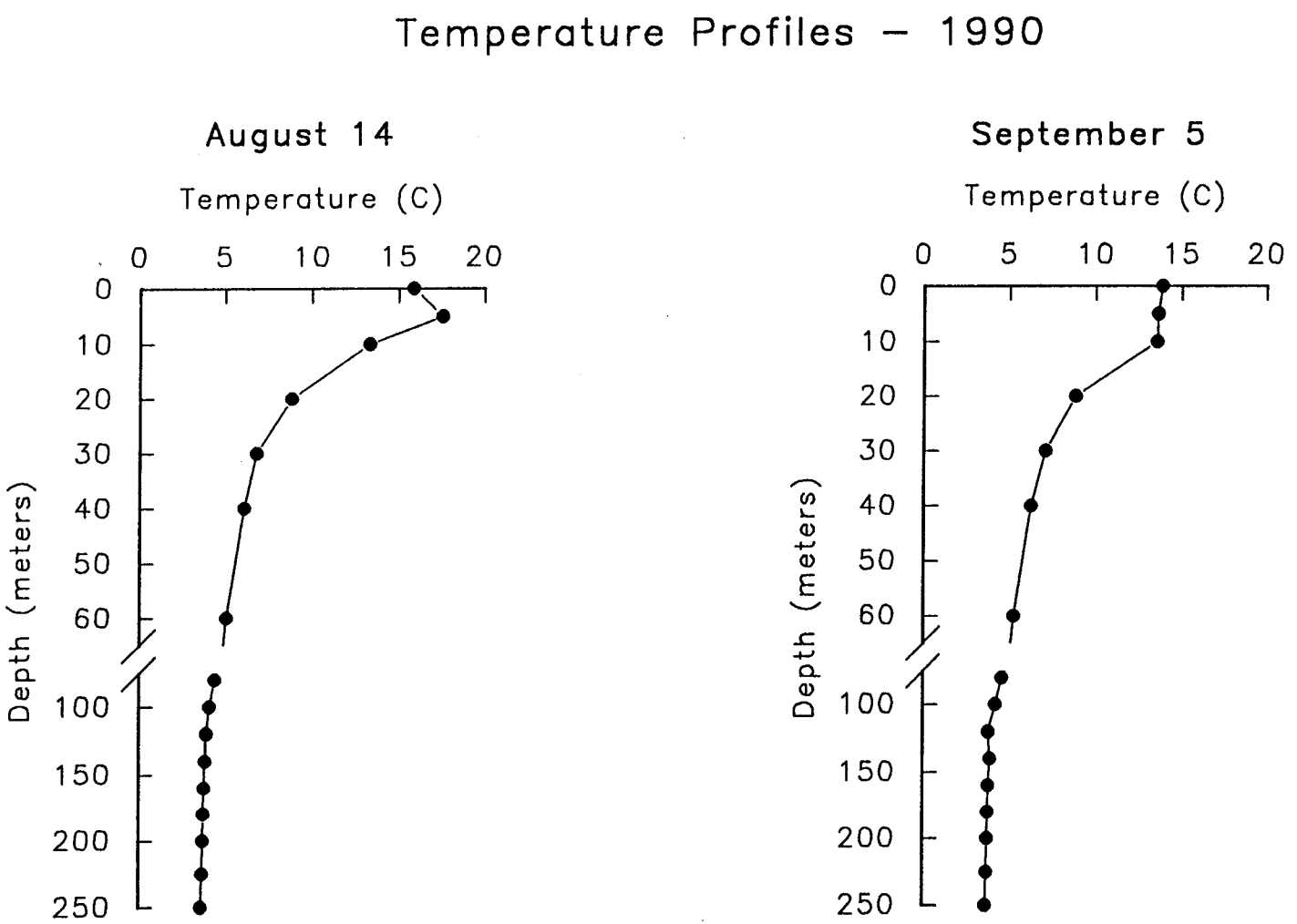


Figure 3. Temperature-depth profiles from teh water surface to a depth of 250 m at station 13 in August and September 1990.

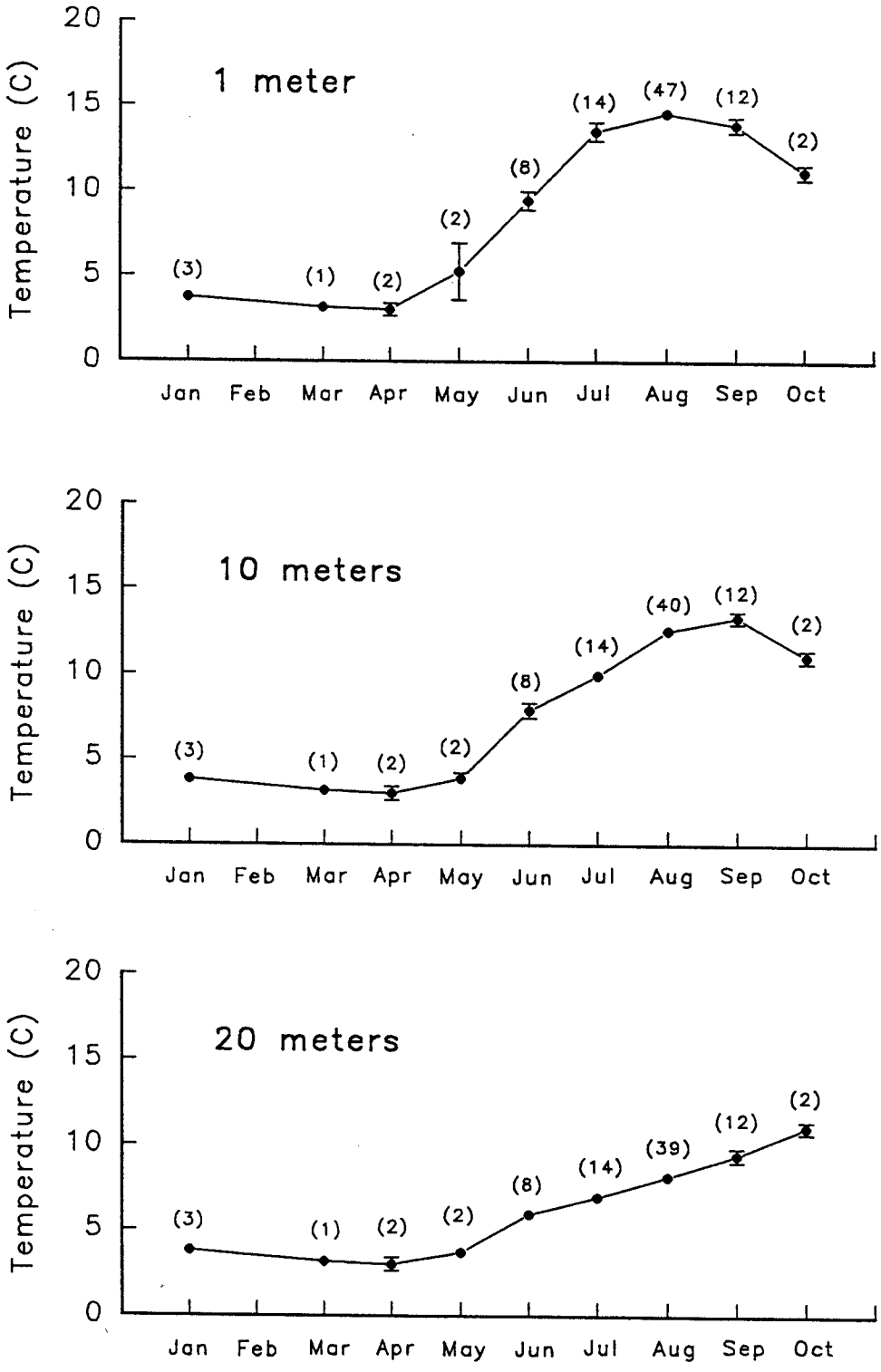


Figure 4. Mean monthly temperatures at the depths of 1 m, 10 m and 20 m at station 13 between 1982 and 1990.

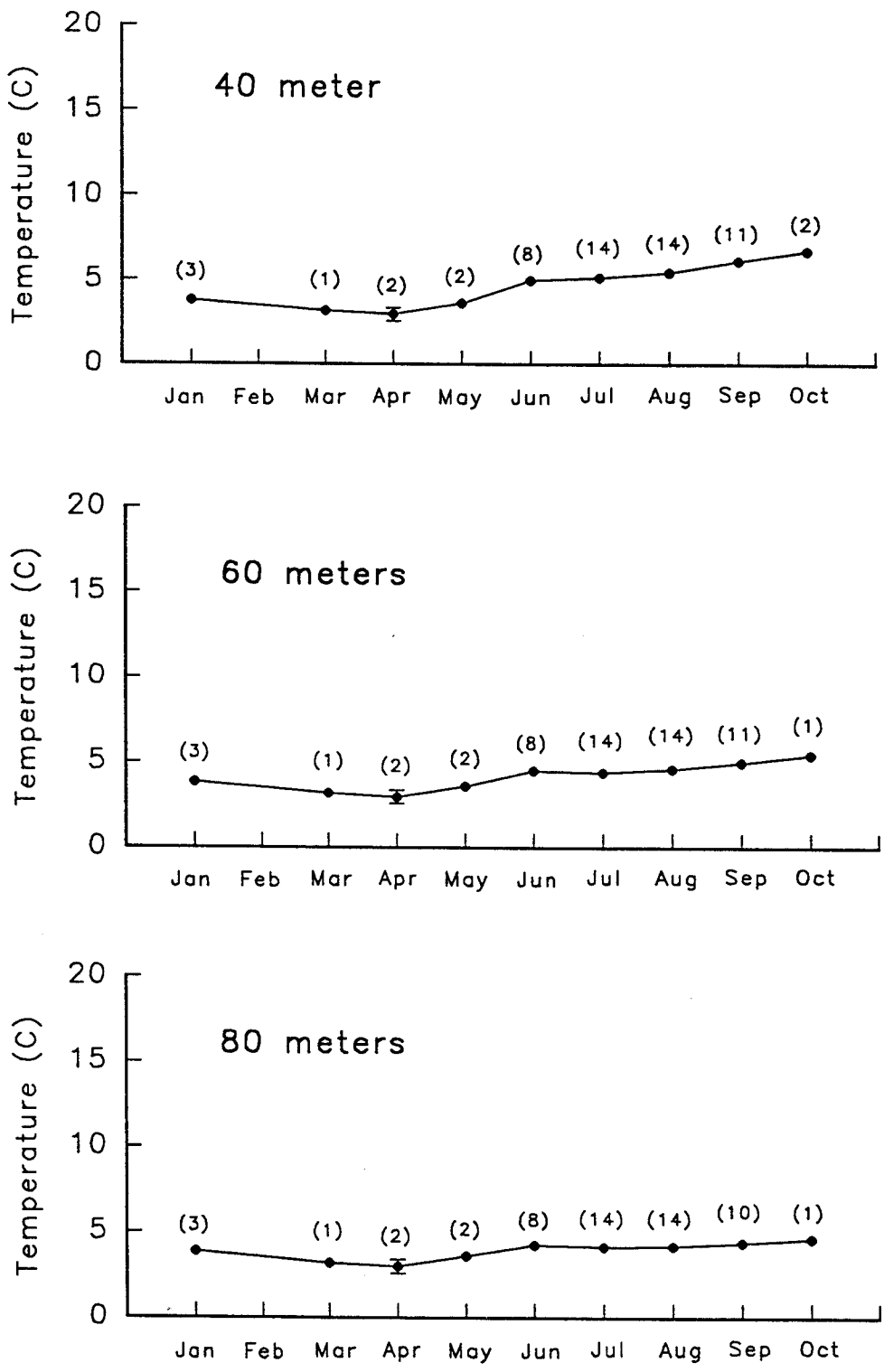


Figure 5. Mean monthly temperatures at the depths of 40 m, 60 m and 80 m at station 13 between 1982 and 1990.

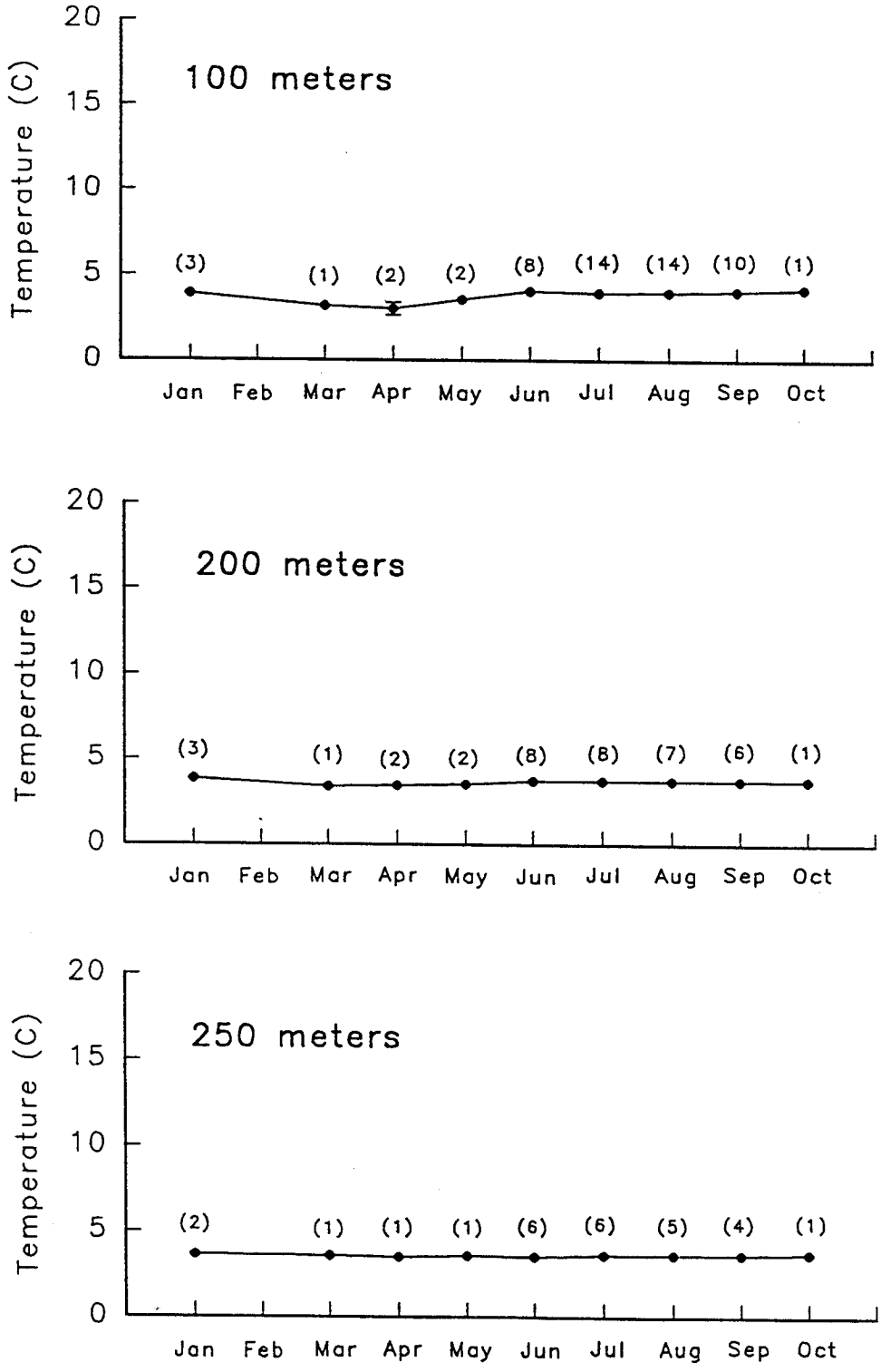


Figure 6. Mean monthly temperatures at the depths of 100 m, 200 m and 250 m at station 13 between 1982 and 1990.

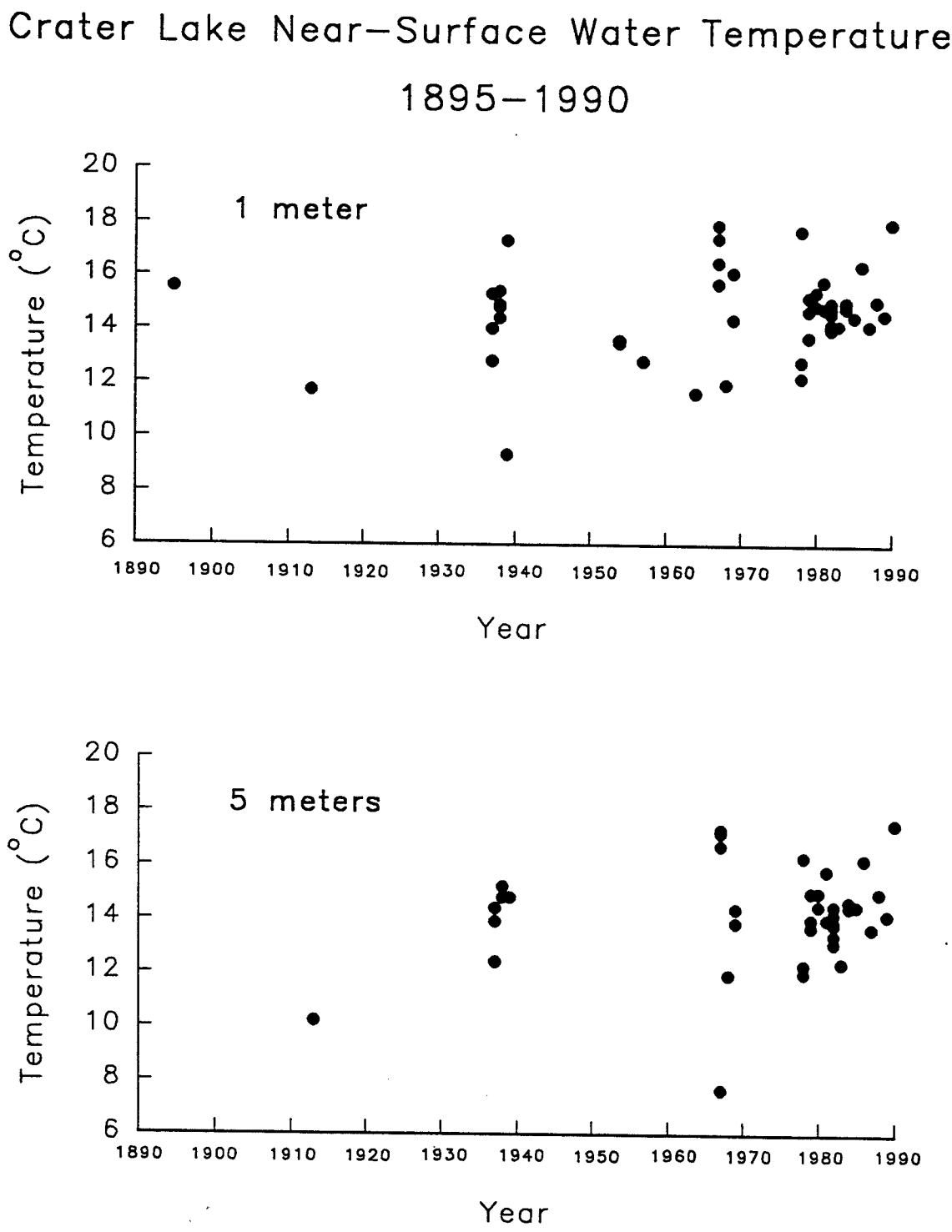


Figure 7. Water temperatures in August at depths of 1 m and 5 m below the water surface of Crater Lake between 1895 and 1990.

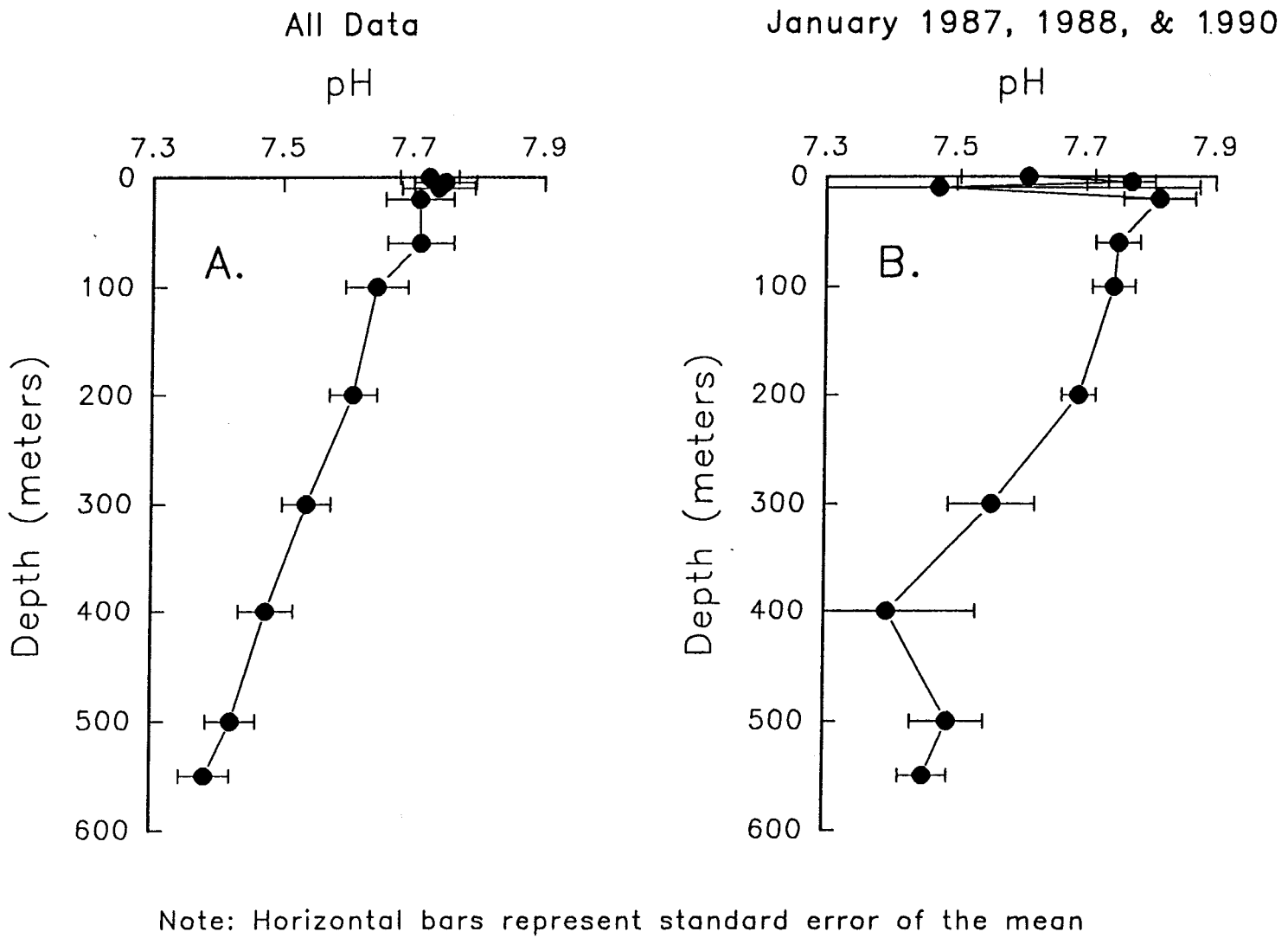


Figure 8. Mean pH depth profile from the water surface to a depth of 550 m for all samples (A) and for the January samples (B) collected at station 13 between 1982 and 1990.

(1982 - 1990) and earlier data collected by the U.S. Geological Survey indicated that there were no obvious changes in the pattern of hydrogen ion activity in the lake since 1961 (Tables 5 and 6).

Total Alkalinity

Mean total alkalinity of all water samples collected at Station 13 between 1982 and 1990 was 27 mg/l. The alkalinity of the near-surface water was slightly less than at greater depths, a difference that was more pronounced in the metaliminion during August (Fig. 9). In general, mean total alkalinity was almost constant in the water column between depths of 100 m and 550 m. Moreover, there were no obvious annual changes in the mean total alkalinity of the lake between 1982 and 1990 (Table 5).

Conductivity

Mean conductivity for all water samples collected at Station 13 between 1982 and 1990 was 115.3 umhos/cm. Conductivity increased between the depths of 200 m and 550 m, reaching a maximum mean value of about 118 umhos/cm near the bottom of the lake (Fig. 10). In the winter and spring the near-surface conductivity was usually lower by 1 or 2 umhos/cm than in the summer and fall when thermal stratification was evident. However, data collected between 1961 and 1990 (Tables 5 and 6) indicated that there were no significant annual changes in the mean conductivity of the lake during this period.

Dissolved Oxygen

The mean concentration of dissolved oxygen was relatively uniform in the water column of Crater Lake in the spring of the year, while in August, when thermal stratification was present, the mean concentration exhibited an orthograde profile in the upper 250 m of the water column (Fig. 11). Below a depth of 250 m there was a slight decrease in the concentration of dissolved oxygen with increasing depth, a pattern that was more evident in

Table 6. Range of selected water quality variables for samples obtained from Crater Lake between 1912 and 1990. All samples were taken near the lake surface from June through September. Conductivity is expressed as μmhos/cm, pH in standard units, and the elements as mg/l. Values for Ca, Mg, Na, K, and S from the present study were obtained since 1986; data for Si was obtained since 1983.

Variable	1912 (Van Winkle & Finkbiner)	1961-1981 (U.S.G.S.)	1982-1990 (Present Work)
pH	---	7.3-7.7	7.1-7.9
Conductivity	---	115-118	80-121*
Si	8.4	8.0-8.9	7.3-9.3
Ca	7.1	6.7-7.3	6.3-7.8
Mg	2.8	2.6	2.6-2.9
Na	11	10-12	10-11
K	2.2	1.7-1.8	1.5-1.9
S	3.7	3.3-3.7	3.1-3/6

*anomalously high value (166 μmhos/cm) measured in July 1984 omitted

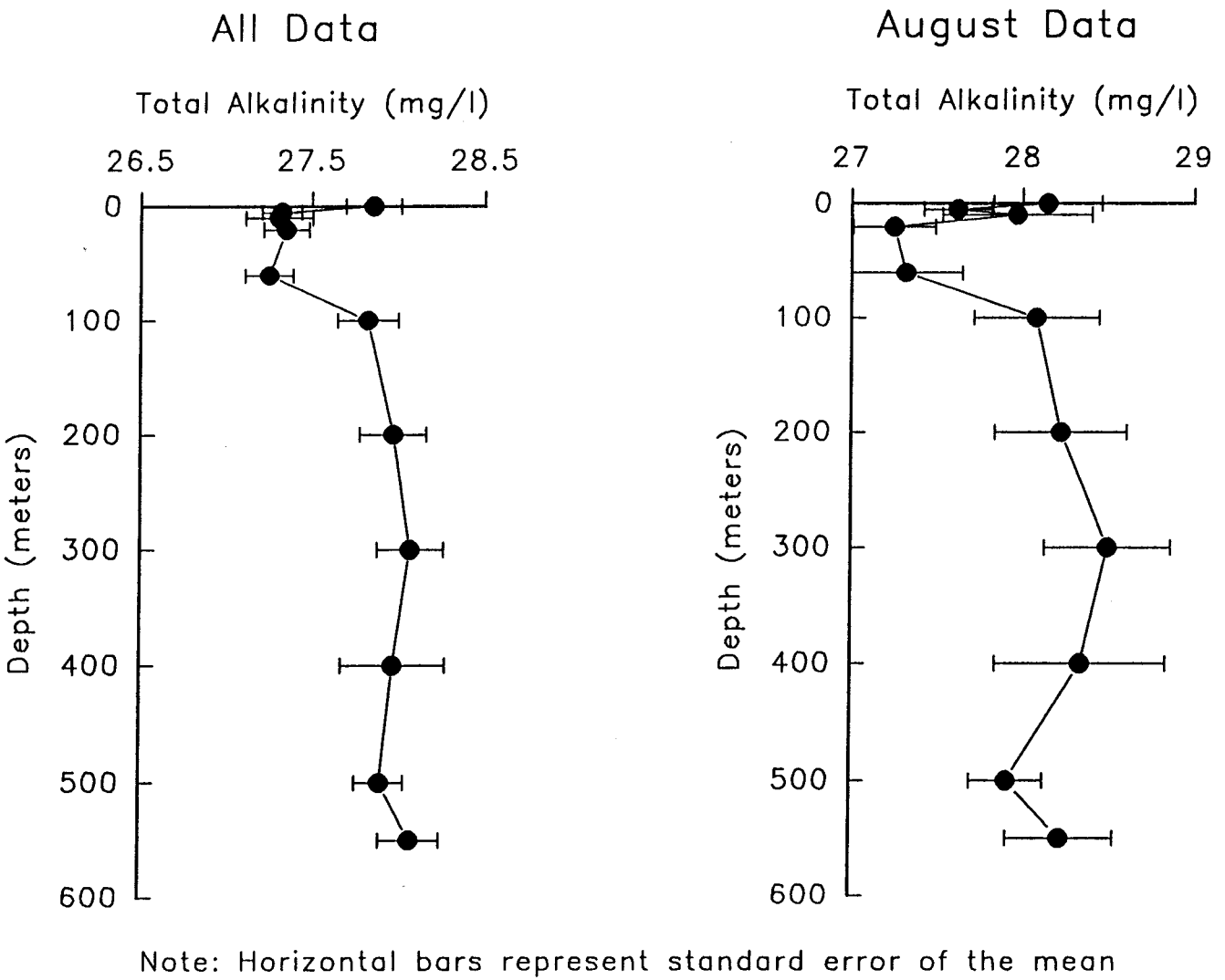
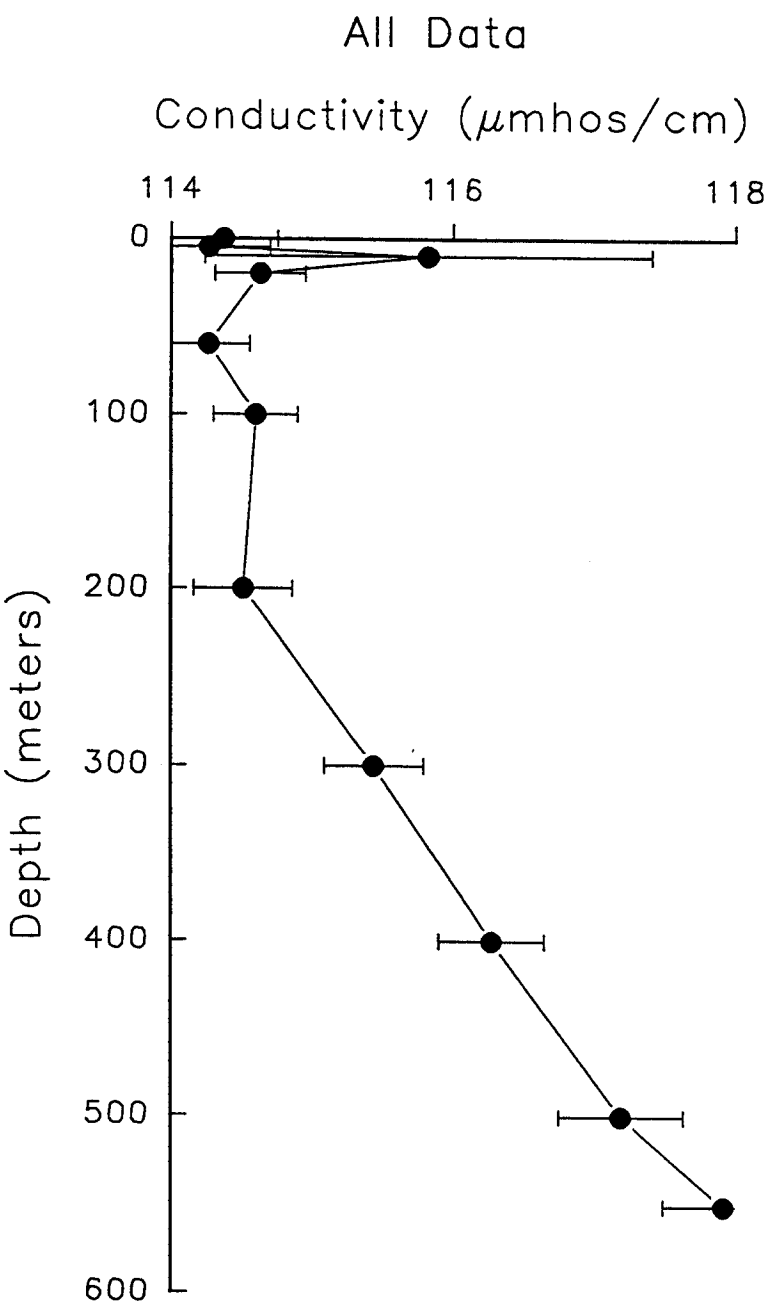


Figure 9. Mean total alkalinity depth profile from the water surface to a depth of 550 m for all samples and for the August samples collected at station 13 between 1982 and 1990.



Note: Horizontal bars represent standard error of the mean

Figure 10. Mean conductivity depth profile from the water surface to a depth of 550 m for all samples collected at station 13 between 1986 and 1991.

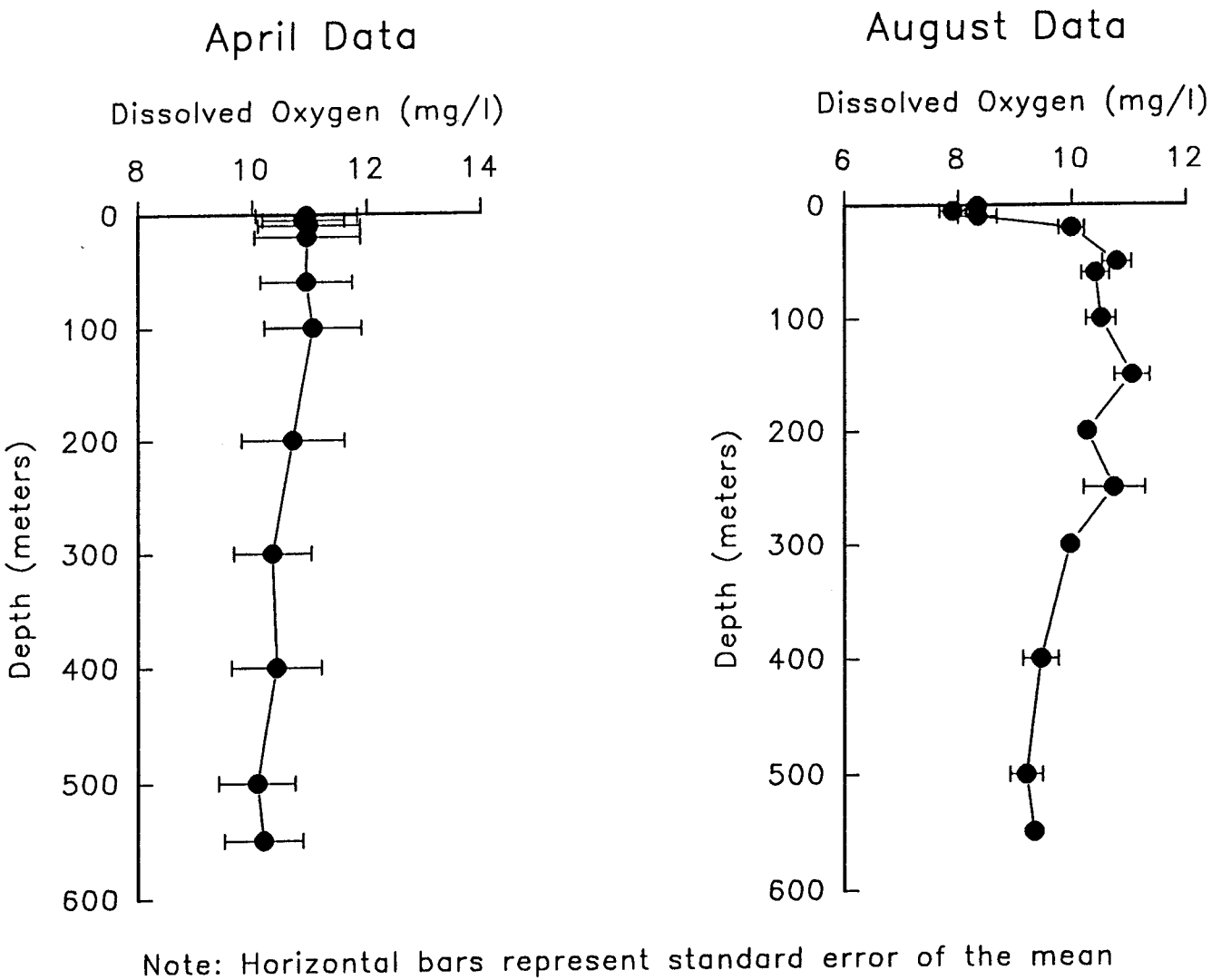


Figure 11. Mean dissolved oxygen depth profile from the water surface to a depth of 550 m for samples collected at station 13 in April and August between 1982 and 1991.

the summer that at other seasons of the year. When thermal stratification occurred, the upper 20 m of the water column usually remained supersaturated with oxygen, often between 105% and 119%, whereas the percentage saturation below 100 m was slightly less than 100% and decreased with depth to about 90% near the bottom of the lake (Fig. 12). Furthermore, the spatial and seasonal patterns of dissolved oxygen in the lake did not exhibit appreciable changes between 1982 and 1990 (Table 5).

Nutrients and Cations

Concentrations of nutrients and cations exhibited little temporal and spatial variation during the 10-year study (1982 - 1990). Orthophosphate phosphorus, nitrate nitrogen, sodium, magnesium, calcium, silicon, and sulfate sulfur increased in concentration with an increase in depth and reached maximum concentrations between a depth of 500 m and the lake bottom (Figs. 13 - 16, Table 7). Nitrate nitrogen was usually below the limits of detection in the upper 200 m of the water column, while Kjeldahl and organic nitrogen decreased in concentration between the depths of 100 m and 500 m (Figs. 13 and 14). All data collected from 1912 to 1990 indicate that there has been very little variation in the annual mean concentrations of nutrients and cations during the past 68 years (Table 6). Without a more intensive sampling regime than the one used in this study (i.e., monthly or biweekly throughout the year), the dynamics of these nutrient profiles is not possible to describe.

Discussion

Crater Lake is unique among the lakes in the Cascade Mountains of Oregon in that it almost always remains free of ice and snow during the winter months. Apparently, the large volume of water in the lake retains enough heat in the winter to keep it free of ice and snow (Hutchinson 1957). Therefore, the fact that the lake had an ice cover at times in

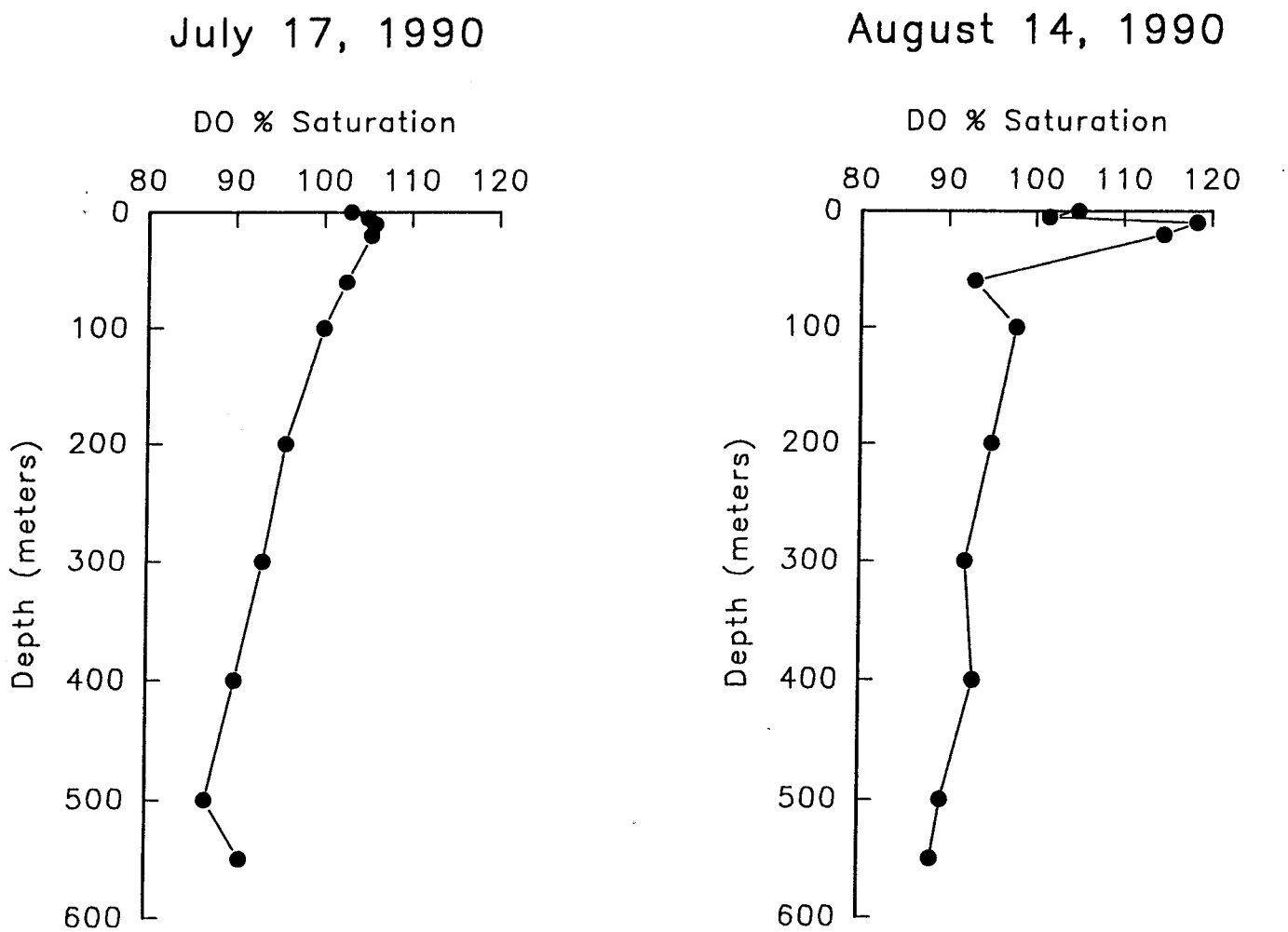


Figure 12. Dissolved oxygen depth profile, expressed as percentage saturation, from the water surface to a depth of 550 m for samples collected on July 17, 1990, and August 14, 1990, at station 13.

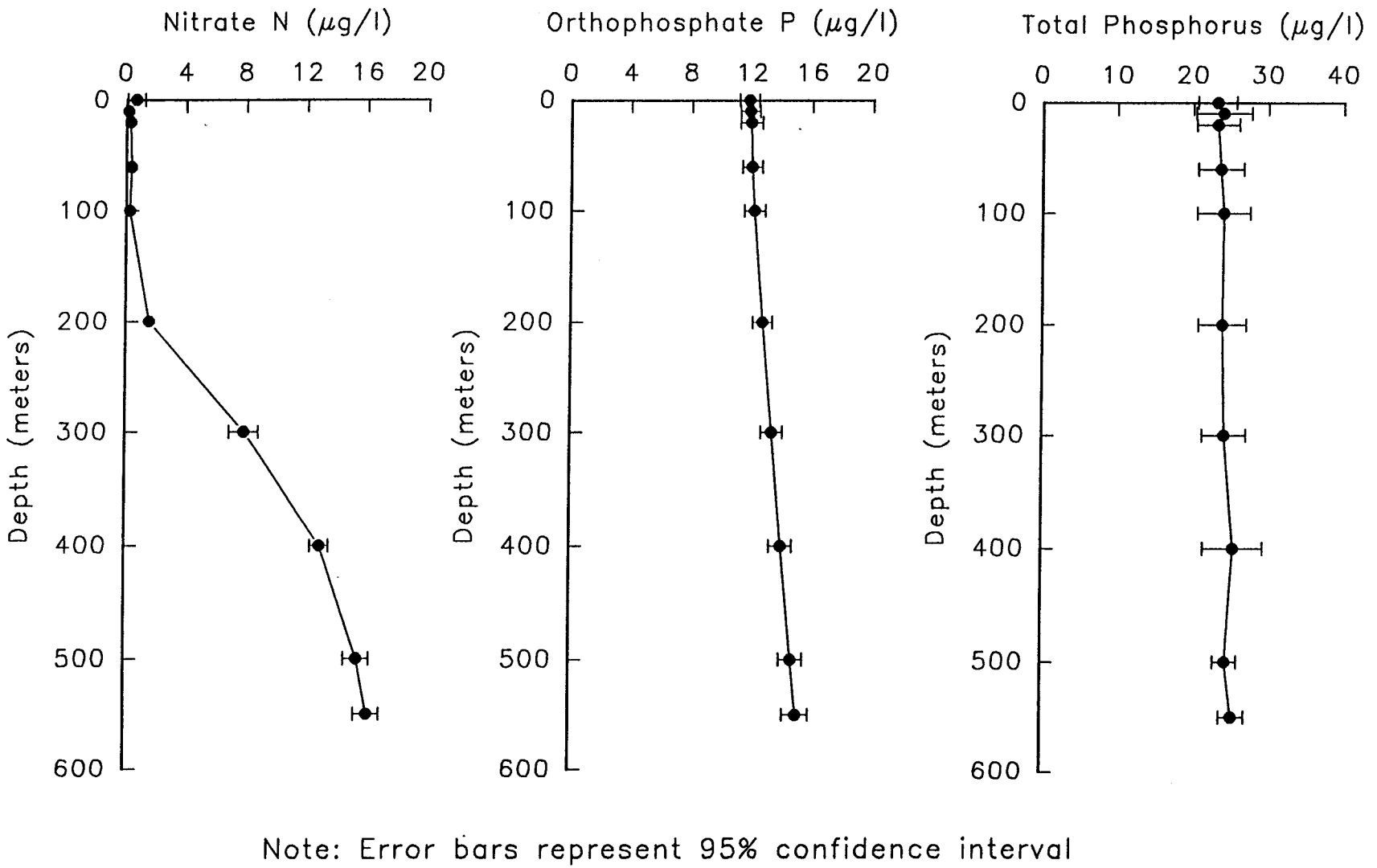


Figure 13. Depth profiles of mean concentrations of nitrate-N, orthophosphate-P and total phosphorus from the water surface to a depth of 550 m for all samples collected at station 13 between 1983 and 1991.

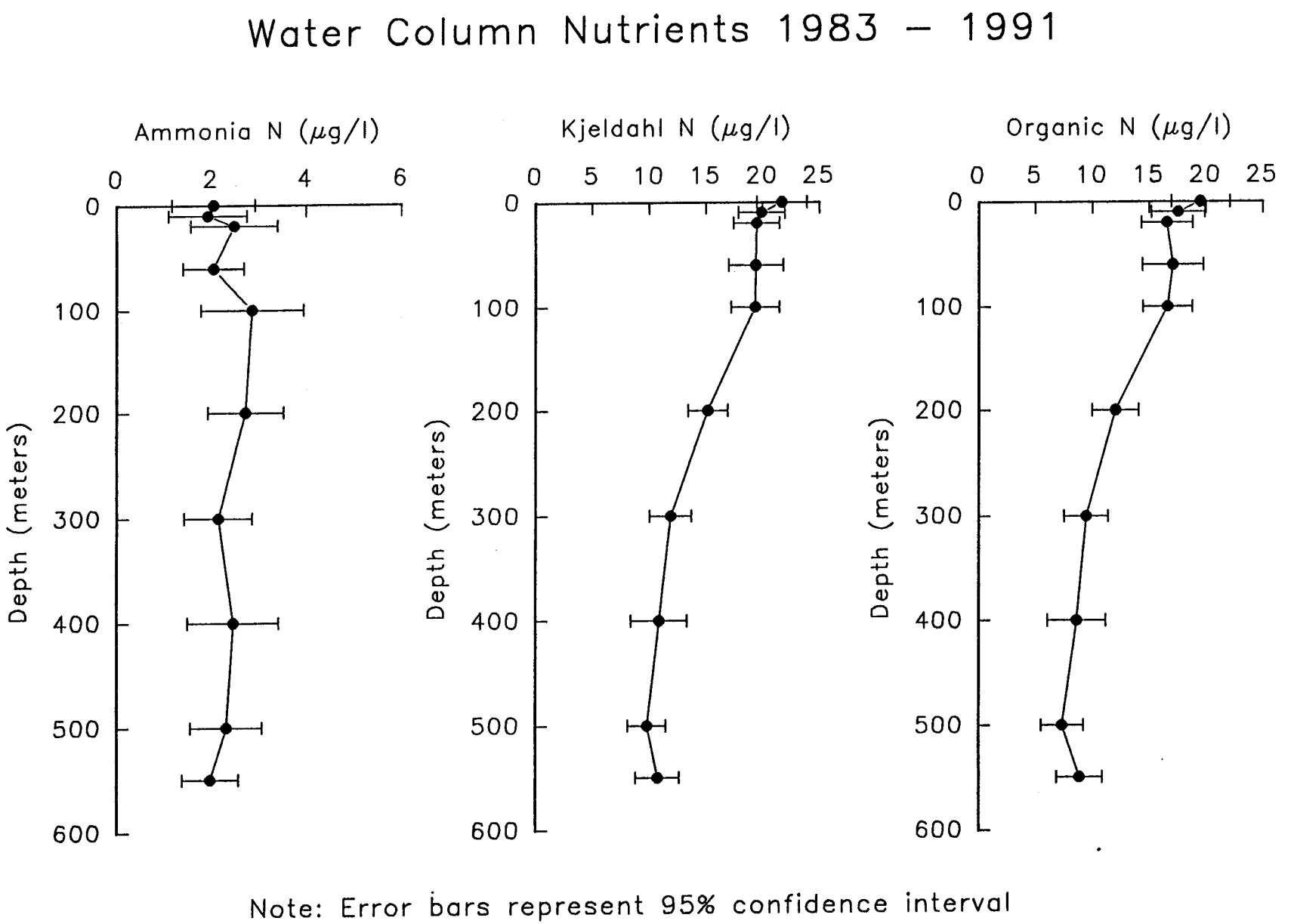


Figure 14. Depth profiles of mean concentrations of ammonia-N, Kjeldahl-N and organic-N from the water surface to a depth of 550 m for all samples collected at station 13 between 1983 and 1991.

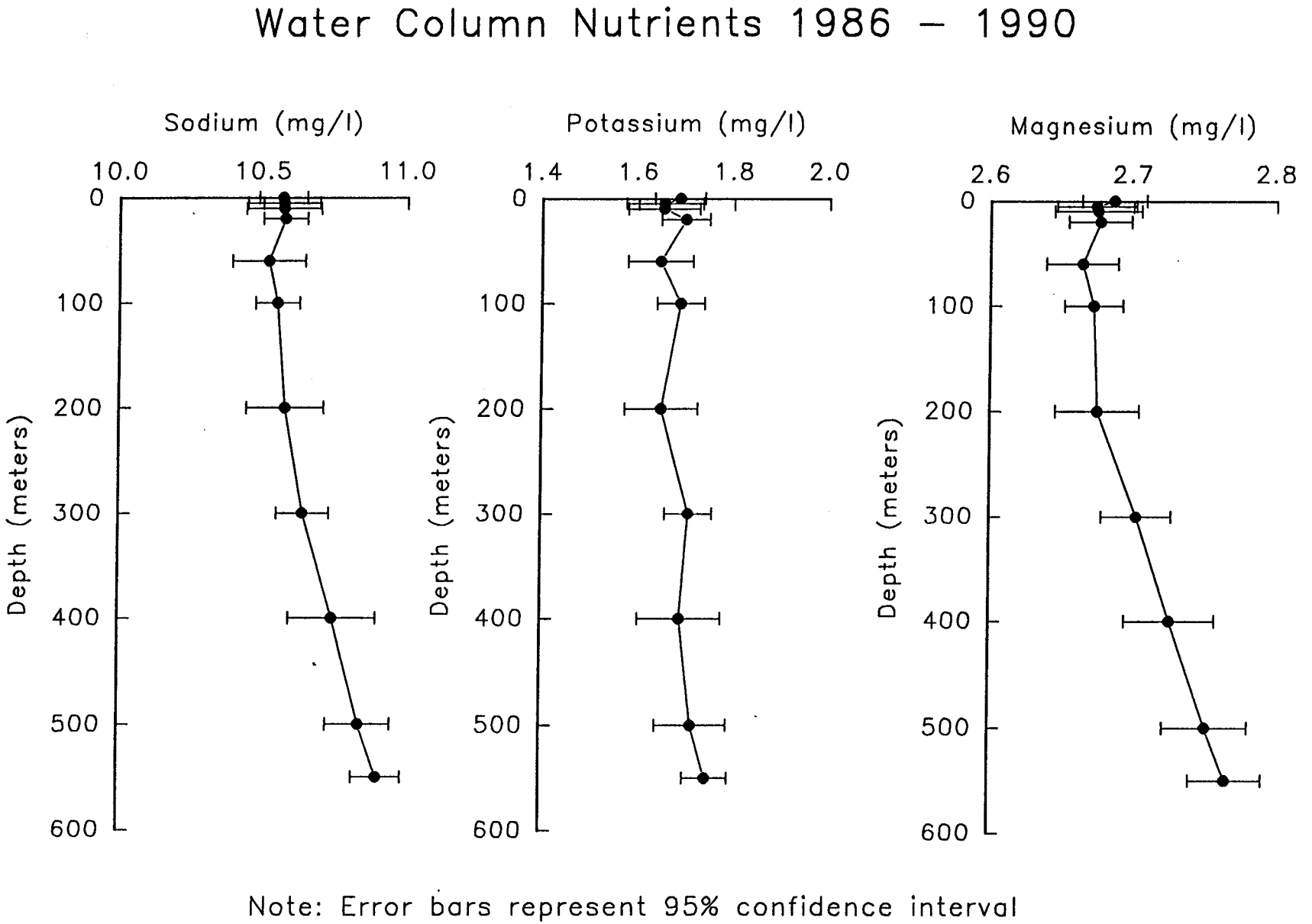


Figure 15. Depth profiles of mean concentrations of sodium, potassium and magnesium from the water surface to a depth of 550 m for all samples collected at station 13 between 1986 and 1990.

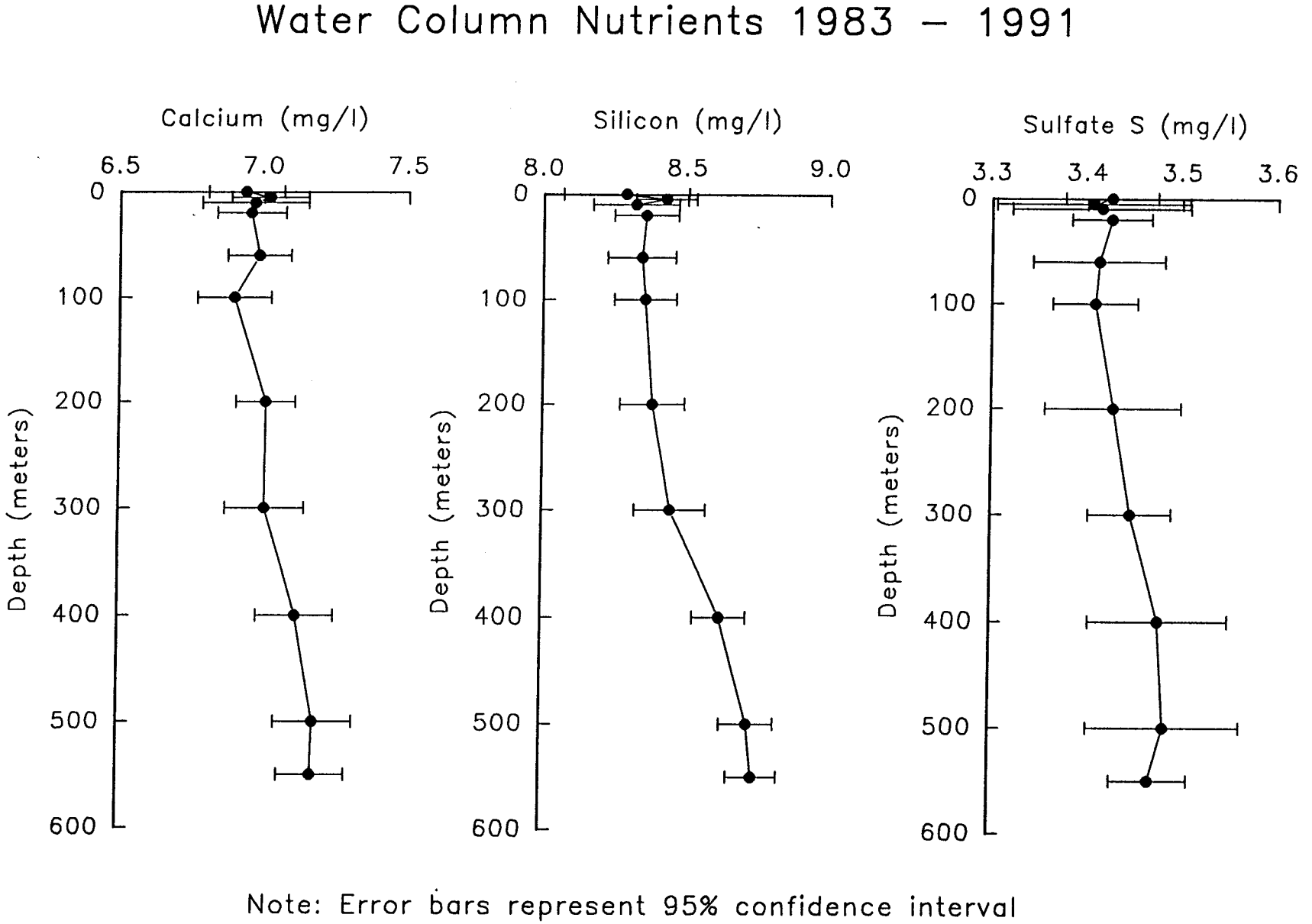


Figure 16. Depth profiles of mean concentrations of calcium, silicon and sulfate-S from the water surface to a depth of 550 m for all samples collected at station 13 between 1983 and 1991.

Table 7. Mean concentrations of selected chemical variables for all samples obtained from the indicated depth intervals in Crater Lake, 1982-1990.

Variable	Depth Interval (meters)		
	0-200	200-550	0-550
Nitrate N (μg/l)	0.61	10.62	6.98
Ammonia-N (μg/l)	2.55	2.34	2.41
Kjeldahl-N (μg/l)	18.52	11.55	14.08
Organic N (μg/l)	15.68	9.09	11.49
Orthophosphate P (μg/l)	12.21	13.88	13.27
Total phosphorus (μg/l)	28.22	29.59	29.09
Sodium (mg/l)	10.56	10.72	10.66
Calcium (mg/l)	6.96	7.09	7.04
Magnesium (mg/l)	2.67	2.72	2.70
Potassium (mg/l)	1.67	1.70	1.69
Silicon (mg/l)	8.36	8.57	8.49
Sulfate S (mg/l)	3.42	3.46	3.45

1985 and 1986 was unusual. The last reported occurrence of an ice cover prior to the 10-year study was in 1949 (unpublished park records). During the three recorded periods when ice was observed on the lake (i.e., winters of 1949, 1985, and 1986), the weather was described as clear and extremely cold, while the lake surface was flat and calm.

Wind action usually mixes the water column of Crater Lake to a depth of about 250 m. A similar depth of mixing has been reported in Lake Tahoe for most years (Goldman et al. 1975). However, unlike Crater Lake, the water column in Lake Tahoe undergoes complete mixing when certain weather conditions are present (i.e., very large storm events during February or March when the lake is isothermal). Also, the thermocline in Lake Tahoe occassionally is disrupted for short periods of time in the summer when energy inputs from wind action are high enough to break down stratification. Complete mixing of the water column in the winter and disruption of thermal stratification in the summer was not observed in Crater Lake, probably because of the relatively short fetch (8 km) and small surface area (48 km^2) associated with the lake.

According the Hutchinson's terminology (Hutchinson 1957), Crater Lake can be classified as a meromictic lake, because some water below the depth of 250 m remains partly unmixed with the main water mass at the circulation periods. However, there is some mixing in the winter and early spring each year when the relatively cold, dense water near the surface sinks and exchanges positions with water in the deep basins of the lake. This process moves nutrient-rich water from locations in the deep lake to the upper 250 m of the water column (see Circulation and Hydrothermal Properties sections), an upwelling phenomenon that is undoubtedly coupled to patterns of primary and secondary production. In addition, the relatively stable thermocline in Crater Lake affects patterns of primary productivity by preventing an occasional recirculation of recycled nutrients into the euphotic zone during the summer and early fall as observed in Lake Tahoe (Abbott et al.1984). Also, because of the great clarity of the lake, the stability of the epilimnion

probably has an important effect on the solar heating of the metalimnion and the vertical distribution of phytoplankton and zooplankton (see Phytoplankton and Zooplankton sections).

Oligotrophic lakes typically are more transparent and lower in concentrations of nutrients and dissolved salts than lakes of higher productivity (Wetzel 1975, Goldman 1983). In oligotrophic lakes, concentrations of dissolved oxygen and nitrate often exhibit orthograde depth profiles during thermal stratification, whereas total phosphorus and ammonia are relatively uniform in concentration throughout the water column (Wetzel 1975). Concentrations of total phosphorus and inorganic nitrogen in the epilimnion of oligotrophic lakes are usually less than 5 μg/l and 200 μg/l, respectively (Wetzel 1975). Chemical and physical properties of Crater Lake that are most consistent with typical oligotrophic characteristics include high transparency, orthograde dissolved oxygen and nitrate depth profiles, and low concentrations of nitrate in the epilimnion. However, cation concentrations in Crater Lake often exceed those in other eutrophic, mesotrophic, and oligotrophic lakes in the Cascade Mountains of Oregon, and are more similar to mean concentrations reported for the streams and lakes of the world (Table 8). High concentrations of cations in Crater Lake, as well as in the other two caldera lakes included in Table 8 (East Lake and Paulina Lake),are associated with inputs of hydrothermal fluids (see Mass Balance and Hydrothermal sections). However, in comparison to other caldera lakes, concentrations of cations in Crater Lake, East Lake, and Paulina Lake are low (Larson 1989). Furthermore, the relatively high concentrations of total phosphorus reported for Crater Lake are in the range usually associated with mesotrophic lakes (Wetzel 1975). Therefore, the chemical and physical properites of Crater Lake are unique and do not conform to the entire range of criteria usually associated with oligotrophic status.

Table 8. Concentrations of selected chemical variables in water samples from near surface waters of eutrophic (E), mesotrophic (M), and oligotrophic (O) lakes in the Cascade Mountains of Oregon. Data for the State of Oregon were obtained from Johnson et al. (1985), while worldwide averages were taken from a publication by Livingstone (1963); the (*) symbol indicates data from the 10-year study.

Lake	Class	Elevation (m)	Area (ha)	Depth (m)	Alkalinity (mg/l)	Cond (μmhos/cm)	pH	T-Phos (μg/l)	Na (mg/l)	K (mg/l)	Ca (mg/l)	Mg (mg/l)	Cl (mg/l)	Sulfate (mg/l)
Diamond	E	1579.8	1300.7	15.8	15	29	9.5	61	3.2	0.8	2.3	1.1	0.9	0.3
Suttle	E	1047.9	102.4	22.9	15	50	8.4	24	2.5	0.8	4.0	1.8	0.6	1.6
East	M	1941.6	422.5	54.9	103	310	7.9	16	23.1	4.0	24.3	11.8	0.9	82.7
Gold	M	1467.0	38.9	13.1	16	33	7.3	47	2.1	0.8	3.2	1.0	0.5	0.7
Marion	M	1258.8	105.6	56.4	18	37	8.8	33	2.6	1.1	4.4	1.5	0.9	0.7
Odell	M	1459.1	1449.6	86.0	13	32	9.3	28	2.4	0.8	2.8	0.9	0.7	0.3
Paulina	M	1929.7	619.6	76.2	340	560	8.3	45	4.5	5.4	25.9	36.4	3.5	5.1
Big	O	1415.5	76.9	23.5	<1	4	7.2	2	0.3	0.1	0.8	0.3	0.6	<0.1
Blue	O	1052.5	21.9	95.7	16	50	6.9	29	2.6	0.9	4.3	2.0	0.6	<0.1
Breitenbush	O	1676.4	26.3	7.6	<1	6	7.6	–	0.5	0.1	0.7	0.2	0.4	0.2
Charlton	O	1734.9	63.1	29.0	2	6	6.8	4	0.4	0.1	0.5	0.1	0.4	0.8
Crescent	O	1474.9	1840.2	80.8	11	26	7.6	62	1.7	0.9	2.4	0.9	–	0.8
Deer	O	1492.3	21.0	7.9	3	12	6.5	17	0.9	0.3	1.1	0.4	0.7	0.7
Devils	O	1658.1	9.3	3.0	10	25	–	72	2.4	0.9	1.4	0.9	0.7	<0.1
Doris	O	1618.5	27.9	29.0	<1	4	–	3	0.3	0.1	0.5	0.1	0.6	0.4
Hariette	O	2057.4	16.2	24.1	<1	3	–	9	0.2	0.1	0.5	0.1	0.6	0.5
Lost	O	958.0	93.5	53.3	2	12	6.6	6	0.8	0.1	1.1	0.4	1.6	0.3
Olallie	O	1504.5	76.1	13.1	<1	3	–	8	0.3	0.0	0.4	0.1	0.5	0.1
Summit	O	1692.6	195.1	19.2	<1	6	6.7	9	0.2	0.1	0.1	0.1	0.3	0.2
Waldo	O	1650.2	2848.8	128.0	<1	3	6.3	9	0.2	0.0	0.4	0.1	0.6	0.3
Crater	O	1882.4	5317.4	588.9	40	108	7.2	17	11.0	1.8	9.3	2.7	9.0	12.4
Crater*	O	1882.4	5317.4	588.9	26-30	80-121	7.1-7.9	13-43	10-11	1.5-1.9	6.3-7.8	2.6-2.9	–	9.4-10.8
Worldwide Mean	–	–	–	–	–	–	–	–	6.3	2.3	15.0	4.1	7.8	11.2

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Chemical Characteristics of Springs

Stanley V. Gregory

(TO BE SUBMITTED)

Dissolved Oxygen in the Deep Lake

James McManus, Robert Collier, and Jack Dymond

Dissolved oxygen is a sensitive tracer of the physical and chemical processes occurring in an aquatic system. Oxygen in excess of atmospheric saturation in the upper water column is caused by photosynthesis, the penetration of solar radiation resulting in *in situ* warming of the water column, and air bubble injection (Jenkins and Goldman 1985; Emerson et al. 1991). The disappearance (consumption) of dissolved oxygen deep in a lake is typically due to the oxidation of particulate organic matter raining out of the euphotic zone. If the photosynthetic component of the oxygen excess in the upper water column is properly constrained, then this component should have the same value (opposite in sign) as the amount of oxygen consumed. In temperate lakes, convective mixing during winter of surface water with deep water results in an increase in dissolved oxygen within the lake. This change in oxygen provides a semi-quantitative estimate for the efficiency and timing of deep-lake mixing.

The goal of this section is to examine the effects of mixing, carbon flux, and hydrothermal inputs on the distribution and budget of dissolved oxygen in the deep water column of Crater Lake. The data set for constraining these processes includes dissolved oxygen samples from 1988-1991, a more limited nutrient data set, estimates of the composition of the hydrothermal fluid, and sediment trap carbon flux estimates.

Methods

Water column samples were recovered using 5-l and 20-l Niskin samplers and 4-l Van Dorn bottles. Water samplers were deployed from the National Park Service (NPS) research boat equipped with a hydrowire. During the summer 1989 field season, discrete bottom water samples also were also recovered using the submersible *Deep Rover* (Dymond et al. 1990).

Temperature, pressure, and conductivity were measured using a SEACAT® model SBE19 (Sea-Bird Electronics Inc.) "CTD". The temperature resolution was ±0.0005°C, and based on calibrations between 1987-1989, the absolute accuracy of the temperature sensor was within

0.001°C. Salinity was determined from *in situ* temperature and conductivity as described by McManus et al. (1992). Density was calculated from the CTD hydrographic data (McManus et al. 1992) and was based on the equation of state for waters in the limnological range as presented by Chen and Millero (1986).

Oxygen samples were analyzed by a whole-flask Winkler titration method with the modifications of Carpenter (1965a, b). An alkaline-iodine fixing solution containing sodium azide was used in samples retrieved near hydrothermal springs to remove potential interferences from reduced iron. The overall precision of the oxygen measurement, based on duplicate sample analysis, was better than 0.5%. Oxygen solubility for Crater Lake was calculated as a function of lake surface elevation, temperature, and salinity (Benson and Krause 1984). The mean barometric pressure was calculated from the altitude-dependent equation given by Mortimer (1981). In discussing the mixing of oxygen-saturated water with deep lake water, we assume that a parcel of water from the upper water column had an oxygen content of 328.5 μM, which is the saturation value for the temperature of the surface mixed layer during winter (~3.6°C).

Nitrate was determined using colorimetric methods described in Strickland and Parsons (1965) and modified for an Alpkem rapid flow analyzer. The precision of the nitrate measurement was ~±0.025 μM. Sodium was determined by flame atomic absorption spectroscopy according to the high precision methods described by McManus et al. (1992). The precision of the sodium analysis for the data presented in this section was ~0.75%. Sediiment traps, with a 0.25-m^2 sampling area, designed and built at Oregon State University (Dymond and Collier 1990) were used to collect particles falling through the water column. Three traps were placed on a single mooring at 200 m, 380 m, and 580 m depths. The 200-m trap was equipped with a five-cup sampler, which allowed for time-series sampling with a two month resolution. Samples were preserved *in situ* using a buffered formaldehyde solution.

Results

Hydrography and the Vertical Distribution of Dissolved Constituents

The upper water column in Crater Lake mixes completely twice annually, during the mid-to-late winter and late spring. During this mixing period, a nearly uniform temperature and density profile is produced in the upper 200 m (Fig. 1). In addition, as a result of this seasonal mixing, the salinity distribution in the upper 200 m is uniform throughout the year (Fig. 1b). As first described by Neal et al. (1971, 1972), the thermal gradient below 350 m is "hyperadiabatic" (Fig. 1a), or approximately two orders of magnitude greater than the adiabatic lapse rate. This thermal gradient in the deep water is due to the active input of hydrothermal fluids and is balanced by an increase in salinity (Fig. 1b), which yields a stable density gradient in the deep lake (Fig. 1c).

The water column of Crater Lake is nearly saturated with respect to atmospheric saturation of dissolved oxygen throughout the year (Fig. 2). This is maintained by rapid vertical mixing, coupled with the relatively low carbon flux through the water column of this oligotrophic system (Dymond and Collier 1990). Likewise, there is little horizontal variability in dissolved oxygen (Fig. 2). In the upper 150 m, supersaturation of dissolved oxygen is typically observed throughout most of the year (Fig. 2). This excess is due to net photosynthetic production in these upper waters and the penetration of solar radiation that causes *in situ* heating of subsurface waters.

Hydrothermal activity in the south basin delivers zero-oxygen water that has high concentrations of chemically reduced species. As a consequence of the oxidation of these reduced species, and dilution of south basin water with this zero oxygen spring water, there are near-bottom heterogeneities in the distribution of dissolved oxygen in the south basin.

Temporal variations in Dissolved Oxygen

The oxygen cycle in Crater Lake includes the mixing of oxygenated upper water with deep lake water followed by the consumption of oxygen in the isolated deep lake basins due to the decomposition of organic matter and the oxidation of hydrothermally-derived reduced species. A time-series of dissolved oxygen shows that the deep-lake (550 m) dissolved-oxygen content

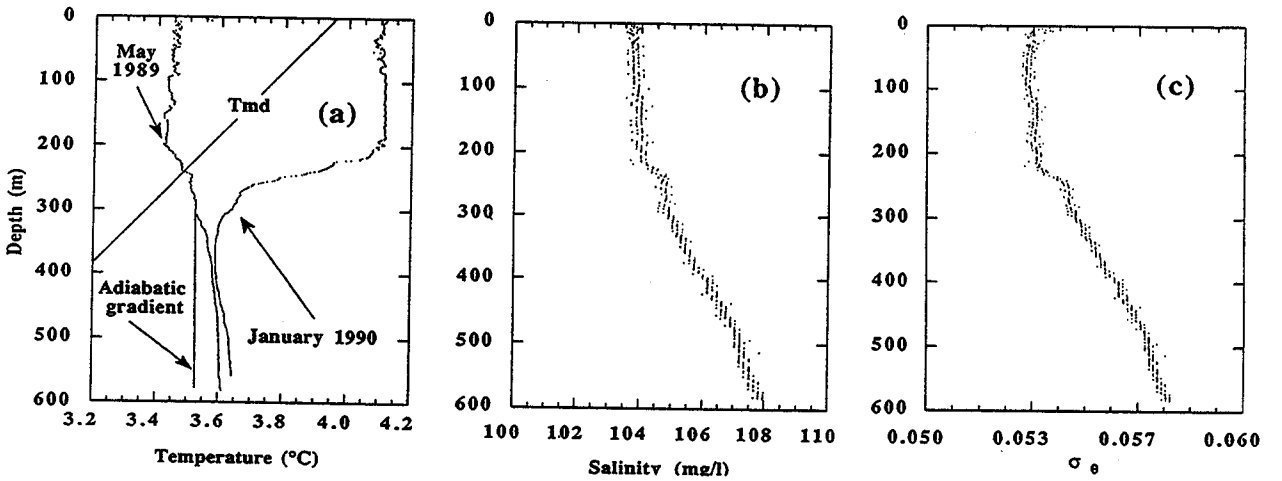


Figure 1. (a) Temperature vs. depth for May 1989 and January 1990. The temperature of maximum density (Tmd) and the adiabatic gradient are calculated from a polynomial presented in Chen and Millero (1986). (b) Salinity vs. depth. (c) σ_θ vs. depth. Note the well-mixed nature of the upper 200 m in the water column of Crater Lake and the increase in temperature, salinity, and density with depth below 200 m.

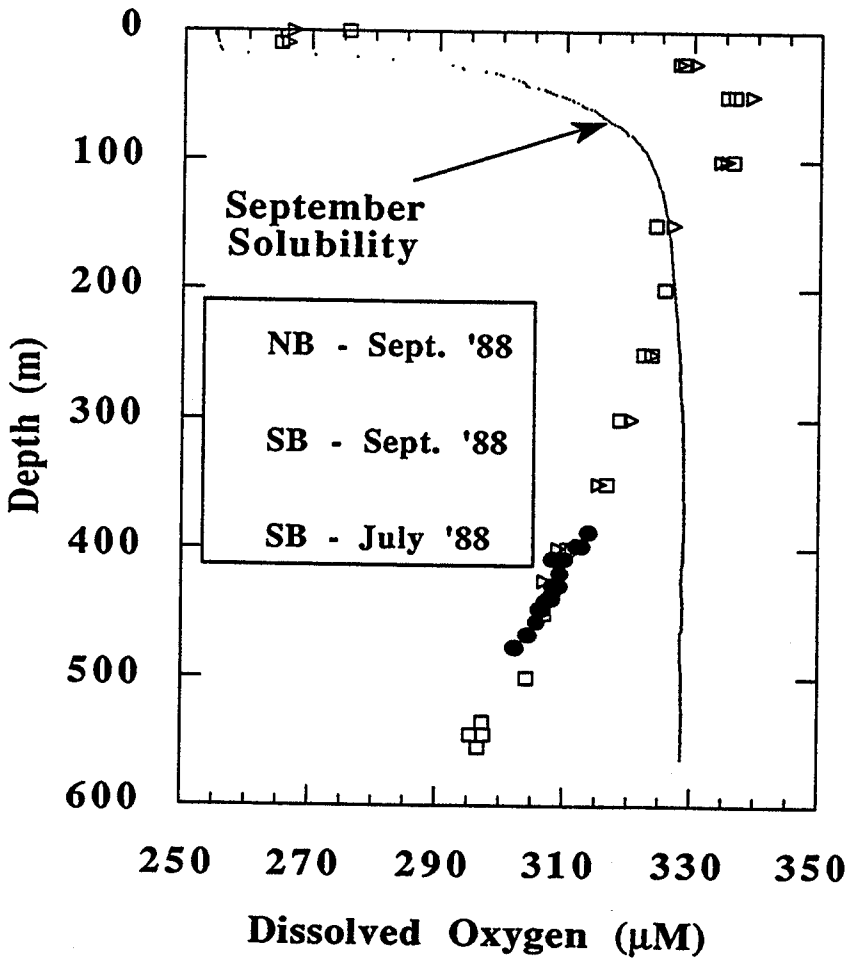


Figure 2. Expanded scale dissolved oxygen (μM) as a function of depth for July and September 1988 in both the south basin (SB) and the north basin (NB) of the lake. Variations in oxygen solubility are primarily a function of temperature (Benson and Krause 1984).

increased from September 1988 to April 1989 by ~10 μM. This increase was followed by a decrease in dissolved oxygen of ~13 μM between April 1989 and January 1990. After January 1990, there was another increase in deep-lake dissolved oxygen accompanied by a decrease in deep-lake temperature due to the partial ventilation of the deep lake with cooler, well-oxygenated surface water (Fig. 3).

The rate at which oxygen decreases in the deep lake varies as a function of depth. At a depth of ~300 m there appears to be little or no change in the dissolved oxygen content throughout the year. The rate of dissolved oxygen decrease at 450 m is 15-20 μmol m^{-3} day^{-1}, and the decrease at 550 m is 40-44 μmol m^{-3} day^{-1}.

The integrated change in the deep-lake (303 to 557 m) dissolved-oxygen inventory, measured between June 1989 and January 1990, is -4.4 mmol m^{-2} d^{-1}. Because the data used to calculate the change in the oxygen inventory only covers depths to 557 m, as opposed to the maximum depth of 589 m, and because the respiration rate increases with increasing depth, the estimated respiration rate is a minimum.

Discussion

Mixing

One approach to constrain the extent of deep-lake mixing during the winter of 1988-89 is to assume that the dissolved oxygen measurement at 550 m for April (307 μM) is a mixture of air-saturated winter water (328.5 μM) and deep lake water (297.4 μM, value for September 1988 in Fig. 3). Under these assumptions, the deep water in April is composed of 30% "new" air-saturated water and 70% "old" deep lake water.

Any deep water oxygen depletion occurring after September and before April will change the mixing estimation made above. Extrapolating the deep-lake dissolved-oxygen consumption rate of ~0.04 μmol $liter^{-1}$ day^{-1} (Fig. 3) to later in the fall and earlier in the winter suggests that the net change in dissolved oxygen was possibly as high as 16.2 μM O_2 at 550 m. This change requires a mixture of 45% air-saturated winter water and 55% deep-lake water. Such a mixture

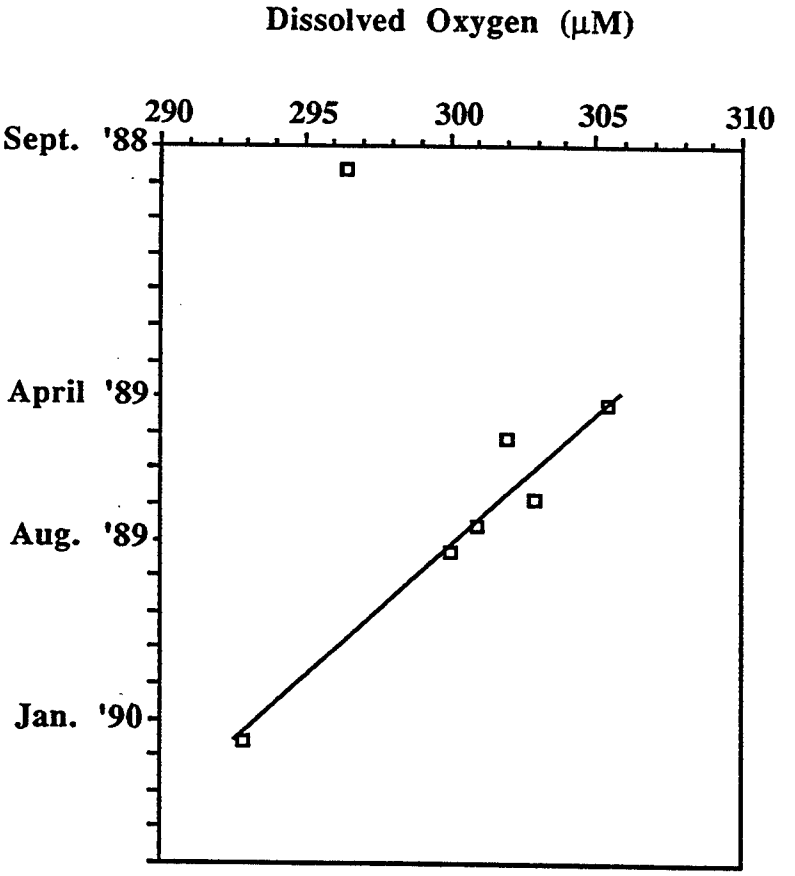


Figure 3. Dissolved oxygen at 550 m as a function of time from April 1989 to January 1990. The dissolved oxygen distribution at depth shows an increase in deep lake oxygen due to mixing followed by a decrease due to the consumption of oxygen. The decrease in dissolved oxygen over time in the deep water column is due to the consumption of oxygen by particulate organic material and hydrothermally-derived reduced chemical species. The line demonstrates a consumption rate of dissolved oxygen of approximately 40 μmol m^{-3} day^{-1}.

implies a deep-lake time-integrated ventilation rate of ~2.5 years. The data are insufficient for the same kind of approximations for 1990; however, the data indicate that some exchange has occurred (Fig. 3). The time scale of vertical mixing calculated here is consistent with the work of Simpson (1970a), who calculated a ventilation rate for Crater Lake on the order of one year, and is also consistent with the recent work of Weiss and Lupton (unpublished).

There appears to have also been some mixing between May and June as indicated by an increase in dissolved oxygen in June relative to May (Fig. 3). This increase in dissolved oxygen is much smaller in magnitude than the changes seen for the winter mixing period. Although it is difficult to constrain this mixing because the analytical uncertainty is large for such a small change, there was also a small decrease in deep lake temperature during this time period, further suggesting that some mixing occurred during spring.

In Crater Lake, the mixing cycle occurs each year. Although the annual efficiency of this mixing is unknown (McManus 1992), dissolved oxygen data taken in July 1989-91 show that the distribution of deep lake dissolved oxygen is consistent from year-to-year (Fig. 4). However, this data does not necessarily demonstrate that the mixing process is constant from year to year. Because primary production is dependent on the upwelling of deep lake nutrients, the carbon flux, which results in deep lake oxygen consumption, could be closely coupled to the extent of mixing. This may lead to the observed consistency in deep oxygen profiles from year to year.

Dissolved Oxygen in the Upper Water Column

Organic matter that rains to the deep lake and is subsequently oxidized has it origins in the euphotic zone of the water column. One method for constraining the flux of organic material out of the euphotic zone is by estimating the amount of excess oxygen generated by primary production (i.e., Jenkins and Goldman 1985). Supersaturation of dissolved oxygen in the upper water column of aquatic systems is commonly observed and is generated by photosynthesis, the penetration of solar energy that heats subsurface waters *in situ*, and air bubble injection. Removal processes for dissolved oxygen include, vertical mixing, respiration, and gas exchange (Jenkins and Goldman 1985, Spitzer and Jenkins 1989). Although we lack the data to constrain all the

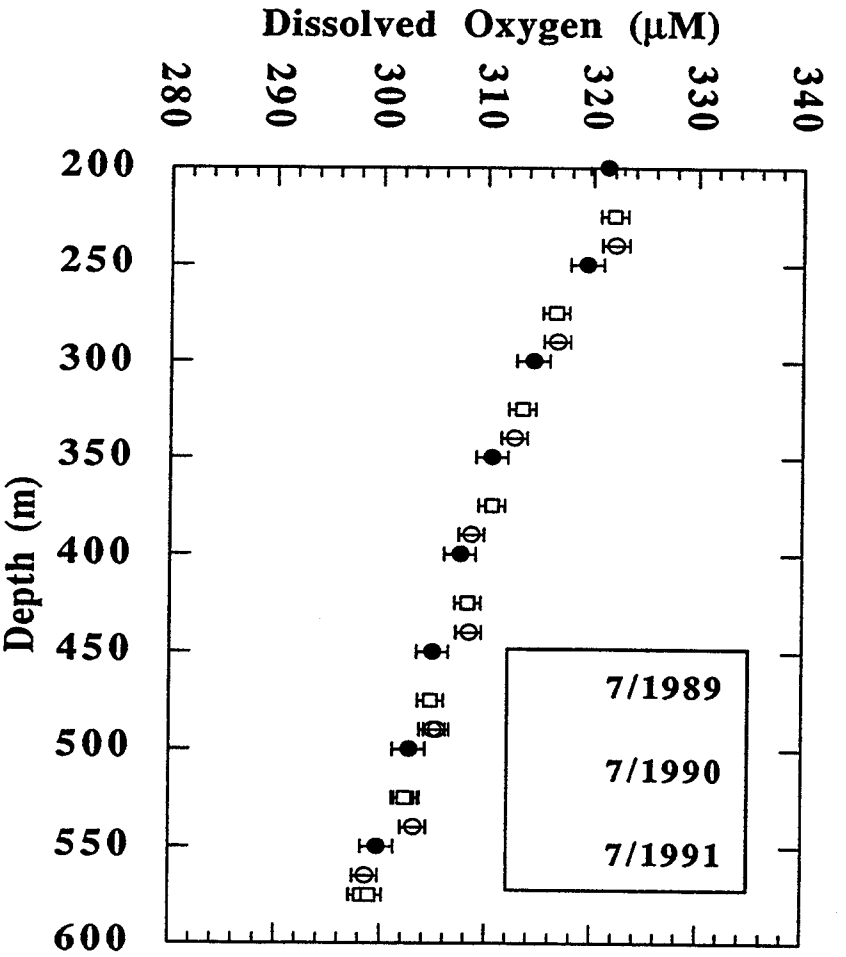


Figure 4. Dissolved oxygen as a function of depth for July 1989-1991. Within the analytical precision of the dissolved oxygen measurement, the vertical distribution of dissolved oxygen is consistent from year-to-year.

processes contributing to the oxygen budget of the upper water column, estimates of the budget can be made which enable the demonstration that there is a sufficient oxygen excess to account for the observed deep-lake respiration rate.

Assuming that the rate of oxygen consumption in the deep lake is driven by the oxidation of organic matter, ~700 mmol m^{-2} of carbon are required to account for the oxygen consumed between 26 June and 19 January. This calculation assumes a ratio of -138O_2:106C (Redfield 1942, Redfield et al. 1963).

Calculations of excess oxygen presented here encompass the region between the surface and 150 m (the compensation depth). Below 150 m, dissolved oxygen is typically less than the saturation value. Although some oxygen consumption is likely to be occurring below this depth, little or no net change in dissolved oxygen is observed from 200 to 300 m between 26 June and 19 January, that is, the supply and removal (respiration) of oxygen are in balance.

If all the supersaturated oxygen (i.e. Fig. 2) were photosynthetically-derived, this would yield an integrated excess in carbon of ~1,150 mmol C m^{-2}. This represents an average value for July 1989-91. Alternatively, considering only the oxygen in excess over the winter saturation value (328.5 μM) an integrated excess of 300 ±100 mmol C m^{-2} is obtained. These estimates are a maximum and minimum respectively. The first estimate assumes that all the supersaturation is due to photosynthesis, which is unlikely to be the case, whereas the second assumes that all the supersaturation produced after spring mixing is due to *in situ* warming of the water column from the penetration of solar energy, also an unlikely scenario. The actual value will likely lie somewhere between these two extremes.

It is useful to consider what fraction of the upper water column supersaturation is needed to balance the deep lake oxygen deficit. If we consider that the particulate organic carbon falling out of the euphotic zone (below 150 m), falls to the deep lake, which has a smaller surface area, then the carbon values based on oxygen supersaturation should be multiplied by a factor that accounts for the differing surface areas between the upper water column and the deep lake. We account for the smaller lake volume from 300 m to the bottom as compared to 0-150 m by multiplying the

calculated carbon inventory value by the ratio of the two volumes (~1.5). The resulting "adjusted" value for the upper limit (1,150 mmol C m^{-2}) gives an oxygen-based carbon value of 1,700 mmol C m^{-2}. Therefore, the deep lake oxygen budget predicts an oxygen consumption that is ~40% of this value or ~60% of the uncorrected value. This range in the photosynthetic fraction is consistent with that found in the ocean environment (Jenkins and Goldman 1985, Spitzer and Jenkins 1989, Emerson et al. 1991).

The ventilation calculations presented earlier in this section are useful for estimating the delivery of a biologically-important nutrient (i.e. nitrate) from the deep lake to the upper water column. This would provide another estimate for the amount of particulate organic material raining out of the euphotic zone. For instance, assuming that 40% of the water below 300 m is replaced with water from the upper lake, then nitrate-rich water from the deep lake will be delivered to the upper 200 m. Because the average concentration of nitrate for the deep lake is ~1 μM, winter mixing will deliver ~5 x 10^6 moles of NO_3^- to the upper lake. The resulting productivity from this added "new" nitrogen will return particulate organic material to the deep lake. This carbon flux will consume deep-lake dissolved oxygen at a rate of ~5 mmoles O_2 m^{-2} d^{-1}, which agrees well with the observed deep lake respiration rate. However, these estimates assume classical stoichiometry between O_2, C, and N which may not be valid for Crater Lake and could therefore make this estimate a minimum.

Without better constraints on the oxygen budget of the upper water column, one can only state that there appears to be sufficient supersaturation of dissolved oxygen in the upper water column to account for the observed oxygen consumption rate based on a traditional oxygen-carbon stoichiometric relationship.

The Influence of Hydrothermal Activity on the Deep-lake Oxygen Budget

Hydrothermal activity delivers anoxic fluid to the deep basins in Crater Lake at a rate of ~200 l iters sec^{-1} (Collier et al. 1991, McManus 1992). Reduced elements carried by this fluid consume deep-lake oxygen and the input of this zero-oxygen fluid dilutes the oxygen dissolved in

the deep lake. Here we will examine the impact of these hydrothermal processes on the oxygen budget of the deep lake.

The dilution of deep-lake water with anoxic fluid would change the dissolved oxygen content by <0.1%. This assumes a minimum deep-lake volume of ~9 x 10^8 m^3 (the volume below 300 m) and a rate of flow of hydrothermal fluid of 63 x 10^5 m^3 yr^{-1} (200 liters sec^{-1}). Therefore, dilution with zero-oxygen water has a negligible effect on the overall oxygen budget of Crater Lake; however, at locations near the source of the anoxic fluid input, it is possible that this mixing of zero-oxygen hydrothermal water will affect the local dissolved-oxygen distribution. This possibility will be examined below.

The oxidation of hydrothermally-derived reduced elements will also consume some deep-lake dissolved oxygen. From our sediment pore water data, an upper limit estimate for the concentrations of reduced metals entering the deep lake is 200 μM for iron and 100 μM for manganese (Wheat et al., in prep.). Assuming that iron and manganese are entering the lake in a reduced form and that exposure to deep-lake water will oxidize these species according to the first two reactions given in Table 1, we can estimate a total oxygen demand associated with these inputs.

At a fluid input rate of 63 x 10^5 m^3 yr^{-1}, the Fe and Mn will consume 4.7 x 10^{11} μmol O_2 yr^{-1}. In the deep lake (below a depth of 300 m) this corresponds to a consumption of ~0.2 μM O_2 yr^{-1} or about 1% of the observed rate of change in dissolved oxygen.

Table 1. Possible oxygen-consuming reactions associated with hydrothermal inputs.

$Fe^{2+} + 3/2H_2O + 1/4O_2$ Æ $FeOOH(s) + 2H^+$
$Mn^{2+} + 1/4O_2 + 3/2H_2O$ Æ $bMnOOH + 2H^+$
$CH_4 + 2O_2$ Æ $CO_2 + 2H_2O$
$H_2S + 2O_2$ Æ $SO_4^{-2} + 2H^+$

Sulfate, measured in hydrothermal end-member samples was found to be as high as 900 μM. Although reduced sulfur (H_2S or HS^-) is often found in hydrothermal systems, it is unlikely

that a significant fraction of the dissolved sulfate entered the lake as H_2S. There are two reasons for suspecting that H_2S is not the primary sulfur species. There is no strong characteristic sulfide odor in any fluid samples, which suggests that the concentrations are well below 10 μM. Furthermore, the oxidation of H_2S generates one mole of H^+ for every mole of O_2 consumed and the pH of the deep lake and the pore waters is generally too close to neutral (between 6 and 8) for this reaction to be significant within the water column.

There are only a few values of methane samples to constrain the input of this constituent. The results indicate that the deep-water-column methane concentration is between 10 and 30 nM; likewise, dive samples ranged between 8 and 23 nM. Water immediately above a box core taken from within a brine had approximately 6 μM methane, indicating that there is some methane present in the reduced fluid.

Assuming maximum concentrations of 10 μM for both H_2S and CH_4, and assuming the oxidation stoichiometry in Table 1, then 40 μM O_2 yr^{-1} will be consumed by the incoming fluid. Following the mass balance arguments used for Fe and Mn, the consumption of oxygen by H_2S and CH_4 will account for <1% of the total oxygen deficit. Therefore, the sum of all hydrothermal oxygen demands is less than 2% of the observed loss of oxygen in the deep lake.

South Basin dissolved oxygen distribution Although hydrothermal activity has a small impact on the overall deep lake oxygen budget, hydrothermal activity strongly influences the local hydrography in the south basin. Dissolved oxygen depletion is most extreme in the south basin and the concentration of dissolved oxygen is correlated with the hydrothermal tracers, temperature and sodium. These correlations suggest that the active input of saline fluids may play a role in the oxygen budget (Fig. 5a, b). In addition, the ΔO_2:ΔNO_3 ratio in this basin is significantly higher than the ratio expected from the oxidation of organic matter which further suggests that particulate organic material is not the only consumer of deep lake oxygen (Fig. 5c).

The lack of dissolved oxygen in fluid samples from brines, located at the bottom of the south basin, indicate that these brines are anoxic. The minor oxygen contents found in the brine sample (Table 2) are probably due to bottom water entrainment at the time of collection and not

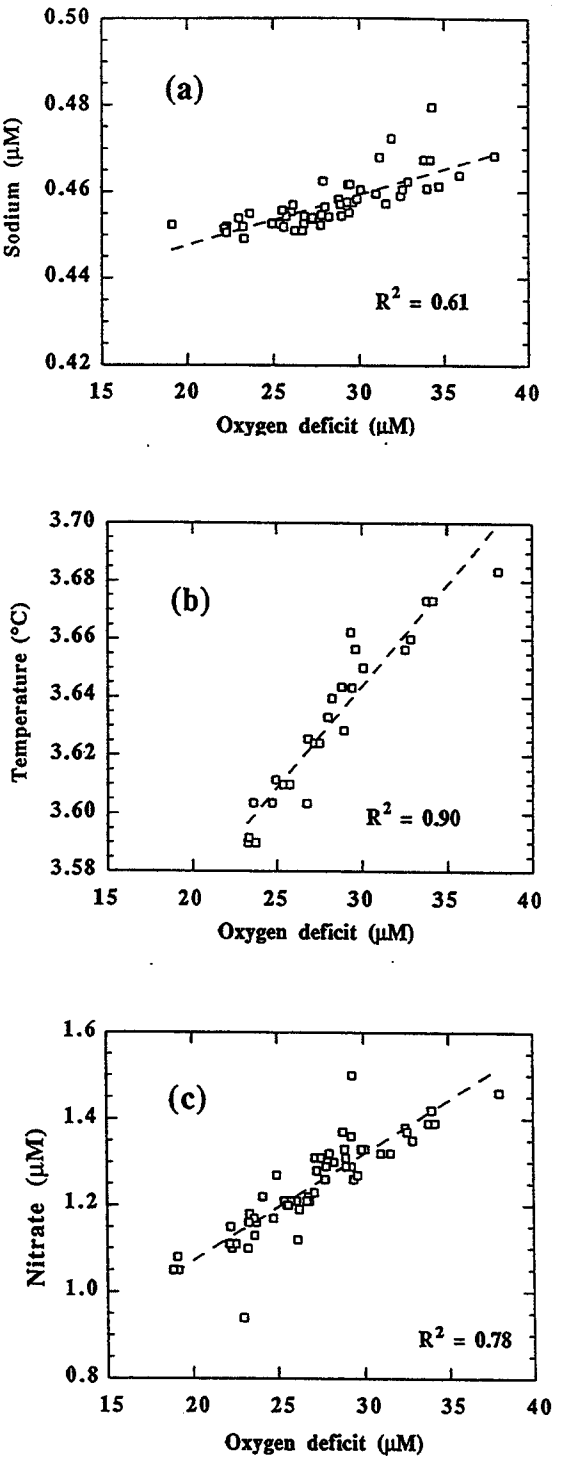


Figure 5. (a) Sodium, (b) temperature, and (c) nitrate as a function of the oxygen deficit in the south basin. The oxygen deficit is defined as the difference between the winter saturation value (328.5 µM O_2) and the measured O_2. Of additional note, $R^2 = 0.93$ for the temperature-salinity relationship and $R^2 = 0.88$ for the salinity-oxygen deficit relationship. The ΔO_2 deficit:ΔNO_3 ratio for (c) is ~40.

from the presence of dissolved oxygen in the brines. Although bacterial mat fluids were always found to contain dissolved oxygen, they were always contaminated with bottom water, and it is unlikely that oxygen is present in the original fluids.

Table 2. DO and Na concentrations in South Basin submersible samples.

Sample or Dive	DO (mM)	Na (mM)	Comments
CD230 S1	17.7	2.36	"Llao's" Pool
CD223 S1	228.2	1.109	Above "Llao's" Pool
CD230 S3	279.2	0.608	Bacterial mat
CD216 S3	294.2	0.480	Bacterial mat
CD223 S3	294.6	N/A	Above pool
CD229 S2	240.7	N/A	Bottom water
CD230 S2	293.8	0.461	Bottom water
CD228 S2	297.3	0.468	Bottom water
CD226 S2	292.6	0.464	Bottom water
CD222 S2	296.6	0.472	Bottom water

Two trends in the oxygen deficit vs salinity relationship for the south basin (Fig. 6) show both the "hydrothermal effect" (dilution plus inorganic oxidation) and the net effect of the oxidation of organic matter and the interaction of hydrothermal fluids with the rest of the south basin waters. The bacterial mat sample from CD230S3 lies along the "hydrothermal" line between the "Llao's Pool" low-oxygen high-sodium end-member and deep lake water (Fig. 6). As stated above, these hydrothermal fluids have enhanced concentrations of reduced chemical species that consume dissolved oxygen after mixing with ambient south basin water. Also, the dilution of deep water with anoxic water will cause a net lowering of the dissolved oxygen content very close to the fluid source. These hydrothermal fluids will also increase the density of near-bottom waters through the addition of salts (McManus 1992). Consequently, the ventilation of these fluids occurs to a lesser degree than in other deep waters, which results in lower oxygen contents in the south basin near-bottom waters.

To quantitatively constrain the influence of hydrothermal activity on the oxygen distribution near the source of the hydrothermal vents, we assume that the hydrothermal fluids enter the lake over an area one tenth the size of the hydrothermal study area (eastern portion of the south basin).

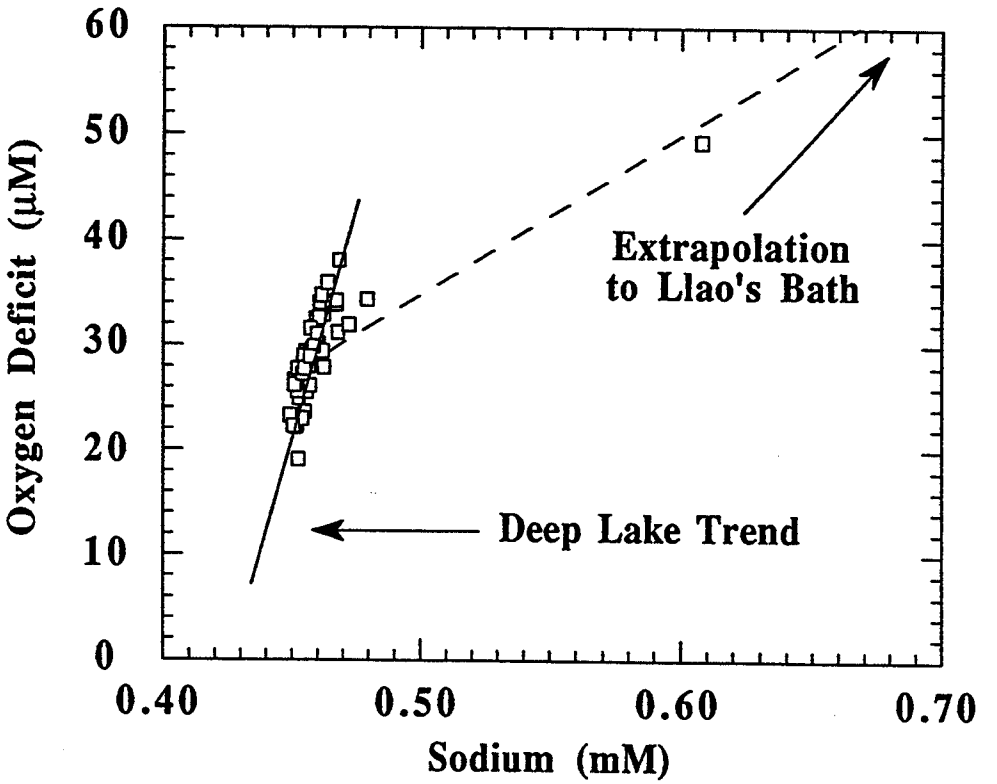


Figure 6. Oxygen deficit vs. sodium for all the South Basin samples including specific hydrothermal features. Both an ambient south Basin trend and a hydrothermal trend are apparent in the figure.

On the basis of the oxygen consumption estimates for the reduced elements from above, and assuming a bottom layer 1 m deep (0.3×10^6 m^3), we obtain an oxygen consumption rate of 6.6 $\mu M\ day^{-1}$. Likewise, this volume will be diluted with anoxic waters by ~6% per day. Although the effects of hydrothermal activity on the deep lake oxygen budget are small, these calculations demonstrate the importance of hydrothermal activity on the local oxygen distribution in the deep south basin.

The linearity between deep lake nitrate and the O_2 deficit (Fig. 5c) suggests that even within the near-bottom hydrothermal fluids the oxygen deficit is driven by the oxidation of particulate organic matter from the upper waters of the lake. However, as mentioned above, the slope of the line in Fig. 5c, shows a $-\Delta O_2:\Delta NO_3$ ratio of ~40, which is much higher than that predicted from classical Redfield stoichiometry where $-\Delta O_2:\Delta NO_3$ = ~9 (Redfield 1942, Redfield et al. 1963). In fact, there are two $-\Delta O_2:\Delta NO_3$ ratios observed for the deep lake (Fig. 7), one in the south basin at depths > 400 m with values between 35 and 40, and another ratio for the rest of the deep lake ~16, which is less-influenced by hydrothermal inputs. The two ratios emphasize the two dominant oxidation processes occurring in the deep lake - the oxidation of organic matter on the oxygen budget of the whole lake, and the oxidation of reduced elements entering the lake.

During the summer of 1989 the C:N ratio was ~15 in the particulate organic material in the 380 and 580 m sediment traps. This is in contrast to the classical C:N ratio of ~7 (Redfield 1942, Redfield et al. 1963). Therefore, both the C:N ratio in particulate material and the $-\Delta O_2:\Delta NO_3$ from the water column ($-\Delta O_2:\Delta NO_3$ = ~16) suggest that the stoichiometry between molecular oxygen, carbon, and nitrogen in the particulate organic material may be non-classical. It is possible that the atypical stoichiometry between carbon, oxygen, and nitrogen, both in particulate material and in the water column, is due to nitrogen limitation. Non-classical stoichiometry between bio-active elements has been reported for Lake Tahoe, which is also an oligotrophic lake where biological production is nitrogen limited (Imboden et al. 1977).

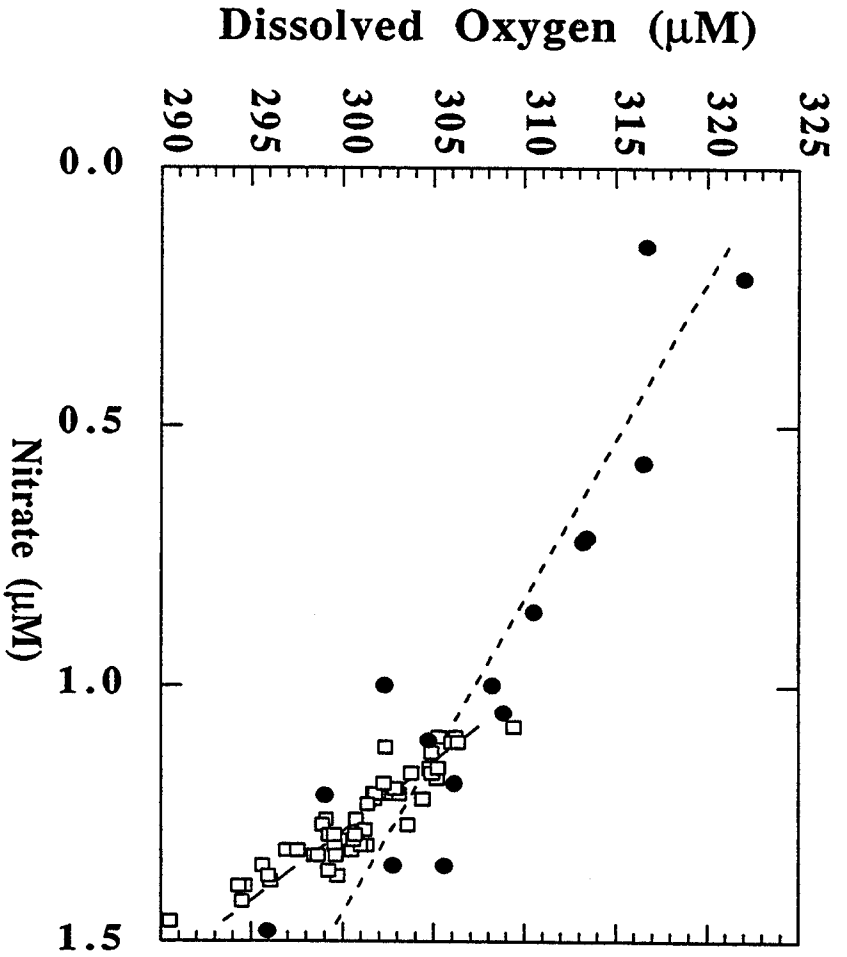


Figure 7. Dissolved oxygen vs. nitrate for the entire water column below 250 m. The data show two relationships; a ΔO_2:ΔNO_3 relationship for the bulk water column (•), and a relationship for the south basin as in Fig. 5c.

On the basis of budget calculations for the hydrothermal study area and the observation that dissolved oxygen in the south basin is 5-15 μM lower than in the north basin, clearly hydrothermal inputs produce small-scale heterogeneity in the south basin dissolved oxygen distribution. Further, the distinct ΔO_2:ΔNO_3 ratio in the deep south basin, compared with the rest of the lake (Fig. 7), indicates that the south basin is influenced to a much greater degree by hydrothermal activity.

Summary

The change in dissolved oxygen over time suggests that the flux of particulate organic material out of the euphotic zone is at least 3.4 mmol C m^{-2} d^{-1}. Although not well constrained, the oxygen budget of the upper water column suggests that this is a reasonable carbon flux estimate. Essentially, if ~40% of the early summer supersaturation of dissolved oxygen in the upper water column is due to photosynthesis, then there is sufficient carbon falling out of the euphotic zone, which will ultimately undergo oxidation, to balance the deep lake oxygen budget.

Hydrothermal activity plays a small role in the overall oxygen budget; however, the active input of reduced fluids influences the local hydrography and bio-active element stoichiometry in the south basin. Mixing calculations suggest that the deep lake mixes with surface water each year and that it would take 2-4 mixing cycles to completely ventilate the deep lake.

Oxygen is a powerful tool for assessing net ecosystem processes, and the ratios between the oxygen deficit and the oxidized solutes can provide both source and process information. This section demonstrates the importance of using a time-series of geochemical tracers to study geochemical cycles. In the case of Crater Lake, a more detailed atmosphere-lake model is needed to refine the estimates of the budgets of the bio-active elements.

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Bulk Atmospheric Deposition

Peter O. Nelson, Joseph F. Reilly, and Gary L. Larson

Atmospheric inputs of chemical components from precipitation and dry deposition, corrected for evapotranspiration, form the baseline composition of lakes from which watershed and in-lake processes affecting lake chemical composition can be assessed (Cook et al. 1987, Munson and Gherini 1991). This section summarizes bulk deposition (precipitation and dry deposition) data collected for Crater Lake during the time period of January 1987 to September 1988. The data are assessed for completeness and accuracy, and compared to other data sets for precipitation/deposition chemistry in the Cascade Mountains.

For Crater Lake, a major source of dissolved and particulate components is expected to be via atmospheric deposition, because lake surface area represents about 78% of the total watershed area, or watershed area (including lake)/lake area ratio of 1.3. This contrasts with a median watershed area/lake area ratio of about 20 for Cascade Mountain lakes (Nelson 1991). Thus, watershed processes for Crater Lake are expected to influence lake chemical composition relatively much less than is typical for Cascade lakes, with resultant chemical composition being more dilute and closer to precipitation composition than is typical.

Methods

Study Area

A bulk-atmospheric-deposition collection station was located on the south-west rim of Crater Lake near Rim Village and north of park headquarters. The station was positioned in an open field removed from the influence of tree litterfall and more than

100 m from the nearest road in an upwind direction from the normally prevailing wind conditions. For Crater Lake, the watershed area is largely delineated by the caldera rim. The location of the collection station was selected to enable collection of atmospheric deposition that represented as closely as possible the deposition to the lake's surface, and to enable access during winter when snow accumulation was high.

The bulk-atmospheric-deposition collection system consisted of a 32-gallon plastic container lined with food-grade plastic bags located about 1 m from ground or snow level. Samples were usually collected at 7-day intervals, although this period varied. This procedure enabled determination of atmospheric deposition in two forms, bulk deposition (wet precipitation plus dry deposition) and dry deposition. For periods where no precipitation occurred (dry deposition), the interior of the collection container was rinsed and the contents diluted to one liter with deionized water and refrigerated one week in the dark prior to filtering. Snow samples were melted overnight prior to filtration.

Samples collected in the field were immediately filtered (prewashed glass fiber filters, 0.75 μm retention) at the Crater Lake laboratory and shipped on ice to the Forest Science Laboratory at Oregon State University in Corvallis. Most of the chemical analyses were conducted at the Cooperative Chemical Analytical Laboratory at Oregon State University, and some were conducted by the Environmental Protection Agency Research Laboratory in Corvallis and the University of Washington, Forest Resources Laboratory in Seattle (Table 1).

Table 1. Sample analysis description.

Analysis	Method*/Modifications**
Cooperative Chemical Analytical Laboratory, Oreg. St. Univ.	
Alkalinity	403, Procedure 4c, titrate to pH 4.5, use 0.02N H_2SO_4. (HCO_3-C)
Ammonia	417F (NH_3-N, 0.005)
Conductivity	205; Wheatstone bridge
Nitrate	418F, Technicon Industrial Method 100-70W. Different formulations for color and ammonium chloride. (NO_3-N, 0.001)
Nitrogen, Total Kjeldahl	Kjeldahl digestion, H_2SO_4, $CuSO_4$/KCl, Nessler finish. (TKN, 0.010)
pH	423; calomel electrode glass pH electrode. Temperature compensator.
Phosphate-Ortho	424F Ascorbic acid reagent:2g/100ml. (PO4-P, 0.002)
Phosphorus-Total	424C, 424F Microwave digestion-60 minutes. 50ml analysis volume, ascorbic acid reagent: 2g/100ml. (P, 0.005)
Silica	Technicon Industrial Method 105-72W. (Si, 0.150)

*Numbers refer to Standard Methods for the Examination of Water and Wastewater 15th Edition, 1980

**Chemical form in which the results are reported is included in parentheses along with the Detection Limit (DL, mg/l)

(continued)

Table 1. Continued.

University of Washington Laboratory	
Chloride	Technicon Industrial Method 99-70W. (Cl, 0.200)
Sulfate	Technicon Industrial Method 105-72W. (SO_4-S, 0.200)
EPA Laboratory	
EPA's Induction Coupled Plasma Atomic Emissions Spectrophotometer is used to determine concentrations of the following components:	
Calcium (Ca, 0.007, 0.067)**	Magnesium (Mg, 0.01, 0.096)
Potassium (K, 0.070, 0.680)	Sodium (Na, 0.010, 0.091)
Boron (B, 0.002, 0.018)	

**Chemical form in which the results are reported is included in parentheses along with the Detection Limit (DL, mg/l) and the Limit of Quality Concentration (LQC, mg/l).

Any analysis below the LQC value has a probable analytical error. The likelihood and magnitude of the error increases as one approaches the detection limit (J. Wagner, U.S. Environmental Protection Agency, pers. comm. 1988). In this study, a result was below the detection limit the policy of the National Atmospheric Deposition Program (NADP) was followed (NADP 1988), i.e., for components that appeared in at least 90% of the sample analyses, one half the detection limit value was used.

Results

Bulk Deposition Concentration

Volume-weighted average concentration in bulk-deposition samples (precipitation plus dry deposition) was determined for each component (Table 2) for the deposition sample collection period (January, 1987 to September, 1988). The component mass collected in each sample was calculated by multiplying each sample concentration by the measured amount of precipitation which fell over the sample collection period.

Table 2. Solute component concentrations for bulk-deposition samples.

Parameter	Concentration*, mg/l
TKN	0.066
NH_3-N	0.025
NO_3-N	0.036
P	0.005
PO_4-P	0.005
SO_4	0.362
Cl	0.375
Ca	0.093
Mg	0.024
K	0.067
Na	0.072
Si	BD**
B	BD
HCO_3	BD

* Annual volume-weighted mean
**Below detection limit

Summation of all sample masses divided by the total volume of precipitation from sample collection periods resulted in the volume-weighted average concentration. The period used in determining the average concentration was normalized to an annual basis.

Dry Deposition Loading Rate

Chemical component masses due to dry deposition were calculated from samples for which no precipitation occurred during the sample collection period. Dry samples accounted for an annual average of 100 days over the study period, 1987 and 1988. An average daily mass deposition was found for each dry sample by dividing the mass collected by the number of days in the sample collection period. An overall average of the entire set of daily averages was calculated and multiplied by the total number of dry

days that occurred annually to estimate the annual mass input to the collection device. This value was then multiplied by the areal ratio of the lake to the collection device to obtain an estimate of annual areal mass loading to the lake (Table 3).

Discussion

Bulk Deposition

Nelson (1991) summarized precipitation chemistry for NADP/NTN sites in western Oregon and Washington for selected variables. The sites are at lower elevations and closer to the Pacific Ocean than is Crater Lake. Duncan and McGinty (1988) summarized winter precipitation chemistry for the Central Washington Cascades. By comparison, concentrations of cations and anions in Crater Lake bulk deposition (T 2) were generally within the low to mid-range of the data sets cited above for the Cascades with the exception of nitrate, which was lower at Crater Lake. Overall, concentrations of bulk-deposition constituents for Crater Lake were probably at or near natural background levels (Galloway et al. 1982, Baker et al. 1991), reflecting little influence from anthropogenic activities.

Bulk deposition contributed less than 5% of the mass lost in seepage from Crater Lake for most chemical components, but was a significant source of mass for the nutrient components. Over 90% of the nitrogen in the lake was derived from bulk and dry deposition (see Chemical Solute Mass Balance section). Concentrations of major cations and anions in precipitation (bulk deposition) were much lower than those in the lake (see Chemical Solute Mass Balance section), despite the limited influence of watershed processes.

Table 3. Dry deposition estimated annual areal loading rate.

Parameter	Loading Rate, kg/km^2-y
TKN	13.6
NH_3-N	1.1
NO_3-N	2.9
P	1.9
PO_4-P	1.3
SO_4	6.5
Cl	17.5
Ca	14.5
Mg	4.1
K	9.4
Na	5.1
Si	BD*
B	BD
HCO_3	BD

*Below detection limit

Cation/anion ratio and measured/predicted conductivity ratio were calculated for each sample as a quality assurance check. Values of these ratios are expected to be near 1.00 for complete water chemical analyses, indicating that key cations or anions have not been omitted or inaccurately determined. Any samples with missing analyses, which affected these calculations were omitted. However, because chloride and sulfate analyses were missed on so many of the bulk-deposition samples in the first year, a median value was entered for the missing values of these components to obtain a representative data set.

The calculated cation/anion ratio median, average and standard deviation for the 51 bulk-deposition samples (samples with precipitation) were 1.18, 1.10 and 0.46,

respectively. Greater variation in the results were observed as the water samples became less concentrated. As concentration values approached the detection limits, as is frequently the case in bulk-deposition samples, analysis inaccuracies created relatively higher errors in the ion totals.

For the calculated conductivity ratio, median, average and standard deviation for bulk-deposition samples were 1.15, 0.89 and 1.42, respectively. The results were greatly affected by four extreme outliers. With the outliers removed the results were 0.90, 0.90 and 0.21, respectively. Increased relative error with high dilution was again indicated. The consistently low values suggested the possibility of a systematic error in the data.

Analysis of variance tests were performed on the bulk-deposition data to check for a systematic error causing the deviation from unity in the ion and conductivity ratios. Evidence was insufficient to prove that a significant difference existed between the component concentration values associated with the "best" ion or conductivity ratios (those near 1.0) and those associated with "errant" ratios (those considerably greater than or less than 1.0).

Overall, data quality ratios were inconclusive in confirming the accuracy for the bulk-deposition samples. Component concentrations in bulk-deposition samples were frequently at, or near, the detection limit, where accurate resolution was difficult to attain. Poor correlation in the bulk-deposition ratio checks may have been caused by the increased effect of analytical errors on the ion sums in the relatively dilute bulk-deposition samples.

Based on the findings of the data review and considering the relative insignificance of the mass input from bulk deposition for non-nutrient components (see

Chemical Solute Mass Balance section), the quality ratios and statistical analysis of the bulk-deposition data indicated that errors present in the data would not greatly influence the mass balance of most components. The complete data set was bulk deposition thus judged to be sufficiently accurate to be used in estimating mass loading of to the lake. A more detailed discussion of the data review is presented in Reilly et al. (1989).

Dry Deposition

No data for dry deposition rates in the Cascade Mountains or western Oregon and Washington were found in the literature to compare with the dry deposition rate data for Crater Lake. Based on annual mass loading to Crater Lake (see Chemical Solute Mass Balance section) dry deposition contributed an estimated 5% to 10% of major base cations (Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+}) and 1% to 5% of acid anions (SO_4^{2-}, NO_3^{-} and Cl^{-}) relative to wet (bulk) deposition. The contribution of dry deposition to the total mass loading to the lake was insignificant for most major cations and anions, but may have been important to the nutrient mass input, as for bulk deposition.

The accuracy of the estimate of mass input to the lake from dry deposition was limited by the sampling method used. The collection device (a dry bucket) failed to accurately simulate the physical transport processes, which are present at the lake surface (NAPAP 1986) and the composition of the atmosphere at the location of the sampling device (the crater rim) was not representative enough of the local conditions on the lake. In addition, the short period of record for the dry deposition data (< 2 years) led to high uncertainty in the data due to the generally high variability of dry bucket deposition rates among sampling periods (Baker 1991).

A wet-pan dry deposition collector located on the lake surface would provide an improved estimate of mass loading (Hicks 1986). Such a device is simple, inexpensive, and accessible to personnel during the summer, when most of the extended, dry collection periods occur. In winter, when a wet-pan collector on the lake would be inaccessible and frozen, snow sampling could provide an indication of atmospheric deposition occurring between precipitation events.

Conclusions

Atmospheric bulk-deposition chemistry for samples collected at Crater Lake during the years 1987-88 was typical of precipitation/deposition chemistry for the Cascade Mountain Range and were near background levels for most constituents, indicating little anthropogenic influence. Dry deposition contributed about 5-10% of wet (bulk)-deposition annual mass loading of soluble chemical components to Crater Lake, although much uncertainty exists in the data. Analysis of data quality for bulk-deposition samples indicated that the data were sufficiently accurate and statistically reliable to produce confident results when the data were used in mass loading calculations. Bulk deposition (wet plus dry) contributed less than 5% of major soluble chemical components in the lake.

Acknowledgements

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Studies of Hydrothermal Processes

Robert Collier, Jack Dymond and James McManus

Background

Crater Lake sits within the caldera of Mt. Mazama, a center of volcanism in the Oregon Cascades for more than 400,000 years (Bacon and Lanphere 1990). The morphology of the lake is largely a consequence of a climactic eruption that occurred 6,845 ± 50 years ago; however, inter-caldera volcanism took place as recently as 4,000 years ago (Bacon and Lanphere 1990). The volcanic morphology provides a basin for what is now the deepest lake in the United States (approximately 590 m). The volcanic terrain strongly limits the nutrient fluxes into the lake, mostly because the lake covers 78% of the total drainage area. Consequently, the lake is highly oligotrophic and one of the clearest lakes in the world.

Our studies of Crater Lake began as an attempt to understand the important physical and chemical characteristics of the lake and the processes that produced some unusual sediment compositions. As we have reported in the past (Collier and Dymond 1988a, Collier and Dymond 1989, Dymond et al. 1989, Dymond and Collier 1990, Collier et al. 1990), a number of these features are consistent with hydrothermal inputs to the lake. Given the location of the lake directly above a relatively recent and major magmatic source (Bacon and Druitt 1988), thermal spring input to the lake would not be surprising. Such a source was first suggested by Van Denburgh (1968), who noted the relatively high sulfate and chloride content of Crater Lake as compared to nearby Davis Lake, and suggested that these two constituents " .... may have been contributed to the lake by thermal springs or fumaroles, probably located below the present lake level. Such springs and fumaroles are a common expression of hydrothermal activity at a site of volcanic eruptions." Van Denburgh did not state whether he thought hydrothermal input was active today. Simpson (1970a) showed that the deep lake had strong gradients in both ^{14}C and the stable carbon isotopes, ^{12}C and ^{13}C. These gradients were consistent with a source of carbon having an isotopic composition similar to magmatic sources. Simpson also constructed a mass balance model which indicated that only a fraction of the ionic content of Crater Lake could be accounted for by known

inputs. He suggested the missing source was the result of "fumarole or hot spring activity near the bottom," and he estimated fluxes from this proposed source.

More recently Williams and Von Herzen (1983) measured high conductive heat flow in certain areas of the lake's sedimented bottom. In one of these areas of high heat flow, they also documented anomalous near-bottom temperatures. This study reinforced earlier work describing the deep temperature structure of the lake as hyperadiabatic (Neal et al. 1971, 1972). On the basis of the heatflow pattern and the water column measurements, Williams and Von Herzen (1983) suggested that there is thermal spring input to the deep lake.

Studies of Crater Lake water composition have provided further support for hydrothermal hypotheses. Thompson et al. (1990) pointed out that Crater Lake has high boron and lithium contents compared to local meteoric water; these elements are typically enriched in thermal waters of volcanic origin. In addition, they showed that chlorine/lithium ratios in Crater Lake waters are very similar to those observed in hot springs from volcanic sources but that these ratios are outside the range of values observed in Mt. Mazama cold springs. Nathenson (1990) demonstrated that a hydrologic model which incorporated precipitation, cold springs, evaporation, and seepage could not account for the major element content of Crater Lake. He suggested thermal springs provide the missing input and, based on geochemical mass balance models, he constrained the input of thermal waters to range between 80 and 1900 l/sec. Nathenson points out that this inflow can easily provide the convective heat flux estimated by Williams and Von Herzen (1983). Nathenson's lower estimate of hydrothermal flux overlaps that of Sorey (1985) who suggested a thermal-spring discharge into the lake of 30 - 150 l/sec.

Evidence of hydrothermal sources to the lake have not gone unchallenged. La Fleur (1987, 1990) argues against any hydrothermal inputs to the lake and suggests that underestimated evaporation rates, fumarolic inputs, and weathering of Mazama ash could account for the anomalous composition of the lake. He suggests that conductive heating rather than convective inputs accounts for the temperature anomalies. La Fleur (1990) proposes that deep springs from caldera wall aquifers can account for the anomalous fluids observed during our 1989 field program.

The question of whether there are hydrothermal sources to Crater Lake has important implications for understanding the lake ecology. For example, the relatively rapid mixing that has been suggested for Crater Lake (Simpson 1970b, Volchok et al. 1970) may be a consequence of hydrothermal inputs to the bottom of the lake. If this is true, temporal variability in this source could impact the nutrient cycling and the plant productivity of the lake. In 1987, in response to the requirement of Public Law 99-591 for identification of significant thermal features in national parks, the National Park Service initiated a three-year program to evaluate possible hydrothermal sources to Crater Lake. The research, which is part of a 10-year limnological study of Crater Lake, is designed to: (1) define the thermal and chemical variability in the deep lake, (2) examine the data for evidence of a hydrothermal source, (3) design and carry out a program that would find possible venting sites and sample any associated fluids, and (4) evaluate alternative mechanisms to explain the observed thermal and chemical variability.

The final report summarizes the field programs and laboratory analyses which have been carried out from 1987 to the present. The results for the 1987 and 1988 field programs also have been reported in Collier and Dymond (1988a), Collier and Dymond (1988b), Collier and Dymond (1989), Dymond et al. (1989), Dymond and Collier (1990), and Collier et al. (1990). During the summer of 1989, our research group spent approximately 35 days at the lake in an expanded program that included the use of the research submersible, Deep Rover. A draft of the report was completed on October 26, 1990 and submitted to a peer review committee chaired by Dr. Charles Goldman. We have considered the evaluations and recommendations of the review committee in the final report of the research submitted May 31, 1991[1]. In addition we have responded to reviews of the draft report by the U.S. Bureau of Land Management and the California Energy Company.

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[1] Collier, R., J. Dymond and J. McManus (1991) Studies of Hydrothermal Processes in Crater Lake, OR., OSU College of Oceanography Report #90-7, 201 pages and 9 appendices.

In Figure 1 we show the major bathymetric features of the lake and the location of what we refer to as the "Detailed Study Area". The Detailed Study Area was a focus of our research operations during the 1987, 1988, and 1989 field seasons. Much of our surface ship sampling has been conducted within this region, and most of the submersible dives that had a hydrothermal focus were carried out within this area. We began our hydrothermal studies here because of the previously reported high heat flow and water column anomalies in this general region (Williams and von Herzen 1983).

During the summer of 1987, our research group spent 20 days at Crater Lake, during which time we performed extensive sampling operations and made thermal and chemical measurements from the surface research vessel. These measurements formed the basis for preliminary mapping of sites with the most anomalous near-bottom water temperatures and salt contents. The 1987 field program also introduced the use of a remotely operated vehicle (ROV) for making detailed observations of the bottom of Crater Lake. Seven ROV deployments were made which provided information on the sediment thickness, the presence of benthic plants and animals, and the existence of unusual precipitates and crusts which were in marked contrast to the normal buff-colored sediments that blanket much of the bottom.

The hydrothermal field program for 1988 was based on three separate expeditions to the lake. In early July, eight days were used to recover and redeploy a sediment trap mooring, establish our navigational stations, carry out several hydrocasts, make numerous CTD casts, and prepare for a major submersible program. In August, our 25 day field program focused on using the submersible, Deep-Rover, to locate, observe, and sample geological, geochemical, and biological features in the deep lake that had been hitherto inaccessible. Although much of our efforts were directed toward the submersible operations, we also carried out bathymetric surveying, conducted hydrocasts, made CTD (conductivity, temperature, and depth) measurements, and collected cores during this period. In September we returned to the lake to recover and redeploy the sediment trap mooring and carry out additional CTD measurements and hydrocasts.

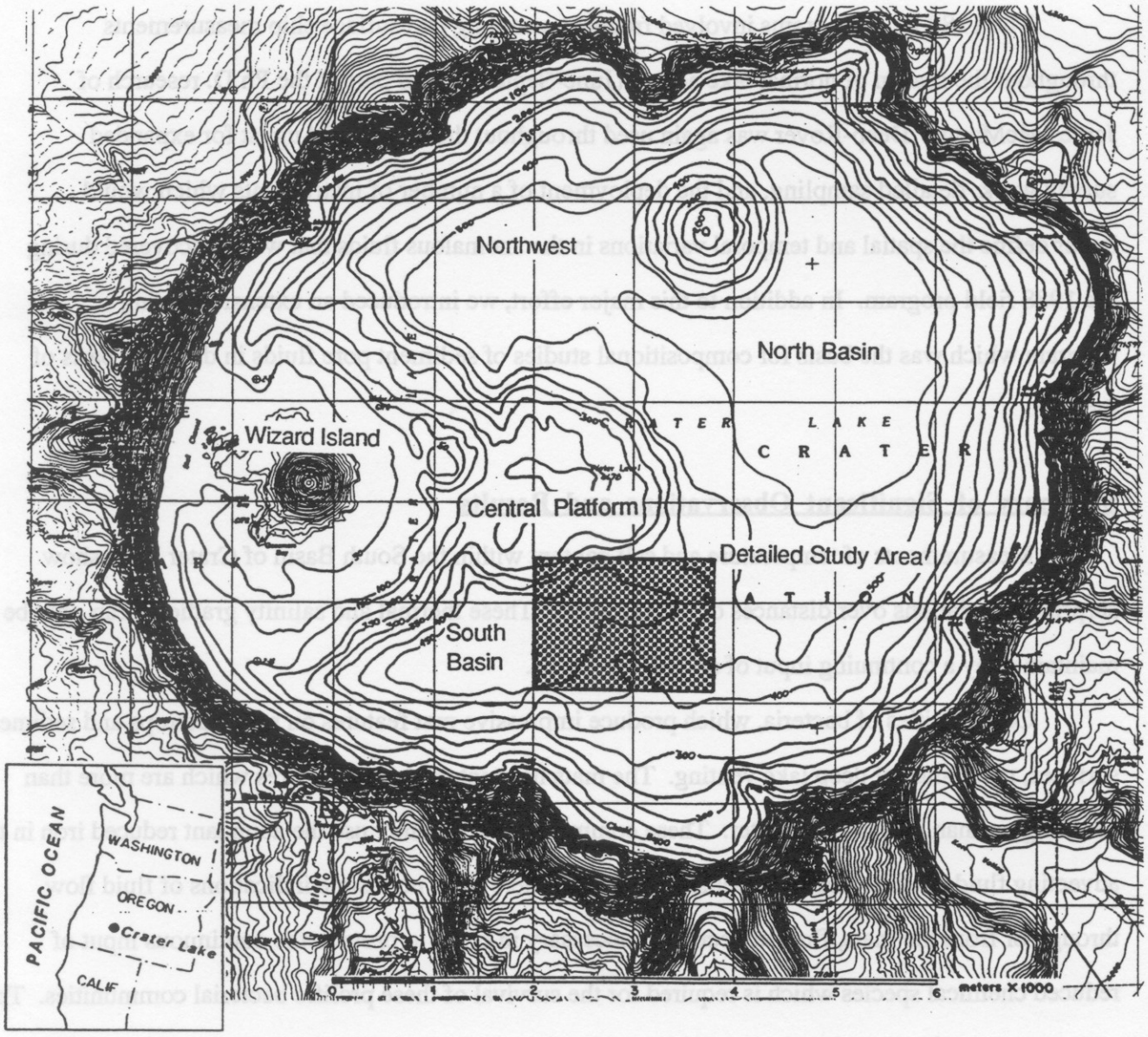


Figure 1. Topographic/bathymetric map of Crater lake, Oregon (42° 56'N, 122° 07'W). The caldera lake has a surface water elevation of 1,883 m and a maximum depth of 594 m. The dotted rectangle denotes the Detailed Study Area. The bathymetry, from Byrne (1965) has been projected onto the USGS 7.5-minute quadranges for Crater Lake East and West.

The 1989 field programs involved frequent sampling and surface ship measurements throughout the season of normal lake access (June-September) as part of the Ph.D. research of James McManus. Deep-Rover was again used throughout the month of August for expanded survey work, detailed sampling, and the deployment of a number of instruments which would better define the spatial and temporal variations in the anomalous fluids that were discovered during the 1988 field program. In addition to this major effort, we introduced an extensive coring program which was the basis for compositional studies of sediment pore fluids in different parts of the lake.

Summary of Significant Observations and Results

Measurements of temperature and salt content within the South Basin of Crater Lake show surprising variations over distances of a few meters. These thermal and salinity gradients can only be maintained by a continuing input of anomalous fluids.

Communities of bacteria, which produce impressive mat features on rock outcrops and sediment surfaces, mark sites of deep lake venting. The mats have internal temperatures which are more than 15°C higher than lake bottom water. These communities apparently use the abundant reduced iron in the advecting fluids to fuel their metabolism. Although there were no visible indications of fluid flow through or from the mats, fluid advection is necessary in order to provide the continuous input of reduced chemical species which is required for the survival of these prolific bacterial communities. The temperature gradients within the mats indicate that the advection rates are as high as 100 mper year. Consequently, the bacterial mats are visual markers of thermally and chemically enriched fluid venting.

Pools of saline water, with major element contents that are approximately ten times greater than background lake values, have been discovered in two widely separated areas of the lake. Sediment pore water compositions from some South Basin cores are similar to those of the pools. The pore water measurements define non-linear gradients which indicate vertical fluid advection rates of up to two meters/year. These measurements as well as the major element compositions suggest that the fluids advecting through the sediments, the brine pools, and the bacterial mats are derived

from a similar source. Results from chemical geothermometry determinations suggest that this source equilibrated with silicate rocks at temperatures ranging from 40 to 165 °C.

Sampling of the mat fluids, the brine pools, and sediment pore waters has dramatically increased the known range of anomalous water compositions within Crater Lake. In the most anomalous fluids, manganese is enriched by as much as a million times and ^{222}Rn is enriched 100,000 times over typical lake values. Helium-3, perhaps the most distinctive indicator of a magmatic source, is enriched 500 times over values for waters in equilibrium with the atmosphere. Striking depletions of ^{14}C in pool fluids and the deep lake waters indicate a magmatic source of "dead carbon" is entering the deep lake. Rare earth element concentrations in lake and sediment pore waters have an abundance pattern which indicate a hydrothermal source. Isotopic compositions of hydrogen in the saline pools clearly show that these anomalous fluids are highly modified lake water and could not have originated outside the lake.

The enhanced salt content of the anomalous fluids enables us to account for the bulk composition of the lake by elucidating the sources of chemical species which were previously unexplained by known water sources such as precipitation and caldera springs. We have identified a third source—a hydrothermal component—as the major influence on lake composition. Using sensitive analytical methods, we have monitored the active accumulation of heat and salt in the deep lake that results from this source. Various mass balance models indicate that a net heat flow of 15 to 30 megawatts (MW) is carried into the lake by thermal fluids. The calculated flow rates for a thermally and chemically enriched fluid are approximately 200-400 l/sec.—roughly two billion gallons per year.

Conclusions

As a result of three years of field studies and our interpretation of these and other data from the literature, we conclude that there <u>are</u> inputs of hydrothermal fluids into the bottom of Crater Lake. The dissolved materials associated with these thermally and chemically enriched fluids, coupled with the overall hydrologic balance, control the observed chemical composition of the lake. Because the hydrothermal input dominates the flux of most dissolved chemicals into Crater Lake, the hydrothermal process is highly significant. Furthermore, the geothermal inputs have a direct effect

on the density structure of the deep lake, and therefore can profoundly affect the rate of heat transport and the redistribution of dissolved salts and nutrients within the body of the lake.

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Particle Flux Measurements

Jack Dymond, Robert Collier, and Gary L. Larson

Lakes reflect a diverse array of influences and processes. Factors such as climate, the erosional/weathering regime of watersheds, and the nature of biologic assemblages all contribute to the character of lakes. Much of the influence of these factors arises because they determine both the flow of carbon and nutrients into the lake and the recycling and redistribution of components within the lake system. In this study we have attempted to define flux of carbon, nutrients, and lithogenic materials into and within Crater Lake, the deepest lake in the US. Our approach relies strongly on the collection of time-series particle flux data.

Settling particulate matter is a dominant pathway for nutrient transfer and element cycling in aquatic systems. Therefore, the collection and analysis of the settling fraction of suspended particles has long been an important tool in biogeochemical studies of lakes (Bloesch and Burns 1980). These studies have helped to understand processes such as sediment focusing (Bloesch 1982, Hilton 1985, Eadie et al. 1990, Baker et al. 1991, Robbins and Eadie 1991, Wieland et al. 1991), particulate removal of pollutants (Eadie and Robbins 1987, Baker, et al. 1991), and nutrient cycling (Premazzi and Marengo 1982). In addition, lake sediment trap studies have been used to determine sources of particulate organic matter in lakes (Meyers et al. 1980, Lee et al. 1987). Recent data has begun to focus on time series trap studies in lakes (Bloesch and Sturm 1986; Pilskaln and Johnson 1991; Robbins and Eadie 1991, Schuler et al. 1991). These new developments in sediment trap instrumentation have vastly improved our ability to interpret flux data and provide a critical tool needed to generate a remotely sensed, long-term evaluation of biogeochemical cycles in lakes.

Although sediment traps were first deployed in lake studies, many recent advances in development and application of sediment traps have been in the ocean research. Sediment traps have become an essential tool for studying a variety of biogeochemical processes in the oceans. Their use has increased our understanding of rates of internal ocean processes and rates of material

transfer between continents and oceans. For example, we now know that particle fluxes are primarily driven by surface biological production (Deuser et al. 1981) and that the material collected in traps has settled at rates much faster (>100 m/day) than is possible with individual particle settling. A variety of aggregation processes that produce fast-settling particles contribute to vertical transport (Fowler and Knauer 1986; Pilskaln and Honjo 1987). Often the particulate flux is episodic (Honjo 1982) or variable over seasonal and interannual scales (Dymond and Collier 1988). The importance of lateral transport and resuspension has been defined through sediment traps (Honjo 1982; Dymond 1984; Walsh et al. 1988; Moore and Dymond 1991). Sediment trap studies have provided the basic data on the export flux of biogenic materials from the euphotic zone (Suess 1980; Martin et al. 1987; Pace et al. 1987) and their recycling and diagenesis within the water column. Finally, flux comparisons between the particulate rain to the seafloor and the burial in sediments have defined benthic diagenesis and the important processes leading to sediment accumulation (Dymond and Lyle 1985; Dymond et al. 1992; Dymond and Lyle in press).
The closed basin nature of Crater Lake suggests that the use of sediment traps could be of particular interest for constraining the overall nutrient and chemical balances of the lake.

Methods

Moored sediment trap deployments were initiated in Crater Lake beginning in July 1983 and have continued without interruption to the present. Although there have been a few changes in our instrumentation and trap locations, the basic design of the experiment has not changed.
The sediment trap design used throughout the experiment is a conical trap based on a design used by (Soutar et al. 1977). It features a relatively steep cone (2:1 height to diameter) with a Hexcell baffle (1 cm opening by 5 cm depth) at the cone mouth to reduce turbulence and produce consistent collection under diverse current conditions. The trap is constructed of fiberglass and plastic to minimize the possibility of metal contamination of the samples. Comparison of this trap design with other cones and cylinders shows very similar particle fluxes. Measurements of ^{230}Th fluxes suggest a collection efficiency of > 80% (Mahannah 1984).

Particles that enter the trap move downward through the relatively still water encompassed by the cone until they enter a sample cup at the base of the cone. For most deployments the sample cup was a 45-x-9-cm acrylic tube. The particulate materials accumulating within this single tube are assumed to represent the integrated flux of setting particles over the deployment period. Beginning in September of 1986, we began deploying a sediment trap with a rotating sample changer with five collecting cups. This trap enabled us to define the particulate flux with greater temporal resolution than is possible with a single-cup trap. The sediment trap cups contained saturated sodium borate-buffered formaldehyde as a bactericide. This resulted in a final cup pH of 8.5 and a concentration of formaldehyde of 2%.

During the first two years of the study, sediment traps had a collection area of 0.10 m^2. These traps were deployed in a paired configuration with identical, single-cup traps suspended side-by-side on a fiberglass framework. During 1983-1985, two of the paired traps were placed on the mooring, one pair at a depth of 200 m and the second 10 m above the lake bottom (~580). The data listed in Table 1 for those years is an average of the measurements made with the two paired cups. In all cases, the fluxes defined by the paired traps agreed to within 10%. Beginning July of 1985, a larger (0.25 m^2), single-cone trap was used in the experiment. Three of these larger traps were placed on the moorings throughout the rest of the time-series (1985-1991) at depths of 200 m 390, and 590 m. During the first deployment of this trap configuration, the deepest trap became fouled in the trap harness and did not collect a sample.

Each year the traps were recovered and redeployed in early July and early September. After 1986 the "winter" deployment (September to July) used the five-cup trap at the 200 m depth. Thus, for this upper trap depth, the summer (July to September) deployment and the winter deployment provided 6, 2-month samples. The sample changer on the trap at the depth of 200 m failed during the winter of 90-91, and only a single 10-month sample was collected. All middle and near-bottom trap data are for a two month summer deployment and a 10-month winter deployment.

Table 1. Fluxes measured in Crater Lake sediment trap experiments. All fluxes are in units of μg per cm^2 per year.

Sample	Depth(m)	Date	Days	Total Flux	C Flux	N Flux	P Flux	Si Flux	Al Flux	Opal Flux
CL-1 upper	200	7/12/83	62	1387	72	6.9		44	10	34
CL-1 lower	457	7/12/83	62	6815	151	24.1	5.5	1903	578	443
CL-2 upper	200	9/13/83	301	362	30	3.5	0.2	94	24	57
CL-2 lower	457	9/13/83	301	2143	141	17.4	1.8	575	144	376
CL-3 upper	200	7/11/84	68	354	57	6.2	—	80	16	80
CL-3 lower	583	7/11/84	68	258	21	1.9	—	68	17	40
CL-4 upper	200	9/18/84	295	603	73	11.6	—	144	28	153
CL-4 lower	583	9/18/84	295	1660	135	20.1	—	429	90	416
CL-5 upper	200	7/11/85	56	231	63	8.8	—	36	6	46
CL-5 middle	390	7/11/85	56	568	142	17.2	—	94	19	94
CL-6 upper	200	9/6/85	305	1618	151	21.4	—	432	81	492
CL-6 middle	390	9/6/85	305	3039	288	34.3	—	800	157	861
CL-6 lower	580	9/6/85	305	3101	222	27.0	—	828	187	700
CL-7 upper	200	7/9/86	56	346	92	9.9	—	52	12	50
CL-7 middle	390	7/9/86	56	926	191	19.5	—	168	37	154
CL-7 lower	580	7/9/86	56	197	36	3.4	—	40	9	36
CL-8 upper cup 1	200	9/4/86	61	37	11	1.1	—	—	1	—
CL-8 upper cup 2	200	11/4/86	61	10	3	0.3	—	—	0.3	—
CL-8 upper cup 3	200	1/4/87	61	124	35	2.2	—	—	3	—
CL-8 upper cup 4	200	3/6/87	61	10	2	0.2	—	—	0.4	—
CL-8 upper cup 5	200	5/6/87	64	575	66	9.7	—	144	27	148
CL-8 middle	390	9/4/86	308	1321	178	18.5	1.5	310	62	331
CL-8 lower	580	9/4/86	308	524	64	7.7	0.6	126	27	115
CL-9 upper	200	7/10/87	62	159	56	8.2	—	—	3	—
CL-9 middle	390	7/10/87	62	327	83	10.1	—	—	10	—
CL-9 lower	580	7/10/87	62	320	68	8.4	—	—	11	—
CL-10 upper cup 1	200	9/11/87	60	110	37	4.4	—	—	2	—
CL-10 upper cup 2	200	11/10/87	60	615	109	11.3	—	—	18	—
CL-10 upper cup 3	200	1/9/88	60	407	70	10.0	—	—	15	—
CL-10 upper cup 4	200	3/9/88	60	549	94	12.4	—	—	22	—
CL-10 upper cup 5	200	5/8/88	59	1187	195	26.0	1.9	—	48	—
CL-10 middle	390	9/11/87	299	653	121	13.8	0.9	—	25	188
CL-10 lower	580	9/11/87	299	375	63	7.6	0.5	—	17	—
CL-11 upper	200	7/7/88	61	375	145	23.1	—	—	5	—
CL-11 middle	390	7/7/88	61	361	124	18.4	—	—	7	—
CL-11 lower	580	7/7/88	61	228	75	9.7	—	—	5	—
CL-12 upper cup 1	200	9/7/88	60	125	51	7.5	—	—	1	—
CL-12 upper cup 2	200	11/9/88	60	284	54	7.3	—	—	12	—
CL-12 upper cup 3	200	1/5/89	60	257	45	6.5	—	—	12	—
CL-12 upper cup 4	200	3/6/89	60	48	12	1.8	—	—	2	—
CL-12 upper cup 5	200	5/5/89	62	3251	292	33.8	3.5	—	195	—
CL-12 middle	390	9/7/88	302	730	91	10.1	0.9	—	41	—
CL-12 lower	580	9/7/88	302	869	101	10.9	1.1	—	49	—
CL-13 upper	200	7/7/89	61	1578	417	31.2	2.3	—	39	—
CL-13 middle	390	7/7/89	61	1664	398	30.5	2.4	—	52	—
CL-13 lower	580	7/7/89	61	1559	378	29.5	2.5	—	50	—

Table 1. Continued.

Sample	Depth(m)	Date	Days	Total Flux	C Flux	N Flux	P Flux	Si Flux	Al Flux	Opal Flux
CL-14 upper cup 1	200	9/7/89	59	123	52	7.4	—	—	1	—
CL-14 upper cup 2	200	11/5/89	60	108	47	9.9	—	—	1	—
CL-14 upper cup 3	200	1/4/90	60	96	36	7.5	—	—	1	—
CL-14 upper cup 4	200	3/5/90	60	58	19	3.0	—	—	1	—
CL-14 upper cup 5	200	5/4/90	67	552	68	8.5	0.6	—	31	—
CL-14 middle	390	9/7/89	306	284	54	7.6	0.5	—	14	—
CL-14 lower	580	9/7/89	306	673	102	13.3	1.0	—	37	—
CL-15 upper	200	7/11/90	69	393	100	9.8	—	—	12	—
CL-15 middle	390	7/11/90	69	188	39	3.5	—	—	8	—
CL-15 lower	580	7/11/90	69	450	57	5.5	—	—	26	—
CL-16 upper	200	9/18/90	294	572	75	8.4	—	—	28	—
CL-16 middle	390	9/18/90	294	302	41	4.4	—	—	15	—
CL-16 lower	580	9/18/90	294	407	53	5.7	—	—	21	—
CL-17 upper	200	7/10/91	69	82	29	3.3	—	—	2	—
CL-17 middle	390	7/10/91	69	48	15	1.3	—	—	2	—
CL-17 lower	580	7/10/91	69	17	3	0.3	—	—	1	—

Annual Trap Data
Sept-Aug.

Sample	Depth(m)	Date	Days	Total Flux	C Flux	N Flux	P Flux	Si Flux	Al Flux	Opal Flux
upper 83-84	200	9/13/83	369	361	35	4.0	0.1	91	23	61
lower 83-84	457	9/13/83	369	1809	123	15.1	1.5		117	307
upper 84-85	200	9/18/84	361	529	70	10.9	—	123	24	132
lower 84-85*	583	9/18/84	361	1445	133	19.1	—	366	76	355
upper 85-86	200	9/6/85	361	1421	142	19.6	—	373	70	424
middle 85-86	390	9/6/85	361	2711	273	32.0	—	702	138	751
lower 85-86	580	9/6/85	361	2651	193	23.3	—	706	159	597
upper 86-87	200	9/4/86	370	156	29	3.7	—	—	6	—
middle 86-87	390	9/4/86	370	1154	162	17.1	1.3	—	53	—
lower 86-87	580	9/4/86	370	490	65	7.8	0.5	—	25	—
upper 87-88	200	9/11/87	361	538	108	14.5	0.3	—	18	—
middle 87-88	390	9/11/87	361	604	122	14.6	0.7	—	22	—
lower 87-88	580	9/11/87	361	350	65	7.9	0.4	—	15	—
upper 88-89	200	9/7/88	363	938	147	14.8	1.0	—	44	—
middle 88-89	390	9/7/88	363	887	142	13.5	1.1	—	43	—
lower 88-89	580	9/7/88	363	985	147	14.1	1.3	—	49	—
upper 89-90	200	9/7/89	367	232	55	7.7	0.1	—	8	—
middle 89-90	390	9/7/89	367	266	51	6.9	0.4	—	13	—
lower 89-90	580	9/7/89	367	632	94	11.8	0.8	—	35	—
upper 90-91	200	9/18/90	363	479	67	7.4	—	—	23	—
middle 90-91	390	9/18/90	363	254	36	3.8	—	—	13	—
lower 90-91	580	9/18/90	363	333	43	4.6	—	—	17	—

* used middle trap for summer of 1985

Average Upper	582	82	10.3	—	—	24	—		
Average Middle	979	131	14.6	—	—	45	—		
Average Lower	1087	108	13.0	—	—	60	—		

The first year of the experiment (1983-4) we deployed the sediment traps in the South Basin (Figure 1). All other deployments (1984-1991) were located in the Central Basin, near Station 13 (see Study Area and Facilities Section). The deep trap on the first deployment was at a depth of 457 m and was located nearer to the steep caldera wall than the deep trap (580m) in the Central Basin deployments. This difference in location lead to a relatively high resuspended sediment flux measured in the deep trap during the 1983-84 deployment.

Results and Discussion

Variability and Composition

In general, the settling particles are composed of materials derived from two major sources: biological production (generally organic matter) and lithogenous material eroded from the caldera walls and carried from other continental sources by winds. The organic matter generally is chemically and microbiologically unstable and the lithogenous component generally is inert with respect to large changes in its chemistry. Total organic carbon was adopted as a proxy all organic matter and aluminum used to represent the lithogenous fraction.

Interannual Variability. We examine the year-to-year variations in fluxes based on a September through August deployment period (Table 1; Figures 2 and 3). During the 8-year experiment, the total (bulk) particle flux to the upper trap (200 m depth) varies by more than a factor of seven. The highest year, 1985-86, is followed by the lowest year, 1986-87. Except for these two extreme years the annual average of the total flux to the upper trap varies by less than a factor of two (426 to 736 $\mu g/cm^2/yr$).

The 1985-86 period is also the year with the highest for a middle trap flux. In general the fluxes for the middle trap are higher than those of the upper trap, which we attribute to sediment focusing (Likens and Davis 1975), whereby particles that settle to the bottom in shallower areas are subsequently resuspended and moved down slope. In some cases, for example 1986-87, there are large differences between the middle and upper trap fluxes.

For the first four years of the experiment, the deep trap collected two to seven times more material than the upper trap. Beginning with the 1987-8 year, however, it is more common for the

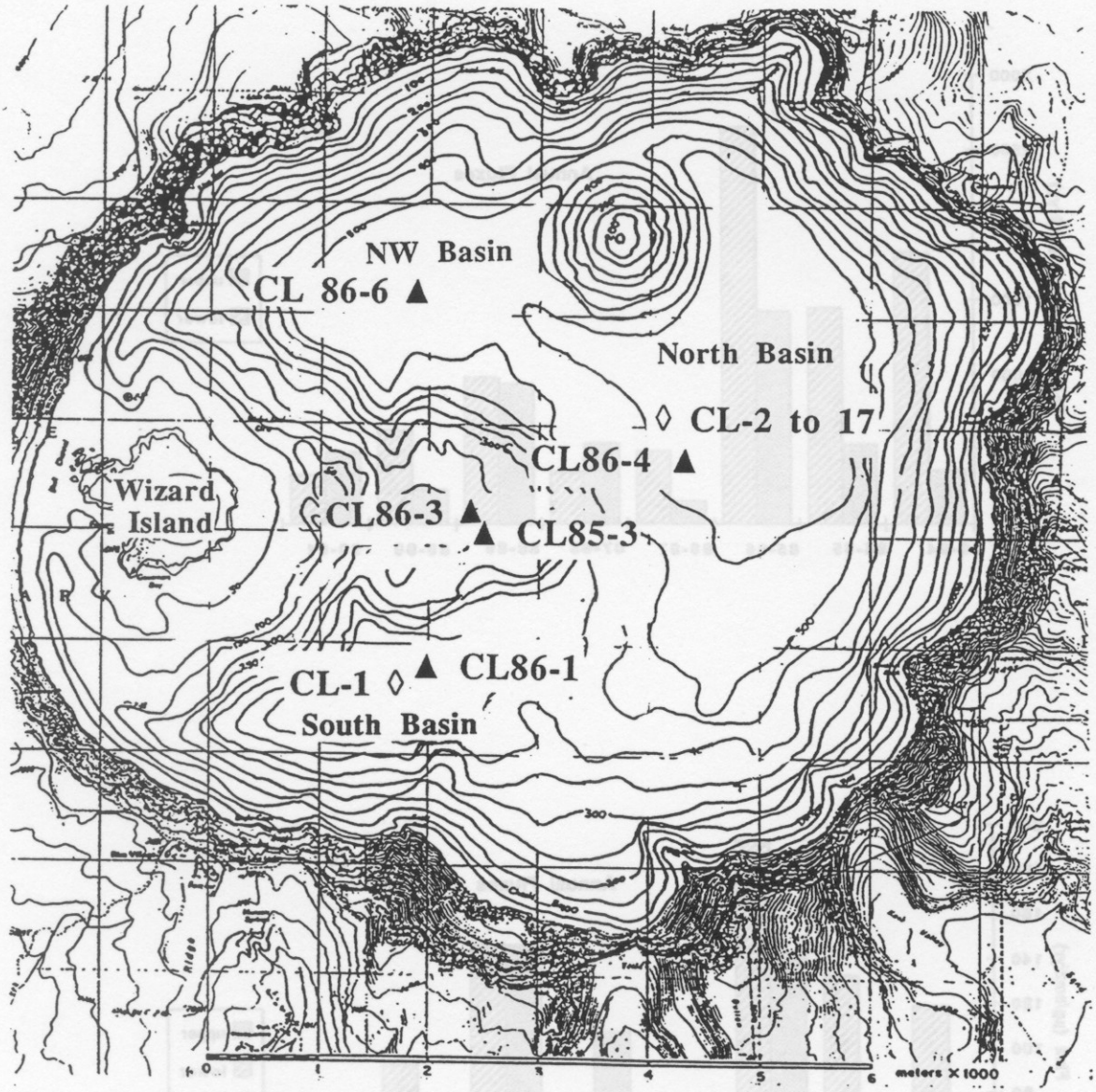


Figure 1. Locations of sediment trap samples are shown by the open diamonds. Note that the location of CL-1 (the 1983-84 trap deployment) is in the South Basin. All other sediment trap deployments are in the North Basin. Filled triangles denote sediment cores. The cores collected in 1986 (CL 86-1 through CL 86-6) were used for the ^{210}Pb measurements. The sedimentation rate of CL 85-3 was determined by ^{14}C measurement of a pine cone.

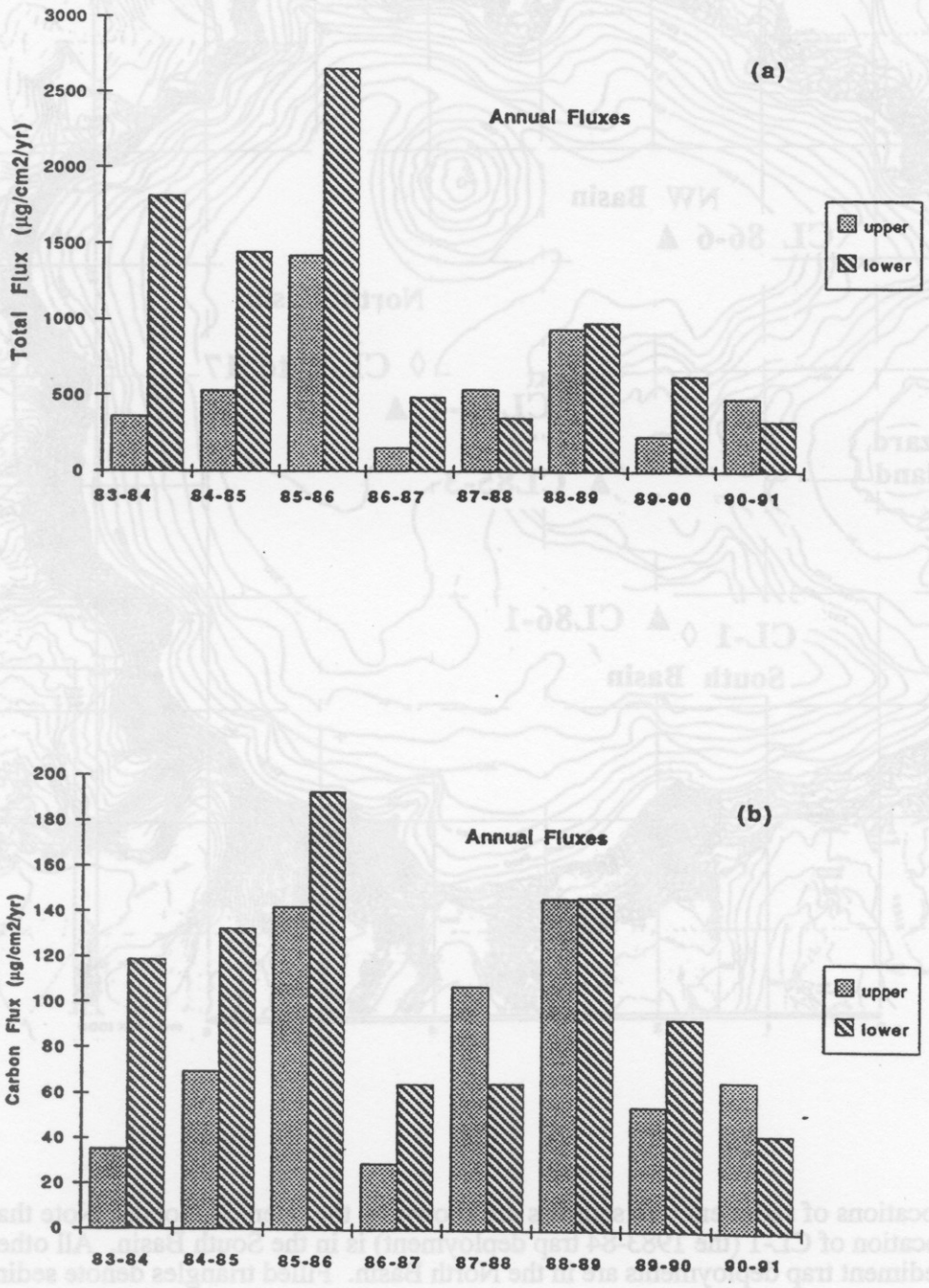


Figure 2. (a) The total annual particulate flux measured in the upper (200 m water depth) and lower (10 m above the bottom) for each of the eight years of our sediment trap experiment. The annual fluxes are determined over the year beginning and ending in September. (b) Annual particulate carbon fluxes measured in the upper and lower traps.

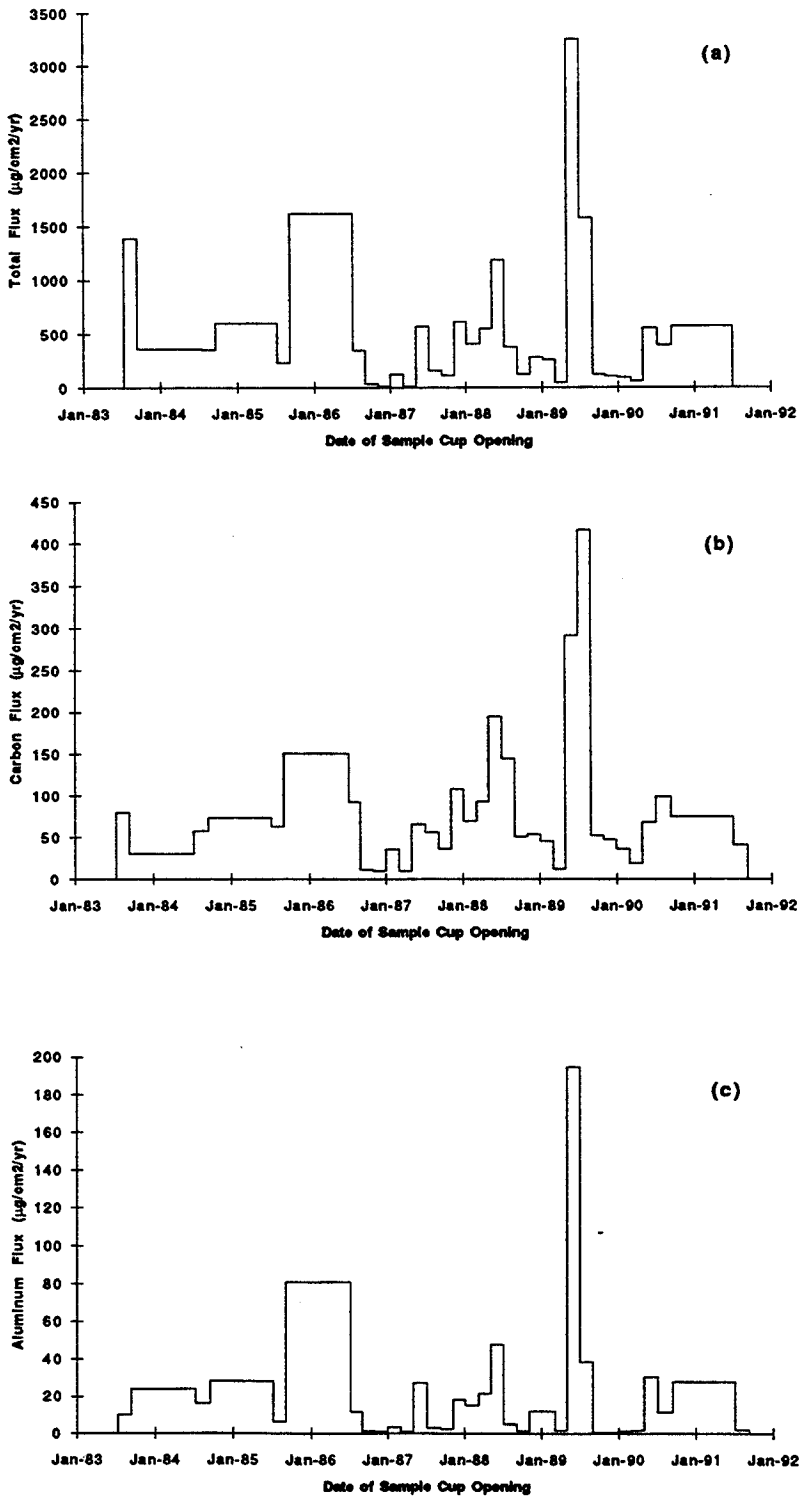


Figure 3. (a) Time-series of total particulate flux measured at depths of 200 m over the duration of the experiment. Early in the experiment, the sampling intervals included a "summer" 2-month sample and a "winter" 10-month sample. Beginning in 1986, a sample changer that collected 2 month samples throughout the year was used. Because the sample changer failed in 1990-91, only a 5-month integrated sample for that interval was collected. (b) Time-series of particulate organic carbon flux measured at 200 m. (c) Time-series of particulate aluminum flux measured at 200 m.

deep trap to collect roughly the same particle flux or in some cases (1987-88 and 1990-91) less material than the upper trap.

Assuming particulate carbon fluxes reflect the biological productivity of the lake, these experiments suggest a possible cyclic component to the general pattern of lake productivity (Figure 2). Lake productivity increased during the first three years (1983-1986) and then decreased sharply. It then increased for the next three years (1986-1989) and has been relatively low for the last two years (1989-1991). This interannual variability in inferred biological productivity of the lake may be a consequence of variable nutrient imputs to the upper lake, a topic which will be discussed in detail later in this report.

Seasonal Variability. Flux variations during the year are best shown by the data from 1986 to 1990 for which the temporal resolution is approximately two months. In Figures 4a-d we compare the total, carbon, and aluminum fluxes for each sample cup during the 1986 to 1990 period. These comparisons reveal that the highest fluxes occur during the May through June collection periods. This pattern is observed not only for total fluxes, but carbon and aluminum fluxes as well, indicating that both the biogenic components of the flux and the alumino-silicate components, which are eroded from the caldera walls reach a maximum in the late spring and early summer. The organic carbon fluxes during the July through August collection period generally are similar or sometimes even higher than that observed for the May through June collections (Figure 4b).

This variability probably reflects seasonal inputs of nutrients and volcanic debris. Nutrient inputs to the euphotic zone derived from mixing of deep waters with upper lake (0-200 m) water occur in the winter and early spring (McManus 1992). In addition, there are nutrient inputs from precipitation which occurs primarily between November and March and from melting of the caldera-wall snow pack that occurs in late spring. The higher biogenic fluxes during May through August may reflect an increase in photosynthetic activity in the upper water column during this period, in response to the winter and spring nutrient inputs, water column stability, and light

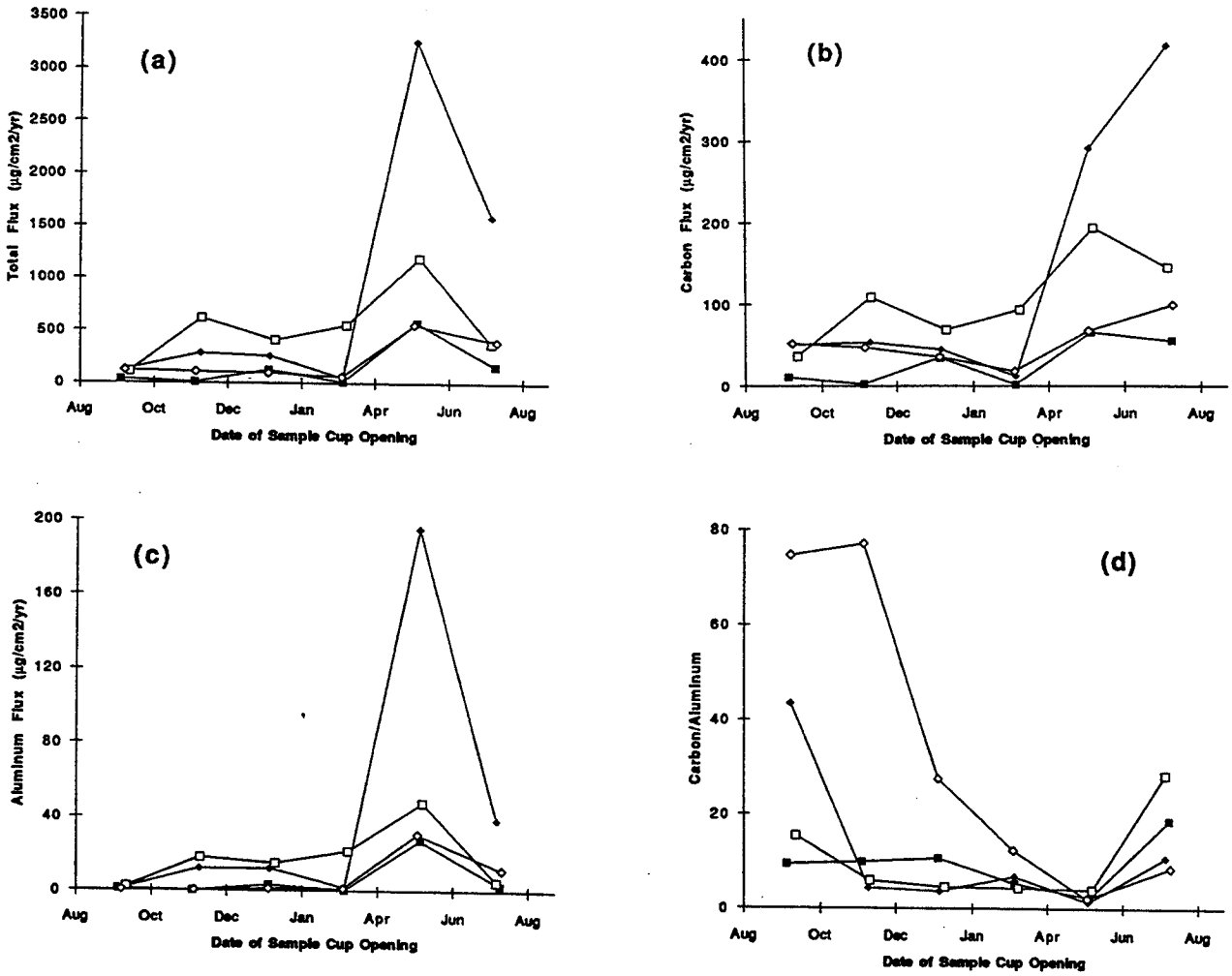


Figure 4. (a) Seasonal patterns of total particulate flux measured at 200 m. Only data from 1986 to 1990 are shown because these are the years during which time-series sample cups were operational on the sediment trap. Filled squares are for 1986-87. Open squares are for 1987-88. Filled diamonds are for 1988-89. Open diamonds are for 1989-90. (b) Seasonal patterns of particulate carbon flux measured at 200 m. (c) Seasonal patterns of particulate aluminum flux measured at 200 m. (d) Seasonal patterns in the organic carbon to aluminum ratio of the settling particulate material. The data are from 200 m.

availability. Generally by July, however, the nitrate levels in the upper 200 m of the lake are below limits of detection.

We expect that the time of maximum input of volcanic debris from the caldera walls would occur during spring, the time of rapid melting of the snow pack. This is also the time of maximum runoff from the caldera-wall springs and a time of frequent rock slides and avalanches. Both processes could account for the peak in the flux of aluminum that is observed during the May through August time period. It is probable that some portion of the aluminum input to the lake is windborne, but significant atmospheric sources from the local terrain are possible only during the snow-free months, which are generally July through October.

Although both carbon and aluminum fluxes peak during the spring and early summer (Figures 4b and 4c), the relative contribution of these two components change over the year. This is most clearly seen by looking at the carbon to aluminum ratios of the sediment trap samples (Figure 4d). The lowest C/Al values occur during the May through June sampling interval corresponding to the time of maximal snow melt and wall runoff. At other times, during periods of very high primary production or during low total flux periods in the fall and winter higher C/Al values occur (Table 1, Figure 4d). For instance, in the fall of 1988 and fall and winter of 1989-90, the relatively small total particulate flux collected was dominated by biogenic material.

Depth Variations in Particle Flux. The computed annual fluxes for each trap are plotted against depth in Figures 5a-c. These figures not only reveal the interannual variations in flux but also changes in flux with depth which help define the processes controlling particle distributions in the lake.

The total flux plot (Figure 5a) shows that two years, 1983-4 and 1985-6, had relatively high fluxes that increased strongly with depth. Increases in flux with depth suggest some type of sediment focusing process (Likens and Davis 1975). In addition to resuspension and downslope particle movement, the focusing process may also involve turbidity currents that are initiated by landslides from the caldera walls. Turbidites have been shown to be common in sediment cores from the lake and can be seen in seismic reflection profiles as well (Barber and Nelson 1990). For

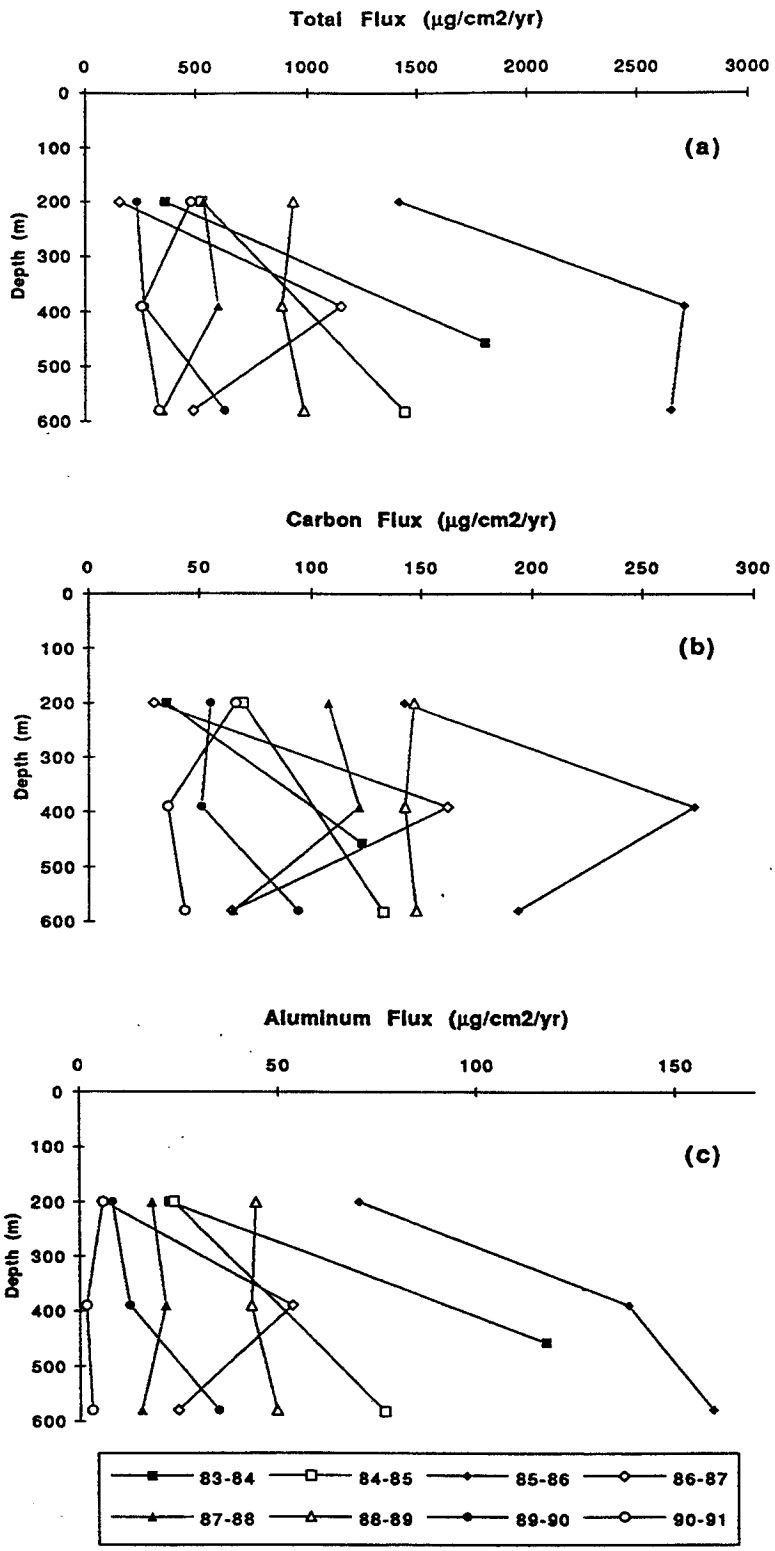


Figure 5. (a) Total particulate flux as a function of water depth shown for each year of the sediment trap deployments. (b) Particulate organic carbon flux as a function of water depth. (c) Particulate aluminum flux as a function of water depth.

either a resuspension or turbidite input of particles the flux would increase with depth and the influence of these deep particle injections would be expected to be greatest near the break in slope between the steep caldera wall and the relatively flat basin floors. The factor of six increase in flux measured in the deep trap relative to the upper trap during 1983-4 most likely reflects its deployment in the South Basin - nearest to the steep caldera walls and to the abundant inter-caldera springs and drifted snow pack along the south rim. This flux to the deep trap in the South Basin could be accounted for by either resuspension or turbidity flows. For the other years, collected in the Central Basin, the focusing effects in total particle flux are not as apparent. Only for 1984-5 is there a major difference between the upper and deep trap fluxes.

Sediment focusing introduces both biogenic and lithogenic components into the deep lake. However, the process is expected to enhance the deep inputs of lithogenic material over those for the biogenic fraction. Resuspension of bottom sediments will introduce particles into the water that have already undergone varying degrees of diagenesis. Much of the organic matter, which falls to the lake floor, decomposes at the sediment-water interface. Therefore, sediments are greatly depleted in organic matter compared to settling particles. (Dymond and Collier 1990) estimate that approximately 90% of the organic carbon undergoes decomposition within the surficial sediment layer. Therefore, resuspended particles should be relatively richer in aluminum than primary particles that have not been resuspended from the bottom. The carbon and aluminum flux data demonstrate this effect. During the sampling periods in which total fluxes were observed to increase with depth (Figure 5a), the carbon flux also increases but not by such a large factor (Figure 5b). For example, the 1983-4 interval, which had a factor of six increase in total flux with depth, has roughly a factor of two increase in carbon flux. In contrast, the aluminum flux for the same year is 10 times higher in the deep trap compared to the upper trap (Figure 5c). This resuspension-driven compositional change is most clearly seen in the systematics of the C/Al ratio (Figure 6a). In all cases the ratio decreases with increasing depth. Such a pattern could also be explained by decomposition of particulate organic matter as it settles through the water column. However, this effect alone would result in a decrease in the carbon flux with depth and no change

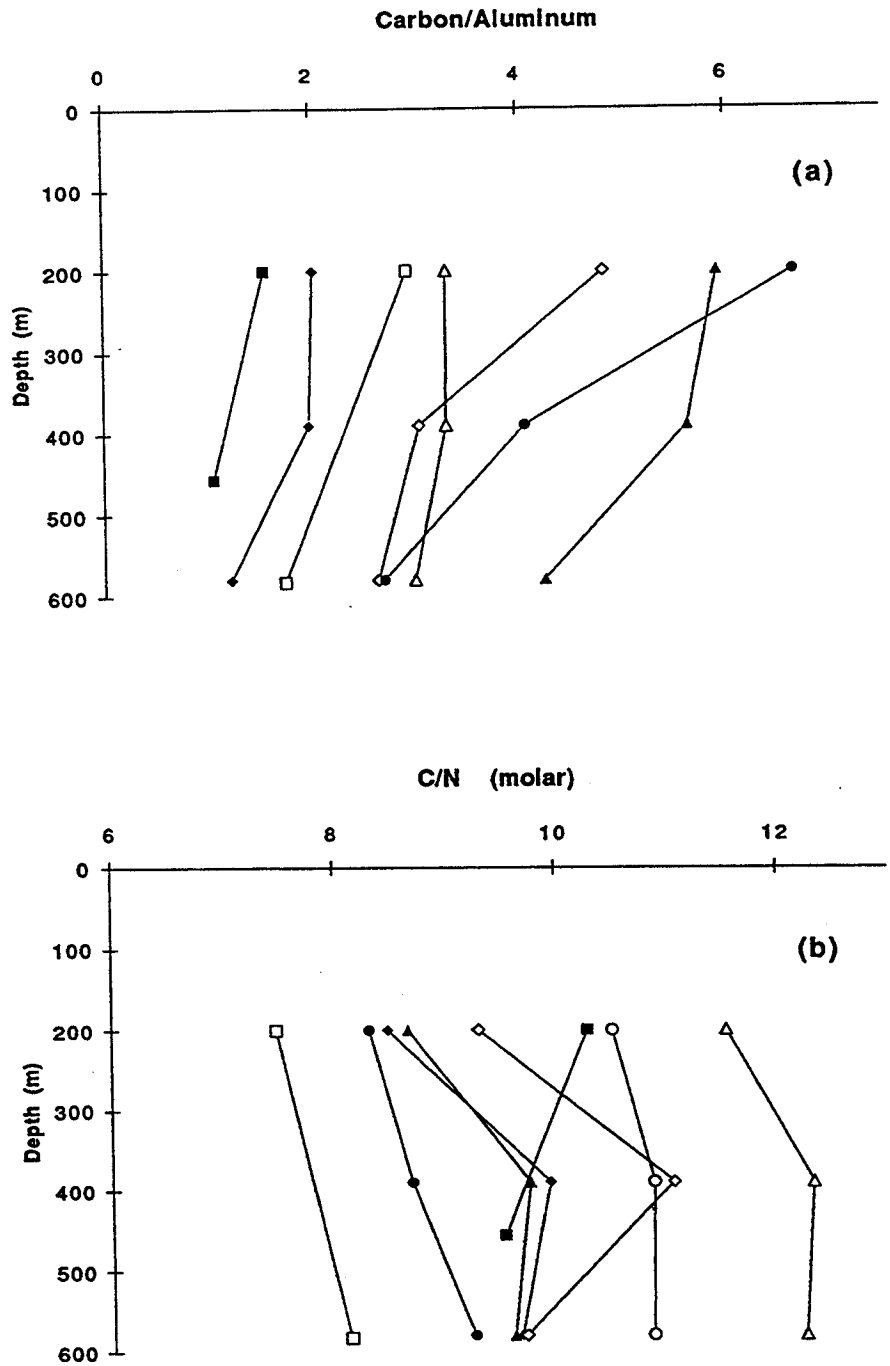


Figure 6. (a) Carbon to aluminum weight ratios in particulate material shown as a function of water depth. (b) Carbon to nitrogen ratios (molar values) shown as a function of water depth.

in the aluminum flux. Because both the aluminum and carbon fluxes increase with depth (Table 1; Figures 5b and 5c), sediment resuspension (i.e. focusing) is the best explanation of the systematic C/Al increase (Figure 6a).

The general trend of increasing C/N values in settling particles (Figure 6b) is also supportive of sediment focusing. Because nitrogen is more quickly regenerated from particles than carbon, early diagenesis will result in an increase in the ratio between the two elements in organic detritus. The depth pattern of C/N despite significant interannual variations in the C/N values. The causes of the interannual variations are less certain but may reflect changes in the lake biological community or variable inputs of terrestrial organic matter that tends to have higher C/N values.

General Composition. As noted earlier, particulate material in Crater Lake can be attributed to two general sources: (1) lithogenic material which is eroded from the surrounding volcanic rocks that comprise Mt. Mazama and (2) biogenous material composed of the hard and soft parts of plankton and other organisms that live in Crater Lake. In addition, there are wind-borne inputs of lithogenous material from more distant sources, atmospherically-carried pollutants, organic matter from local vegetation, and precipitates from the hydrothermal venting in the deep lake. We believe these latter sources to be a relatively minor contribution to the total particle flux, however, for individual elements or certain compounds these sources could dominate. For example, it is possible that aerosol lead originating from industry and automobile emissions may dominate the natural lead content in lake particles (Collier et al. 1990). At certain times of the year pollen sources from local trees contribute to a visible layer on the lake surface and organic compounds from terrestrial vegetation probably could be detected in sediment trap material. Because of the high arsenic content of some of the hydrothermal precipitates recovered from the bottom of Crater Lake (Collier et al. 1991), this source may predominate over other sources of arsenic in particles.

If the biogenic material from lake organisms and local sources of lithogenous material are the dominant contributions to the particulate flux, some simple normative calculations can define the relative importance of the two sources. The proportion of total organic matter can be estimated by multiplying the carbon flux by the constant 2.5, which is derived from the assumption that

organic matter has a composition similar to carbohydrates and which is similar to the "Redfield" composition for algae (Stabel 1985, Kilham 1990). If aluminum has only a lithogenic source we can compute the lithogenic contribution from our knowledge of the aluminum contents of typical Crater Lake rocks. Fine material from scree slopes and major outwashes from springs have an average aluminum content of 8.9% (Collier, et al. 1991). Therefore, total aluminosilicate percentage is 100/8.9 or 11.2 times the aluminum content. The third particulate component contributing significance mass is opal from diatom frustules, which was directly measured in the samples from the first three years of sediment trap deployments (Table 1). From these normative calculations the sum of organic, lithogenous, and opal fluxes can be determined:

Eq. 1 $$\text{Normative Sum of Fluxes} = 2.5 \times C + 11.2 \times Al + \text{opal}$$

If it is true that these three components dominate the particulate flux in Crater Lake, the normative sum of fluxes should approximate the total flux measured in the sediment trap. Comparison over the first three years shows that the sum of fluxes is within 5% of the total measured flux in nearly all cases.

During the 1983-86 interval, the biogenic components (organic matter and opal) in the upper traps averages approximately 50% of the flux. During this interval, the lower traps contain approximately 40% biogenic (proportioned as roughly equal parts opal and organic matter) and 60% lithogenous. Although we have not analyzed for opal in samples since 1986, some sense of the proportion of biogenic component can be made from the carbon to aluminum ratios. Using our normative constants for transforming carbon and aluminum into organic matter and lithogenous material , we can define a constant to transform the C/Al elemental ratios (Figures 4d and 6a) into the ratio of total organic mass to lithogenous mass. As discussed above, the C/Al values are highest in the upper traps where annual average values greater than eight are observed. The normative model indicates that on average this particulate material in upper traps contains twice as much organic matter as it does lithogenous component. For some summer and fall samples the C/Al values are over 40 (Figure 4d) suggesting that these are times when the biogenic component (organic plus opal) is more than 90% of the particulate flux.

We now consider the question of what components - lithogenic or biogenic - dominate the *fine* particle field (as opposed to the larger settling fraction). This question is relevant to the issue of lake clarity because fine, suspended particles have the greatest influence on lake clarity. Our only direct estimate of the fine particle composition is based on the large particle flux collected by the traps. As noted above, the settling particle flux measured at 200 m water depth is composed of roughly equal parts by weight of lithogenic and biogenic material. This is most likely to be a minimum estimate of the biogenic contribution to the *fine* suspended particle field in the upper water column. The continual decomposition of particles settling from the upper lake (0 to 50m) due to bacterial oxidation and zooplankton metabolism would only lower the content of organic matter collected by the traps below the euphotic zone.

An indication of the significance of organic matter to suspended particles can be seen in the time-series of trap fluxes which have shown that the carbon-to-aluminum ratio varies strongly during the year. These data demonstrated that during the months when most observations of lake clarity have been made (July and August) the biogenic components dominate the settling flux. The beam transmissometer data, which is most sensitive to the fine suspended particle fraction, always shows that the maximum light absorbance is nearly coincident with the chlorophyll maximum (see Transmissometer Section). This demonstrates that the suspended particle field, as well as the settling fraction, is dominated by the biogenic fraction.

Relationship of Particle Composition and Fluxes to Precipitation. Approximately 78% of the precipitation that reaches the lake falls directly on the lake surface while the remaining fraction falls on the small watershed represented by the caldera walls and Wizard Island. Precipitation falling directly on the lake surface introduce atmospheric aerosols and nutrients to the upper lake. Precipitation that falls on the caldera wall is a major mechanism for introducing lithogenic material to the lake and introduces additional nutrients to the upper lake (Gregory et al. 1990).

Particles from the May through June interval, commonly the time of peak total flux in the lake (Figure 4a), contain significant organic matter but are particularly enriched lithogenic material (Figure 4d). We suggest that this input is a response to the time of peak snow melt within the

caldera walls. If this is true, we might expect a correlation between annual precipitation and the flux of lithogenic particles collected with the sediment traps. Although the existing data show a significant but not especially strong correlation (Figure 7a). The weakness in the correlation probably reflects a more complicated input process resulting from variability in the character of runoff/erosion from year to year. In years in which the snow melt is more gradual the erosional effects may be less severe or there may be fewer landslides.

Organic matter flux and total annual precipitation at the lake are not significantly correlated (Figure 7b). Although precipitation introduces nutrients to the upper lake, we will show later in the report that this source is small compared to the nutrients recycled into the upper lake from mixing with the hypolimnion. Interestingly, the C/Al values and the annual precipitation are inversely correlated (Figure 8a). This relationship suggests that despite the weak influence of annual precipitation on the magnitude of the fluxes, higher precipitation enriches the settling particles in lithogenic components relative to organic components. The positive correlation between C/N values and precipitation (Figure 8b), although not as strong, could be due to enhanced terrestrial inputs of organic matter during years with high precipitation.

A variety of other large scale variables might also affect the particle flux. These could include could include factors such as lake level which changes the character of the littoral depositional zones. However, we do not at this time have specific hypotheses about other relationships nor enough data to assess them.

Flux Evaluation and Modelling

These studies of the lake were guided by a conceptual model of the critical fluxes that control the movement of elements through the system. Over appropriate time scales (~years) the allocthonous (outside) inputs of elements to the lake must be balanced by processes that remove them from the lake. This steady-state hypothesis requires that the sediment burial fluxes plus the outputs from seepage must equal the allocthonous inputs from the atmosphere and runoff from the caldera wall. The equation for this total lake balance is:

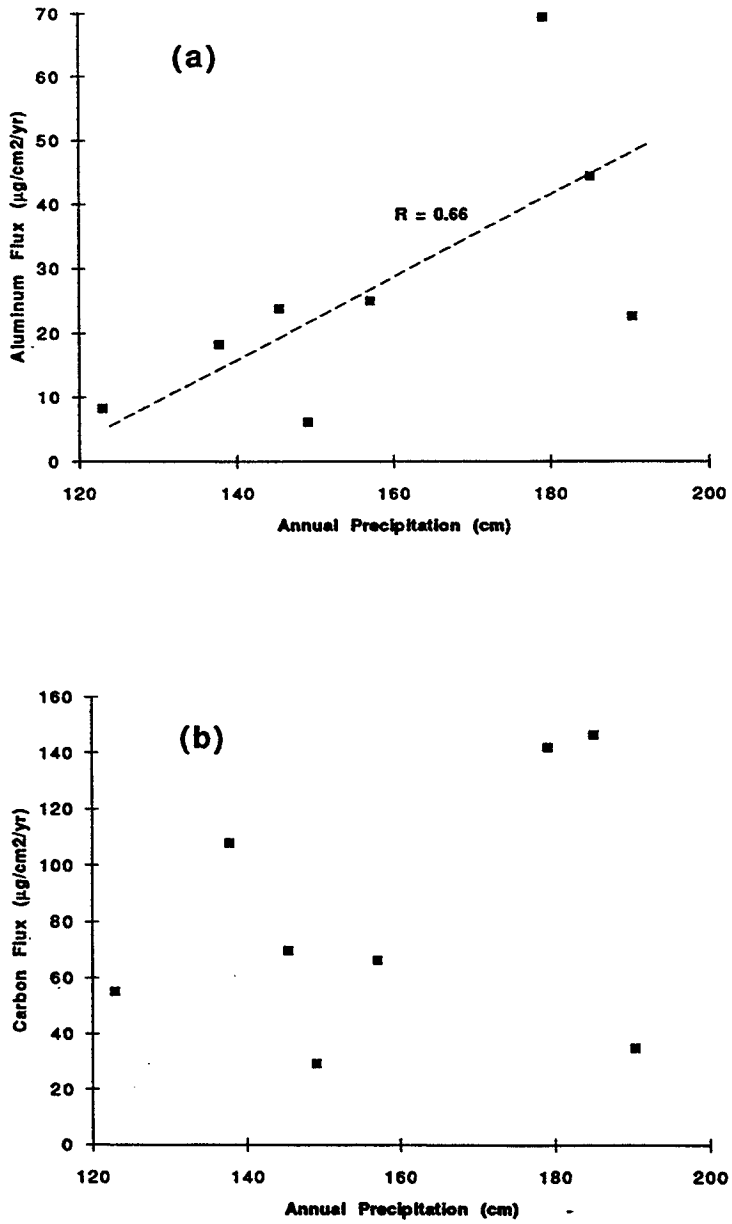


Figure 7. (a) The relationship between the annual particulate aluminum flux measured at 200 m water depth and the total annual precipitation. (b) The relationship between annual carbon flux and annual precipitation.

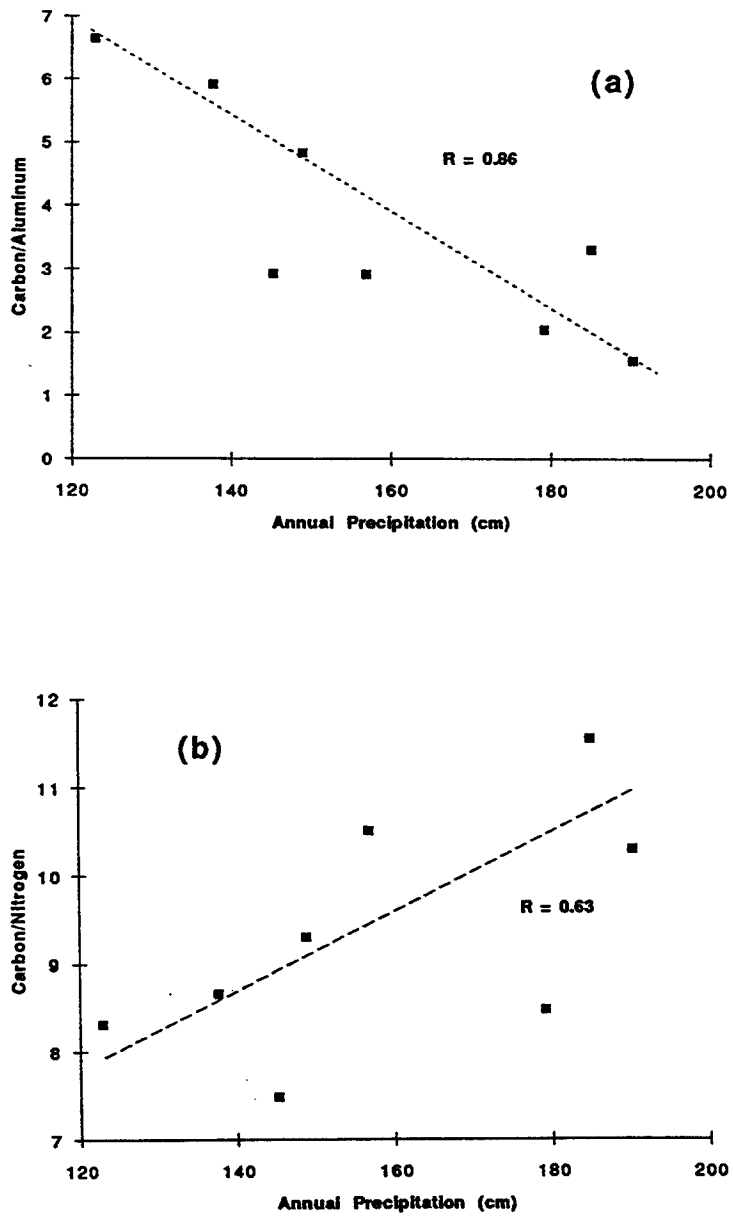


Figure 8. The relationship between carbon to aluminum ratios in particulate material from 200 m (annual data) and precipitation. Figure 8. The relationship between carbon to nitrogen ratios in particulate material from 200 m (annual data) and precipitation.

Eq. 2: $F_a + F_r = F_b + F_o$

F_a equals the atmospheric inputs, F_r equals the inputs from runoff, F_b equals the sediment burial rate of a given component, and F_o equals the loss by seepage through the lake floor.

This simple "one-box" model is useful to gain a view of the whole-lake system at steady state. Previous steady state box models have been used to describe lake systems (Snodgrass and O'Melia 1975, Lam et al. 1982, Imboden and Schwarzenbach 1985) and the oceans (Broecker and Peng 1982). We have already applied a similar box model in our discussion of the impact of hydrothermal inputs on the dissolved materials in the lake (Collier, et al. 1991, Collier et al., in this report; Nelson et al., this report). This type of model is especially simple for materials that are highly soluble, such as sodium and chloride, and which do not participate significantly in biological particulate matter cycles. In this case, the total output flux (F_o) is simply the product of the average lake concentration and the rate of water seepage. In the case of materials that are effectively insoluble, such as aluminum, which are bound in particulate matter, the sediment burial flux should equal the total input flux. However, in order to evaluate the lake's *internal* nutrient cycles, we will need to increase the complexity of this model by partitioning the lake into upper and deep lake compartments. These additional compartments make it possible to incorporate both the primary production of organic matter in euphotic zone and its transfer and remineralization in the hypolimnion.

Accumulation of Materials in Lake Sediments. Over appropriate time scales the burial of carbon, nutrients and metals in Crater Lake sediments should approximate *net* inputs of these materials from external sources. Rearranging Eg. 2, this balance is expressed as:

Eq. 3 $F_b = F_a + F_r - F_o$

where the atmospheric (F_a) and runoff sources (F_r) minus the total outflow from the lake floor ($F_o = F_{o,upper} + F_{o,deep}$) is equal to the burial flux (F_b). The sediment burial flux for any element is defined by:

Eq. 4. $F_b = C \times S \times \rho$

where C is the concentration of any element in the sediment (ppm), S is the linear sedimentation rate in units of cm/y, and ρ is the dry bulk density of the sediment in units of gm/cm^3.

Determination of sedimentation rates in aquatic systems is usually accomplished by measuring the decay of an appropriate radioactive isotope at depth in a sediment core. For lakes this is usually ^{210}Pb with a 22.4 year half life or ^{14}C with a 5,700 year half life. We have used both types of data to estimate the sedimentation rates in Crater Lake. Carbon-14 dating in Crater Lake sediments is complicated by the fact that carbon with no ^{14}C activity ("dead carbon") is introduced into the deep lake by the input of hydrothermal fluids (Collier, et al. 1991). This input of carbon produces older apparent ages (lower ^{14}C activity) in the waters of Crater Lake and in the plankton which grow in these waters. Consequently, the bulk organic carbon in sediments that accumulate in Crater Lake have older apparent ages than would be expected. For example, ^{14}C measurements of total organic carbon from a Wizard Platform sediment core reveal a surface sediment age of approximately 3,000 years (S. Robinson and H. Nelson,US Geological Survey, personal communication, February 1987). Because there are no sources of "old" carbon in the volcanic terrain of the Crater Lake caldera, this age reflects the hydrothermally modified ^{14}C activity of the lake waters. In contrast, a small pine cone recovered from a depth of 20-22 cm in a Wizard Platform sediment core produced a ^{14}C age of only 1,600 years. Because land vegetation derive their carbon directly from the atmosphere, this age should be representative of the time when the cone was formed. The ^{14}C age of the bulk organic matter at that same depth revealed an age of 5300 years, which is in excess of the age of the pine cone by roughly the same amount as the age off-set of surface sediments. These data suggest Wizard Platform sediments are accumulating at a rate in the range of 0.013 cm/y (based on pine cone) to 0.016 (based on the slope of the apparent ages of total organic matter; S. Robinson, personal communication, February 1987). Because the Wizard Platform cores are from a water depth of approximately 300 m, they represent a part of the lake that does not experienced as much sediment focusing as the deep basins. Therefore, we expect these sedimentation rates to be a minimum for the lake as a whole.

We measured ^{210}Pb in four cores collected from Wizard Platform and from each of the deep basins (Figure 1). The cores used for the ^{210}Pb measurements were collected with a small box-type corer that recovered what appeared to be a perfectly intact sediment-water interface. We expect little or no coring artifacts with this corer. These data have been corrected for ^{210}Pb supported by ^{226}Ra decay by measuring ^{210}Pb in deeper layers of several cores. Measurements of ^{210}Pb in samples from >30 cm in the sediment reveal that the 210Pb which is supported by ^{226}Ra decay is approximately 0.5 dpm/g, and this value was subtracted from each of the measurements to estimate the unsupported ^{210}Pb. Water contents and wet bulk sediment density were measured at each sampling depth as well, and these data were used to compute the dry bulk density at each sampling depth. ^{210}Pb activity/cm^3 (corrected for ^{226}Ra decay) varies log-linearly with depth (Figure 9a-c) which can be interpreted in terms of sedimentation rate according to the equation:

Eq. 5. $$A = A_0 e^{-\lambda S \cdot z};$$

where A is the activity measured at depth, z, A_0 is the unsupported ^{210}Pb activity at time zero, 1 is the decay constant of ^{210}Pb, and S is the linear sedimentation rate. Best fits through the data predict sedimentation rates that range from 0.066 cm/year at Wizard Island to 0.156 cm/year in the South Basin (Figure 9a-c). The rate for the Wizard Island core is 4 to 5 times greater than the rate estimated from ^{14}C dating. Although the rates determined by the two methods were done on separate cores (^{14}C on CL85-3; ^{210}Pb on CL86-3), they were collected within 200 m of each other (Figure 1) and would not be expected to display significant differences in sedimentation rate. Therefore, the ^{14}C and ^{210}Pb comparison suggests that the ^{210}Pb activity in the core is strongly influenced by bioturbation which mixes young, surficial sediments with older, more deeply-buried sediments (Guinasso and Schink 1975, Robbins et al. 1978). Although extensive bioturbation in a very deep, oligotrophic lake like Crater Lake seems surprising, we have recovered worms that are a few centimeters long in cores and observed some larger worms with video transects of the lake floor using a remotely operated vehicle.

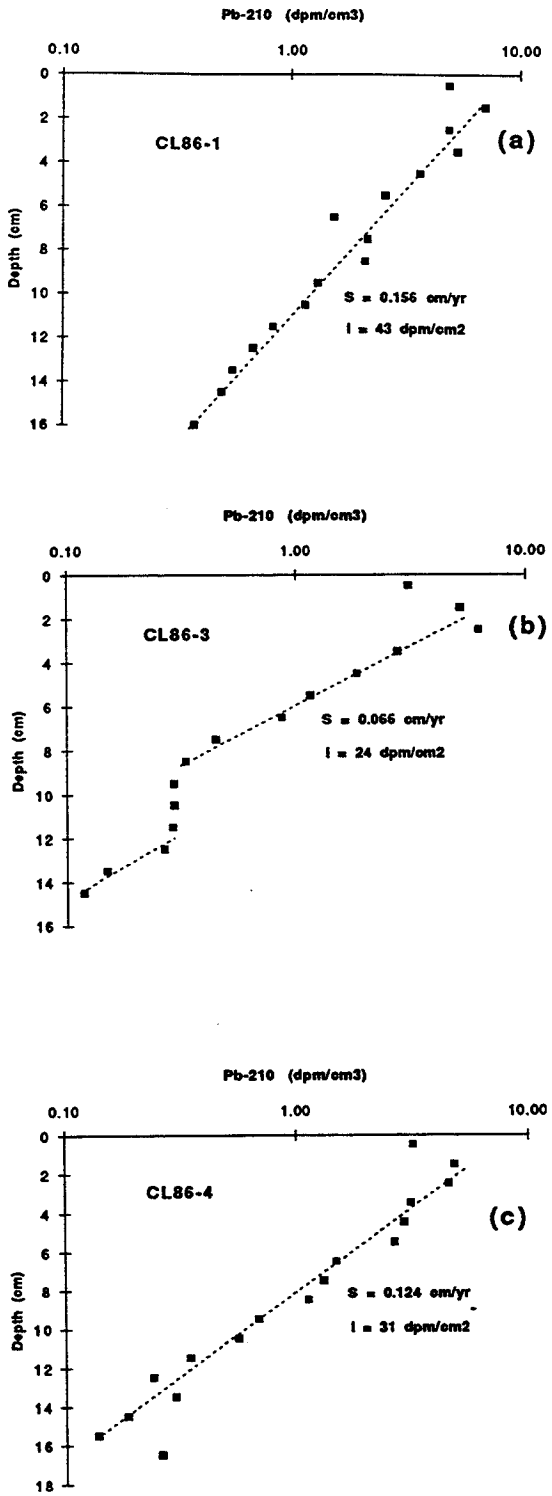


Figure 9. (a) Activity of ^{210}Pb as a function of depth in the sediment for CL 86-1 (South Basin core). Activities are corrected for ^{226}Ra-supported ^{210}Pb. "S" refers to the sedimentation rate that assumes the decrease in activity with depth is a result of closed system radioactive decay. "I" refers to the inventory of unsupported (excess) ^{210}Pb activity in the core. (b) Activity of ^{210}Pb as a function of depth in the sediment for CL: 86-3 (Wizard Platform core). (c) Activity of ^{210}PB as a function of depth in the sediment for CL 86-4 (North Basin core).

Assuming both bioturbation and sedimentation are significant, the change in ^{210}Pb activity with depth is defined by the following equation (Anderson et al. 1988):

$$\text{Eq. 6:} \qquad A = A_o \exp\left[\frac{(S - S^2 + 4D_b \lambda)^{1/2} \cdot z}{2D_b}\right];$$

where D_b is a bioturbation mixing coefficient which has units of cm^2yr^{-1}. All other symbols are the same as in Equation 5.

If we assume that the true sedimentation rate for the Wizard Platform is given by the ^{14}C age of the pine cone in the nearby core (CL85-3; 0.013 cm/yr), we can solve for the bioturbation coefficient using the ^{210}Pb-depth profile in the CL86-3 core. This calculation suggests a bioturbation coefficient of 0.3 cm^2yr^{-1}. Assuming, this bioturbation coefficient applies to all cores within the lake we can compute a bioturbation-corrected sedimentation rate for the other cores (Table 2 and Figure 10a-c). We have no direct data to support the assumption of constant bioturbation rates for the basins and Wizard Platform sediments. It is reasonable to expect that bioturbation rates are a function of specific sediment quality and the size of the benthic community. Because the benthic community relies on nutrition from organic matter that settles from the euphotic zone, variations in the particulate flux of carbon could cause variations in the bioturbation rate. The sediment trap data (Table 1) shows that the differences in carbon flux between the middle trap with a depth similar to the Wizard Platform and the deep trap, which is 10 m above the bottom, are on average less than 10%. For this reason we believe a constant bioturbation rate in basin and Wizard Platform sediments is a reasonable first-order assumption. The correction for bioturbation reduces the estimated sedimentation rate for the two deep basin cores by roughly a factor of two.

Using Equation 4 and data for the dry bulk densities in the cores and concentrations of various elements measured in the cores we can compute the accumulation rates of these elements in sediments from different parts of the lake (Table 3). Because of the range in sedimentation rate and dry bulk density, our estimates of total accumulation rate vary by nearly a factor of 20. The greater bulk density in the basins is probably a consequence of a greater fraction of lithogenic

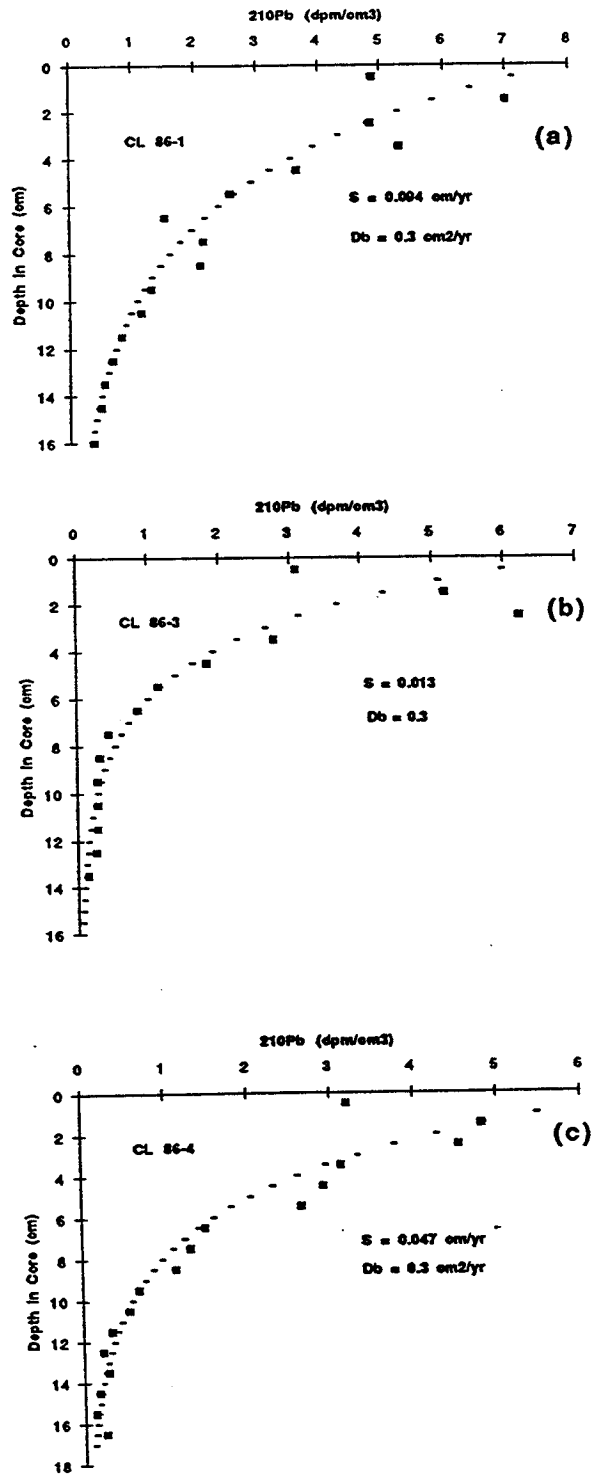


Figure 10. (a) Model of ^{210}Pb activity in CL 86-1 incorporating both sedimentation and bioturbation (Eq. 6). Bioturbation coefficient, D_b of 0.3 is computed from ^{14}C data of CL 86-3 (Table 2) and is assumed to apply to all sediments in the lake. Dashed line indicates the fit to the ^{210}Pb data using the sedimentation rate, S, and the bioturbation coefficient shown. (b) Model of ^{210}Pb activity in CL 86-3 incorporating both sedimentation and bioturbation. (c) Model of ^{210}Pb activity in CL 86-4 incorporating both sedimentation and bioturbation.

material and less organic matter in these cores (Table 3). The lithogenic material has a higher grain density and also produces a sediment fabric with a lower water content compared to organic-rich materials.

Table 2. Sedimentation rate data for Crater Lake cores.

Core	Location	Method	Estimated Sedimentation Rate (cm/yr)
CL 85-3	Wizard Platform	^{14}C (pine cone)	0.013
USGS 80-7	Wizard Platform	^{14}C (total carbon)	0.016
CL 86-1	South Basin	^{210}Pb	0.094
CL 86-4	North Basin	^{210}Pb	0.047

Table 3. Accumulation rate data for Crater Lake cores.

Core	Dry Density (g/cm^3)	Sedimentation Rate cm/yr	% Al	% C	%N	Accumulation Rates ($\mu g/cm^2/yr$) Total	Al	C	N
86-1(SB)	0.38	0.094	8.80	1.32	0.20	35,700	3140	470	71
86-3(WP)	0.14	0.013	7.66	3.24	0.49	1,820	140	59	8.9
86-4(NB)	0.23	0.047	7.90	2.08	0.32	10,800	850	220	35

Sediment focusing is responsible for the variation in accumulation rates as down-slope transport of sedimentary materials accumulate in the deep basins. This process also accounts for the lower carbon and nitrogen contents in the basin sediments because resuspension of bottom sediments introduces sedimentary materials that have undergone early diagenesis and loss of organic matter. Basin deposits are also subject to turbidity inflows which may be initiated by landslides from the steep caldera walls and slumping from shallower sediments. In effect, the basin sediments represent a dilution of the vertically settling particulate material by laterally

introduced material that is rich in aluminosilicates from the caldera walls. The higher sedimentation rates represent a greater fraction of lateral input and more dilution by lithogenic material. This view of lake sedimentation implies that the South Basin, with the highest sedimentation rates, lower concentrations of carbon and nitrogen, and higher fluxes of aluminum, is receiving greater sediment focusing than the North Basin. This may seem surprising since the North Basin has a maximum depth that is roughly 100 meters deeper than the South Basin. Nonetheless, several other lines of evidence support this interpretation.

First, we have computed the inventory of ^{210}Pb in each of the cores in which ^{210}Pb measurements were made. These measurements reveal that the highest inventories are in the South Basin (43 dpm/cm^2) followed by the North Basin (31 dpm/cm^2) and the Wizard Platform (24 dpm/cm^2). Because the ^{226}Ra contents of the lake water are very low (Collier, et al. 1991), the sources of excess ^{210}Pb in sediments is greatly dominated by atmospheric sources. It is reasonable to assume that the inputs of ^{210}Pb to the surface of the lake are relatively constant. Any differences in the accumulation of lead (reflected by the inventory in the sediments) probably results from advection and redistribution of ^{210}Pb on particles after it enters the lake. The factor of two higher inventory of ^{210}Pb in the South Basin sediments compared to Wizard Platform sediments is a clear indication of sediment focusing. The nearly 40% higher inventory in the South Basin compared to the North Basin indicates greater focusing in the South Basin.

Greater focusing in the South Basin is also supported by the very strong differences in upper trap (200 m) and the deep trap fluxes (10 meters above the bottom) during the first sediment trap experiment (1983-84) carried out in Crater Lake. This experiment, which was the only sediment trap deployment that was not deployed in the North Basin, recorded five to six times higher flux in the deep trap compared to the upper trap—a greater difference than observed in any of the subsequent North Basin traps (Table 1). Also, the carbon to aluminum ratio in the deep trap from the South Basin was lower than those observed in any of the deep traps from the North Basin, a clear indication of strong lithogenic input.

The greater sediment focusing may reflect the proximity of the center of the South Basin to the caldera wall. The center of the South Basin is approximately 1.5 km from the shoreline, whereas the center of the North Basin is approximately 2.5 km from the shoreline. The south caldera wall also has the majority of the subaerial springs and certainly the largest springs that flow into the lake. These springs have high flows during times of snow melt and probably transport significant material to the lake from the caldera walls. Finally, the South Basin is nearly encompassed by relatively shallow parts of the lake. To the north of the South Basin is the Wizard Platform, to the west is Wizard Island and the relatively shallow waters that surround it, to the south is the caldera wall, and to the east is Chaski Slide, a major caldera wall landslide that extends approximately two kilometers away from the shoreline. These shallow areas are probably an important source of advected sediments into the South Basin.

^{210}Pb Balance. Because the source of ^{210}Pb in the lake is predominantly from the atmosphere and is carried to the lake by precipitation and runoff, evaluating the balance between sediment accumulation of ^{210}Pb and the flux measured by sediment traps can help to reveal lake processes. From the inventory of ^{210}Pb in each of the cores (Figure 9a-c, Table 4), the flux of ^{210}Pb required to maintain that inventory can be estimated from Equation 7:

Eq. 7. $$^{210}\text{Pb flux (dpm/cm}^2\text{/y)} = {}^{210}\text{Pb inventory (dpm/cm}^2\text{)} \cdot \lambda$$

Where λ is the decay constant of ^{210}Pb ($\lambda = 0.031$ years^{-1}). Table 4 lists the results of this calculation for the deep basin and Wizard Platform cores.

As discussed previously, the observation that the highest inventory is found in the South Basin is evidence that this site has relatively high sediment focusing. Also of interest, however, is a comparison between the ^{210}Pb flux measured by sediment trap and our estimate of the flux required to support the inventory. We have measured the ^{210}Pb flux in two sediment traps, one a middle trap (380 m) and one a deep trap (580 m). The fluxes measured were 0.34 and 0.27 dpm/cm^2/yr respectively. Thus, the measured trap fluxes of ^{210}Pb are two to four times lower than the burial fluxes implied by the inventory in the sediment cores (Table 4).

The apparent mismatch between fluxes required by the sediment inventory and the measured ^{210}Pb fluxes may also be a consequence of sediment focusing. ^{210}Pb differs from other components of the particle flux because it is apparently removed by biological scavenging of dissolved ^{210}Pb. Lead is also a refractive element, which is not recycled like nutrients and other labile elements. This has been shown by studies in the deep ocean in which the measured particulate inputs of ^{210}Pb are equal to the fluxes required to support the inventory of ^{210}Pb in the sediments (Moore and Dymond 1988).

Because the lake surface accounts for 78% of the total lake watershed, ^{210}Pb input to the lake is distributed relatively evenly over the lake surface, in contrast to lithogenous components which have a predominately lake margin source. If biological particle fluxes throughout the lake are adequate to strip the ^{210}Pb relatively quickly after it enters the lake, the flux of ^{210}Pb carried by settling particles will be relatively uniform. Therefore, it is reasonable to assume that the input of ^{210}Pb to the lake is given by the measured sediment trap flux (an average of 0.31 dpm/cm^2/yr) times the area of the lake (53.2 km^2). This estimate is similar to a ^{210}Pb flux of 0.16 dpm/cm2/yr measured in glacial ice from Mt. Olympus, Washington (Windom, 1969), a site 600 km north of Crater Lake. The sediment trap estimate is also comparable to values predicted for the west coast of North America (0.5 to 0.8 dpm/cm^2/y) using a global ^{210}Pb flux model (Turekian, et al., 1987). The sediment trap flux measured in our sediment traps suggests 1.6 x 10^{11} dpm of ^{210}Pb activity are introduced to the lake each year.

Because of the strong variability in the burial rates observed between the two basins and the Wizard Island Platform, it is difficult to predict the whole-lake ^{210}Pb inventories. Nonetheless, to provide a first order examination of the ^{210}Pb budget in the lake we will assign our South Basin measurement of ^{210}Pb inventory to the part of the South Basin deeper than 450 m. We will also assume that the portions of the lake outside the South Basin which are deeper than 400 m have ^{210}Pb inventories equivalent to the value measured in our North Basin sediment core. Because submersible dives indicate very little sediment accumulates on steep slopes and at depths less than 300 m (Collier, et al. 1991), we will assume there is no sediment accumulation on the very steep

topography of Miriam cone and at depths less than 300 m. Using this areal breakdown of inventories, we compute that 2.1×10^{11} dpm of ^{210}Pb activity is carried to the sediment each year. Therefore, the estimate of total ^{210}Pb burial in lake sediments is within 25% of the total input estimated by the sediment trap data. These results suggest ^{210}Pb activity in the lake sediments can be accounted for by a relatively homogenous input to the lake surface, removal by biological activity, and downslope transport to basins which accumulate most of the ^{210}Pb (68%) that enters the lake.

Table 4. ^{210}Pb inventory in Crater Lake sediments and estimate of flux required to support the inventory.

Core	Location	Inventory (dpm/cm^2)	Flux required to support the inventory ($dpm/cm^2/yr$)
CL86-1	South Basin	42.7	1.3
CL86-3	Wizard Platform	25.6	0.74
CL86-4	North Basin	31.3	0.98
CL86-6	NW. Basin	31*	0.97

*Because this core did not penetrate as deeply, the estimate of inventory is more uncertain than for the other cores.

Aluminum Budget. Because of the high concentration of aluminum in the Earth's crust, aluminum can be used to define lithogenous sources to the lake. Also, the low aqueous solubility and association with refractive minerals means that nearly all of the particulate aluminum reaching the lake will become part of the sediment record (Dymond and Lyle 1985; Dymond and Collier 1990; Dymond and Lyle, in press). Using the measured accumulations of aluminum in sediments (Table 3) and the same areal distribution of burial fluxes used for the nitrogen and ^{210}Pb budgets, we compute a total burial of 1.7×10^8 g of aluminum each year in Crater Lake sediments. Of this, 34% is deposited in the South Basin, 59% is deposited in the North and Northwest Basins, and only 7% is deposited on Wizard Platform and the other intermediate depth areas.

The estimates of total inputs of aluminum to the lake sediments are much greater than the inputs measured by sediment traps deployed in the Central Basin. The average aluminum flux estimated from the particulate flux measured at 200 meters during the eight years of sediment trap deployments is 27 $\mu g/cm^2/yr$ (Table 1). Given a lake area of 53.2 km^2, the trap flux (measured at 200 m) accounts for 0.15×10^8 g of aluminum each year. Thus, aluminum associated with the particle flux at 200 m water depth is only 9% of the total sedimentation of aluminum (1.7×10^8 g/yr) that we estimated for the whole lake.

We believe the marked difference between measured particulate aluminum fluxes and sediment burial fluxes reflects fundamental lake processes. Because the lake margin is the predominant source of aluminum-bearing particles, there may be significant lateral gradients in the particle flux. Therefore, a sediment trap deployed at 200 meters, but closer to the caldera wall, would be expected to record higher aluminum fluxes than our trap deployed in the center of the North Basin. In addition, the computed sediment accumulation represents a temporal integration of the aluminum inputs over several half-lives of ^{210}Pb (decades to a century) in contrast to the eight-year record provided by our sediment trap deployments. If landslide and turbidite events are a significant source of particulate material to both the margins of the lake and the deep basins on this time scale, we may not have sampled these unusual events during our time-series of sediment trap deployments. Finally, the inputs of material to the basins is likely to occur mostly in the near-bottom layer. The sediment-focusing process is likely to involve repeated resuspension processes which transports material that temporarily settles to the bottom downslope. The resuspension is not likely to move material very far above the bottom so that particles travel downslope as a very near bottom nepheloid layer. This type of sediment transport is not likely to be collected in our deepest trap which is 10 meters above the bottom. Although the aluminum flux in the deep trap is roughly double that observed in the upper trap (Table 1), this flux increase cannot account for the high aluminum flux implied by the sediment burial rates (Table 3).

Nitrogen Budgets and Particulate Organic Matter Cycles

Whole-Lake Nitrogen Budget. We have used the areal distribution of burial fluxes developed for our whole-lake ^{210}Pb budget to determine the whole-lake nitrogen accumulation. Based on the same sedimentation-rate assumptions we calculate that 4.5×10^5 moles of nitrogen accumulates in lake sediments each year. This suggests that the deep basins, which account for 26% of the lake area, accumulate 87% of the nitrogen that makes it into the sediment record (Table 5). Intermediate depth areas, such as the Wizard Island Platform and the Chaski Slide area on the south side of the lake, comprise 17% of the lake and account for 13% of the buried nitrogen. The shallow areas and areas of steep topography account for 55% of the lake area but accumulate very little nitrogen.

Table 5. Percentages of total lake inputs accumulating in various lake areas.*

Area	% of total lake area	% of total N accumulation	% of ^{210}Pb inputs buried	% of total Al accumulation
Wizard Platform and intermediate depth areas	17	13*(0.8)*	32*(1.9)*	7*(0.4)*
South Basin	3.5	21*(6.0)*	11*(3.1)*	34*(9.7)*
North Basin	22.6	66*(2.9)*	57*(2.5)*	59*(2.6)*

* Values in parentheses indicate extent of focusing that is implied by the percent of total accumulation divided by the percent of total lake area. Larger values indicate greater relative focusing.

Seepage of nitrogen can be estimated from Crater Lake's hydrologic budget which indicates that seepage accounts for 51% of the total water loss (Redmond 1990). This amounts to 6.75×10^{10} l/yr. We have partitioned this loss according to the lake areas deeper and shallower than 200 m. Because 73% of the lake area is deeper than 200 m, we will assume that 4.96×10^{10} liters/year seep from the deep lake and that 1.79×10^{10} liters/year are lost from the

upper lake - however, we have no direct way of evaluating this partitioning. The total nitrogen content of the upper lake is roughly 0.05 μmolar resulting in a very small seepage loss ($<10^3$ moles/yr), whereas the deep lake has a nitrogen content of approximately 1.0 μmolar resulting in a whole-lake loss of nitrogen of 0.5×10^5 moles/yr by seepage.

Runoff and precipitation inputs of nitrogen can be estimated from measurements of nitrogen in precipitation that were made over an 18-month period. A volume-weighted estimate of the total nitrogen concentration in precipitation is 4.4 μmolar (Reilly et al. 1989). If we assume that this concentration estimate applies for runoff as well as direct precipitation on the lake, the total exogeneous inputs of nitrogen can be computed as the product of total water inputs - 1.31×10^{11} l/yr (Redmond 1990; Collier, et al. 1991) and the nitrogen concentration in precipitation. This results in an input estimate of 5.8×10^5 N moles/yr.

Using these estimates of nitrogen fluxes, we find the exogenous sources of nitrogen to the lake (precipitation and runoff) balance very well with the losses of nitrogen to the sediments and by seepage.

$$\text{(precipitation + runoff)} \simeq \text{(burial + seepage)}$$

$$(5.8 \times 10^5 \text{ moles/year}) \simeq (4.5 \times 10^5 + 0.5 \times 10^5) \text{ moles/year}$$

Given the possible errors in estimating the exogenous nitrogen inputs and the assumptions that we chose to estimate the total lake accumulation of nitrogen in sediments, close agreement does not prove our estimates and assumptions are valid. It does show that reasonable assumptions concerning sediment focusing and accumulation in the basins can produce a balance in the exogenous nitrogen budget. If these assumptions are wrong, there must be counter-balancing errors in the estimates of nitrogen inputs to the lake. If the estimates are valid, however, it indicates that roughly 90% of the nitrogen which enters the lake from precipitation is buried in sediments, the rest is lost by seepage.

Internal Nitrogen Cycling. As is the case in any oligotrophic ecosystem, carbon, nitrogen and other essential nutrients in Crater Lake are extensively recycled. The recycling, which takes place in all parts of the lake (e.g. within the euphotic zone, throughout the deep lake water column, and

on and within lake sediments), is a result of heterotrophic and inorganic processes. Although recycling has a variety of impacts on the lake, the most fundamental result of recycling is to make nutrients available to support many cycles of production before they are finally removed from the system by sediment burial or lake seepage. In effect, this increases the overall productivity of the lake far above a level that could be supported by a single-pass of nutrient imputs through the lake.

Because nitrogen in the upper lake is below the detection limit during most of the year while phosphorus remains abundant (Larson, this report), it is assumed that nitrogen is the limiting nutrient. The whole-lake nitrogen budget discussed in the section above describes the flow of nitrogen into and out of the lake, but nitrogen recycling within the lake provides the dominant short-term controls on the productivity that can be maintained in the sunlit portions of the water column.

A conceptual model of productivity that has been developed for the ocean (Eppley and Peterson 1979) also has value in examining lake biological processes of lakes (Caraco et al, 1992). This model partitions the primary productivity into two parts. "New productivity" is the portion that is supported by the direct input of *new* nutrients to the euphotic zone, which includes surface inputs as well as upwelling from the hypolimnion. The portion that is based on the recycling of nutrients *within* the euphotic zone referred to as "recycled productivity". Total primary production is the sum of these two types and is the value that would be measured by an 'instantaneous' ^{14}C primary production experiment. In the oceans, recycled productivity exceeds new productivity by factors ranging from two to more than ten times (Eppley and Peterson 1979).

For Crater Lake, the sources of nutrients that can support new productivity are precipitation, runoff, and mixing of deep water with surface water. These processes and sources can be formalized by expanding the one-box, whole-lake budget model to a two-box model that partitions the lake into a shallow, nitrogen-depleted euphotic zone box (0-200 m) and a deep hypolimnion box (Figure 11). The upper box receives nutrients (nitrate and phosphate) from runoff (F_r), the atmosphere (F_a), and upward mixing of deep lake water (F_u). Nutrients are removed by particle settling (F_p), downward mixing of surface water (F_d), and outflow seepage ($F_{o,upper}$). The nutrient fluxes into the deep box (F_p and F_d) are balanced by upwelling (F_u), particle burial (F_b),

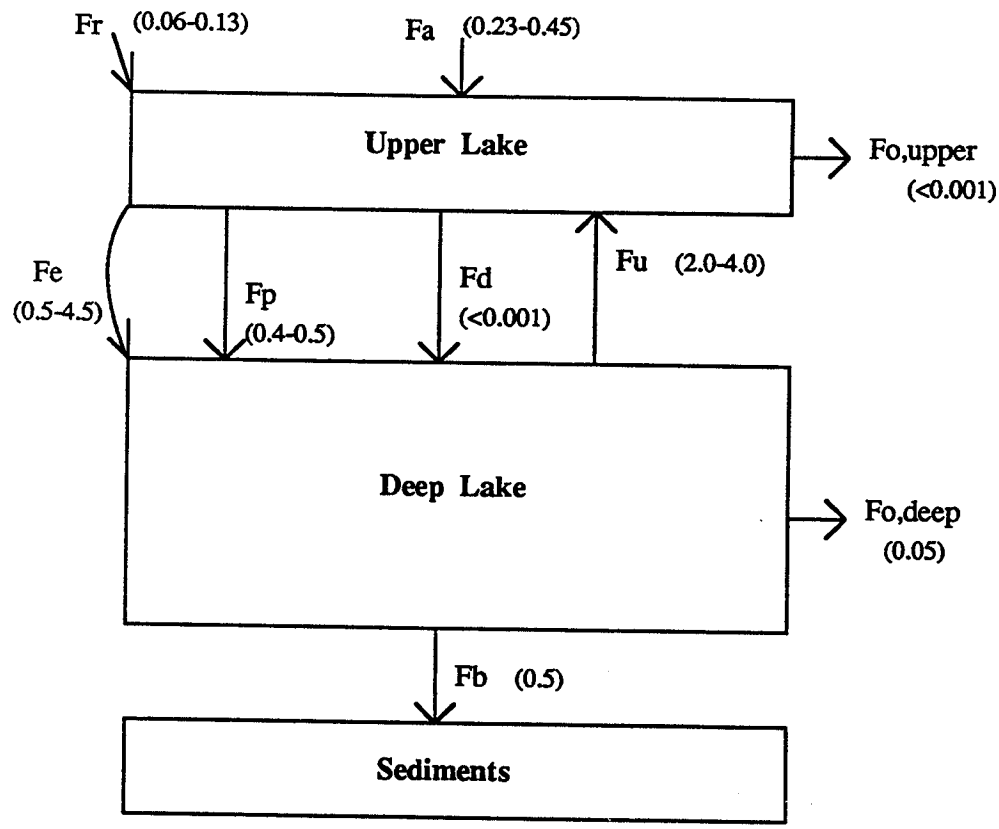


Figure 11. Box model of Crater Lake showing three reservoirs of organic matter and nutrients: upper lake (0-200 m), deep lake (>200 m), and sediments. Exchange of dissolved and particulate materials into the system and between the reservoirs are represented by the various flux arrows: F_a equals the atmospheric inputs; F_r equals the inputs from runoff; F_u represents nutrients transported by upward mixing of deep water; F_d is flux from the upper lake by downward mixing; Fo equals the looss from the lake by seepage through the lake floor, $F_{o,upper}$ is seepage losses from the upper lake and $F_{o,deep}$ is seepage from the deep lake. Nutrients removed from the upper lake by particle settling are designated at F_p. F_b equals the sediment burial rate of a given nutrient. F_e is a hypothesized "edge flux" - the transport of particulate materials from the lake margins to the deep lake by resuspension and near-bottom advection. Estimated of the individual fluxed of nitrogen, which is believed to be the limiting nutrient, are shown by values in parentheses, in units of 10^6 moles/year. F_e is computed from the lack of balance between estimated nitrogen fluxes into and out of the upper lake.

and outflow seepage ($F_{o,deep}$). Over appropriate time scales the system will be at steady state for the bio-active elements such that the inputs will equal the outputs. The mass balance equation for the shallow box is:

Eq. 8: $$F_a + F_r + F_u = F_{o,upper} + F_d + F_p ;$$

whereas the steady state balance for the deep hypolimnion box is:

Eq. 9: $$F_p + F_d = F_u + F_b + F_{o,deep}.$$

We will now use these equations to evaluate the relative significance of different physical processes (quantified as model parameters) on the particulate nitrogen fluxes in Crater Lake. The sediment burial term, F_b, in the whole lake nitrogen budget (e.g. Eq. 2) can be transformed by assuming that a fixed fraction of the particulate nitrogen which falls to the deep lake is buried and the rest is recycled (Broecker 1971).

Eq. 10: $$F_b = \alpha \cdot F_p$$

where, α is the fraction of nitrogen which is buried.

Substituting into Eq. 2:

Eq. 11: $$F_a + F_r = \alpha \cdot F_p + F_o.$$

In order to directly examine the effects of deep-lake recycling on the particle flux, we solve for F_p:

Eq. 12: $$F_p = [(F_a + F_r) - F_o]/\alpha .$$

In order to evaluate the influence of deep lake mixing on particle flux we will consider the upper lake nitrogen balance. Equation 7 can be simplified because there is essentially no dissolved nitrogen in the upper lake (<200 m). Therefore, seepage ($F_{o,upper}$) and downward mixing (F_d) account for a very small fraction of the nitrogen removal. As a result, the flux of particulate nitrogen (F_p) should balance inputs from upward mixing (F_u) and exogenous sources ($F_a + F_r$):

Eq. 13: $$F_p = F_a + F_r + F_u .$$

We can make estimates of the amount of particulate recycling, α, in the deep lake from comparison of sediment trap and sediment data. If particulate aluminum is conservative, differences between the N/Al values observed in deep sediment traps and surficial sediments will

be due to nitrogen recycling. The ratio of N/Al values of deep traps with the N/Al in surficial sediments indicates that 79 to 90% of the nitrogen is recycled (Dymond and Collier 1990). This suggests α in Crater Lake ranges between 0.1 and 0.21.

As discussed above, measurement of the average nitrogen in precipitation (4.4 μmoles/l) and the assumption that water introduced from runoff has the same nitrogen contents indicate 5.8 x 10^5 moles of nitrogen enter the lake from precipitation and runoff. We have not accounted for a possible sampling contamination blank in this estimate. Also, because nitrogen in precipitation was measured only for one year, we do not have a measure of the variability of this input. We will assume that 5.8 x 10^5 moles N/year is a possible maximum input from precipitation and runoff and have evaluated the effects of varying this input by a factor of two (from 2.9 to 5.8 x 10^5 moles N/year).

We will evaluate the effects of varying the deep lake ventilation rates which are equivalent to deep water residence times of 2 and 10 years. Based on tritium measurements in Crater Lake, Simpson (1970b) estimated that the lake mixes over time scales of a few years. The observed rate of deep water exchange with oxygen (McManus 1992) requires a residence time of about 2-3 years. Recent measurements of chlorofluorocarbon in Crater Lake (R. Weiss, unpublished data) suggest an average age of the deep waters of Crater Lake of approximately three years (Collier, et al. 1991). Therefore, the available data is most consistent with complete exchange of deep lake water occurring within 2 to 4 years (McManus et al., unpublished data, University of Southern California and OSU, October 1992).

Assuming the lake is at steady state, we use Equations 11 and 12 to define the mixing rates, nitrogen recycling, and nitrogen inputs from precipitation and runoff that are compatible with the observed upper and deep lake nitrogen concentrations. The equations can be used to generate a field of values that are compatible with these parameters (Figure 12). This field is an effective visual tool for defining the magnitude of lake processes. For example, if the deep water residence time lies between 2 and 4 years, the extent of recycling must be higher than 79% ($a<0.21$). Also with this mixing rate and $a = 0.1$, the precipitation and runoff input of nitrogen must be somewhat

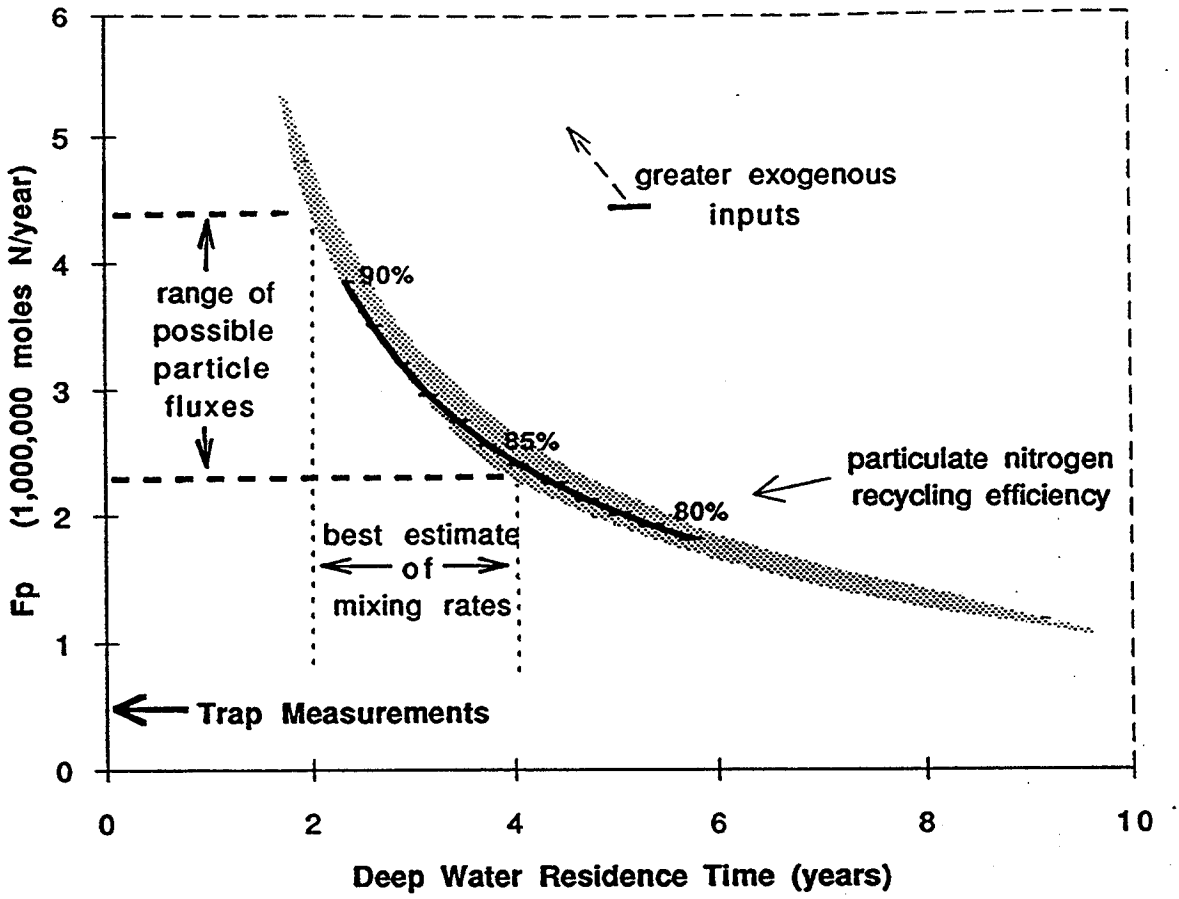


Figure 12. The modeled relationship between deep water residence time (a function of the vertical mixing rate) and the settling flux of particulate nitrogen in Crater Lake. The relationship is derived from equations 12 and 13 by independently estimating values of the exogenous nitrogen inputs ($F_a + F_f$) and the deep lake recycling fraction ($1-\alpha$). The observed dissolved distribution of nitrogen is also imposed such that F_o is determined from the seepage rate and F_u is determined from vertical mixing rate (see text). Setting this group of parameters to the 'most reasonable' values (see text) requires a particulate nitrogen flux out of the euphotic zone of 2.5 to 4.5 x 10^6 moles/year - considerably greater than the 0.4-0.5 x 10^6 moles/year collected by the sediment traps (shown by arrow on N axis). The dark curve is generated under the conditions of $F_a + F_r = 0.44 \times 10^6$ moles/year with tick marks for the particulate nitrogen recycling efficiencies (79-90% or $\alpha = 0.21$-0.10). The stippled field includes the complete range of estimates for F_u and F_p that result by including all model parameter estimates. The result of increasing our estimate for exogenous inputs ($F_a + F_r$) moves the curves towards the upper left of the field as shown.

smaller than our upper estimate of 5.8 x 10^5 moles/year. Likewise, for a deep lake residence times of 2 to 4 years, the annual particulate N flux must lie between 2.3 and 4.4 x 10^6 moles, regardless of the extent of recycling or precipitation and runoff inputs. Only with relatively low recycling rates, low precipitation inputs, and slow deep-lake mixing can particulate nitrogen fluxes approach values as low as 1.0 x 10^6 moles/yr.

These model-based estimates of the downward flux of particulate nitrogen (F_p) can be compared to the flux of nitrogen, which has been directly collected by sediment traps deployed at a depth of 200 m. The average flux of nitrogen measured in the 200-m traps is 10 $\mu g/cm^2/yr$ (Table 1). Multiplying this value by the area of the lake (53.2 km^2), results in the total particulate nitrogen flux for the lake: 5.3 x 10^6 g/year or 3.8 x 10^5 moles/year. This sediment trap estimate of total nitrogen flux leaving the euphotic zone (through 200 m) is 2.5 to 10 times smaller than the flux required to balance the upper lake nitrogen budget. This significant disagreement in flux estimates must be carefully considered as it may demonstrate errors in any of the direct measurements (traps, reservoir concentrations, mixing rates) or errors in the assumptions of the box models. Perhaps more significantly, it may suggest processes which we have not yet considered.

First we will consider possible errors in the trap flux estimates in order to account for the low nitrogen fluxes observed. Trap-related errors could result from several possible sources. The first question is whether the trap is collecting the vertical particle flux with 100% efficiency. Certain trap designs and hydrodynamic conditions can lead to under-trapping (Gardner 1980, Baker et al. 1988). However, the general trap design we use in Crater Lake has been shown to have efficiency near 100%. A similar trap, deployed in the central Pacific, was >80% efficient based on ^{230}Th collection inventories (Mahannah 1984). As shown by other studies, most of the collection artifacts are created by hydrodynamic effects around the traps in high-current environments which do not exist in the deep water column of Crater Lake. Measured current speeds in Crater Lake average approximately 1 cm/sec (McManus et al. unpublished, University of Southern California and OSU, October, 1992), well below speeds that might cause inefficient particle collections (Gardner 1980, Baker, et al. 1988). Also, if bulk collection efficiency were

low, we would also have observed more severe problems with the comparison between ^{210}Pb fluxes and the whole-lake ^{210}Pb budget. Therefore, we do not feel that a low trapping efficiency is the cause of low organic matter fluxes into the traps.

A related trapping artifact is the change in flux and particle composition that can result from substantial zooplankton activity that may occur within the trap cone and/or cup. The problem of "swimmers" has been well discussed in the literature (Lee et al. 1988), and they may play a role in Crater Lake. These effects are more likely to be a problem in the shallow traps which are at depths where zooplankton are more abundant. Zooplankton 'invaders' can result in a decrease in the collected flux (mobile organisms feeding within the cone) or in an increased flux (swimming organisms that get poisoned by formaldehyde in the trap cup). Most studies suggest that swimmers result in flux increases, not decreases (Silver and Gowing 1991). Over the past few years, we have observed an increased number of chironomid larvae in the cups, which may be 'swimmers', but the overall chemical composition and systematics of flux with increasing depth suggests that swimmers are not a big problem.

Another trapping artifact relates to the chemical preservation of the particles once they enter the trap. Experiments show that formaldehyde is an effective particle preservative and eliminates significant microbial degradation (Lee et al, 1992). However, extremely 'labile' organic fractions can become dissolved in the trap cup preservative solution after the particles enter the cup. Unless these solutions are carefully collected and analyzed as part of the sample, several tens of percent of the total flux can be lost. There is also some small fraction of this loss that diffuses out of the traps while they are still collecting and cannot be recovered. Because it is impossible to measure DOC in formaldehyde, we have monitored this loss to solution indirectly by the analysis of dissolved P in the cup solution. This approach assumes a Redfield ratio of the soluble P to determine a 'worst estimate' of the amount of total organic matter lost to the cup solutions. While we have generally found that the soluble P projects this magnitude of loss (25% average), we are unable to see any systematics to this release. Our experience with marine particulate matter suggests that the loss predicted on the basis of P is an over estimate of the total organic matter lost, because P appears to

be the most labile organic component. Therefore, our nitrogen fluxes are probably no more than 25% low on average, which would increase our estimate of the trap-defined fluxes to 0.5 x 10^6 moles N/year. Therefore, this concern can not account for the discrepancy with our nitrogen budget.

The differences between the models and the trap flux observations could also result from errors in model parameters or structure. The upper 200 meters of the lake are consistently depleted in dissolved nitrogen (Larson et al., this report), clearly showing that all new inputs of nitrogen must be quantitatively removed by settling particles. We have a high degree of confidence in this assertion. Therefore, we will examine those parameters which make up the estimate of the nitrogen inputs - the allocthonous inputs and the vertical mixing flux from the hypolimnion.

Although the estimate for the primary source of nitrogen to the whole-lake system (atmospheric input and runoff) is based on just an 18-month record of precipitation compositions and monthly precipitation records, this term is less than 20% of the upper lake budget. Therefore, even errors greater than the factor-of-two range used in Figure 12 would not produce a balance between model and trap measurements.

The extent of particle recycling has a significant impact on the range of possible particle fluxes, which are compatible with observed lake nitrogen distributions (Figure 12). However, the model shows that for a deep-water residence time of two to four years the fraction of nitrogen recycled must lie between 85 and 90%. Therefore, it seems unlikely that the extent of recycling can lie outside the range indicated by a comparison of N/Al values in Crater Lake sediments and sediment trap materials (79 to 90%).

The vertical mixing flux is computed from the product of the average deep-lake nitrate concentration of approximately 1 μM (see Larson et al., this report) and the vertical mixing rate. Although the mixing rate is perhaps the most indirect and 'model-dependent' estimate used, it has been independently derived using a variety of tracers. These include the rate of oxygen consumption and ventilation in the deep lake (McManus et al. this report) as well as the observed penetration of surface-derived tritium (Simpson 1970) and freon (Weiss, unpublished, University

of California, San Diego, June, 1991). These estimates, which range between 1-3 years for the average ventilation age of the deep lake, are supported by a set of 'limnologically consistent' observations related to the rates of hydrothermal processes (Collier et al. 1991). Therefore, we feel that this parameter is quite well constrained and supports the model calculation for the introduction of new nitrogen from the hypolimnion. Although the model-based estimates of particulate nitrogen flux depend strongly on the ventilation rates (Figure 12), even deep water residence times of 10 years (Figure 12) cannot account for the particulate nitrogen fluxes measured with sediment traps.

It is also instructive to apply this model to other nutrients, in particular, phosphorus. Phosphorus is not strongly depleted in the surface lake and is probably not limiting to growth. Although we do not have as much sediment trap flux data for this nutrient (Table 1), we can still apply the same box model used for nitrogen. The surface lake is depleted in dissolved P with respect to the deep lake by approximately 0.1 μM. Given our estimate of the vertical mixing rate, this results in a average vertical flux of 2 to 4 x 10^5 moles P/yr. The estimates of exogenous P inputs (Reilly, et al. 1989) add approximately 0.6 x 10^5 moles P/yr. The sum of the upwelled and exogenous sources must equal the particulate P flux - 2.6 to 4.6 x 10^5 moles P/yr. We can compare this model estimate to the equivalent model estimate for nitrogen and to the direct trap measurements. The particulate nitrogen fluxes derived from the box model (F_p = 2.5 to 4.5 x 10^6 moles N/yr) are approximately ten times higher than the phosphorus flux. In spite of the large approximations involved, the possible range of N/P flux ratios include the 'Redfield' algal composition ratio (~16:1) observed elsewhere (Redfield 1934, Kilham 1990). The model estimate can also be compared to the particulate trap flux for phosphorus. A representative trap flux is about 2 x 10^4 moles P/yr with an N/P ratio ranging from 10:1 to 20:1. As is the case for nitrogen, this measured flux is only ~10% of that required by the observed distribution of dissolved P (box model result). This lends further support to the argument that the traps are under-sampling all components of the settling particulate organic matter.

In summary, we are faced with an apparent paradox. The steady state composition and physics of the lake require an organic matter flux which is at least several times higher than that measured by the sediment traps deployed in the center of the lake. This apparent discrepancy exists for organic carbon as well as for nitrogen and phosphorus. The observed rate of oxygen consumption in the deep lake, which must be supported by a steady supply of organic matter from the euphotic zone, is at least two times larger than the flux of organic carbon measured by the traps (McManus et al., this report). There appears to be a mechanism to move particulate organic matter into the hypolimnion that "bypasses" the traps.

Significance of Lake Margins as Major Sources of Biogenic Particles

We hypothesize that 'edge-effects' are supporting significant production not collected by the traps and that this particulate flux is focused into the deep basins where it is remineralized, consuming oxygen, and regenerating nitrate. These edge effects, which result in higher production, might include enhanced vertical mixing across the thermocline due to frictional shear introduced by surface waves, internal waves, and seiching. If there is greater productivity near the margins of the lake than the central lake, more particulate material will settle to the shallower areas of the lake and the frictional shears will eventually move the detritus downslope, all the while undergoing diagenesis, carbon oxidation, and nutrient regeneration. We propose that biogenic detritus in the shallow areas around Wizard Island and on the steep caldera walls accumulates seasonally, primarily during the late spring and summer months. Resuspension may occur either by winter storms or possibly through mixing events.

We have also not made any estimate for the production of periphyton and mosses attached to the walls of the caldera. These plants have been shown to account for the dominant fraction of the productivity in the littoral zone of Lake Tahoe and Crater Lake (Loeb et al. 1983). However, much of the littoral periphyton productivity in these lakes is due to nitrogen fixing species (Loeb and Reuter 1981) and would not be a major sink for new nitrogen. Crater Lake, with its steep subaqueous caldera walls and great clarity, is perhaps highly suitable for substantial growth of attached macrophytes to great depths. At water depths greater than 60 m nitrogen-fixing species

are not significant (S.Loeb, personal communication, University of Kansas, September, 1992). A number of transects to define the plant growth on the caldera wall were made in 1988 and 1989 using a manned submersible (Collier, et al. 1991). Although these plants were most abundant between 30 and 80 m, moss was also collected and observed at depths below 100 m. Detrital patches of moss were observed as deep as 545 m, and clumps of moss are common in sediment cores collected in the deep basin. These deep occurrences of moss indicate that macrophytes become detached from the rocks and move downslope where they decompose in the deep lake or are buried in the sediments. While the growth and transport of these plants is apparent, it is difficult to quantify their impact on the overall nutrient cycle of the lake.

An important implication of our "edge-effect" hypothesis is that the margins of the lake and the extensive shallow regions around Wizard Island have much higher nutrient inputs and biological productivity than the open lake. Depending on the assumed lake ventilation rate, upwelling and precipitation introduce 2 to 10 times more nitrogen to the upper lake than we measured with central lake sediment traps. The discrepancy may result from an equivalent higher new production occurring at the lake margins. We show this productivity in Figure 11 as an edge flux of 5 to 45 x 10^5 moles/year of particulate nitrogen leaving the euphotic zone.

If the new production in the lake and resulting particulate organic matter settling is 2 to 10 times greater than that measured by central-lake sediment traps, do the variations in trap-based carbon and nitrogen fluxes reveal anything about whole-lake productivity variations? Our "edge-effect" hypothesis implies that 50 to 90% of the biological activity occurs in the shallow areas around Wizard Island and near the caldera walls. Because the particulate organic detritus from this biological production moves into the deep lake basins by near-bottom transport, it seems possible that the variability in central-lake sediment trap fluxes is disconnected from the predominate biological activity that occurs along the margins. Perhaps the factor of five variability in particulate carbon fluxes that we observed over the duration of our sediment trap experiment (Table 1), reflects more effective horizontal transport away from lake margins to central lake traps by storms or other processes. Alternatively, the variability may indicate interannual differences in upward

mixing of deep lake nutrient source which influences both the margins and the central lake areas. If this is the case, sediment trap measurements, although not an absolute measure of whole-lake productivity, serve as a relative indicator of its interannual biological production. We cannot sort out these questions from the existing data, however, future studies, which attempt to define the horizontal gradients in total primary productivity of the lake and which link independent measures of deep lake mixing with particle fluxes, can lead to a much clearer definition of lake processes and budgets.

Implications of the Nitrogen Budget for Primary Production

Estimates of deep-lake mixing can be used to define the expected quantity of new productivity in Crater Lake. As we discussed above, the most probable age of the deep waters of Crater Lake is in the range of two to four years (Collier, et al. 1991) which leads to an input of 2 to 4 x 10^6 moles of nitrate to the upper lake each year by deep-lake mixing. We have also estimated that precipitation and runoff inputs of nitrogen to the lake range from 0.29 to 0.58 x 10^6 moles/year. These 'best estimates' suggest the annual nitrogen input to the euphotic zone ranges between 2.3 to 4.6 x 10^6 moles.

Because deep-lake mixing provides 80 to 90% of the total nitrogen inputs to the upper lake, one would expect that year-to-year variations in deep-lake mixing would produce variability in new production for the lake. We cannot yet test this hypothesis, although significant interannual variations have been discussed. On-going studies of lake physics coupled with the continuation of particle flux measurements could provide the necessary data. Because the annual nitrogen fluxes to the euphotic zone are five to nine times greater than the sum of burial and seepage removals, typically nitrogen atoms entering the euphotic zone must be recycled in the deep lake and upwelled many times before being buried in the sediments or removed from the lake by seepage.

The input of nutrients to the euphotic zone can be thought of as an estimate of the lake's "new production". Primary production during the summer is approximately 30 mg $C \cdot m^{-2} \cdot hr^{-1}$ (12-hour day, average since 1983, G. Larson , this report). Assuming a Redfield ratio of C/N, our estimate of the total new nitrogen introduced to the euphotic zone suggests new production is

only 3 to 5 % of the total primary productivity of the lake. These calculations further demonstrate that nitrogen is *very* efficiently recycled *within* the euphotic zone (as well as in the deep lake) which supports a level of total primary production that is roughly 25 times higher than could be supported without recycling.

The estimates of nutrient inputs to the euphotic zone can also provide an independent estimate of deep-lake recycling when these fluxes are compared with the burial rate of nitrogen (0.45×10^6 moles N/yr). At steady state, the input flux of new nutrients to the euphotic zone must be balanced by removal of nutrients accompanying settling particulate organic matter. Thus, 2.3 to 4.6×10^6 moles N/year should accompany particles that settle into the deep lake. The estimate of nitrogen burial rate implies 80 to 90% of the particulate nitrogen reaching the deep lake is recycled, an estimate very similar to the range determined by comparison of N/Al values measured in sediment and sediment-trap materials (Dymond and Collier 1990).

Our nitrogen budget also makes it possible to evaluate the significance of nitrogen inputs from Spring 42, located on the caldera wall below the lodge. This spring has consistently shown relatively high concentrations of nitrate (Larson 1988, Gregory, et al. 1990, Larson et al. 1990). These elevated concentrations are probably anthropogenic. They might have already impacted the nutrient budget of the lake and, more specifically, the clarity as measured by Secchi disk depths (Larson et al. 1990). If we assume the average concentration and flow rate estimates from Larson et al. (1990), 250 μg N·Liter^{-1} @ 2 Liters·sec^{-1}, and extrapolating these estimates over the whole year, we calculate an annual input of approximately 1×10^3 moles N. This is 0.2% of the direct flux to the lake surface estimated from atmospheric deposition and other runoff sources and is roughly 0.03% of the estimate for the total new nitrogen fluxes (including deep lake mixing) added to the euphotic zone each year. While this anthropogenic nitrogen may have local effects near the source, it is overwhelmed by atmospheric inputs and other exogenous runoff sources. When we include the deep-mixing source of nitrogen in considering the upper lake budget, it is difficult to see how this specific flux could have a detectable impact on production and whole-lake clarity.

Summary and Conclusions

Settling particle fluxes measured near the center of Crater Lake reveal large interannual variations in lithogenic components (a factor of eight to nine) and biogenic components (a factor of five). The lithogenic flux variations may be related to interannual differences in precipitation which influence the amount of particles washed from the atmosphere and the amount of material eroded from the caldera wall during snow melt. The variability in biogenic fluxes does not correlate with variations in annual precipitation, an observation consistent with our estimate that this source contributes less than 30% of the annual input of nutrients to the upper lake. Seasonal variations in organic carbon show that the highest fluxes of both lithogenic and biogenic components occur during the late spring and summer (May-August). This timing is probably controlled by the juxtaposition of maximum sunlight, lake stratification, and nutrients introduction through deep lake mixing and snow melt .

Our whole-lake budget, which is based on measurements of sediment accumulation, estimates of nutrient input from precipitation and runoff, and estimates of lake seepage, indicates that nitrogen and ^{210}Pb sources to the lake balance removal fluxes to within 30%. The internal lake budget reveals the importance of recycling. Productivity based on the input of new nutrients to the euphotic zone ("new production") is only about 4% of total primary productivity, demonstrating the importance of recycling in the euphotic zone. Carbon burial is less than 10 % of new production, which indicates that nutrients are recycled many times in the deep lake before they are finally removed by burial or seepage.

A major mismatch in the internal nitrogen budget of the lake exists, however. Although the rates of nitrogen input must be equal to outputs over the annual cycle, fluxes of nitrogen, which enter the euphotic zone of the lake by deep lake upwelling, precipitation, and runoff, are 2 to 10 times larger than the nitrogen fluxes we measured in lake sediment traps deployed in the central lake . We cannot account for this discrepancy through errors in any of our measurements or flux estimates. We propose, therefore, that this discrepancy reflects "edge effects", whereby enhanced nutrient fluxes at the lake margins, result in greater biological productivity near the caldera walls

and in the shallow regions around Wizard Island. We propose that the biogenic detritus from this enhanced productivity is resuspended seasonally and transferred from the margins to the deep lake by winter storms and possibly mixing events. The importance of this type of sediment focusing is supported by both the systematic decrease in particulate carbon/aluminum values with increasing sediment trap depth and by submersible studies which reveal a lack of significant sediment accumulation on the steep caldera walls and shallower portions of the lake.

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CHEMICAL SOLUTE MASS BALANCE OF CRATER LAKE, OREGON

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In 1982, the National Park Service initiated a 10-year program of study with the objectives of more fully describing the chemical, physical, and biological processes of Crater Lake. Collection of solute chemical data began in 1987 for the lake and its major input sources, atmospheric deposition and caldera spring runoff. This study is a synthesis of solute chemical data in the form of a mass balance of the major chemical components for Crater Lake.

Terms included in the steady-state mass balance for Crater Lake were external inputs from atmospheric deposition and spring runoff, internal processes of solubilization and precipitation of lake sediments and suspended solids, internal biological assimilation and removal by cellular deposition, seepage from the lake, and a previously unknown (unquantified) source term which was subsequently confirmed to be hydrothermal inflow. To perform the solute mass balance, new hydrologic information was employed for atmospheric precipitation, lake evaporation, runoff, and seepage.

The lake, because of its unique physical characteristics (Table 1), is well suited to mass balance modeling. Surrounded by steep walls, the water surface occupies 78% of the catchment basin. Located high in the mountains, the only inlets are a number of springs supplied by rain and melting snow stored within the rim. There is no surface outlet. Evaporation and seepage help maintain the lake at a relatively constant level, though the surface elevation has varied by as much as 4 m since 1900.

Chemistry data provided by the National Park Service (NPS) (Larson 1985, Larson 1986, Larson 1987) was used to perform a chemical solute mass balance of the

Table 1. Physical Characteristics of Crater Lake (Phillips 1968).

Elevation of surface	1,882 m
Area of surface	53.15 km^2
Total area of basin	67.8 km^2
Volume	17.3 km^3
Maximum depth	589 m
Average precipitation	171 cm/yr
Residence time	156 yr

lake system. The data set was more complete than those previously available for the lake and watershed. In addition to the extensive lake and spring sampling, and the first on-site precipitation collection, new hydrologic data (Redmond 1989) and lake sediment chemistry data (Dymond and Collier 1989) enabled improved estimation of the mass input and output terms. The mass balance approach was used to evaluate the proposal of previous investigators (Phillips 1968, Thompson et al. 1987) that additional source(s) must be present to account for the anomolously high dissolved chemical component concentrations (solutes) in Crater Lake compared to the input sources and to other nearby surface waters (Eilers et al. 1987).

Methods

Sample Collection

The data collection period under consideration ran from January, 1987 through September, 1988. Figure 1 shows the approximate locations of the data collection sites at Crater Lake. A bulk atmospheric deposition collection station was located on the rim of the caldera near Rim Village. Samples were collected in a 32-gallon plastic container lined with food-grade plastic bags. Samples usually were collected at 7-day intervals, although this period varied. Snow samples were melted overnight. All samples were

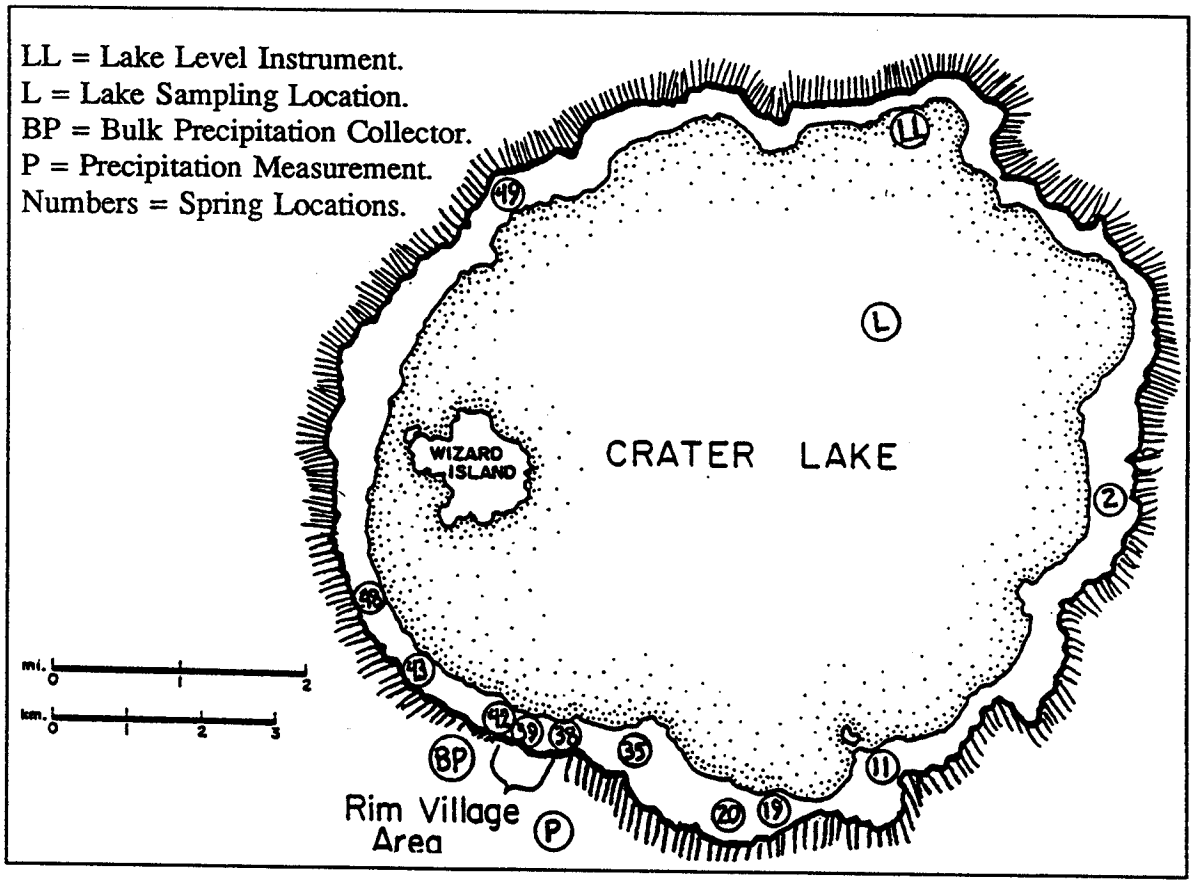


Figure 1. Sample collection and measurement sites at Crater Lake.

filtered (Larson 1987). For periods when no precipitation occurred (dry deposition), the interior of the collection container was rinsed and the contents diluted to one liter with deionized water and refrigerated one week in the dark prior to filtering.

Over 40 springs emanate along the caldera walls and flow into the lake. Some flow year round, while others are ephemeral. A numbering system initiated by the NPS is used here to designate spring location (Fig. 1). Ten springs, chosen to include those representative of the range of water quality characteristics recorded in 1983 and 1984, were sampled (see section - Water Quality of Caldera Springs). Particular emphasis was placed on springs in the Rim Village area, where visitor facilities are provided (Larson 1985, Larson 1987).

Lake water samples were obtained using 4-liter Van Dorn bottles at intervals planned to reveal the concentration profile of the lake. Measurements were taken at 0, 5, 10, 20, 60, 100, 200, 300, 400, 500 and 550 meters at station 13 (see Study Area and Facilities section). For both lake and springs, the sampling was generally monthly through the summer months (June - September) with occasional winter and early spring trips. Lake sampling during winter months was restricted due to the inaccessibility of the lake caused by severe weather and deep snow. The amount of precipitation was measured with a gage at park headquarters and recorded daily. Daily lake level readings are available from a gage maintained by the U.S. Geological Survey on the lake at Cleetwood Cove (see Study Area and Facilities section).

Sample Analysis

Three laboratories were employed for sample analyses: The Cooperative Chemical Analytical Laboratory at Oregon State University, Corvallis, where all samples were initially shipped; Environmental Protection Agency (EPA) Research Laboratory, Corvallis; and University of Washington, Forest Resources Laboratory, Seattle. A summary of the analyses is presented in Table 2.

Detection limits (DL, mg/l), are included in parentheses (Table 2) along with the chemical form in which the results are reported. The second number in the EPA analyses refers to the Limit of Quality Concentration (LQC). Any analysis below this value has a probable analytical error. The likelihood and magnitude of the error increases as one approaches the detection limit.

Where a result was below the detection limit the policy of National Atmospheric Deposition Program (NADP) was followed (Anonymous 1988). For those components which appear in at least 90% of the sample analyses, one half the detection limit value was used.

Summary of Data Review

A cation/anion ion balance was calculated from the data for each sample. The resulting median, average, and standard deviation of the cation/anion ratios were, respectively: 0.98, 1.02, and 0.05 for lake water samples; 0.96, 1.00 and 0.35 for spring water samples; and 1.18, 1.10 and 0.46 for precipitation samples. A greater degree of spread in the results was observed as the water samples became less concentrated. As the concentrations approach the detection limits, as was frequently the case in

Table 2. Sample analysis description.

Analysis	Method*/Modifications (Chemical form, Detection Limit)
OSU Laboratory	
Alkalinity	403, Procedure 4c, titrate to Ph 4.5, use 0.02N Na_2CO_3, use 0.02N H_2SO_4. (HCO_3-C)
Ammonia	417F (NH_3-N, 0.005)
Conductivity	205; Wheatstone bridge
Nitrate	418F, Technicon Industrial Method 100-70W. Different formulations for color and ammonium chloride. (NO_3-N, 0.001)
Nitrogen,	Total Kjeldahl digestion, H_2SO_4, $CuSO_4$/Kcl, Kjeldahl Nessler finish. (TKN, 0.010)
pH	423; calomel electrode glass pH electrode. Temperature compensator.
Phosphate-Ortho	424F Ascorbic acid reagent:2g/100ml. (PO4-P, 0.002)
Phosphorus-Total	424C, 424F Microwave digestion-60 minutes. 50ml analysis volume, ascorbic acid reagent: 2g/100ml. (P, 0.005)
Silica	Technicon Industrial Method 105-72W. (Si, 0.150)
UW Laboratory	
Chloride	Technicon Industrial Method 99-70W. (Cl, 0.200)
Sulfate	Technicon Industrial Method 105-72W. (SO_4-S, 0.200)
EPA Laboratory	
EPA's Induction Coupled Plasma Atomic Emissions Spectrophotometer is used to determine concentrations of the following components:	
Calcium (Ca, 0.007, 0.067)	Magnesium (Mg, 0.01, 0.096)
Potassium (K, 0.070, 0.680)	Sodium (Na, 0.010, 0.091)
Boron (B, 0.002, 0.018)	

Detection limits (DL, mg/l), are included in parentheses along with the chemical form in which the results are reported. The second number in the EPA analyses refers to the Limit of Quality Concentration (LQC). Any analysis below this value has a probable analytical error. The likelihood and magnitude of the error increases as one approaches the detection limit. (Wagner, 1988)

Where a result is below the detection limit the policy of National Atmospheric Deposition Program (NADP) was followed (NADP, 1988). For those components which appear in at least 90% of the sample analyses, one half the detection limit value is used.

*Numbers refer to Standard Methods for the Examination of Water and Wastewater 15th Edition, 1980.

precipitation and spring samples, analysis inaccuracies create relatively higher errors in the ion totals.

A conductivity ratio (measured/calculated) was computed for each sample. The resulting median, average and standard deviation for lake, spring and precipitation samples were, respectively: 0.94, 0.94, and 0.02; 0.94, 0.93, and 0.10; and 0.90, 0.90 and 0.21. Increased relative error with high dilution was again indicated.

Analysis of variance tests were performed on the precipitation data to check for a systematic error causing the deviation from unity in the ion and conductivity ratios. Evidence was insufficient to suggest that a significant difference exists between the component concentration values associated with the "best" ion or conductivity ratios (those near 1.0) and those associated with "errant" ratios (those considerably greater than or less than 1.0).

Based on the findings of the data review, the data set was judged to be sufficiently accurate to be used in the mass balance analysis.

Results and Discussion

Solute Mass Balance Model

Figure 2 depicts the lake's hydrologic and chemical inputs and outputs. Precipitation is the lake's primary source of water. It falls directly on the lake surface, or is stored temporarily on the caldera walls where it later appears as surface or subsurface springs. Infiltration of groundwater from outside the crater rim and flow emanating from under the lake floor are other potential sources. Water losses from the lake include seepage through the lake bottom and evaporation. The hydraulic components transport chemical solute mass to, or from, the lake. Mass transport of

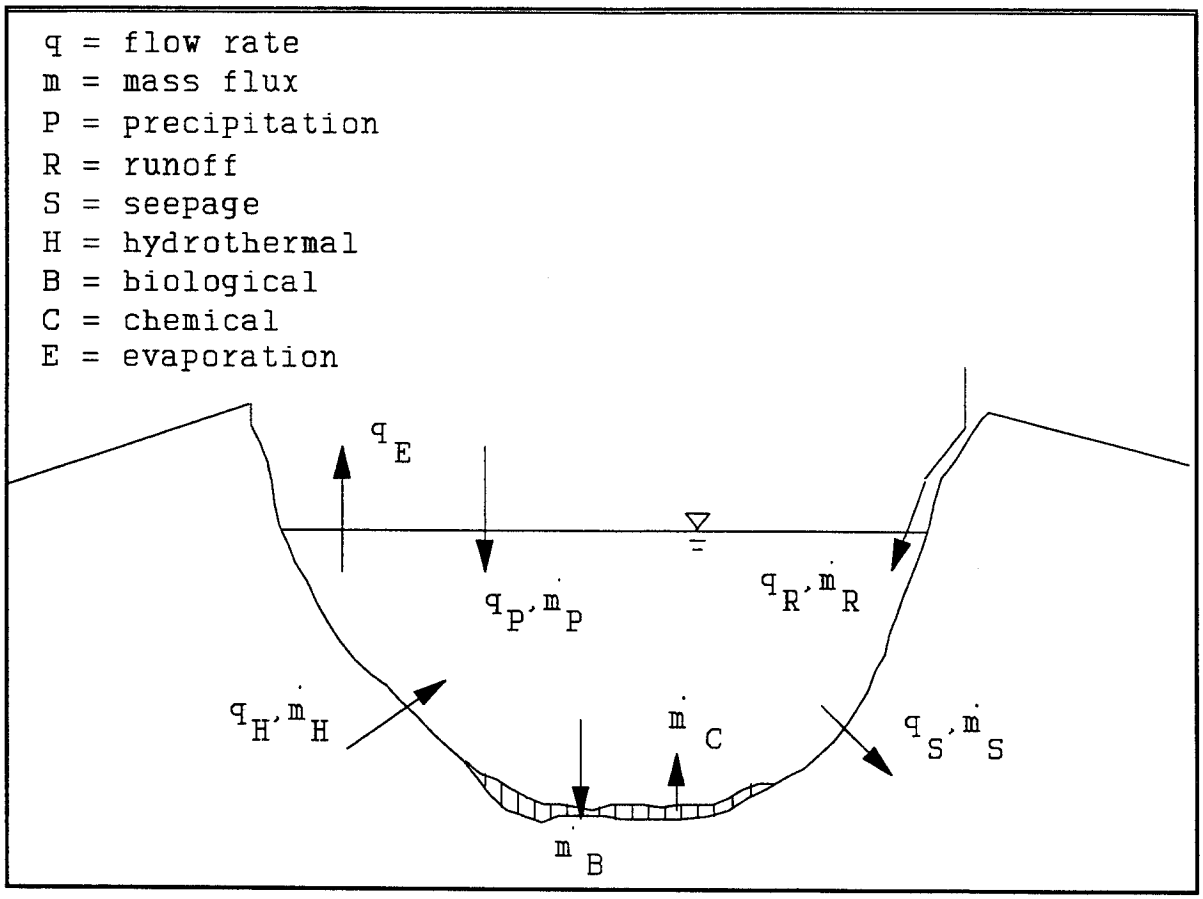


Figure 2. Hydraulic flow and mass transport paths predicted for Crater Lake.

chemical components can also occur through biological processes and through precipitation or dissolution of solid mineral phases.

Initial development of the mass balance excluded mass transport components ofwhich little was known, (e.g. chemical, biological and hydrothermal) and considered those which were readily estimated. An unknown term was included which summarizes the influence of excluded processes. Each of these processes was evaluated as to its importance in making up the unknown. A positive convention (input) was adopted for the unknown, recognizing that the processes making up the unknown may cause a component's mass in the lake to increase or decrease.

The exchange of mass in a dynamic system may be expressed as:

(1) Rate of mass accumulation = Rate of mass inputs - Rate of mass outputs + Rate of internal mass generation

This applies to water as well as to any chemical component of the selected control volume.

For water in the lake volume (non-steady state), a hydrological mass balance can be written:

(2) $dLL = (q_P + q_R - q_S - q_E)/A_L$

where dLL is the change in water mass expressed as lake level (m) and the lake area, A_L (m^2), is considered constant for small changes in lake level due to the steep caldera walls.

At steady state (constant lake level), dLL = 0, and (2) becomes:

(3) $q_P + q_R = q_E + q_S$

The mass balance of soluble chemical component i over the lake volume is written:

(4) $dM_i/dT = \dot{m}_{iP} + \dot{m}_{iR} - \dot{m}_{iS} - \dot{m}_{iE} + \dot{m}_{iU}$

where dM_i/dt is the rate of accumulation of mass for component i in the lake and "U" represents any unknown mass transport process. A positive (input) convention has been used here for the unknown source(s), recognizing that there may exist both inputs and outputs of mass that are not accounted for in the initial analysis.

The rate of mass transport of component i carried in water stream J is:

(5) $\dot{m}_i = q_J c_{iJ}$

At steady state (component mass in the lake constant), $dM_i/dt = 0$, and assuming no mass transport in evaporation (nonvolatile components), equation (4) becomes:

(6) $\dot{m}_{iP} + \dot{m}_{iR} + \dot{m}_{iU} = \dot{m}_{iS}$

The mass balance was performed on an annual basis. The mixing time for the lake has been shown to be on the order of one year (Simpson 1970, Volchack 1970) so this basis should suit the system. The model assumes a steady-state chemical composition in the lake, a reasonable assumption based on little change in chemical solute concentrations in 75 years (Van Winkle 1913). Mass transport in the major hydraulic components, precipitation, runoff and seepage, was calculated from equation (5) using annual flow rates and component concentrations estimated in the following sections. Equation (6) will then be solved for $\dot{m}_{iU}$ leading to discussion and estimation of other mass transport processes.

Hydrology of the Lake System

Recent research has provided new insight into the hydrology of the lake. Using precipitation and lake level data from 1961 to 1988, Redmond (1989) developed the following linear correlation:

(7) $dLL = 1.457P_h - 2.465$

where dLL is change in lake level (m/yr), and P_h is measured precipitation at park headquarters (m/yr). This relationship is a solution of the more general mass balance, equation (2). The hydraulic inputs to the lake, direct precipitation and runoff, are represented by $1.457P_h$ and the outputs, seepage and evaporation, by -2.465 (m/yr). Equation (7) is used in estimating the four hydrologic components needed for calculating the component mass balances.

Inputs: Precipitation and Spring Flow. Total water flow to the lake is represented by $1.457P_h$ in equation (7). This term is comprised of precipitation which enters the lake directly, q_P, and indirectly, transported from the watershed to the lake as runoff, q_R, in the basin springs. Assuming that no springs exogenous to the Crater Lake watershed flow into the lake (Phillips 1968), that precipitation was evenly distributed over the land and water portions of the basin, and neglecting evaporation in the watershed, the two input components can be separated out of the overall input term by using the areal fraction of each. Solution of equation (7) for precipitation, q_P (m^3/yr), and runoff, q_R (m^3/yr), yields:

(8) $q_P = (A_L/A_B)(dLL + 2.465)A_L$

(9) $q_R = (A_W/A_B)(dLL + 2.465)A_L$

where A_L, A_B and A_W are the flat-map areas (m^2) of the lake, basin (mouth of caldera) and watershed, respectively. Using lake level data provided by the NPS for the study period (January 1, 1987 through September 28, 1988) the average annual values for q_P and q_R are 77.3×10^6 m^3/yr and 21.3×10^6 m^3/yr, respectively.

Estimated Hydrograph. The term for the total rate of water input to the lake from equation (7) can be written:

(10) $1.457P_hA_L = q_P + q_R$

Under the previous assumption that distribution of precipitation was even over the land and lake surface in the basin, the direct precipitation component of the total input is written:

(11) $q_P = (A_L/A_B)(1.457P_h)A_L$

Substituting (10) and (11) into (7) and solving for q_R (with the ratio $A_L/A_B = 0.78$) yields:

(12) $q_R = (dLL + 2.465 - 1.142P_h)A_L$

If the annual loss term, 2.465 m/yr, is assumed constant over the year, equation (12) can be transformed to a daily basis. Dividing (12) by 365 (days/yr) yields:

(13) $q_R = (dLL + 6.753x10^{-3} - 1.142P_h)A_L$

where dLL and P_h are now expressed in m/day and q_R is m^3/day.

Precipitation and lake level data presented graphically by Redmond (in Larson 1987) were used in equation (13) to estimate the hydrograph for the basin (Fig. 3).

The assumption that the loss term, seepage plus evaporation, is constant throughout the year, limits the accuracy of the correlation. The seepage component would likely remain constant (Redmond 1989), but evaporation would not. Previous researchers (Phillips 1968, Simpson 1970) proposed that the summer evaporation is considerably greater than winter. The opposite may be true. Direct solar radiation effects in summer are dampened by slack winds and deep penetration of the solar rays allowed by the unusually pure water. The lake usually does not freeze in winter and higher winds and a favorable temperature gradient encourage moisture transfer (Mahrt 1983). The negative runoff numbers on the hydrograph in December and January support the argument for greater evaporation in winter. Since the minimum value for q_R is zero (and winter time spring samples show that this minimum has not been reached), a

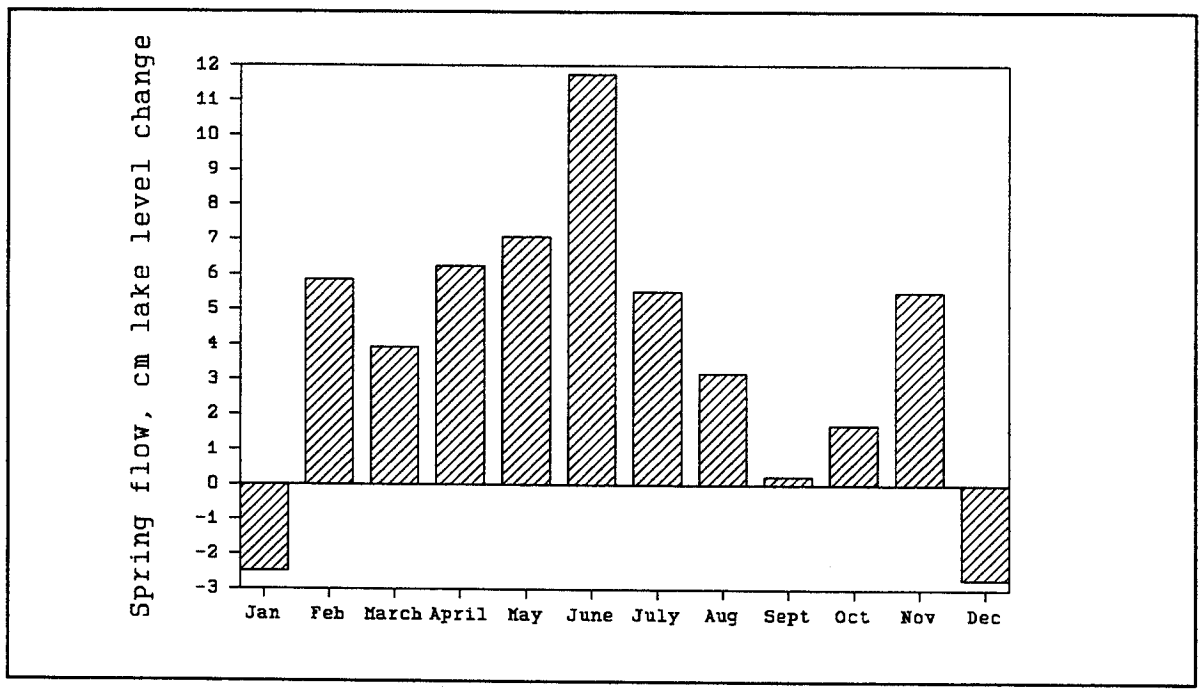


Figure 3. Estimated hydrograph for Crater Lake basin, assuming constant lake evaporation rate.

negative value for runoff can be explained only by a value for the loss term higher than assumed, or by an underestimate of rainfall. The most likely explanation is the evaporation term. The factors affecting evaporation of Crater Lake have yet to be studied in depth, and for this reason, the results of the hydrograph are used only in a qualitative sense, to indicate likely trends.

Measurements of the flow rate of Spring 42 made on July 2, 1987 and August 24, 1987 (Hurley 1988) confirm the trend of spring flow in summer depicted on the hydrograph. The July flow rate was approximately 6 l/s and that in August 0.05 l/s. While the method employed (bucket and stopwatch) is approximate, the large difference indicates that spring flow has decreased markedly over the summer, as predicted by the estimated hydrograph.

Outputs: Seepage and Evaporation. In January, 1985 and again in December, 1985 the lake surface completely froze, prohibiting evaporation. Only one other time (1949) in the past 40 years has the lake surface completely frozen (Redmond 1989). The first event coincided with a period of very little precipitation and the second, none at all. The lake level fell at an average rate of 0.347 cm/day (Redmond 1989). Two components remain in the hydrological mass balance, equation (2), under the special conditions encountered, seepage and runoff. The seepage rate is equal to the lake level change rate plus the runoff rate in January and December. Based on the hydrograph, December and January runoff rates are the lowest of the year, and are assumed to have a negligible effect on the seepage rate estimated from the observed lake level decrease rate. The annual rate of seepage based on the average daily lake level drop is 67.3×10^6 m^3/yr. Estimated annual evaporation, calculated by the difference between the total annual loss, $2.465A_L$ m^3/yr and the seepage estimate, is 64×10^6 m^3/yr.

Chemical Composition of Hydraulic Transport Paths

Precipitation Solute Concentrations. Volume-weighted average concentration in precipitation was determined for each component (Table 3) for the deposition sample collection period (January, 1987 to September, 1988). The component mass collected in each sample was calculated by multiplying each sample concentration by the measured amount of precipitation which fell over the sample collection period. Summation of all sample masses divided by the total volume of precipitation from sample collection periods results in the volume-weighted average concentration. The period used in determining the average concentration was normalized to an annual basis.

Spring Solute Concentrations. Detailed hydrologic information from the basin was lacking, necessitating use of the annual basin spring flow estimated above, and an annual component mean concentration in calculating the mass loading in springs ($\mathring{m}_{iR} = c_{iR}q_R$). Spatial and temporal variations in spring concentrations complicate accurate determination of a representative c_R. The variability in concentration among springs and within individual springs over an annual period is exemplified by calcium (Fig. 4).

Most components that exhibit temporal variability behave similarly to calcium (Fig. 4). Concentrations of components in springs are high in winter, often peaking in late winter, reach a minimum in spring, during snowmelt, and rise throughout the dry summer. The pattern was inversely related to the annual hydrograph and was evidently a dilution effect (Gregory 1989). This relationship supports using an annual mean value for each spring, since the mass transport would be reasonably constant throughout the year (increased c values are accompanied by decreased q values resulting in constant mass transport rate). Because relative rates of discharge among springs are not known,

Table 3. Solute chemical component concentrations for precipitation, spring runoff and lake water at Crater Lake.

	CONCENTRATION (mg/l)			
	[1]Precip. (c_{iP})	[2]Runoff (c_{iR})		[3]Lake (c_{iL})
		(Q_1)	(Q_3)	
TKN	0.066	0.025	0.028	0.0187
NH_3-N	0.025	0.003	0.004	0.0018
NO_3-N	0.036	0.017	0.062	0.0035
P	0.005	0.025	0.081	0.0292
PO_4-P	0.005	0.040	0.056	0.0137
SO_4	0.362	0.714	13.6	10.1
Cl	0.375	0.449	0.659	9.34
Ca	0.093	2.35	6.94	6.86
Mg	0.024	0.603	2.02	2.70
K	0.067	0.735	1.34	1.749
Na	0.072	2.55	3.17	10.6
Si	0	11.8	16.1	8.30
B	0	0	0	0.347
HCO_3	0	31.0	37.0	35.4

[1]Annual volume-weighted mean.
[2]Estimated mean annual lower and upper quartile values.
[3]Annual volume-weighted mean.

the upper, Q_3, and lower, Q_1, quartile values from the spring mean annual concentration data are used to bracket expected overall spring component concentrations.

Lake Solute Concentrations. The mass of a solute chemical component in the lake was divided by the lake volume to calculate the component concentration, c_{iL}, which was used to determine the mass loss in seepage. The total mass of component in the lake was found by summing the mass of eleven volume elements defined by the depth intervals used in the sampling program. The elemental mass was calculated from the concentration for that element's depth multiplied by the area of the lake at this depth

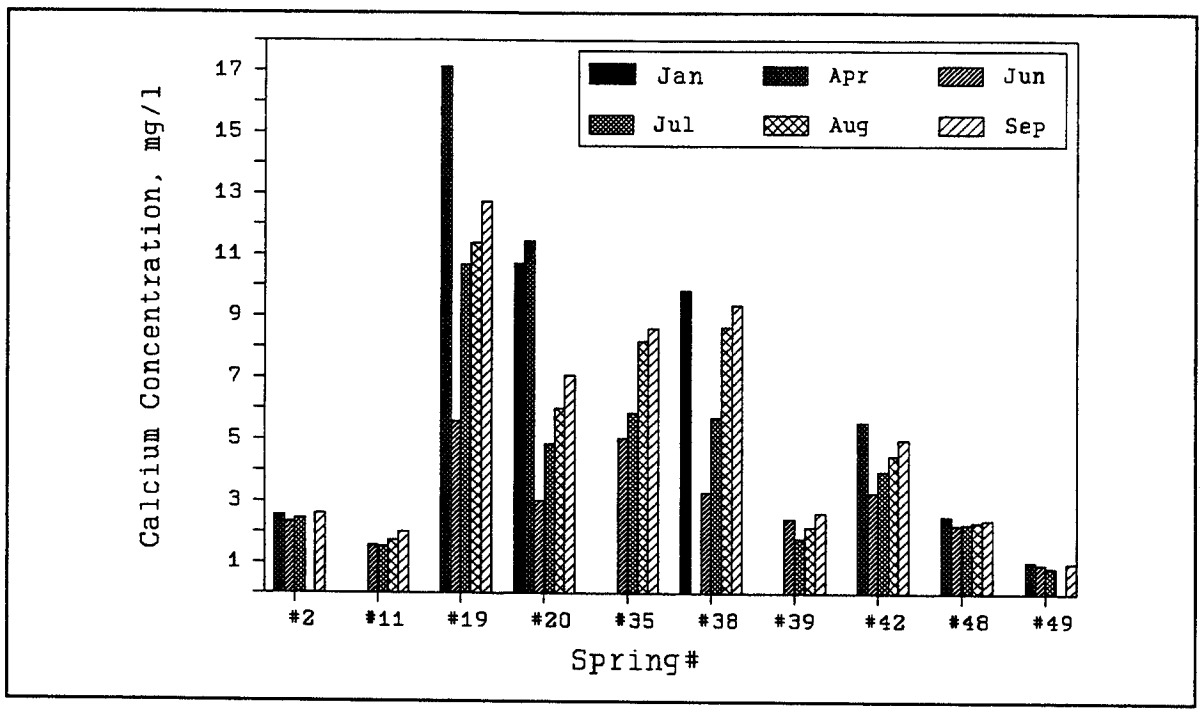


Figure 4. Example of the variability in Crater lake spring concentraton; Calcium, 1987.

and the distance between the depth intervals. Lake areas were taken from Byrne (1965). The lake volume was from Phillips (1968) adjusted for lake level variations from the mean level of 1,882 m. To account for temporal variations in concentration an annual average was taken of all individual depth-weighted averages, and was used for the final annual mean concentration, c_{iL}.

Mass Inputs and Outputs

Dry Deposition Mass Input. Mass due to dry deposition was calculated from samples for which no precipitation occurred during the sample collection period. An average daily mass deposition was found for each dry sample by dividing the mass collected by the number of days in the sample collection period. An overall average of the entire set of daily averages was calculated and multiplied by the total number of dry days occurring annually to estimate the annual mass input to the collection device. This value was then multiplied by the areal ratio of the lake to the collection device to obtain an estimate of annual mass loading to the lake.

Preliminary Mass Balance. Component mass transport in precipitation, springs and seepage was calculated from equation (5) using the appropriate annual flow rate and concentration values estimated above. Dry deposition mass input was combined with the precipitation mass input to form $\dot{m}_{iP}$, total input from atmospheric deposition. These transport terms are used to solve for $\dot{m}_{iU}$ in equation (6) (Table 4). Positive values of $\dot{m}_{iU}$ indicate that an additional output(s) was required to complete the mass balance, while negative values for $\dot{m}_{iU}$ indicate that an additional input(s) must be present to fulfill the mass balance requirement. Evaluation of processes which may account for the unknown and close the mass balance are presented below.

Table 4. Preliminary mass balance results.

	$\dot{m}_{iP}$		$\dot{m}_{iR}$		$\dot{m}_{iS}$	$\dot{m}_{iU}$	
	WET	DRY	(Q_1)	(Q_3)		(Q_3)	(Q_1)
TKN	5060	653	419	596	1260	5049	4870
NH_3-N	1950	53	64	79	122	1940	1950
NO_3-N	2810	138	362	1320	2350	4040	960
P	369	90	1130	1730	1960	229	-371
PO_4-P	366	65	863	1200	923	709	371
SO_4	28000	313	15200	288000	679000	-362687	-635487
Cl	29000	842	9560	14000	629000	-585158	-589598
Ca	7190	697	50100	148000	462000	-306113	-404013
Mg	1870	195	12800	43000	180000	-134935	-165135
K	5200	452	15700	28500	117000	-82848	-95648
Na	5590	244	54300	67500	716000	-642666	-655866
Si	0	0	251000	343000	559000	-216000	-308000
B	0	0	0	0	23300	-23300	-23300
HCO_3	0	0	661000	788000	2380000	-1592000	-1719000

All units kg/yr. 1

Biological Processes. The biogenic production of diatoms depletes silica from the lake. An ongoing study of lake sediments employing sediment traps includes data that allow an estimation of the magnitude of the silica loss term. Opal flux at a depth of 200 m has ranged from 54 to 380 mg SiO_2/cm^2-yr (Dymond and Collier 1989). Of this, 80% was shown to be recycled into the water column (Dymond and Collier 1989). Based on the highest flux, the amount of silica lost to the sediments was determined to be 13,800 kg/yr (as Si). This is just 3% of the mass lost in seepage, and is assumed negligible.

Biological activity has an important effect on the mass content of the nutrient components in the lake. Results from the calculation of the mass balance (Table 5) could be used as an approximation of the net depletion of the nutrient components from

Table 5. Fraction of sediment dissolution required to account for 10% of the calculated component mass deficit, based on data from two sediment cores.

	10% Component Mass Deficit (10^3 kg/yr)	Approx. Wt% of Component in Sediment	Component Mass Deposited (10^3 kg/yr)		Required Fraction Dissolved	
			Core 79-1	Core 85-3	Core 79-1	Core 85-3
Ca	30.6	2.5	60	22	0.34	0.58
Mg	13.5	1.2	29	11	0.32	0.55
K	8.27	1.0	24	8.8	0.26	0.48
Si	21.6	26	624	228	0.03	0.09

the lake due to biological processes. Loss of the nitrogen and phosphorus, assimilated by algae, occurs when cell material settles to the lake bottom and is buried in sediments. A detailed accounting of the mass movement of the nutrient components in the lake was not attempted. Proper evaluation of these complex processes was beyond the scope of this report. Also, the relatively small amounts of the nutrient components present in the various transport paths increases their sensitivity to the errors introduced in the approximations made in calculating the mass balance.

Chemical processes. Equilibrium solubility calculations show the lake to be chemically under-saturated, therefore the process of sediment dissolution is favored over precipitation. Dissolution of caldera geologic material, which enters the lake as suspended solids in springs and with landslides, is a potential source of component mass. The kinetics of these processes in Crater Lake are unknown, but information is available which allows estimation of their relative importance to the mass balance of some components to be made.

U.S. Geological Survey ^{14}C measurements of organic material in two sediment cores indicated a rate of deposition of 9.5 cm/1000 yrs for core 79-1, obtained from the South basin at a depth of 450 m and 30 cm/1000 yrs for core 85-3 from the Wizard Island platform, about 250 m deep. The density of core 79-1 was 0.6 g/cm^3 and of 85-3, 0.25 g/cm^3 (Collier et al. 1991). The calculated mass flux over the entire lake for the two depths using these data and lake area versus depth data from Byrne (1965) are 880,000 kg/yr and 2,400,000 kg/yr, respectively. The increased flux with depth is explained as a resuspension of material from the sides of the lake (Dymond and Collier 1989). Using the weight percentages of calcium, magnesium, potassium and silica in the sediment cores (Dymond and Collier 1989), the annual component mass deposited was calculated (Table 5). The fraction of mass which must dissolve to account for 10% of the mass deficit calculated in the preliminary mass balance (Table 4) was then determined (Table 5) for comparison purposes.

The fraction dissolved for the cations is large enough to have caused a noticeable difference between the downcore sediment composition and the composition of the sediment trap. No such difference was evident (Collier et al. 1991) and therefore, the dissolution reaction appears to have little significance in the mass balance for these components. The much smaller dissolution fraction required to account for 10% of the silica deficit makes it possible that dissolution of sediments could have a noted affect on the mass of this component in the lake.

Hydrothermal Source Hypothesis. Several investigators have proposed a hydrothermal source under the lake floor as an explanation for observed anomalies in lake solute concentrations. Solute mass balance (Van DenBurgh 1968; Collier and Dymond 1988, 1989) and heat flux calculations (Williams and Von Herzen 1983; Collier

and Dymond 1988, 1989), chemical relationships (Thompson 1987; Collier and Dymond 1988, 1989) and lake sediment composition (Collier and Dymond 1988, 1989) have been used to support this hypothesis. Evaluation of the viability of such a source as an explanation of the mass deficits observed in the elemental components is presented below.

Replacing the unknown term with a hydrothermal term the mass transport relationship (6) becomes:

(14) $\dot{m}_{iP} + \dot{m}_{iR} + \dot{m}_{iH} = \dot{m}_{iS}$

where:

(15) $\dot{m}_{iH} = c_{iH}q_H$

and

(16) $\dot{m}_{iS} = c_{iL}q_S$

The seepage rate was determined, under the special conditions mentioned previously, assuming that it was the only significant flow term. The presence of a hydrothermal flow component changes this condition to:

(17) $-0.00347 = (q_H - q_S)/365A_L$

where the observed lake level decrease has been converted to m/day.

Substitution of equations (15), (16) and (17) into (14) and solving for the hydrothermal flow rate, q_H, gives:

(18) $q_H = (\dot{m}_{iP} + \dot{m}_{iR} - 67318c_{iL})/(c_{iL} - c_{iH})$

The components that exhibit mass deficits are common constituents of hydrothermal springs. Chemistry data from five Oregon Cascade hydrothermal springs (Table 6; Mariner, et al. 1974), chosen as possibly representative of the expected composition in a Crater Lake hydrothermal source, were used to estimate c_{iH} in equation

Table 6. Chemical composition of five Oregon Cascades hydrothermal springs (Mariner, et al., 1982) and hydrothermal fluids from bottom of Crater Lake (Collier et al., 1991).

	Hot Spring Concentration (mg/l)					
	Belknap	Cougar Reservoir	Breitenbush	Olene Gap	Austin	Crater Lake Hydrothermal Fluids*
Ca	210	225	100	40	35	38
Mg	0.2	0.1	1.3	0.2	0.1	53
K	15	6.3	31	7.2	7.1	17
Na	690	392	720	190	300	118
SO_4	170	260	140	400	140	85
Cl	1300	788	1300	59	430	71
B	6.4	5.1	4.1	1.0	2.6	--
Si	45	23	39	46	35	33
HCO_3	17	19	142	53	56	530

*Maximum value of fluids sampled at lake bottom (mixture of hydrothermal fluids and overlying water column)

(18). Also shown for comparison in Table 6 are the maximum concentrations of hydrothermal fluids sampled at the bottom of Crater Lake by Collier et al. (1991). The Crater Lake fluids are from pools and bacterial mats and, thus, are comprised of mixtures of hydrothermal fluids and overlying lake water.

Equation (18) was solved for q_H using the high and low concentration for each component, c_{iH}, among the five hot springs, at both the high and low quartile average basin spring values, resulting in a range of predicted hydrothermal flow rates for each component. A discrete value common to the predicted flow ranges for six of the nine components is q_H = 120 l/s (3.78 x 10^6 m^3/yr). Rearranging equation (18), and using q_H = 120 l/s, the composition of a hydrothermal source which accounts for the calculated mass deficits was predicted (Table 7). Comparison of the composition predicted using q_H = 120 l/s with the cited composition range shows that magnesium, silica, and bicarbonate require hydrothermal concentrations higher than those observed in cited

Table 7. Predicted composition of a hydrothermal source that accounts for Crater Lake mass deficits compared to cited hot springs.

	Chemical Composition (mg//l)		
	Cited Range	Predicted (q_H = 120 l/s)	
		(Q_1)	(Q_3)
Ca	35-225	114	88
Mg	0.1-1.3	46	38
K	6.3-31	27	24
Na	190-720	180	180
SO_4	140-400	175	105
Cl	59-1300	162	165
B	1-6.4	6.4	6.4
HCO_3	17-142	500	450
Si	23-45	90	65

Oregon Cascade springs, although within the measured compositions of Crater Lake hydrothermal fluids for magnesium and bicarbonate (Collier et al. 1991). The required bicarbonate concentration, 450 mg/l to 500 mg/l, is commonly found in Oregon hot springs outside the Cascades (Alvord 1,196 mg/l; Weberg 1,710 mg/l; Unnamed (near Harney Lake) 566 mg/l), the required silica concentration of 65 mg/l to 90 mg/l is not uncommon to Oregon hot springs (Mickey Springs 93 mg/l; Hot Lake 89 mg/l), and the required magnesium concentration, 38 mg/l to 46 mg/l, is reached in several hot springs of the Washington Cascades (Summit Creek 93 mg/l; Longmire 170 mg/l; Bubbling Mike 100 mg/l) (Mariner et al. 1982). Thus, it would be realistic for a Crater Lake hydrothermal source to exhibit the composition calculated with a flow rate of 120 l/s, which is 5.6% of the presumed seepage rate.

Based on both mass balance modeling and direct heat and salt flux calculations, Collier et al. (1991) estimate the hydrothermal flow into Crater Lake between 200-400 l/s.

Summary of Mass Balance. Current research at Crater Lake has produced extensive information enabling an accurate estimation of the hydrologic and chemical components of the lake system mass balance. An extreme imbalance in the major chemical components (Na, Ca, K, Mg, SO_4, Cl, Si and HCO_3) has been calculated. The mass lost in seepage of these constituents exceeds the mass input from recognized sources by up to 13 times (Cl).

Assumptions associated with the hydrology of the Crater Lake system limit the accuracy of the mass balance results. The errors introduced by these assumptions are conservative with respect to the magnitude of deficits predicted in the mass balance and therefore do not weaken the conclusion that an unknown (unquantified) source(s) of solutes is present in the lake. Seepage rate was considered equivalent to the decrease in lake level under conditions of no precipitation and no evaporation (lake surface frozen). Runoff was assumed negligible at the time these special conditions occurred (January and December). Any contribution by runoff causes an increase in the seepage rate estimate, and consequently an increase in the mass output from the lake. The calculated mass deficits are, therefore, underestimates. Based on annual spring flow and the estimated hydrograph, the addition of runoff may increase the seepage estimate by 5%. Estimation of the total spring flow assumed zero evaporation in the watershed. If watershed evaporation were considered, a lower spring discharge estimate would result, and, consequently, decreased mass input to the lake. The deficit values calculated assuming no watershed evaporation are therefore underestimates. Precipitation was assumed evenly distributed over land and water surfaces in the basin. An uneven distribution would result in changes in the estimates for spring flow and direct lake precipitation. Phillips argued that avalanching of snow from the crater walls reduces the

precipitation effective in producing runoff by approximately one-third. The calculated runoff (spring flow) assuming evenly distributed precipitation was probably overestimated, and the calculated mass deficits were therefore underestimated.

Lack of detailed spring flow information increased uncertainty in the calculated mass balance. Use of upper and lower quartiles of the mean annual spring concentrations was one way to bracket a representative concentration for use with annual spring discharge in mass input estimates. Further study of the relative flow rates among the springs throughout the annual hydrographic cycle will allow an improved estimate of the mass input to the lake from springs. Calculation of runoff from Redmond's relationship (equation 7) provided an estimate of the annual hydrograph, but more information on annual variations in lake evaporation is needed to use such calculations quantitatively.

The accuracy of the estimate of mass input to the lake from dry deposition was limited by the sampling method used. The collection device (a dry bucket) fails to simulate the physical transport processes that are present at the lake surface (NAPAP 1986) and the composition of the atmosphere at the location of the sampling device (the crater rim) is not representative of the local conditions on the lake. The contribution of dry deposition to the total mass input is insignificant for elemental components, but may be important to the nutrient mass totals (Table 6) .

The relative importance of component mass input to the lake from precipitation (wet plus dry deposition), springs, and unknown (unquantified) sources is summarized in Table 8. The values for chemical components were computed as the percentage of mass lost in seepage, which must equal the total inputs required to balance the system. The values for nutrient components, which yield net positive results in the mass balance

Table 8. Percentage of mass inputs to Crater Lake by precipitation, springs, and unknown sources.

	Precipitation	Spring*	Unknown
TKN	93.2	6.8	(80.1)
NH_3-N	96.9	3.1	(94.1)
NO_3-N	89.1	10.9	(94.5)
P	28.9	71.1	(10.1)
PO_4-P	33.3	66.7	(43.3)
Ca	1.8	32.0	66.2
Mg	1.1	23.9	75.0
K	4.9	24.4	70.7
Na	0.8	9.4	89.8
SO_4	4.1	42.6	53.3
Cl	4.7	2.2	93.1
B	0.0	0.0	100
Si	0.0	61.4	48.6
HCO_3	0.0	33.1	66.9

* High quartile C_R used.

Parenthetical values represent the % of mass lost in unknown processes and likely represent biological uptake and subsequent loss of cellular components to the sediments.

calculations, were determined from the percentage of the total component mass inputs. The largest source(s) of input for the major chemical components is the unknown, except in the case of silica. Precipitation contributes less than 5% of the mass lost in seepage for the major chemical components, but is a significant source of mass for the nutrient components. Over 90% of the nitrogen in the lake is derived from bulk deposition. The unknown nutrient output (shown in parentheses) represents the percentage of the total mass removed through biological processes. Use of the high quartile mean annual spring estimate in calculating the relative mass inputs in this study yielded conservative

estimates of the magnitude of the unknown source of the chemical components and of the percentage of nutrient mass from precipitation.

Estimation of the contribution of component mass by chemical dissolution of caldera wall material deposited on the lake bottom showed this process to be an unlikely major source of calcium, magnesium, and potassium but potentially a major source of dissolved silica.

A hydrothermal source hypothesis is shown to be compatible with the calculated mass flow rate of unquantified sources to Crater Lake. A hydrothermal source, similar in chemical composition to Cascade Range hot springs and with a discharge rate 5.6% of the estimated seepage flow rate, accounts for the mass imbalance estimated in lake components. Further, the calculated hydrothermal flow rate and chemical composition are in good agreement with results reported by Collier et al. (1991) which represent both direct measurements and calculated values.

Conclusions

Based on a chemical solute mass balance model, mass inputs of major solute chemical components (Na, Ca, K, Mg, SO_4, Cl, Si and HCO_3) from recognized sources (atmospheric deposition and caldera springs) do not equal the mass output in seepage from Crater Lake. One or more previously unquantified sources must be present in the lake or watershed system to account for the calculated input mass deficits which range from about 50 to 90% of mass output. A hydrothermal source with a flow rate of approximately 6% of the seepage rate and chemical composition similar to Cascade hydrothermal springs could account for the calculated input mass deficits for major solute chemical components. Atmospheric bulk deposition (wet plus dry) accounts for

about 90% of nitrogen and 30% of phosphorus input to Crater Lake. A net removal of nutrients from the lake occurs through internal biological processes, but accurate determination of the extent of these processes was beyond the scope of this study.

Glossary of Symbols

q = flow rate of water, volume/time
$\dot{m}$ = rate of mass transport, mass/time
c = concentration, mass/volume
M = mass (of solute component)
T = time
A_B = basin surface area ($=A_W$ + AL)
A_W = watershed surface area
A_L = lake surface area
Q_1 = lower quartile of a data set
Q_3 = upper quartile of a data set
LL = lake level
V_L = lake volume

Subscripts:

i = chemical component index
W = watershed
P = precipitation
R = spring runoff
S = seepage
H = hydrothermal
E = evaporation
C = chemical
B = biological
L = Lake
U = unknown (unquantified)

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Clarity of Crater Lake Measured with a Secchi Disk

Gary L. Larson and Michael Hurley

The first recorded measurement of the clarity of Crater Lake was made on a hazy August day in 1896 by Diller (1897) using a white 24.4-cm-diameter dinner plate (Table 1). The first Secchi disk readings were recorded in August and September of 1913 with a 12-cm Secchi disk (Kemmerer et al 1924). Additional readings using 20-cm Secchi disks were made at irregular intervals in the 1930's (Hasler 1938, Farner 1939), 1954 (Fairbanks and Rowley 1954), 1960 (H. Nelson, U.S. Geological Survey, pers. comm., 1992), and the late 1960's (D. Larson 1972). Annual Secchi disk clarity measurements were recorded between 1978 and 1981 (D. Larson 1984) and 1982 and 1991 (G. Larson 1991). The deepest Secchi disk readings recorded in Crater Lake prior to the present study were in the 39 - 40 m range in July and August (Hasler 1938, Larson 1972).

The objectives of this study were to (1) evaluate the Secchi disk readings from Crater Lake relative to seasonal and annual changes between 1978 and 1991, and (2) assess if the clarity of the lake had changed by comparing the Secchi disk readings collected from 1978 to 1991 with readings collected prior to 1978.

Methods

A 20-cm black and white disk was used to determine Secchi disk clarity at Station 13 from 1982 through 1991. The readings were determined as the mean of descending and ascending values. Three readings were recorded on most occasions, usually by two or more observers. All reported measurements were made between 10:00 and 14:00 hours under clear or high-haze sky conditions and with the lake surface exhibiting calm to rippled conditions. Measurements recorded prior to this study were made at a variety

of lake locations, including many locations in the lake that were poorly documented. With the exception of those measurements recorded in 1954, the late 1960's, and between 1978 and 1981, observers did not record weather and lake surface conditions. Data collected between the late 1960's and in 1978 and 1981 were provided by Douglas Larson.

Results

The clarity of Crater Lake exhibited a considerable amount of variation between 1978 - 1991 (Table 1). For June, July, August, and September, monthly Secchi disk readings generally increased in depth between 1978 and 1988 and then decreased in depth between 1989 and 1991 (Fig. 1). The shallowest reading (21.9 m) was recorded in August of 1982, and the deepest reading (39.2 m) was recorded in June of 1988 (Table 1).

Although the data were limited for certain seasons between 1978 and 1991, Secchi disk clarity appeared to be high in January, low in March and April, increasing in May, high in June, decreasing in July, low in August, and increasing in fall (Fig. 2). For June through September, however, the seasonal pattern of Secchi disk clarity was not consistent among years, which made it difficult to predict patterns of change from year to year (Fig. 3). Storm events may have played an important role in the yearly patterns. For example, Secchi disk readings dropped from 37.2 m to 28.2 m between early and late July 1985, and weather conditions were stormy during the time period between these readings.

The deepest Secchi disk readings recorded during the present study occurred near mid-day, under clear skies, and with a flat-calm lake surface. Effects of less-than-optimal

Table 1. Mean, minimum and maximum Crater Lake Secchi disk readings per month from 1896 to 1991.

Year	Month	N*	Mean Secchi Reading (m) (S.D.)	Minimum Secchi Reading (m)	Maximum Secchi Reading (m)
1896	Aug	1	30.0 (-)	-	-
1913	Aug	1	25.0 (-)	-	-
	Sept	1	27.0 (-)	-	-
1937	Aug	3	38.3 (2.1)	36.0	40.0
1938	Aug ?	2	28.5 (2.1)	27.0	30.0
1939	Aug	3	31.3 (1.5)	30.0	33.0
1954	Aug	1	33.5 (-)	-	-
1960	July	2	29.5 (5.0)	26.0	33.0
1968	June	1	31.0 (-)	-	-
	July	1	36.0 (-)	-	-
1969	July	1	39.0 (-)	-	-
	Aug	2	35.5 (5.0)	32.0	39.0
1978	July	2	29.0 (1.4)	28.0	30.0
	Aug	4	29.3 (0.5)	29.0	30.0
1979	June	1	28.3 (-)	-	-
	July	1	31.1 (-)	-	-
	Aug	2	26.0 (4.3)	22.9	29.0
1980	July	3	34.3 (3.6)	30.2	36.5
	Aug	2	29.9 (2.8)	27.9	31.9
1981	July	3	29.2 (0.5)	28.7	29.7
	Aug	2	30.1 (1.4)	29.1	31.1
1982	July	6	28.7 (0.4)	28.4	29.3
	Aug	6	24.3 (1.7)	21.9	26.7
	Sept	2	25.9 (0.1)	25.8	26.0
1983	June	1	29.0 (-)	-	-
	July	7	30.0 (1.2)	27.5	31.5
	Aug	2	29.3 (1.8)	28.0	30.5
	Sept	1	25.2 (-)	-	-
1984	July	2	31.1 (1.2)	30.3	32.0
	Aug	2	29.8 (1.8)	28.5	31.0
	Sept	2	31.3 (0.4)	31.0	31.5
1985	July	2	32.7 (6.4)	28.2	37.2
	Aug	1	27.1 (-)	-	-
	Sept	1	28.3 (-)	-	-

Table 1. continued

Year	Month	N*	Mean Secchi Reading (m) (S.D.)	Minimum Secchi Reading (m)	Maximum Secchi Reading (m)
1986	March	1	26.2 (-)	-	-
	May	2	30.0 (0.7)	29.5	30.5
	June	1	33.2 (-)	-	-
	July	4	32.0 (1.3)	30.9	33.4
	Aug	5	28.1 (2.2)	25.9	31.5
	Sept	2	29.8 (2.1)	28.4	31.3
1987	April	1	28.6 (-)	-	-
	June	3	36.4 (0.2)	36.2	36.5
	July	2	33.9 (3.3)	31.5	36.2
	Aug	3	31.6 (2.4)	30.0	33.7
	Sept	2	32.8 (0.9)	32.2	32.5
	Oct	1	35.8 (-)	-	-
1988	June	3	37.7 (1.6)	36.1	39.2
	July	2	34.4 (0.4)	34.1	34.6
	Aug	2	31.1 (0.6)	30.7	31.5
	Sept	2	33.4 (1.1)	32.6	34.2
1989	April	2	26.9 (0.1)	26.8	27.0
	May	1	32.3 (-)	-	-
	June	1	31.8 (-)	-	-
	July	4	31.4 (2.2)	29.2	34.4
	Aug	1	27.4 (-)	-	-
1990	Jan	1	34.8 (-)	-	-
	June	1	29.5 (-)	-	-
	July	2	29.4 (0.9)	28.8	30.1
	Aug	3	27.5 (1.8)	25.5	28.9
	Sept	1	27.6 (-)	-	-
1991	June	1	35.8 (-)	-	-
	July	2	29.9 (3.3)	27.6	32.2
	Aug	3	22.9 (1.9)	21.3	25.0
	Sept	3	26.4 (3.5)	22.8	29.7

*N refers to the number of days readings were recorded per month.

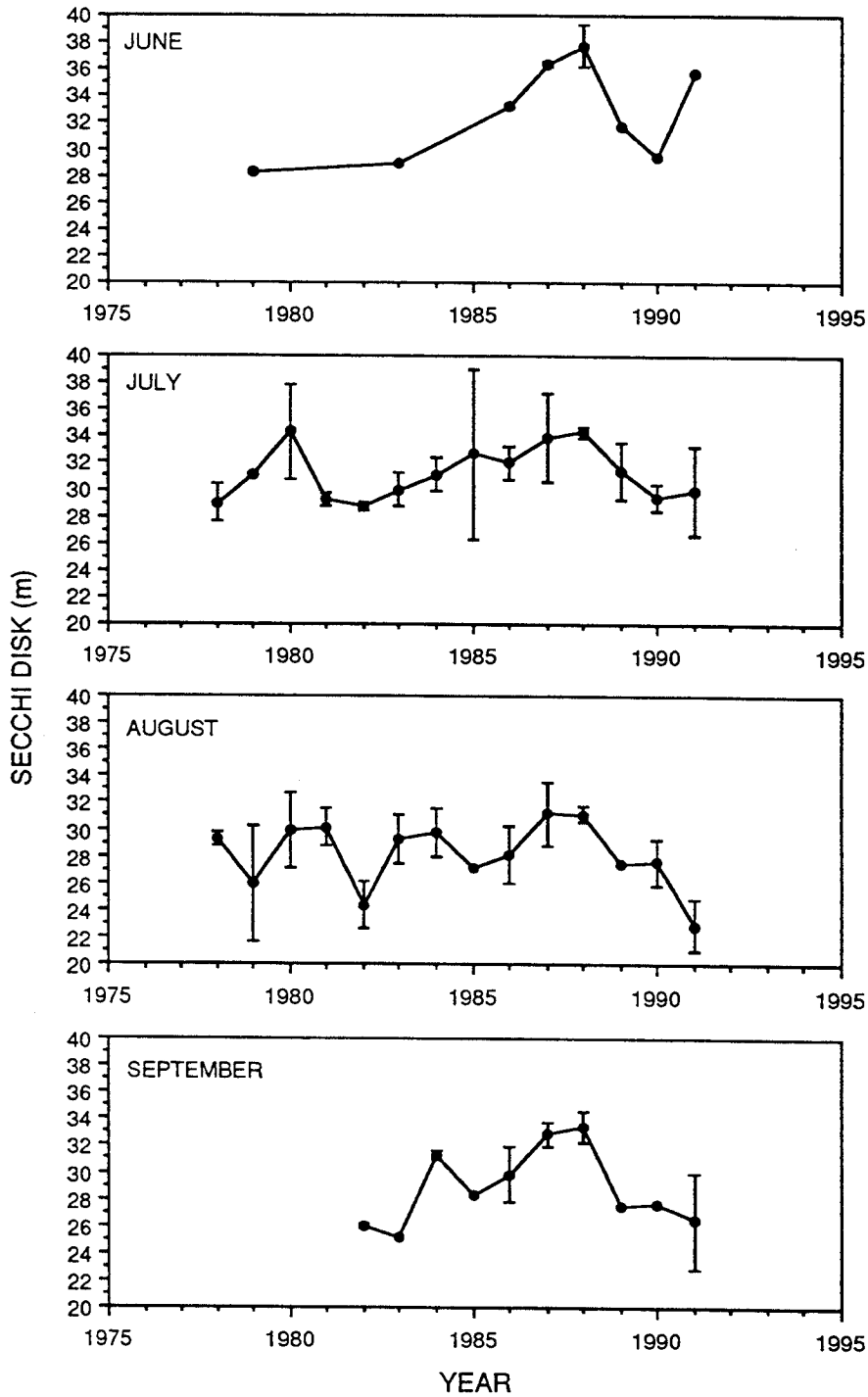


Figure 1. Mean Crater Lake Secchi disk readings (+/-1 standard deviation) for June, July, August, and September from 1978 to 1991

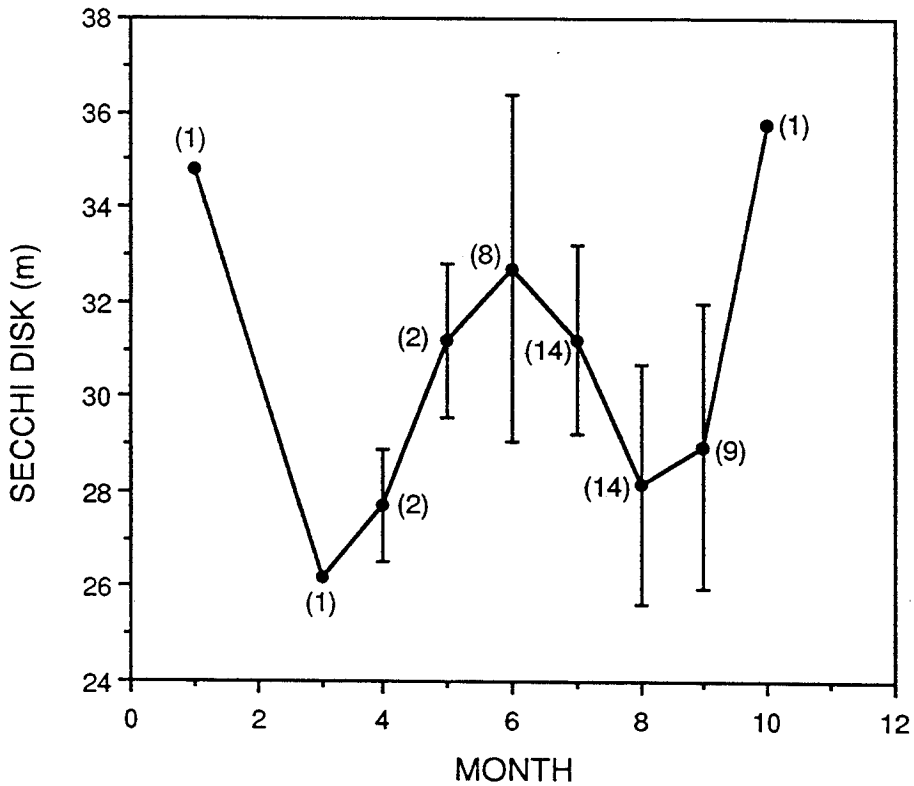


Figure 2. Mean Crater Lake Secchi disk readings (+/-1 standard deviation) per month from 1978 to 1991. Sample sizes are indicated in the parentheses.

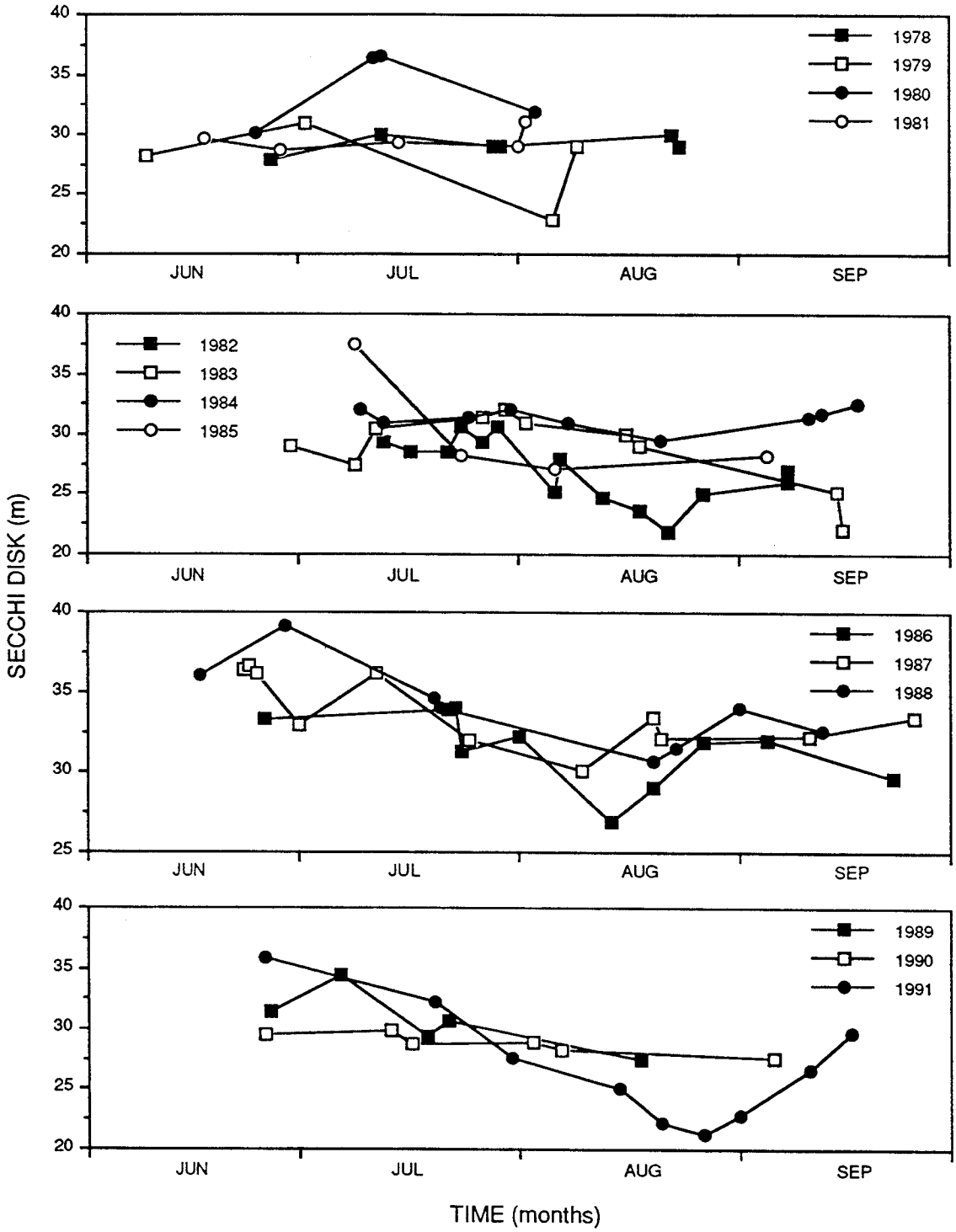


Figure 3. Crater Lake Secchi disk readings in June, July, August, and September from 1978 to 1991.

viewing conditions on Secchi disk readings were difficult to assess, yet some pertinent observations were recorded. The lake surface was flat calm when the 39.2 m reading was made in June 1988. Small drops of water fell from the research boat onto the lake surface during this observation and the reading briefly decreased to 37 m. Similarly, a single drop of water on the lake surface caused a decrease in Secchi disk clarity from 35.6 m to 34 m in June 1991. Wind caused the lake surface to ripple on many occasions, which resulted in a loss of clarity. For example, the lake surface was flat calm on August 19, 1986, and the Secchi disk reading was 27.8 m. The reading was 25.8 m only one day later at the same location but with the lake covered by 2.5-cm-high ripples. Secchi disk readings were even more reduced under stormy conditions. In 1968 the Secchi disk reading was 36 m under calm surface conditions in July, whereas the reading was only 18 m in August under stormy conditions (D. Larson 1983).

Secchi disk readings recorded between 1978 and 1991 were very similar to readings recorded between 1896 (Diller's dinner plate) and 1969 (Fig. 4; Table 2). Since 1978, only the deep readings recorded by Hasler (1938) in August 1937 and Larson (1972) in July and August 1969 were deeper than other August readings. However, some of the readings recorded since 1978 in June and July were similar to Hasler's and Larson's readings.

Variation in the abilities of observers to see the Secchi disk affected the depth readings. Three experienced observers collected comparable data in 1986. One observer tended to record shallower readings (McCrea) and another tended to record deeper readings (Brady) than the third observer (Table 3). Differences between deep and shallow readings averaged 1.1 m. The greatest difference was over 2 m on 22 July.

With the exceptions of Secchi disk and phytoplankton data collected in late July

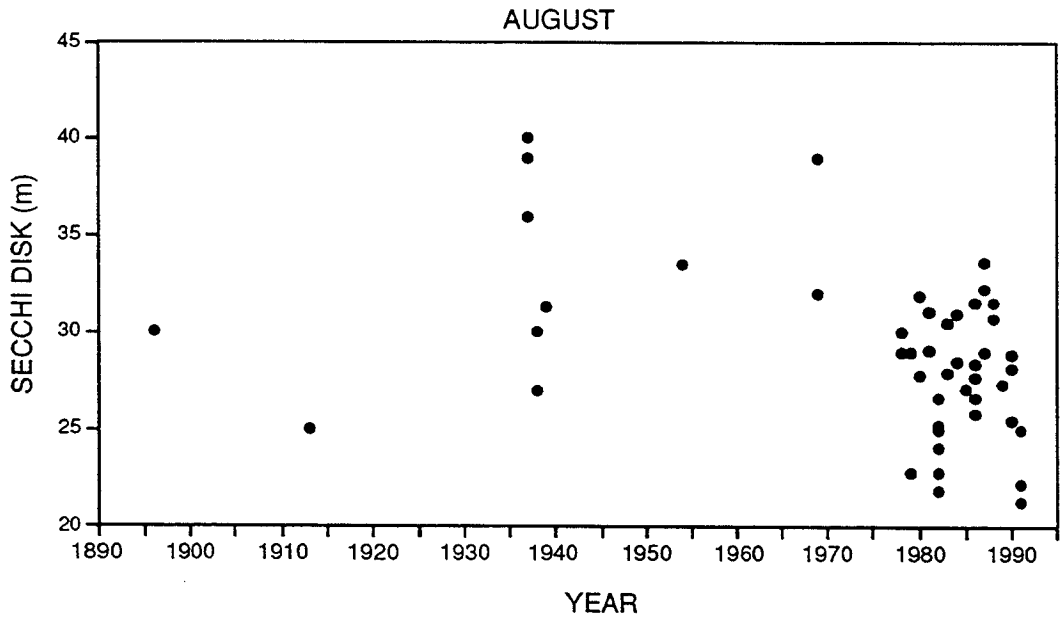


Figure 4. Mean daily Crater Lake Secchi disk reading in August from 1896 to 1991.

Table 2. Comparative mean Crater Lake Secchi disk readings taken in July and August between 1896-1969 and 1978-91.

Period of Observation	Months	N	Secchi Disk Clarity (m)	Standard Deviation
1896-1969	July and August	10	32.7	4.6
	July	3	34.8	4.7
	August	7	31.7	4.5
1978-1991	July and August	28	29.7	2.7
	July	14	31.2	2.0
	August	14	28.2	2.5

Table 3. Comparable mean Crater Lake Secchi disk readings in July, August and September of 1986 by Mark Buktenica, Steve Brady and Jerry McCrea.

Date		Secchi Depth (m) by Observer		
		Buktenica	Brady	McCrea
July	21	33.22	33.67	-
	22	32.97	33.69	31.35
	23	31.13	-	30.68
	30	28.63	30.33	-
	31	30.66	31.33	-
Aug	4	28.97	28.58	27.67
	19	-	28.40	27.26
	20	26.23	-	25.52
	26	31.21	31.83	-
Sept	4	30.60	32.10	-

and August of 1985 and August and September of 1986, there appeared to be a significant negative relationship between Secchi disk readings and phytoplankton cell densities between 1985 and 1990 for the months of June, July, August, and September ($r^2 = 0.712$, $p < 0.05$) (Fig. 5). The relationship between the two variables was unclear in late July and August of 1985 and August and September of 1986. In addition, no significant relationship was found between chlorophyll and Secchi disk clarity in Crater Lake (Larson and Hurley 1988).

Discussion

The depth at which a Secchi disk disappears is a function of the contrast between the light reflected from the Secchi disk and the scattering and absorption of incident light by water molecules, dissolved substances, and particles in the water column (Wetzel 1975). Particles are key to altering this optical contrast in lakes with low concentrations of dissolved and colored substances, such as Crater Lake. A hypothetical relationship between Secchi disk clarity and particle density is hyperbolic (Fig. 6). Thus, a small change in particle density in very clear lakes will correspond to large increases or decreases in Secchi disk clarity. However, the effects of different kinds, sizes, and shapes of particles on the optical properties of water in clear lakes are important to Secchi disk clarity (Edmondson 1956, Halicki 1958, Jewson 1977, Gordon and Wouters 1978, and Bertoni and Callieri 1981). For this reason, the hyperbolic relationship between particle density and Secchi disk clarity is actually a family of curves depending on the optical properties of the particle communities.

Dynamics of Secchi disk clarity in Crater Lake are undoubtedly related to changes in abiotic and biological particles. The apparent relationship between

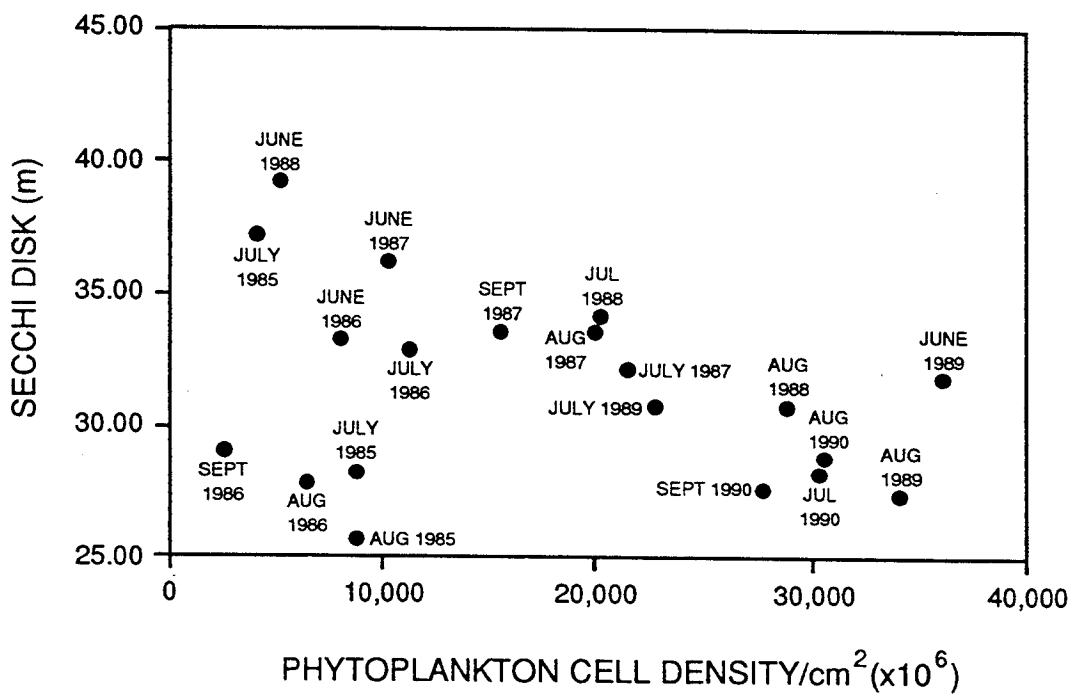


Figure 5. Relationship between Secchi disk readings and phytoplankton cell densities integrated to the Secchi depth in Crater Lake from 1985 to 1990. Two July 1985 data points are shown. The point on the far left of the graph represents a late June phytoplankton sample and an early July Secchi disk reading.

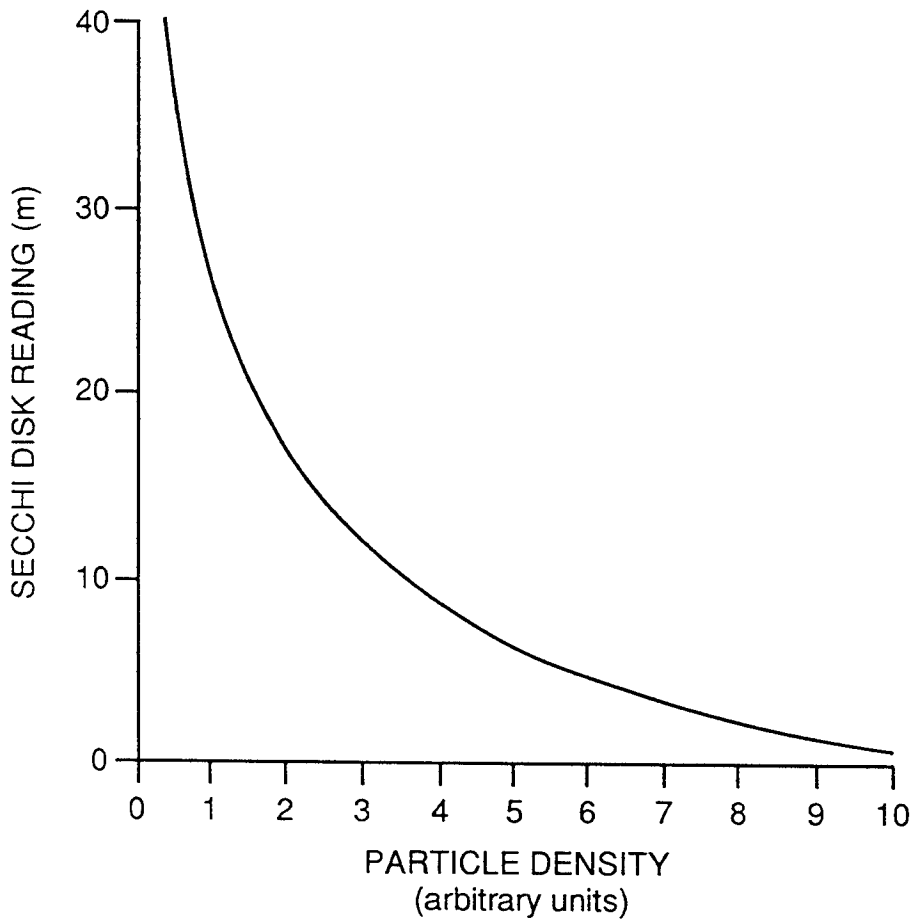


Figure 6. Hypothetical relationship between Secchi disk readings and densities of particles with constant optical characteristics (after Larson and Hurley 1988).

phytoplankton cell density and Secchi disk clarity between 1985 and 1990 (Fig. 5) suggests that algal cell density can be important to the clarity of Crater Lake. The role of abiotic particles to the apparent relationship is unknown. Some of the data from 1985 and 1986, however, do not support the relationship between algal density and Secchi disk clarity (Fig. 5). As mentioned earlier, the Secchi disk reading dropped from 37.2 m to 28.2 m after a storm in July of 1985. Although no algal density data were available from early July, phytoplankton were sampled in late June. If it is assumed that the cell density was similar in late June and early July, the data point that represents the Secchi disk reading lies close to the area projected from the line through the June and July 1986 data and the 1987 - 90 data. Thus it appears that the change in clarity in July was due mostly to non-algal particles, possibly abiotic ones. Data collected between 1985 and 1990 illustrates some of the roles and interactions of abiotic particles and biological particles relative to the Secchi disk clarity of Crater Lake. Based on the hyperbolic relationships previously mentioned between Secchi disk clarity and particle densities and types, the July and August 1985 and August and September 1986 data are probably located on different hyperbolic curves than the rest of the data collected between 1985 and 1990 (Fig. 5).

Seasonal changes in Secchi disk clarity of Crater Lake showed some general patterns, but it was difficult to predict the patterns from year to year. Nonetheless, clarity appears to be low in late winter and early spring during the avalanche and snow melt runoff periods. Clarity increases as snow melt runoff subsides and reaches its maximum in June and early July. As the lake surface warms, clarity declines and is lowest in August. This is the period when the lake is thermally stratified and the epilimnion probably serves as a collector of colloidal particles from the caldera walls and

the atmosphere, and as the primary habitat for certain phytoplankton taxa. Clarity increases in the fall, probably due to deepening of the epilimnion because of fall winds, thus diluting the colloidal material and reducing the densities of the phytoplankton (see Transmissometer section). Fall storms, however, could be associated with an increase in the density of abiotic particles, which may explain the reduced Secchi disk readings in the fall of some years (Fig. 3).

The Secchi disk data base assembled since 1978 illustrates the magnitude of the annual and seasonal dynamics and variability of the clarity of Crater Lake. The deepest August Secchi disk readings taken in 1937 and 1969 are about 25% deeper than those taken in August from 1978 through 1991. However, given the sensitivity of the Secchi disk in clear lakes relative to small changes in particle densities and lake surface conditions, it seems likely that the conditions required to obtain 39 and 40 m readings are rare rather than typical of Crater Lake. A. Hasler (University of Wisconsin, pers. comm., 1985) suggested that a lack of rain during the 1937 field season was responsible for reduced erosion and thus the unusual clarity of the lake in 1937. Farner (unpublished annual report, Crater Lake National Park) commented that the low readings in 1938 were due, in his view, to mud slides. Similar qualitative observations of mud flows and turbidity from caldera streams were made during the period of 1982 through 1991 which appeared to correspond to periods of reduced Secchi disk depth. Thus it seems reasonable to conclude that the Secchi disk clarity of Crater Lake is dynamic relative to both short-term and long-term changes. Although the environmental conditions and time of day were not recorded for readings prior to 1968, with the exception of 1954, the data collected between 1896 and 1969 appear to be fairly consistent with most of the recent observations. These results suggest that the "old" data

may be fairly representative of the Secchi disk clarity during those periods of time.

Although the analysis of Secchi disk records collected between 1896 and 1969 and 1978 and 1991 suggests that the data sets are fairly comparable, this result does not imply that Crater Lake has not changed through the years. Changes in nutrient input from the atmosphere (see Bulk Atmospheric Deposition section) and potential local sources of nutrients (see Springs section) may have some long-term roles to play in the productivity of Crater Lake. The extent that Crater Lake may have changed is not known because it is difficult to assess the natural variability of the Secchi disk readings relative to any changes caused by anthropogenic activities. The absence of Secchi disk readings in the range of 39-40 m in August between 1978 and 1991 may be a sign of change, but if the reading in August 1954 is real, then the problem of separating the natural Secchi disk dynamics from long-term changes remains unresolved. A much longer data set will be needed to document such changes in Crater Lake.

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Photometer

Gary L. Larson and Michael Hurley

Submarine photometers have been used for many years by limnologists to assess how the spectral composition and intensity of incident solar radiation changes as a function of lake depth (Hutchinson 1957). The first submarine photometer study at Crater Lake was conducted in June of 1936 using a Weston Cell photometer (Brode 1938). Additional photometer measurements were made in July of 1940 using a Weston Cell photometer (Utterback et. al 1942) and in the late 1960's using a Kahl photometer (model 268-WA310) (Larson 1972). Photometric measurements were resumed in 1980 using a Kahl photometer (model 280-WA350) (Dahm et al. 1990) and continued during this study. The instruments were not inter-calibrated for purposes of data comparison.

The objectives of this study were to: (1) use current photometric instrumentation to measure the spectral distribution of clear, blue, green, and red incident solar radiation as a function of depth in Crater Lake; (2) examine seasonal and annual changes in the depth of 1% of the incident light for each color based on measurements made in this study and comparable measurements collected from 1980 to 1984; and (3) assess the relationship between the depth of penetration of 1% of total surface incident light (425-655 nm) and measurements of lake clarity made with a Secchi disk.

Methods

Submarine photometer data were collected from 1985 to 1989 at Station 13 in Crater Lake (see Study Area and Facilities section) using a Kahlsico instrument (model 268Wb365/TD) with clear, blue, red, and green filters. The instrument was deployed near mid-day and a deck cell was used to calibrate variations in incident solar radiation

during each deployment. Sampling dates and types of photometer data collected, including observations prior to this study, are presented in Table 1. The initial reading with the submarine cell, which was 1 cm below the lake surface, was considered to register 100% of incident radiation. Readings from the deck cell and submarine instrument were compared on the deck of the research boat before and after each deployment.

The Kahlsico instrument was deployed to a maximum depth of 150 m. Spectral measuring ranges for the clear, blue, green, and red filters were 425-655 nm, 400-500 nm, and 500-570 nm, and 580-670 nm, respectively. Measurements of water clarity were taken with a Secchi disk when the photometer was deployed in as many instances as possible. In some cases, Secchi disk observations were not possible because lake surface conditions were too poor for use of the disk. In those instances, Secchi disk readings taken a few days before or after deployment of the photometer were used for comparison with the photometer data.

Results and Discussion

The extreme clarity of Crater Lake was evident from the depths to which each color of light penetrated into the lake. Two examples for periods with deep and shallow Secchi disk readings are shown in Figures 1 and 2. In each example, blue light penetrated to the deepest depths, followed by green, white, and red light. The depth of penetration of 1% of the incident blue light exceeded 80 m in each example.

Seasonal changes in the depth of penetration of 1% of the incident radiation for each filter for the period 1980-1989 are shown in Figures 3 and 4. Although limited data were available for some months, in general, depths were shallow in April, increased in

Table 1. Photometer sampling dates between 1936 and 1989 at Crater Lake. The available data for each filter on each sampling date are indicated by "X".

Year	Month	Day	Clear Filter	Blue Filter	Green Filter	Red Filter
1936	June	22	X			
1940	July	18?	X			
1968	June	15	X	X	X	
1969	July	16	X	X	X	X
	August	5	X	X	X	X
1980	July	10	X	X	X	X
		23	X	X	X	X
	August	12	X	X	X	X
		27	X	X	X	X
1981	July	14	X	X		X
	August	10	X	X	X	X
1982	July	16	X	X	X	X
		29	X	X	X	X
1983	July	15	X	X	X	X
		28	X	X	X	X
		29	X	X	X	X
1984	July	30	X	X	X	X
1985	July	16	X	X	X	X
	August	6	X	X	X	X
	September	16				X
1986	May	28		X	X	
	July	22			X	
		23	X	X	X	X
		31	X	X	X	X
	August	13	X	X	X	X
		20	X	X	X	X
1987	April	13	X	X	X	X
	June	22	X	X	X	X
	July	23		X	X	X
	August	18		X	X	X
	September	15	X	X	X	X
1988	June	30	X	X	X	X
	July	19	X	X	X	X
		20	X	X	X	X
	August	16	X	X	X	X
	September	1	X	X	X	X
		13	X	X	X	X
	October	25	X	X	X	X
1989	April	6	X	X	X	X
	May	12	X	X	X	X
	June	26	X	X	X	X
	July	6	X	X	X	X
		18	X	X	X	X
	August	17	X	X	X	X
	September	12	X	X	X	X

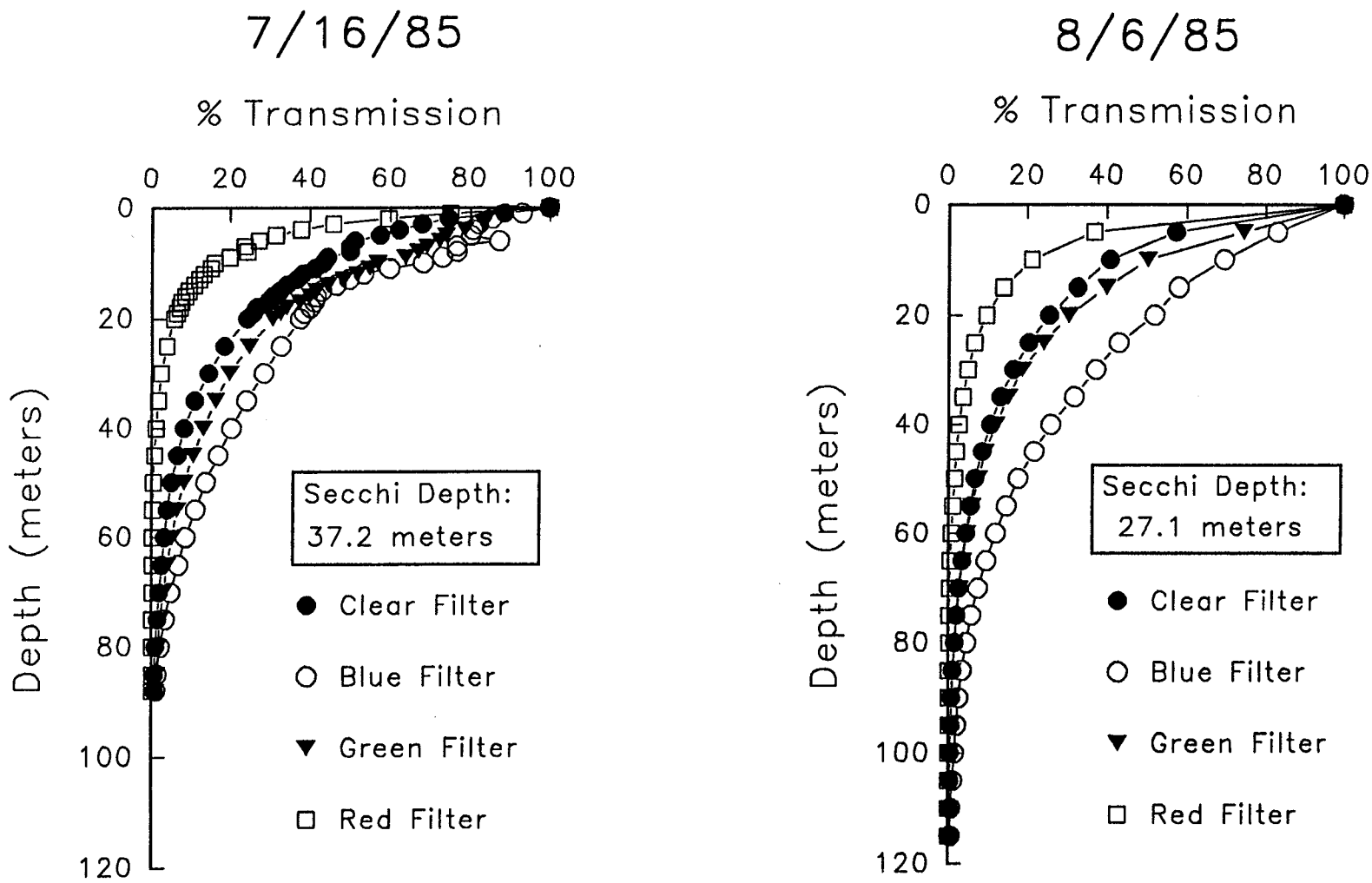


Figure 1. The percent transmission of incident solar radiation as a function of lake depth in Crater Lake for the clear, blue, green and red filters in July and August 1985.

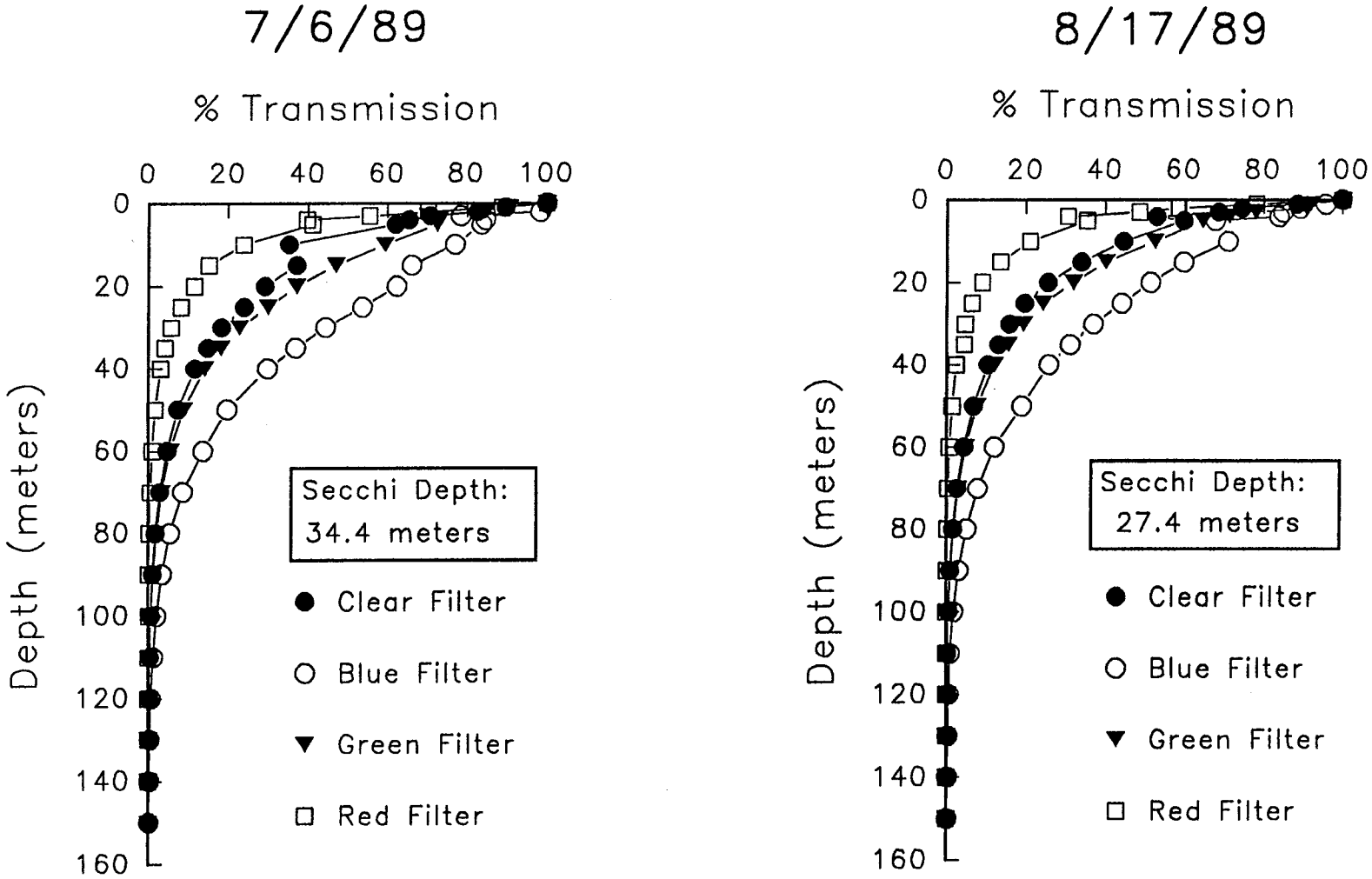


Figure 2. The percent transmission of incident solar radiation as a function of lake depth in Crater Lake for the clear, blue, green and red filters in July and August 1989.

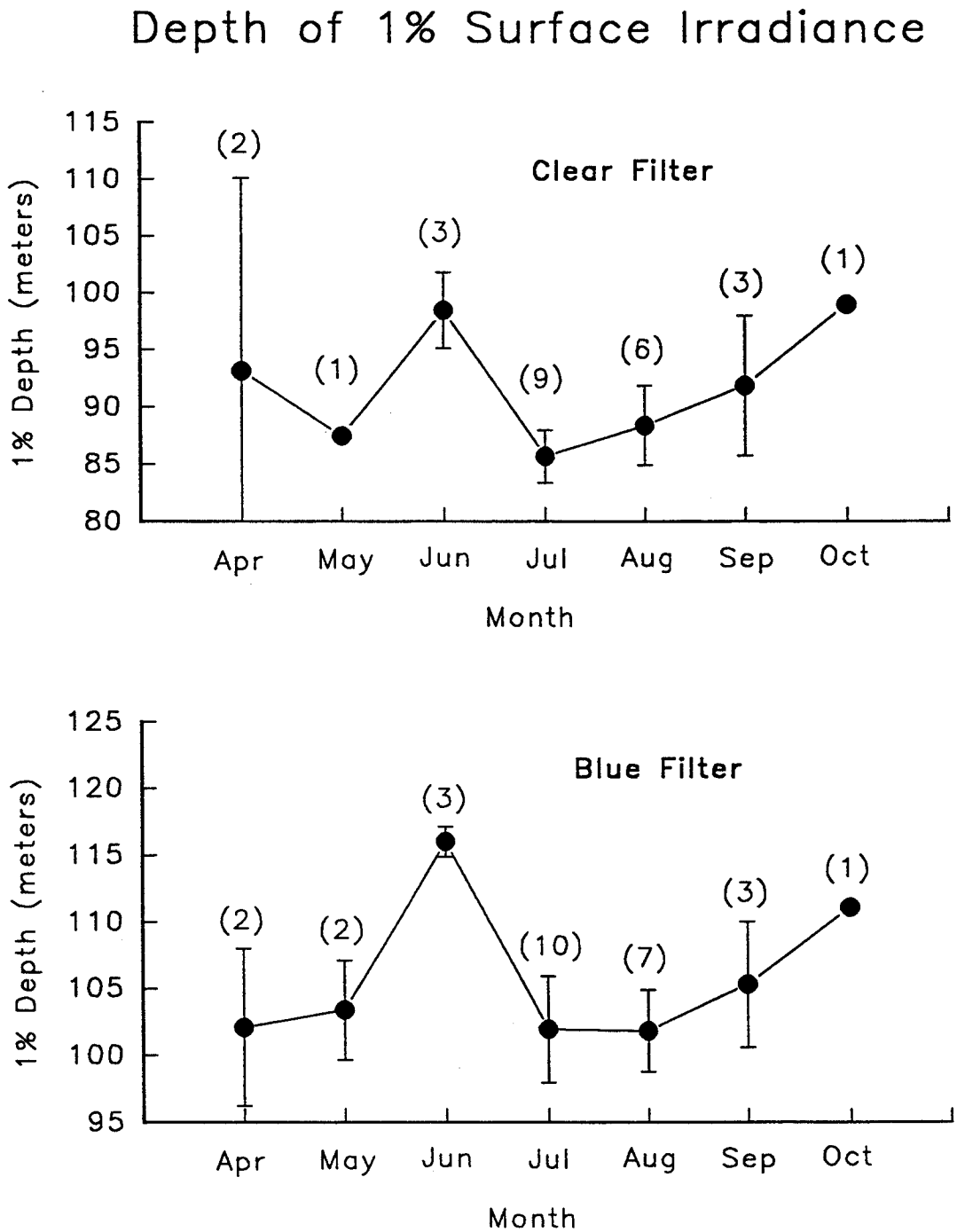


Figure 3. Monthly mean depths of 1 percent transmission of incident solar radiation for the clear and blue filters in Crater Lake from 1980 to 1989. Sample sizes are shown in parentheses.

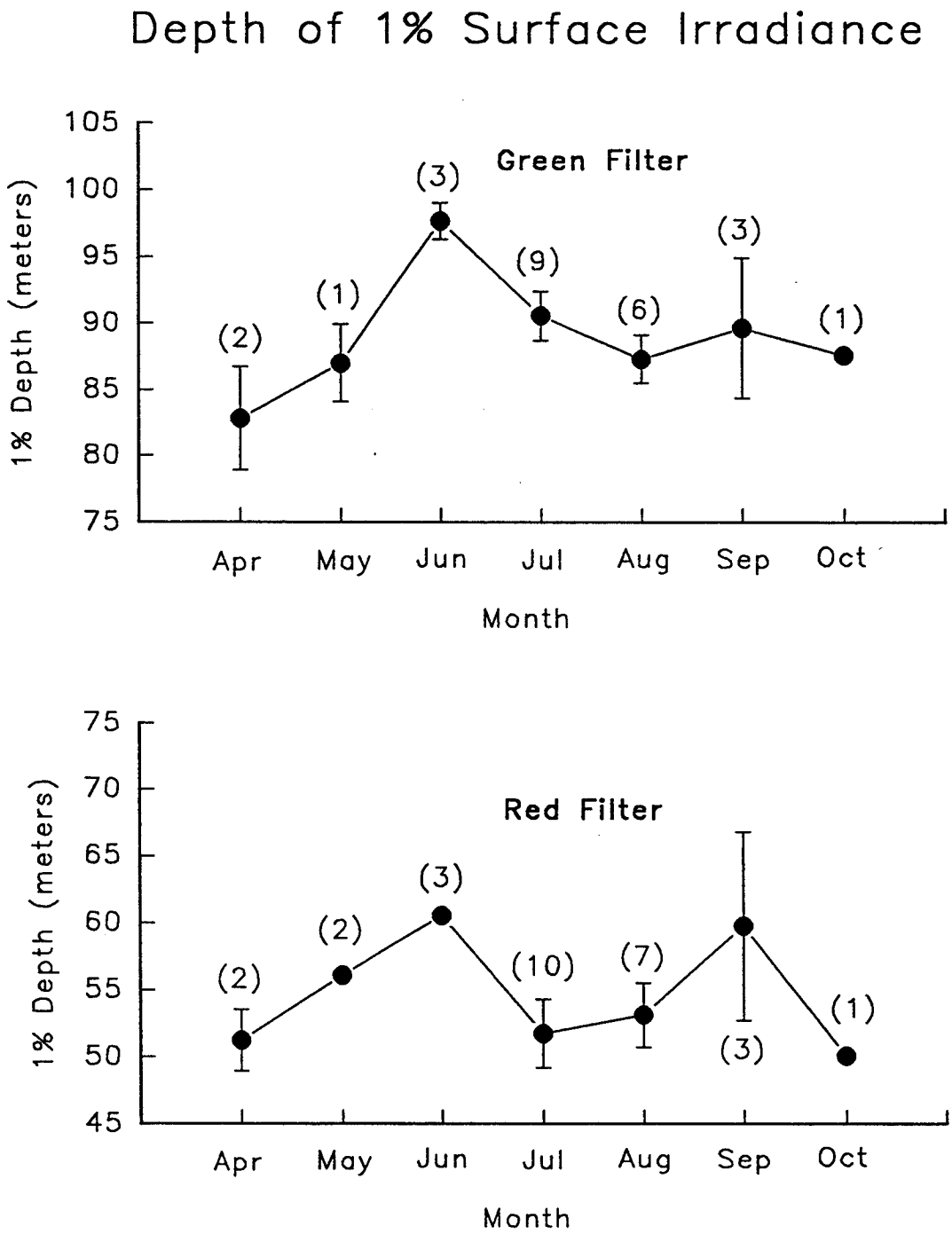


Figure 4. Monthly mean depths of 1 percent transmission of incident solar radiation for the green and red filters in Crater Lake between 1980 and 1989. Sample sizes are shown in parenthesis.

May and June to a maximum in June, decreased in July and August, and increased in the fall. The relatively shallow depths in spring occurred during the period of avalanche and snow-melt runoff. The clear-water period of 1% light levels period in June corresponded to reduced snow-melt runoff and initial heating of the lake surface, which reduced the amount of mixing in the upper portion of the water column. The shallow depths of 1% light levels in July and August occurred when the lake was thermally stratified. When the lake was stratified, the shallow epilimnion probably served as a collector of phytoplankton and particles from atmospheric deposition, landslides, and littoral erosion due to wave action during summer storms. The increased depth of transmission of 1% of the incident light in the fall was due to dilution of the epilimnetic particles as the epilimnion increased in depth during fall storms (see Transmissometer section).

These trends appear to be within the range of values recorded in the past, with the exception of data collected for the red filter in 1969. Perhaps the wavelength range of the filter used in 1969 was narrower than the ones used between 1980 and 1989. The red filter used since 1985 has a relatively wide range in wave length, extending into the near-yellow range (Clarke 1939). Perhaps this explains the greater depth measurements for penetration of 1% of incident red light during recent studies compared to earlier studies.

For the period of 1980 through 1989, the mean depth of 1% penetration of incident light (425-655 nm) was 85.7 m in July and 88.4 m in August. The 1% depth in July ranged between 82.3 - 84.8 m between 1980 and 1985, and then ranged between 90.3 m and 99.5 m between 1986 and 1989 (Fig. 5). For August, the 1% depth ranged between 74.7 m and 89.0 m from 1980 through 1985 and then ranged between 86.1 m and 103.4 m from 1986 through 1989 (Fig. 6). Brode (1938) estimated the 1% depth at

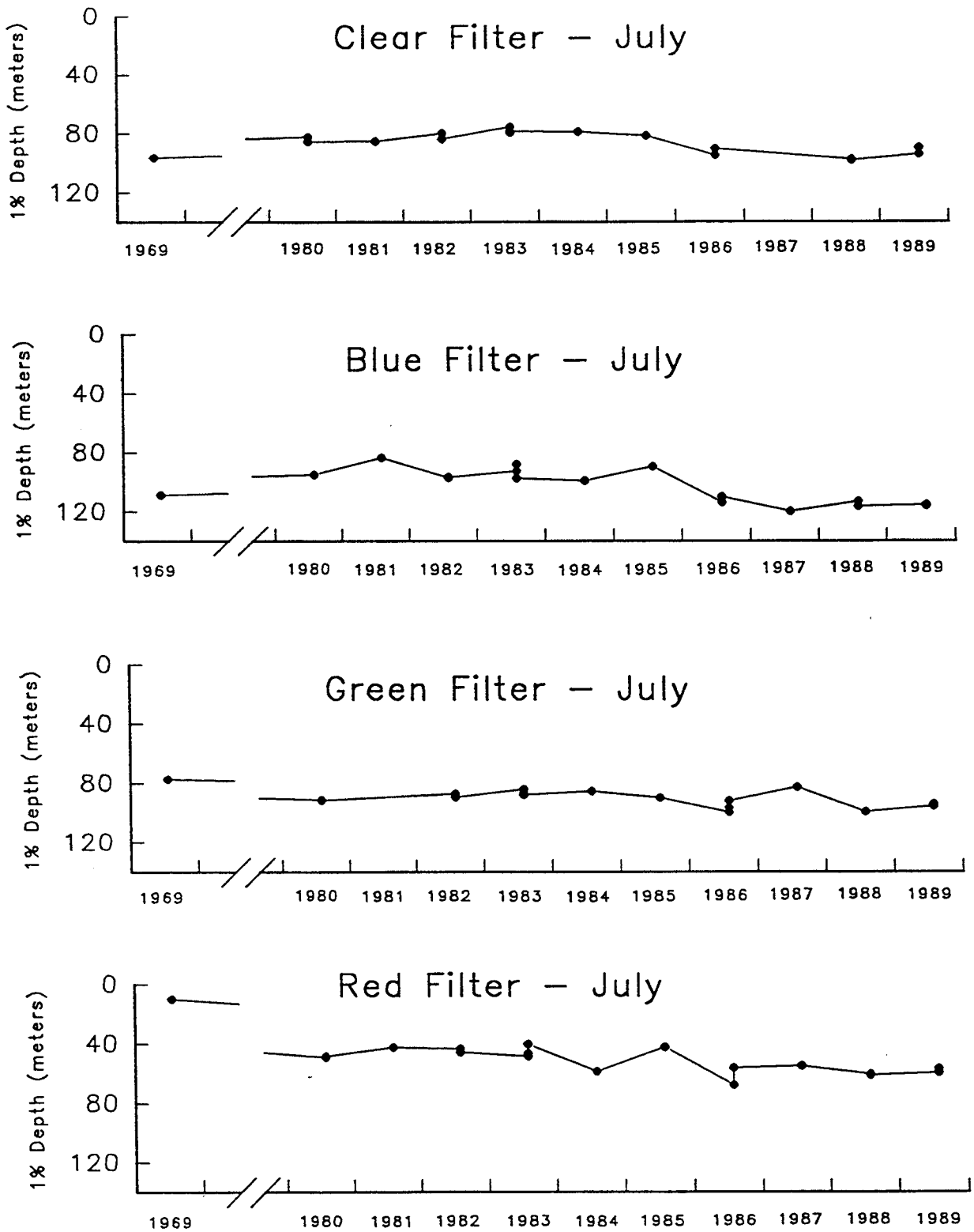


Figure 5. The depths of 1 percent transmission of incident solar radiation for clear, blue, green, and red filters in Crater Lake in July of 1969 and between 1980 and 1989.

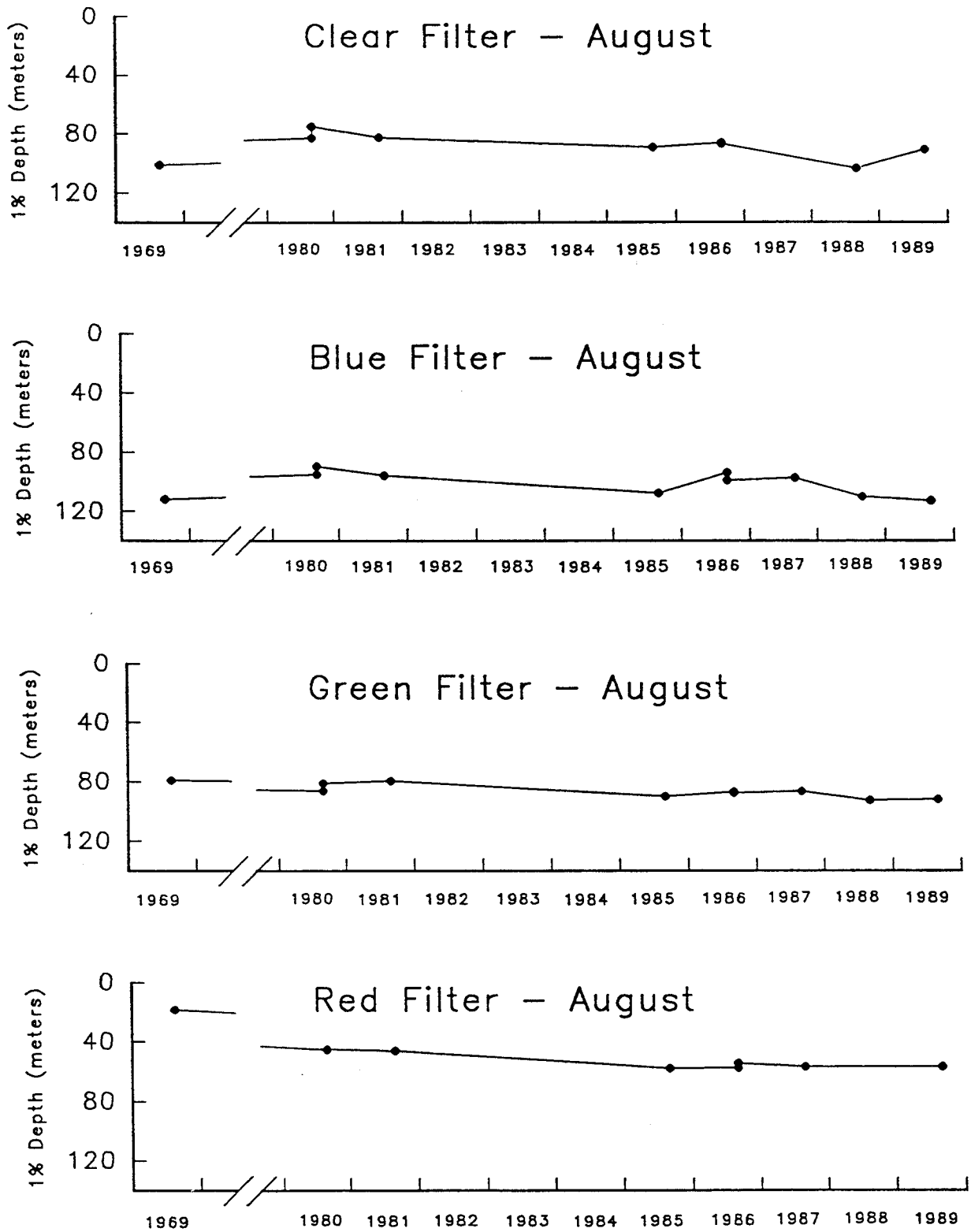


Figure 6. The depths of 1 percent transmission of incident solar radiation for clear, blue, green, and red filters in August of 1969 and between 1980 and 1989.

between 100 m and 110 m in June 1936. The 1% depth in July 1940 was between 80 m and 90 m (Utterback et al 1942). In 1968, the 1% depth in June was 90 m, whereas the 1% depth in August of 1969 was 100 m (Figs. 5 and 6, Larson 1972). Smith et al (1973) determined that the 1% depth in July, 1969 was about 77 m using a Scripps spectroradiometer, whereas, Larson (1972) estimated the depths to be 90 m using a photometer.

The mean depth of 1% penetration of blue light between 1980 and 1989 was 102.0 m in July and 101.8 in August. From 1980 and 1985, the depth of 1% blue light ranged between 83.5 m and 99.3 m in July and 89.6 m to 107.5 m in August (Figs. 5 and 6). During the period from 1986 through 1989, the 1% depth ranged between 110.1 m and 119.8 m in July and 94.2 m and 112.8 m in August. In July 1968 and August 1969, the depth of 1% of blue light in Crater Lake was between 100 m and 110 m (Figs. 5 and 6; Larson 1972).

The mean depth of the 1% penetration of green light between 1980 and 1989 was 90.5 m in July and 87.3 m in August. During the period from 1980 to 1985, the depth of 1% green light ranged between 84.2 m and 91.6 m in July and 78.9 m to 89.8 m in August (Figs. 5 and 6). From 1986 through 1989, the depth ranged between 82.6 m and 99.7 m in July and 86.4 m and 92.7 m in August. In 1969, the depth of 1% green light was 70 m in July and 79 m in August (Figs. 5 and 6; Larson 1972).

From 1980 through 1989, the mean depth of 1% penetration of the red light was 51.8 m in July and 53.1 m in August. Between 1980 and 1985, the depth of 1% red light ranged from 42.1 m to 58.6 m in July and 46.8 m to 57.9 m in August. The depth of 1% red light ranged between 55.0 m to 67.8 m in July and 54.6 m to 57.6 m in August from 1986 through 1989. In 1969, the depth of 1% red light was 10 m in July and 18.6 m in

August (Figs. 5 and 6; Larson 1972).

The relationship between July and August Secchi disk clarity and the depth of transmission of 1% of incident light (425-655 nm) was not statistically significant ($p=0.05$, $r=0.231$, $n=28$) although some seasonal and annual trends were similar in both data sets (see section - Clarity of Crater Lake Measured with a Secchi Disk). Both data sets showed increasing depths in July and August. Depths were shallower in both data sets in the mid-1980's, increased through 1988, and decreased in 1989.

Conclusions

Although it was impossible to compare all photometer data, the data collected since 1980 suggests that the depth of penetration of 1% light in Crater Lake undergoes seasonal and long-term changes. The evidence is insufficient to conclude that the lake has changed in spectral composition or in depth of light penetration.

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Transmissometer

Michael Hurley and Gary L. Larson

The density, composition, distribution, and dynamic interactions of particles in lakes affect water clarity (Hutchinson 1957). Transmissometers are used to determine spatial distributions of particles in lake waters at any depth, whereas Secchi disks and photometers provide information on near-surface clarity and depth of surface light penetration (Bertoni and Calleri 1981, Stewart and Martin 1982, and Johnson and Merritt 1979). Attenuation coefficients of transmissometer beams are correlated to the densities of suspended particles; therefore, a transmissometer measurement can be used as a proxy for particle concentrations (Spinrad 1986).

The possibility that clarity of Crater Lake was changing prompted a 10-year study of a variety of characteristics of the lake (see Introduction section). As part of that study, a transmissometer was used to characterize the vertical and seasonal distribution and density of particles in the upper 200 m of the water column of the lake. A second objective was to evaluate the relationships between Secchi disk readings in the lake and particle measurements taken with a transmissometer in the upper 40 m of the water column.

Methods

From 1987 through 1989, a beam transmissometer was used to assess light transmission and spatial distributions of particles in Crater Lake. Water clarity was assessed using a standard 20-cm-diameter black and white Secchi disk. All measurements were at a site designated as Station 13 (see Study Area and Facilities section). Transmissometer and Secchi disk measurements were taken on the same date

and at the same time except when viewing conditions were too poor for measurements with the disk. On those occasions, measurements with the Secchi disk were postponed, usually only a couple of days, until viewing conditions improved. Sampling during 1989 was the most extensive, with measurements taken from April through October.

The transmissometer was a Seatech beam transmissometer powered by a Seabird Seacat Profiler (Model SBE19). The transmissometer had a nearly monochromatic wavelength of 660 nm with a path length of 25 cm. The unit recorded two readings per second as it was lowered into the lake at a rate of about 1 m per second. The volume of data was reduced by averaging all values at one-decibar intervals with the Seabird Binavg Program. The methods associated with the Secchi disk readings are described in the section, Clarity of Crater Lake Measured with a Secchi Disk.

The transmissometer was calibrated periodically using filtered distilled water (91.3% transmission) provided by Seatech. The accuracy of measurements in Crater Lake were assumed to be within 0.5% (Spinrad et al 1989), a precision of about 20 - 25% relative to the range of percent transmission in Crater Lake. The precision among deployments of the transmissometer was improved by normalizing the data to a clear-water layer in the lake at a depth between 300 m and 400 m. Deep-water transmission values from 12 deployments at different locations on the lake were within a range of 0.05% on June 27, 1989. Therefore, it was assumed that the deep clear-water layer was spatially homogeneous throughout the year. Immediately after calibrations by the manufacturer, the transmission values in the deep clear-water layer were equal to transmission values of filtered distilled water.

The attenuation of light from a beam transmissometer is caused by absorption (a) and scattering (b) of light by particles, water, and dissolved substances (Equation 1).

Equation 1: $C = a + b$

Particle volume should be linearly proportional to the logarithm of transmission. Equation 2 is the derivation of the attenuation coefficient for the beam transmissometer, where T=transmission and z=distance of light path (0.25 m).

Equation 2: $C = -(\ln T/z)$

The attenuation coefficient can be further broken down into components that affect light attenuation (Equation 3).

Equation 3: $C_t = C_w + C_b + C_d + C_i + C_o$

C_t (or C) is the total beam attenuation coefficient, C_w is the extinction coefficient for pure water, C_b includes all living particles, C_i is for inorganic particles, C_d is for detritus, and C_o is for dissolved substances. The influence of dissolved matter on beam light attenuation is insignificant, since the wavelength of 660 nm is insensitive to dissolved organics (Zaneveld and Bartz 1984) and light extinction due to particulates is much greater than that for dissolved organics and detritus in oligotrophic waters (Keifer 1984). The value for C_w is a constant of 0.364 which corresponds to 91.3% transmission for filtered distilled water (Zaneveld and Bartz 1984). For this study, the extinction coefficient for particles ($C_p = C_b + C_d + C_i$) could be determined by Equation 4.

Equation 4: $C_p = C_t - C_w$

The beam attenuation coefficient is highly correlated with total suspended matter (Spinrad 1986). The relation between the attenuation coefficient and particles may differ by an order of magnitude depending on the absorption and scattering properties of the particles. Cumulative attenuation of light to a specific depth represents the amount of light attenuated by particles to that depth. The Secchi depth is inversely proportional to the sum of the beam attenuation coefficient and the diffuse attenuation coefficient, K'

(Preisendorfer 1968, Davies-Colley 1988) as in Equation 5, where Sd is the Secchi disk reading, Cps is the average cumulative extinction coefficient, K is the diffuse attenuation coefficient, and A is the negative log of the irradiance in the dominant waveband at the Secchi disk depth divided by the dominant waveband at the lake surface (Megard and Berman 1989).

Equation 5: $Sd = A(Cps + K')^{-1}$

The average attenuation coefficient to the depth of the Secchi disk was considered to be independent of the diffuse attenuation coefficient (Horjerslev 1986). The variability of diffuse light values was quite high at the lake surface, and thus, was not used owing to precision requirements of the Crater Lake data. For consistency of analysis, the average particulate attenuation coefficient, $\overline{C}p$, was used to determine Secchi disk-beam attenuation relations and water column transparency.

The cumulative beam attenuation coefficient also can be considered as a wavelength-specific (660 nm) diffuse-light extinction coefficient for a depth interval, and thus, can be substituted in equations for photometers for diffuse light. Equations to describe Secchi disk and light extinction are derived from Lambert-Bouger Law, and can best be described by a power equation, $S = mx^b$ (Megard and Berman 1989). The exponent b is -1, thus reciprocal transformations of the data should be performed. Also, linear regressions should pass through the origin (Megard and Berman 1989). Substituting the average cumulative extinction coefficient, $\overline{C}ps$, for the diffuse attenuation coefficient, K', yields Equation 6, which was used to regress beam attenuation against Secchi depth.

Equation 6: $S_d^{-1} = A^{-1}(\overline{C}_{ps})$

Results and Discussion

Between 1987 and 1989, values of the beam transmissions from the surface to a depth of 200 m ranged from 87.35 to 90.45% for a range of 3.1% transmission. A range of 4.5% was observed for the entire water column over all seasons. The deepest Secchi disk readings and the highest beam transmission values in the upper 40 m stratum occurred in 1988; the lowest transmissions and shallowest disk readings occurred in 1989 (Table 1). Even lower transmission values and shallower Secchi disk readings were recorded occasionally in near-shore areas of the lake during periods of snow avalanche and spring runoff (Larson 1990).

The distribution and dynamics of particles is important in understanding variability in water clarity and Secchi disk readings. From early summer through fall, transmission profiles of the water column varied from year-to-year (Fig. 1). A typical profile had zones with relatively low transmissions, with clear layers above and below the zones. The most notable zone of low transmission in the 0 m and 200 m stratum in 1987 and 1988 was located at a depth between 60 m and 120 m (Fig. 1). This was the portion of the water column with the highest measurements of primary production and total chlorophyll (see Phytoplankton section). In 1989, the minimum transmission layer developed in the metalimnion between July and September. The clearest waters occurred at the surface and in deep waters below the minimum transmission layer (300-400 m).

The turbid and clear portions of the transmission profiles in the upper 40 m of the lake were related to the magnitude and dynamics of the Secchi disk readings. Maximum surface water clarity and Secchi depths occur when the surface water clear layer is most developed and when surface and metalimnetic minimum transmission peaks

are least developed. The highest Secchi recordings were made during such conditions (Fig. 2). The disk usually disappeared from view below the minimum transmission peaks (see arrows on Fig. 2). The shape and change in per cent transmission profiles closely corresponded with the thermocline (Fig. 2). Although an ephemeral upper metalimnetic minimal transmission peak between 15 and 30 m formed in 1987 and 1989, this peak was the dominant minimum transmission layer in 1989.

Small temporal changes in the transmission profile and corresponding water clarity can be extreme and rapid in response to certain climatic events that influence thermocline migration, nutrient replenishment, and the particulate regime. For example, in 1989 after a windstorm on June 28 and 29 and a rain storm on July 18 and 19, the percent transmission profile, thermocline, and water clarity changed rapidly. The maximum summer secchi depth was recorded on July 6, 1989 (34.4 m) and the maximum transmissometer reading was on June 30, 1989. (Fig. 2). This period of maximum water clarity was due to storm action causing downward migration of the thermocline and dilution of particles in the weak epilimnion. However, by August 17, 1989, the Secchi disc depth had decline to 27 m. During this time, the minimum transmission layer migrated from 50 m to 18 m and the minimum transmission value changed from 88.1% to 87.4%. The rate of ascent of the minimum transmission peak was 0.75 m per day between June 26 and July 17, 1989 but accelerated to 3.5 m per day after the July storm for an ascent of 14 m in 4 days.

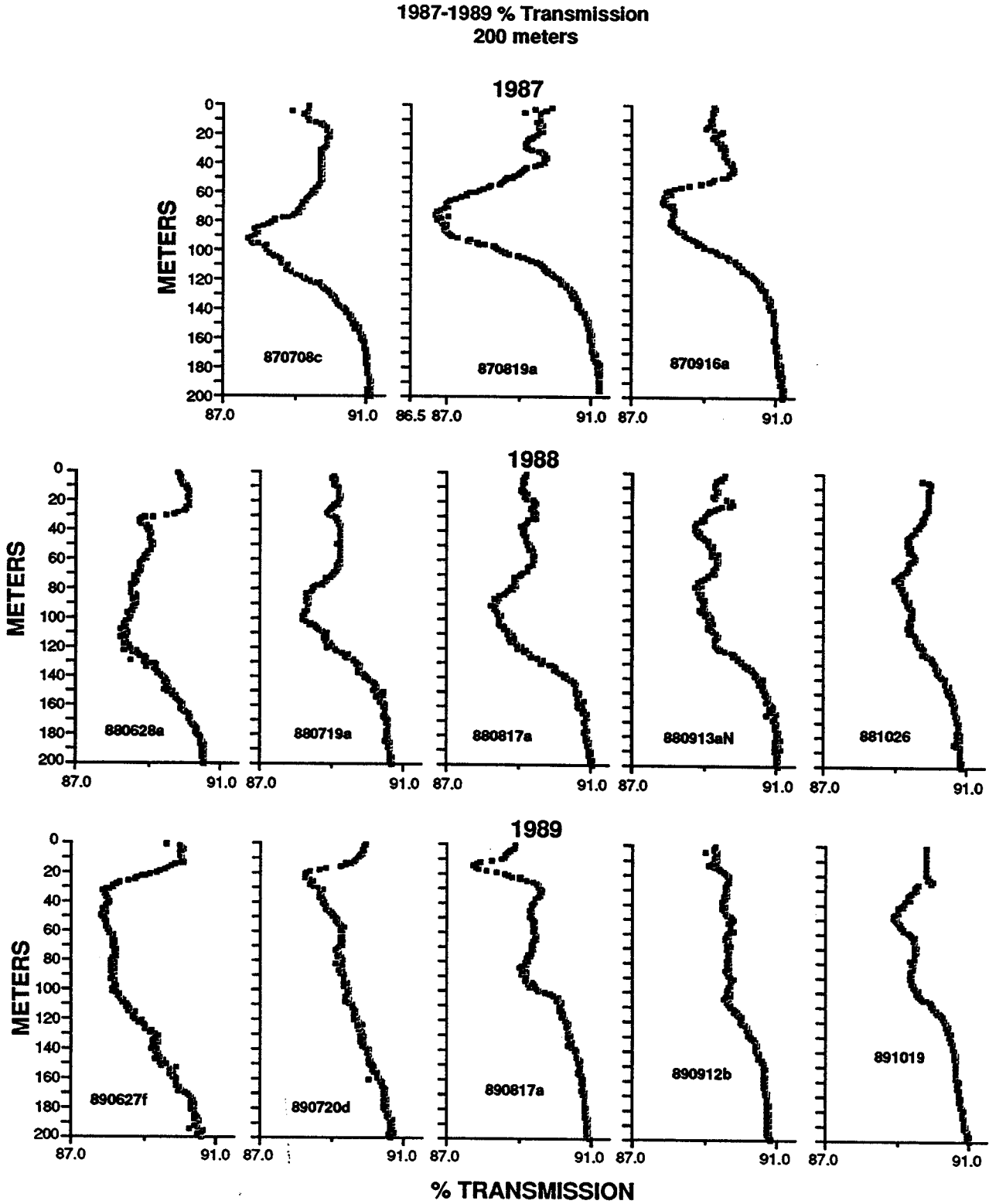


Figure 1. Percent beam transmission profiles from 0 to 200 mm from 1987-1989.

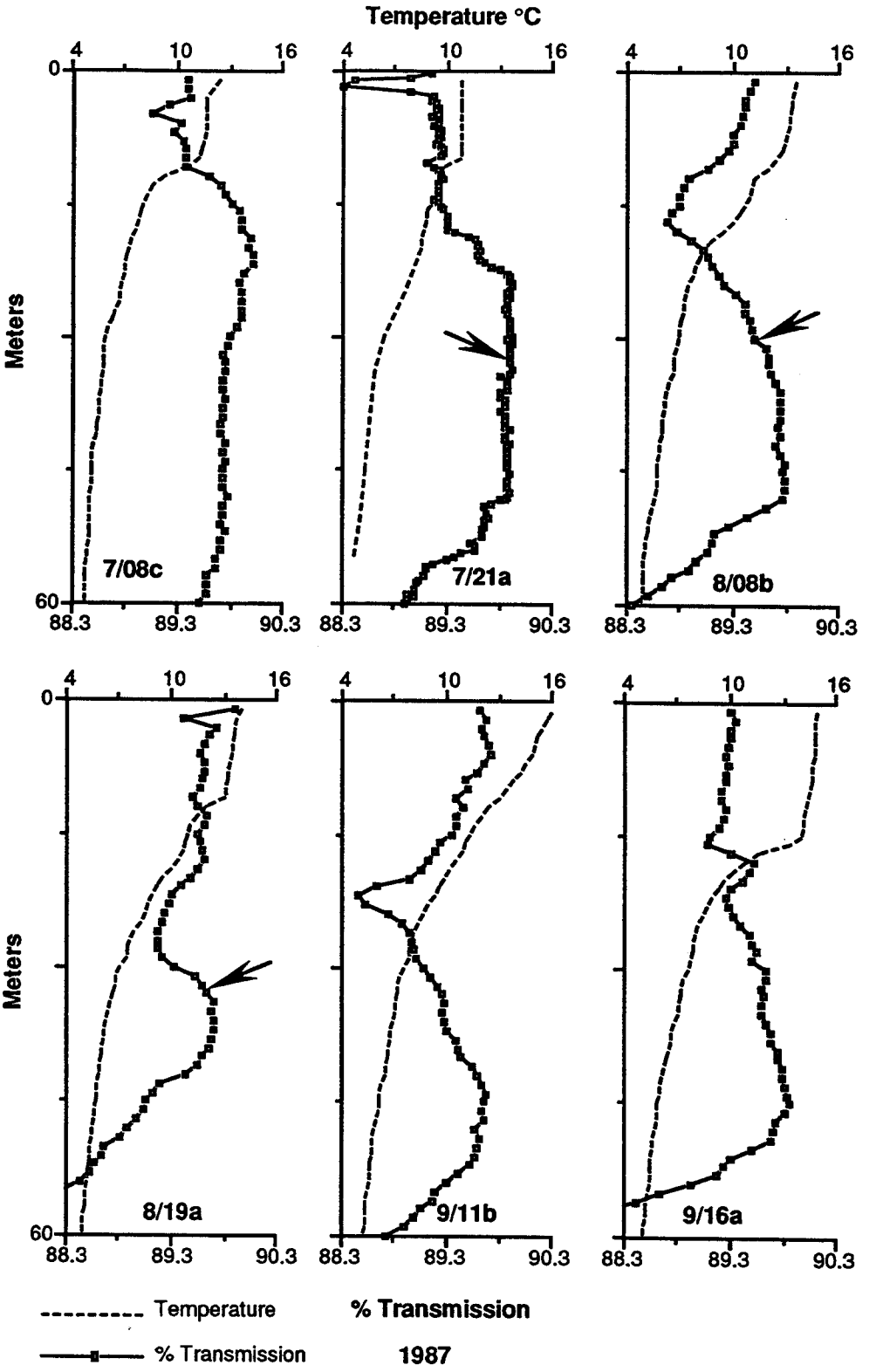


Figure 2. Percent beam transmission and temperature profiles from 0 to 60 m from 1987-1989.

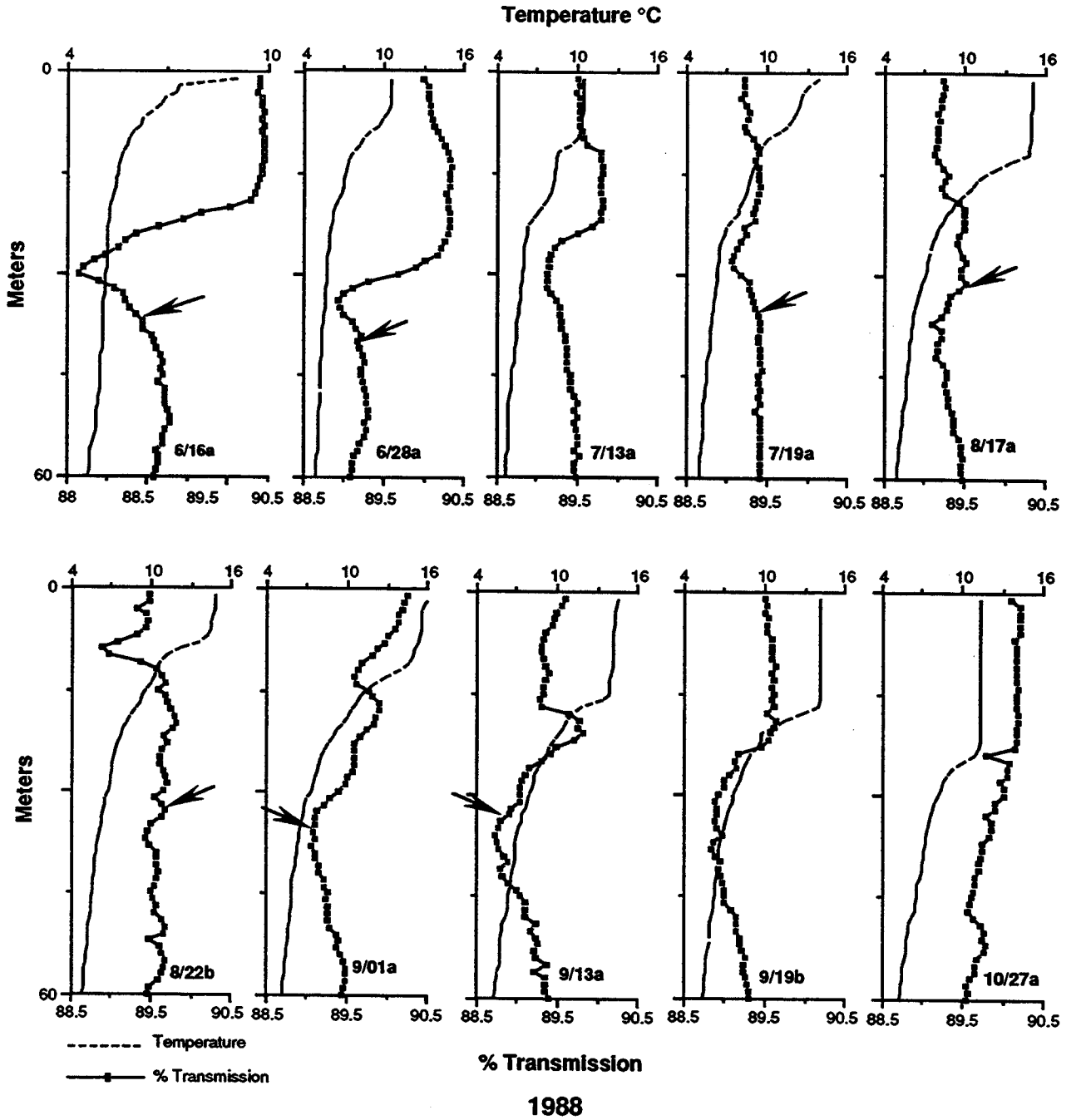


Figure 2. Continued.

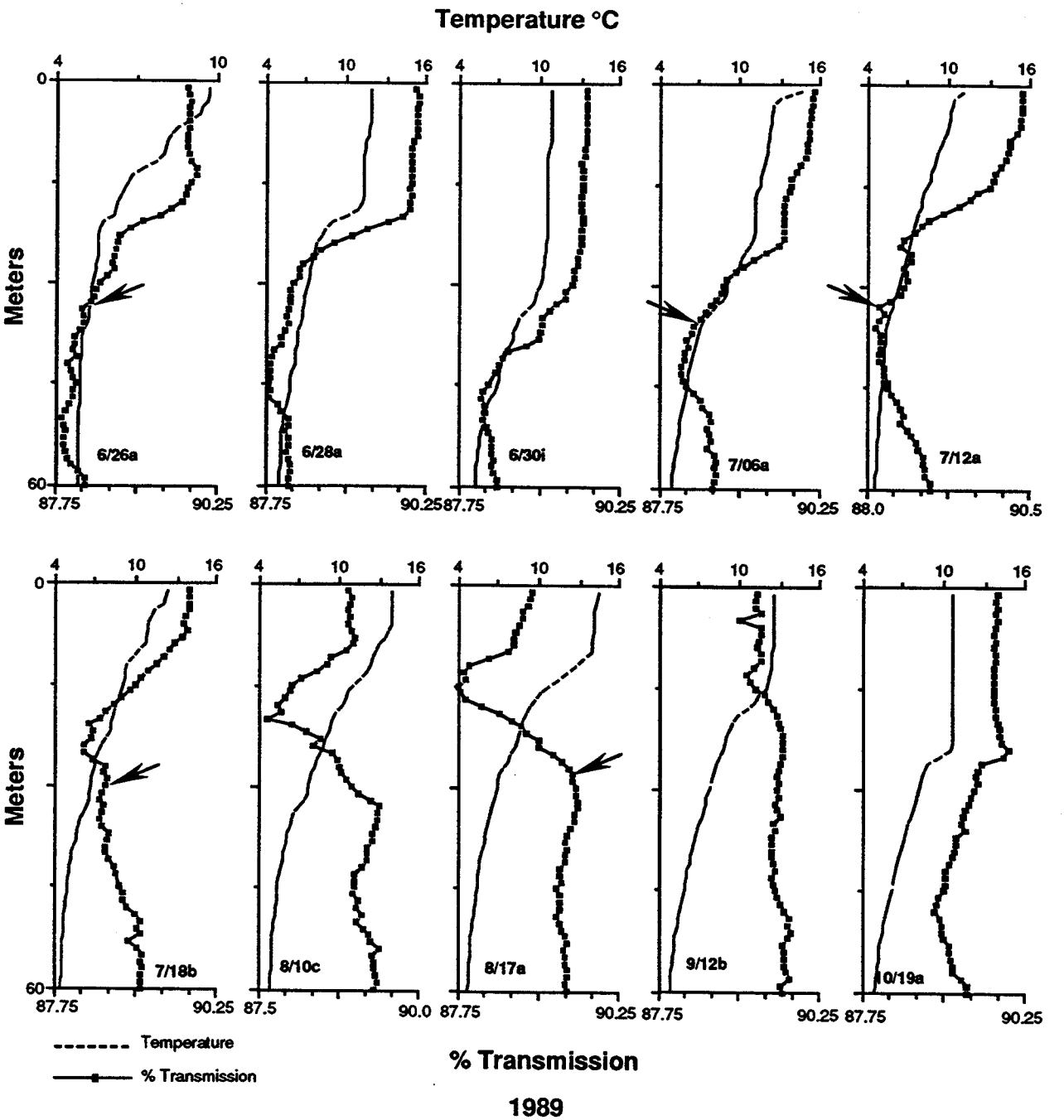


Figure 2. Continued.

Table 1. Minimum and maximum summer and fall Secchi disk readings and percent transmissometer beam transmissions from 1987 - 1989. Transmissometer data from 0 - 40 m.

	Secchi (m)				% Transmission		
Year	Range (m)	%	Min	Max	Range	Min	Max
1987	6.5	18	30	36.5	1.6	88.4	90.0
1988	8.4	21	30.7	39.2	2.4	88.1	90.5
1989	6.8	19	27.5	34.3	2.7	87.7	90.4

Water clarity at the surface of Crater Lake in winter was equivalent to the average transparency of the water column to the depth of mixing. For example, during April of 1989 (Fig. 3), a reverse thermocline developed at about 125 m and corresponded with low beam transmission (86.8%) from the surface to a depth of 125 m and a shallow Secchi disk reading of 26 m. By May, the depth of mixing increased to about 230 m and the reverse thermocline was significantly reduced. At that time, the Secchi disk reading was 33.5 m and the beam transmission was 89%. The increase in Secchi disk clarity and transmission between April and May was probably due to dilution of particles because the standing crops of particles were the about the same (15.5 vs 15.6) as determined by integrating Cp to the mixing depths.

Transmissometer values corresponded to clarity measurements taken with the Secchi disk for the years 1987 and 1989 (Fig. 4). The high correlation between the Secchi disk and transmissometer beam attenuation was especially significant considering that the Crater Lake data included only a small range of the data usually used to generate Secchi disk and light attenuation relationships (e.g., Megard and Berman 1989),

and the data are located on the vertical portions of hyperbolic curves between Secchi disk clarity and particle densities, where large changes in clarity occur with relatively small changes in particle density (Larson and Hurley 1988). Based on these relationships, integrated transmissometer values from depths of 0 - 30 and 0 - 40 m appeared to be useful proxies for Secchi disk measurements (Fig. 5). As Secchi depths becomes shallower, variability between Secchi and C_p 0-40 m becomes more variable, thus shallower Cp values should be used for shallow Secchi depths.

The dominant pattern in Crater Lake was for the water column to exhibit maximum clarity early in the summer and minimum clarity in mid- to late summer. The processes driving the development of surface transparency maxima and minima need to be identified in order to understand seasonal and long-term changes in Crater Lake clarity. Summer surface transparency maxima are associated with weak thermocline development, both in early summer before the onset of stable stratification and in fall with the decay of the thermocline. Exceptionally clear near-surface waters are associated with the early summer transparency maxima, especially those with deep Secchi depths (i.e., June 1987, Secchi depth of 39 m, Fig. 2). The duration of maximum surface transparencies are short, lasting only about one or two weeks with about a three-to-five-week interval between the maximum and minimum values.

Development of minimum surface transparencies was associated with thermocline development in a stable water column and an increase in phytoplankton cell bio-volume. Summer surface transparency minima usually occurred in mid to late August and early September when the thermocline was most developed and the water column most stable. During the minimum period of surface transparency, phytoplankton cell bio-volumes and associated Cp values from the surface to a depth of 40 m showed high correspondence.

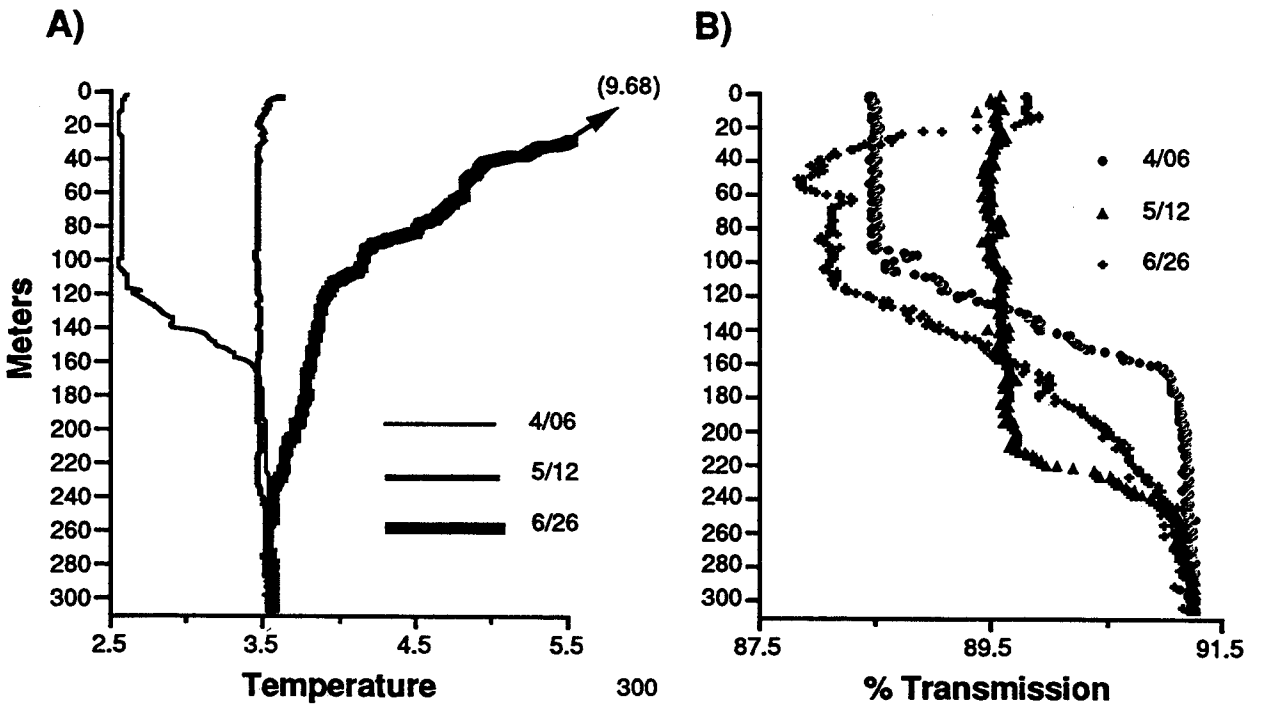


Figure 3. Temperature (A) and percent beam transmission (B) profiles from April to June, 1989.

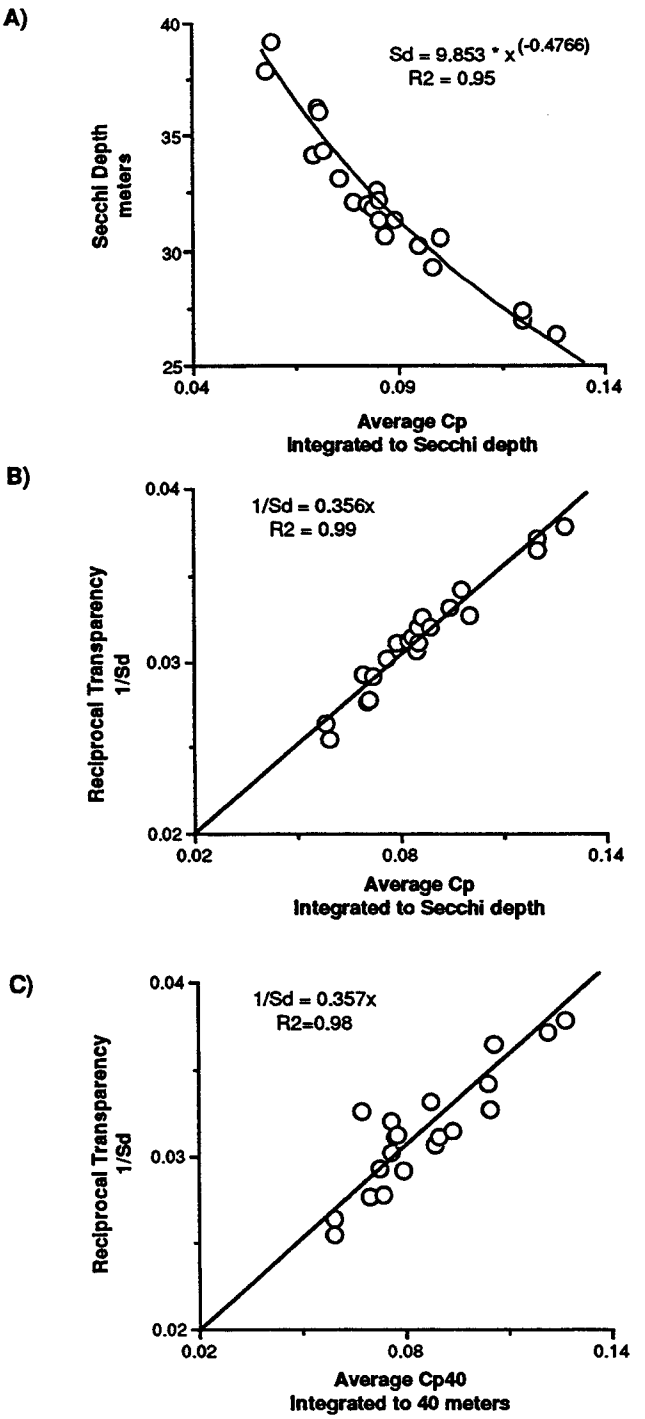


Figure 4. Relationships between Secchi disk readings and beam attenuation coefficients. A) power curve fit between the average attenuation coefficients integrated to the Secchi disk depth and Secchi disk readings. B) Linear regression through the origin between average attenuation coefficients integrated to the Secchi disk depths and the reciprocal Secchi disk depths. C) Linear regression through the origin between the average attenuation coefficients integrated to 40 m and the reciprocal Secchi disk depths.

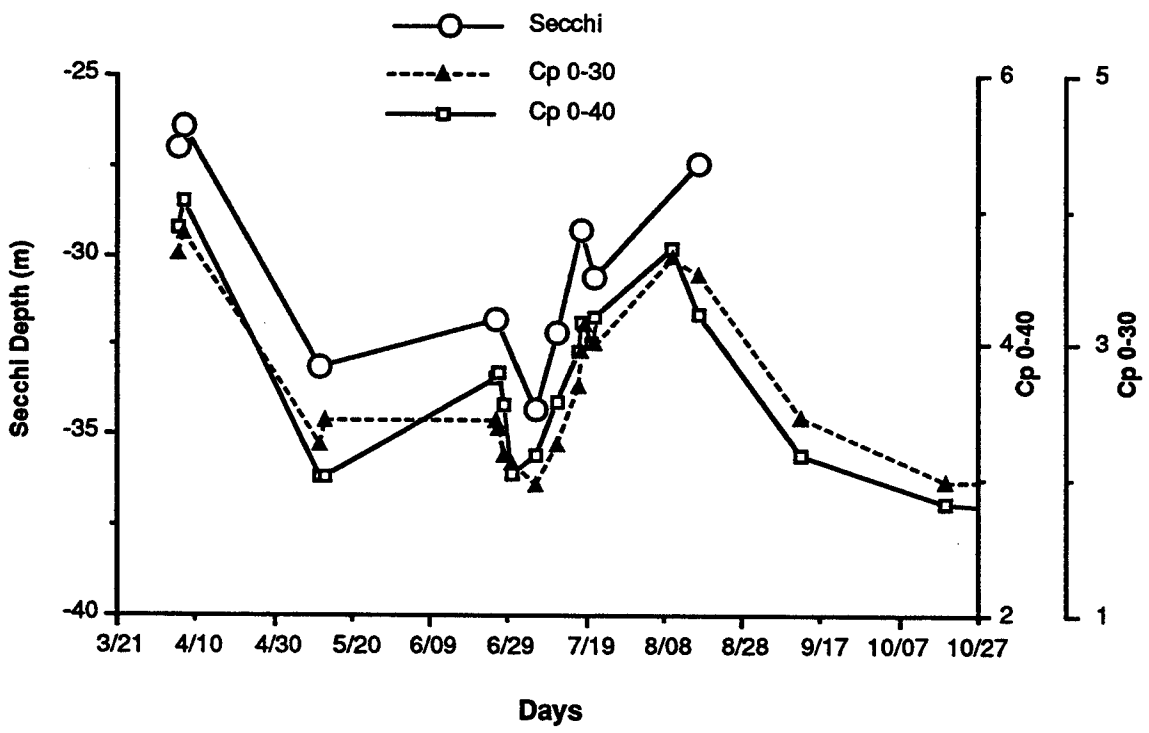


Figure 5. Secchi disk depths and the average attenuation coefficients integrated to 30 m and 40 m from April through October, 1989. Secchi disk readings could not be taken after August 8 because the lake surface was too rough.

For example, in August 1989 r-squared between the two variables was 0.85. Because the Secchi disk reading was 27.4 m, phytoplankton cell bio-volume in the epilimnion and metalimnion appeared to explain a significant proportion of variability in surface clarity. At that time, the dominant algal taxon in the 0 - 20 m stratum was *Nitzschia gracilis*, whereas the minimum transmission layer was characterized by small chlorophytes and chrysophytes. The fact that phytoplankton cell biovolume and water clarity in the upper-most stratum of the water column were interdependent with thermocline development, suggested, however, that other factors could have influenced water clarity.

Particles originating from the atmosphere, shoreline erosion from wave action during storm events, landslides, runoff from caldera streams, and phytoplankton may contribute to the turbidity of Crater Lake, particularly during periods of thermal stratification when the shallow epilimnion may serve as a collector of particles. However, interannual climatic fluctuations affect yearly variability in thermocline development, nutrient dynamics, and primary production/chlorophyll (Strub et al. 1985, Goldman et al. 1989). Seasonal patterns of mixing and stratification are considered the "master variable" for phytoplankton development and, thus, are probably important to particle abundance and distribution (Sommer 1985). The thermocline provides a physical structure for differential spatial and temporal community development. Phytoplankton populations often develop maxima at the metalimnion (Baker and Brook 1971), which corresponds to the metalimnetic layer of minimum transparency in Crater Lake. Furthermore, changes in the depth of the epilimnion results in a corresponding shift in particle densities and shapes of the light attenuation profiles (Kling 1988). Development of a stable pcynocline is a barrier to mixing and advective processes and allows differential development of the surface waters from those below the pcynocline.

Conclusions

Seasonal particulate/transmission profiles develop from a homogenous, well-mixed water column in winter to early spring to a well-defined profile by mid to late summer. Development of the particulate profile parallels that of the physical development of the water column. Development, distribution, and dynamics of the particulate profile affects surface water clarity as historically measured with the Secchi disk. Consistent patterns of seasonal surface transparency maxima and minima are observed. Surface transparency maxima generally occur in late spring to early summer at a period of physical and ecological transition at the onset of thermocline development. Surface transparency minima usually occur at mid to late summer and are associated with maximum water column stability.

Seasonal and short-term variability in water clarity can be explained by changes in the physical structure of the water column and concomitant changes in the particulate/transmission profile. Downward migration of the thermocline/pycnocline by storm events and deepening of the winter/spring deep-water mixing layer can initially dilute particles and increase water clarity. Surface transparency maxima and seasonal changes due to storm events are quite ephemeral, and changes in particle regimes and water clarity can be rapid. Sampling strategies must be structured to effectively monitor these changes for a better understanding of the fluctuations in water clarity at Crater Lake. Sampling at least once a week is considered necessary to identify transparency maxima and the physical and biological factors related to their formation and decay.

The transmissometer data is well correlated with Secchi depths and surface phytoplankton, and thus, serves as a good proxy for Secchi depths to monitor water clarity. Long-term trends in the clarity of Crater Lake are difficult to detect because of

variability in seasonal transparency of the lake. Changes in surface transparency are related to thermocline development and water column stability, and also are influenced by phytoplankton community development, weather, landslides, atmospheric deposition, storm events, and stream runoff. A much larger data set will be required to detect long-term changes in the clarity of Crater Lake.

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Crater Lake Color

Gary L. Larson

Most studies conducted to detect any changing optical properties of Crater lake have focused on comparing past and present readings taken with Secchi disks and photometers. However, changes through time in the scattering of light as it enters the water can also indicate changing optical properties. A small amount of impurities can drastically change the distribution of wavelengths of scattered light and, thus, effect the color of the water.

Pettit (1936) conducted light scattering experiments using water from Crater Lake. In August 1934 and July 1935, he collected water just below the surface of the lake and examined the non-resonant scattering of the light under controlled laboratory conditions as an indication of water purity. He concluded that the amount of backward-scattered light in water from Crater lake was intermediate to that of distilled water with dust and distilled water without dust. This study was conducted to (1) determine seasonal and annual changes in the color of water of Crater Lake from 1986 to 1989, and (2) compare the results of this study with results of Pettit (1936).

Methods

The analyses were based on the assumption that water molecules behave like an electric dipole, which results in an elastic differential scattering cross-section proportional to $\lambda^{-4} \cos\theta^2$, where λ is the incident wavelength and θ is the angle of scattering (Fontana 1989). Thus, the water molecule radiates more strongly at short wavelengths and preferably in the forward and backward directions. In contrast, large particles, e.g.,

suspended sediment and pollen, scatter visible light independent of wavelength. In addition, there also is inelastic scattering with enhanced absorption at long wavelengths. In the visible wavelengths, absorption in distilled water is greatest in the red region, shows a dip in the green region, and rises again slightly in the blue region (Fontana 1989).

Crater Lake water was analyzed by measuring the ratio of backward-scattered light ($\theta \sim 135°$) to transmitted light ($\theta \sim 0°$) in a 3-liter plexiglass apparatus (Fig. 1). The scattering cell was covered with a plexiglass lid. The lamp contained a hot tungsten filament and the light was focused in the center of the cell using a camera lens. The transmitted light and backward-scattered light were focused at the entrance slit of a monochromator and subsequently recorded with a photomultiplier and associated linear amplifier. Because the spectrum of the tungsten lamp was not constant and depended on the age of the filament and the length of time the lamp was on, the recordings were ratios of backward-scattered light to transmitted light normalized to 600 nm. Thus, the ratio of the normalized backward scattering to normalized transmitted light was independent of the spectral profile of the tungsten lamp and any varying effects of temperature. Readings were recorded manually in 1986 and 1987. In 1988 and 1989 the equipment was interfaced with a computer in order to record a large number of measurements at 20 nm intervals between the wavelengths of 400 and 600 nm. This prohibited measurements at 450 and 550 nm. The goal was to have the computer automatically change the monochromator settings, record and store the signals, and perform a variety of other tasks such as averaging data and calculating ratios. Although the apparatus used in this study was markedly different in shape from the bulb flask used

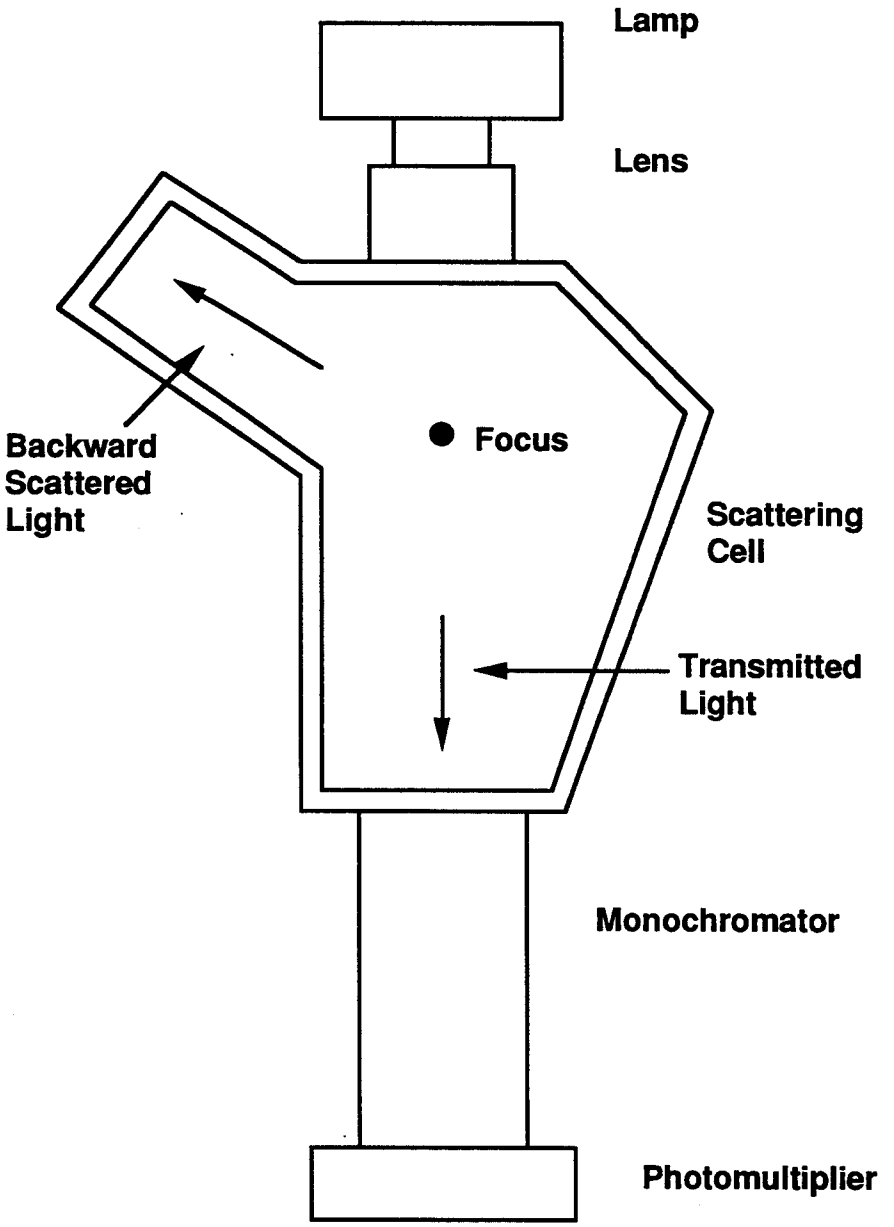


Figure 1. Diagramatic representation of the scattering cell used in the lake color experiments. The monchromater can be moved to also record backward scattered light.

by Pettit (1936), the physical principals were the same. The use of a monochromator and photomultiplier increased the sensitivity of the experimental results of this study (Fontana 1989). Results from a test with distilled water filtered through a glass filter with a pore size of 1.2 μm and Pettit's test with dust-free distilled water were similar (Table 1).

Water samples were collected at the main sampling station (Station 13) on Crater Lake (see Study Area and Facilities section) from a depth of 1 m using a van Dorn water sampler. Each water sample was drained into three acid-washed polyethylene bottles and stored on ice in the dark in a cooler. The samples were transported to a laboratory in the Physics Department, Oregon State University within 24 hr after collection and either processed the same day or refrigerated for processing the next day. All samples were processed at room temperature. Each set of samples was allowed to stand in the apparatus for at least 1 h before processing.

Table 1. Ratios of backward-scattered light to transmitted light (normalized to 600 nm) as a function of wavelength for pure water (theoretical Rayleigh scattering), dust-free distilled water, and distilled water filtered through a glass filter (1.2-μm pore size).

Wave Length nm	Theoretical Rayleigh scattering	Dust-free distilled water (Pettit 1936)	Filtered (present work)
600	1.00	1.00	1.00
550	1.41	1.35	1.22
500	2.07	1.85	1.85
450	3.16	2.80	2.91
400	5.06	4.50	4.98

Results and Discussion

For the most part, results of this study were comparable to results of Pettit (1936) (Table 2). Compared to Pettit's results, ratios observed in this study at 550 nm were about the same, those at 500 nm were slightly higher, and those at 450 nm were slightly lower. The ratios at 400 nm were similar to Pettit's value of 4.10 but ranged from 3.27 to 4.85 (Table 2). The most important ratio for comparison of Pettit's results and those from the present study were at 400 nm. This ratio measures the enhancement of blue light over the other colors in the scattered light. Based on the July and August data collected from 1986 to 1989, only the August 1986 and July 1987 ratios were markedly lower than Pettit's reading of 4.1 (Fig. 2). The ratio in July 1988 was substantially higher than Pettit's ratio. It appeared, therefore, that in some cases Crater Lake water was not as blue as it was in August 1934 and July 1935.

Considerable seasonal variation was observed in lake color (Fig. 2). Although the data varied considerably, the ratio at 400 nm was lowest in January, April and May, increased between June and August, and decreased slightly in September. The lowest values in July and August were recorded in 1987 and 1986, respectively (Fig. 2). Samples collected in July 1987 and August 1986 and those collected in January, April and May contained a lot of particles (Fontana 1988). The origin of the particles was unknown, but they may have been a combination of phytoplankton, pollen, and particles from shore erosion, snow and rock avalanches, and intracaldera streams. For samples collected on the same dates and at comparable depths, there were no statistically significant relationships ($p > 0.05$) between the 400-nm-normalized ratios and phytoplankton cell biovolumes ($r = 0.011$; $n = 18$) and densities ($r = 0.319$; $n = 18$).

Table 2. Ratios of backward-scattered light to transmitted light (normalized to 600 nm) as a function of wavelength for unfiltered Crater Lake water in August 1934 and July 1935 (Pettit 1936) and samples collected during the period from May 1986 to September 1989.

	Wavelength (nanometers)												
Sample date	400	420	440	450	460	480	500	520	540	550	560	580	600
5/28/86	3.41	3.36	3.04	2.72	2.38	1.86	1.49	1.33	1.27	1.13	1.13	1.04	1.00
6/25/86	3.83	3.62	2.98	2.70	2.39	1.91	1.53	1.26	1.19	1.14	1.12	1.07	1.00
7/07/86	3.98	3.31	2.77	2.55	2.30	1.95	1.53	1.43	1.38	1.30	1.24	1.08	1.00
7/24/86	3.99	3.28	2.68	2.49	2.29	1.84	1.47	1.34	1.26	1.20	1.13	1.05	1.00
8/20/86	3.29	2.74	2.33	2.15	2.01	1.67	1.42	1.32	1.25	1.23	1.17	1.05	1.00
9/17/86	3.76	3.04	2.53	2.35	2.18	1.87	1.47	1.32	1.22	1.17	1.13	1.04	1.00
1/18/87	3.56	2.84	2.28	2.22	2.05	1.84	1.44	1.33	1.31	1.21	1.17	1.07	1.00
4/14/87	3.61	3.06	2.54	2.34	2.12	1.89	1.49	1.37	1.27	1.22	1.16	1.04	1.00
6/23/87	3.65	2.97	2.52	2.34	2.13	1.83	1.49	1.37	1.27	1.22	1.15	1.03	1.00
7/23/87	3.37	2.88	2.38	2.18	2.01	1.67	1.41	1.26	1.23	1.17	1.15	1.03	1.00
8/19/87	4.25	3.38	2.81	2.57	2.36	1.93	1.58	1.40	1.28	1.23	1.15	1.05	1.00
9/16/87	3.69	2.93	2.51	2.32	2.19	1.83	1.53	1.36	1.28	1.21	1.18	1.07	1.00
6/30/88	4.14	3.08	2.46	–	2.46	1.94	1.57	1.33	1.15	–	1.08	1.06	1.00
7/21/88	4.54	3.09	2.49	–	2.41	1.91	1.38	1.34	1.31	–	1.05	0.98	1.00
8/16/88	4.09	3.35	2.62	–	2.27	1.93	1.53	1.31	1.38	–	1.16	1.11	1.00
9/13/88	4.09	3.39	2.88	–	2.39	1.98	1.60	1.48	1.38	–	1.21	1.09	1.00
10/26/88	4.85	3.79	3.19	–	2.54	2.15	1.76	1.52	1.35	–	1.23	1.08	1.00
4/07/89	3.15	2.60	2.02	–	1.84	1.55	1.29	1.16	1.12	–	1.07	0.98	1.00
5/13/89	3.49	2.76	2.52	–	2.20	1.80	1.31	1.25	1.14	–	1.05	0.98	1.00
6/28/89	3.65	2.65	2.41	–	2.11	1.75	1.39	1.28	1.22	–	1.12	0.99	1.00
7/12/89	3.86	3.05	2.45	–	2.22	1.79	1.36	1.25	1.13	–	1.02	1.06	1.00
8/17/89	3.88	3.11	2.72	–	2.39	1.94	1.46	1.23	1.25	–	1.08	1.04	1.00
9/12/89	3.27	2.75	2.09	–	2.00	1.78	1.53	1.19	1.11	–	1.05	1.04	1.00
*July/ August (1934-1935)	4.10			2.80			1.35			1.20			1.00

*Pettit (1936). The author presented summary data only.

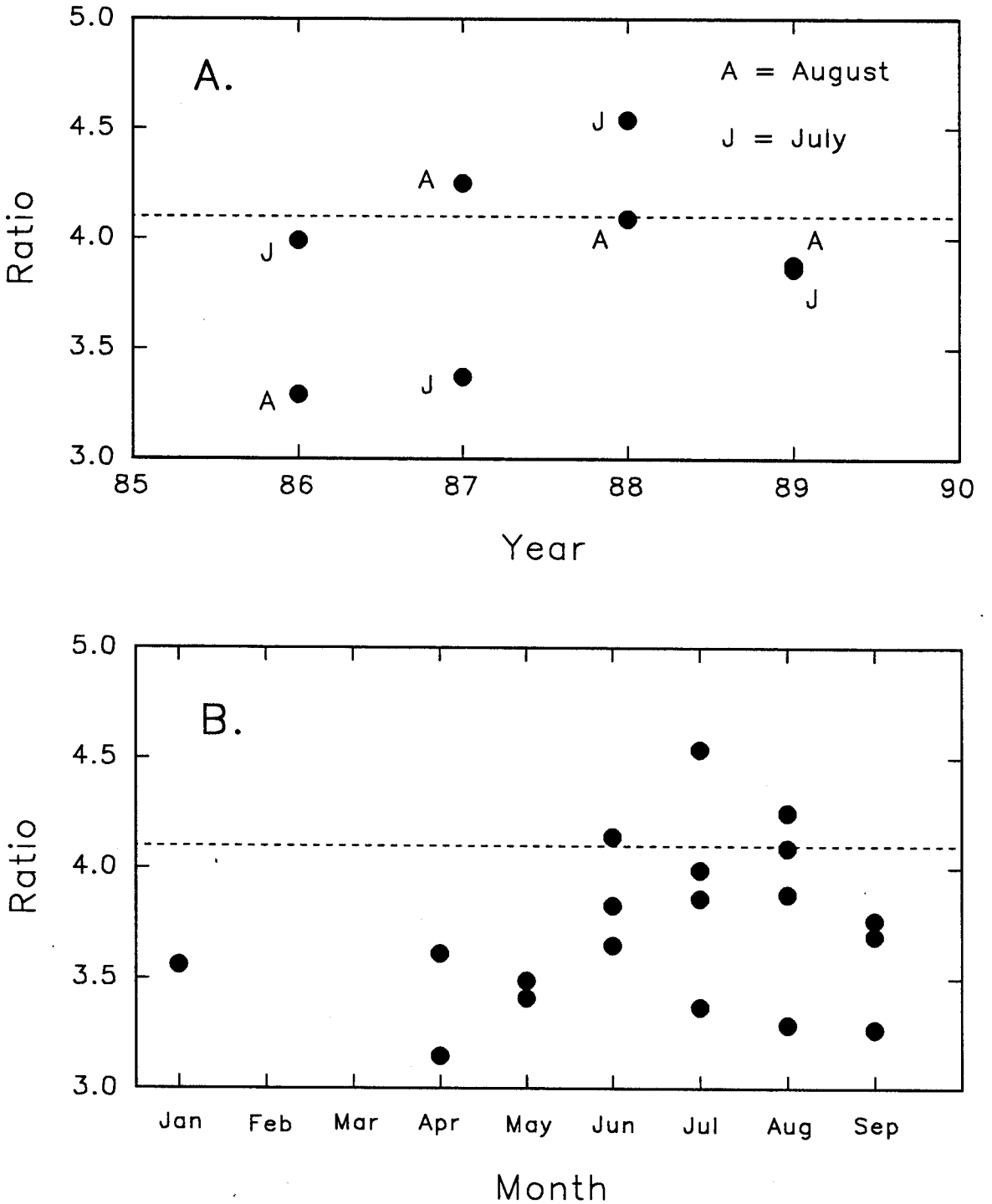


Figure 2. Ratios of backscatter light to transmitted light at 400 nm (normalized to 600 nm) in July and August (upper graph) and by month (lower graph) during the period from 1986 to 1989. The ratio of 4.10 determined for Crater Lake water in July and August of 1934 and 1935 by Pettit (1936) is indicated by the dashed line.

Acknowledgments

Peter Fontana, Physics Department, Oregon State University, constructed the test apparatus and conducted the experiments.

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Phytoplankton

C. David McIntire, Gary L. Larson, Robert Truitt, and Mark Buktenica

The taxonomic structure and primary productivity of phytoplankton assemblages in Crater Lake have been investigated using quantitative methods only recently (Larson and Geiger 1980, Larson 1984, Larson et al., 1987, Debacon and McIntire 1990, 1991). From the analyses of samples obtained at an intensive study site during the summers of 1978, 1979 and 1980, Larson et al. (1987) proposed a three-tier structure to describe vertical distribution of phytoplankton populations in Crater Lake. This conceptual model was based on the prominence of three taxa: *Nitzschia gracilis*, which was dominant in the upper 20 m of the water column; *Tribonema* sp., a dominant between 80 and 120 m; and *Stephanodiscus hantzschii*, which was concentrated between 160 and 200 m. Furthermore, it was hypothesized that the vertical distribution of these taxa in the water column is predictable during the summer months, and that because of their tolerance for extreme environmental conditions, namely low nutrient concentrations, they tend to perpetuate low species diversity and high dominance within their respective assemblages through the process of competitive exclusion. The study by Larson et al. (1987) also revealed a deep-water chlorophyll maximum between 100 and 140 m below the water surface during the summer (1981 and 1982), and a primary production maximum at a depth of 80 m (July 1983).

Phytoplankton data presented in this report represent a 10-year period of sampling, from August 1981 through September 1990. The objectives of the phytoplankton study were to describe the seasonal and annual dynamics of phytoplankton assemblages at an intensive study site in Crater Lake and to generate and test hypotheses that could account for the vertical and seasonal distribution and abundance of the constituent algal populations. Variables expressing taxonomic structure, primary productivity, and phytoplankton biovolume and biomass (i.e., the concentration of chlorophyll) were examined relative to

their spatial and temporal dynamics, with particular emphasis on mechanisms accounting for the positions of the primary production and chlorophyll maxima in the water column. In addition, the data provided the opportunity to examine hypotheses and the model of community structure proposed by Larson et al. (1987).

Sampling

For analytical purposes, research related to the taxonomic structure of the phytoplankton was divided into three time periods: (1) a preliminary study of netplankton and nannoplankton (1982-84); (2) an extended study of netplankton and nannoplankton (1985-88); and (3) a more recent study that included netplankton, nannoplankton, and some picoplankton, mostly cyanobacteria between 1 and 2 um in diameter (1989-90). In this report, size ranges for netplankton, nannoplankton, and picoplankton are defined as greater than 20 μm, 2 to 20 μm, and less than 2 μm, respectively.

Table 1. Summary of the three time periods of phytoplankton sampling and the corresponding taxonomist, sample size, and whether or not small cells of cyanobacteria were included in the count.

Time Period	Taxonomist	# of Cells Counted per Sample	Picoplankton (< 2 m) Counted in Sample
1982 - 84	S. Geiger	100	No
1985 - 88	M. Debacon	300	No
1989 - 90	R. Truitt	300	Yes

Because of the length of the program, there was a different taxonomist involved in the examination of samples obtained during each of the three time periods (Table 1). After the preliminary study, the number of organisms counted in each sample was increased from 100 to 300, a sample size more suitable for the estimation of community

composition parameters (McIntire and Overton 1971). Moreover, a preliminary analysis of data collected from 1985 through 1987 indicated a lack of correspondence between the depth profiles of total cell biovolume, C^{14} primary production, and chlorophyll concentration, an observation that stimulated interest in picoplankton dynamics. Consequently, when R. Truitt joined the research team, the decision was made to include small cells (to an approximate size of 1 μm) in the counts of each sample, a procedure that had relatively little effect on estimates of total cell biovolume, but a much greater effect on estimates of community composition parameters based on cell density. In spite of inconsistencies related to taxonomic interpretation (three taxonomists), sample size, and inclusion or exclusion of organisms less than 2 μm in diameter, multivariate statistical procedures revealed strong, interpretable patterns in the phytoplankton for each of the three time periods, and continuity in the dynamics of some dominant taxa over the entire 9-year study.

All phytoplankton samples were obtained with 4-liter Van Dorn bottles which were spaced along a cable that could be lowered to any depth in the lake. The sampling strategy used early in the 10-year study of Crater Lake phytoplankton was based on a grid system developed by Hoffman (1969). The grid consists of 31 sections, most of which are approximately 2.6 km^2 in area (Fig. 1). During the preliminary study of netplankton and nannoplankton, samples were obtained from locations corresponding to grid numbers 13 and 23, henceforth designated as Station 13 and Station 23. The preliminary study was designed to investigate both vertical and horizontal distribution and abundance of phytoplankton populations, and included samples obtained in July, August, and September of 1982, 1983, and 1984. During most of the 1982-1984 cruises, samples were taken at the water surface and at depths of 10 m, 20 m, 40 m, 60 m, 80 m, 100 m, 120 m, 140 m, 160 m, 180 m, and 200 m below the surface.

An analysis of the 1982-1984 samples indicated that the taxonomic structures of phytoplankton assemblages at stations 13 and 23 were similar for corresponding times and depths. Consequently, beginning in 1985, intensive sampling of the phytoplankton was

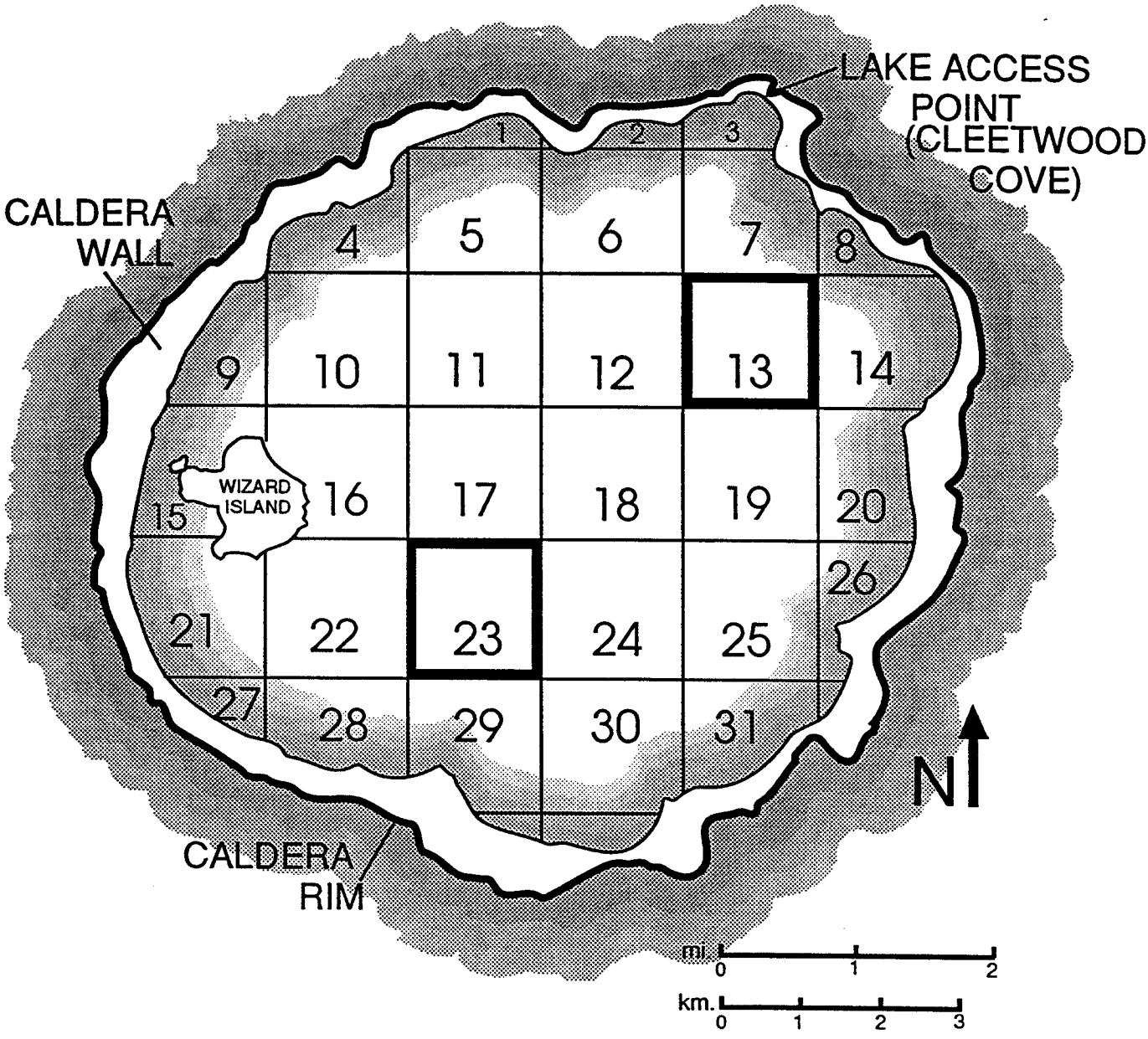


Figure 1. Grid system for the Crater Lake ecosystem established by Hoffman (1969), indicating locations of intensive phytoplankton sampling (Station 13 and Station 23).

confined to Station 13, a strategy that permitted more frequent sampling and direct comparisons with chemical and physical data collected from the same location. The complete set of species-abundance data representing the period between June 1985 and September 1990 consisted of 410 samples collected on 33 different dates from 13 depths (0, 5, 10, 20, 40, 60, 80, 100, 120, 140, 160, 180, and 200 m below the surface). Samples were obtained during all seasons of the year: 19 dates in the summer (June, July, August), 3 dates in the winter (January), 5 dates in the spring (March, April, May), and 6 dates in the fall (September, October). The only missing observations from this data set were values for the 5 and 10 m depths in September 1986 and from 180 and 200 m in September 1987. In addition, there were a few samples taken from depths below 200 m (225, 250, 275, 300, 350, 400, 450, 500, and 550 m). Data derived from these samples were incomplete and were not included in the statistical analysis of taxonomic structure.

Measurements of carbon-14 primary production and chlorophyll a concentration in the water column also were obtained during the 10-year study. The investigation of phytoplankton primary production began in August 1986 and continued through September 1990. In contrast, the chlorophyll data set is relatively large, and consists of measurements obtained at various seasons of the year between 1984 and 1990.

Water samples for estimates of carbon-14 primary production were taken from depths down to 180 m -- more specifically, at the water surface, and at 5, 10, 20, 30, 40, 60, 80, 100, 120, 140, 160, and 180 m below the surface. Water collected from each depth was transferred to one 125-ml transparent bottle and one 125-ml black bottle. The samples were inoculated and incubated *in situ* for 4 hr, usually between 11:00 and 15:00 hr. All measurements were made at Station 13. Data presented in this report include estimates of net primary production for selected days in 1986 (late summer), 1987 (winter, spring, summer, early fall), 1988 (winter), 1989 (spring, summer, early fall), and 1990 (winter, summer, early fall). Unfortunately, the isotope inoculum used during the spring and

summer of 1988 apparently was contaminated, a problem that prevented acceptable estimates of primary production for that period of time.

Water samples for the analysis of chlorophyll concentration were collected between June 1984 and September 1990 at Station 13 from depths of 0, 5, 10, 20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 225, 250, 275, and 300 m below the lake surface. Samples from a depth of 30 m also were obtained in 1989 and 1990. All water samples for chlorophyll analysis were taken with 4-liter Van Dorn bottles at the same time that water was obtained for C-14 incubation and taxonomic analysis of phytoplankton assemblages.

Laboratory Methods

For the taxonomic analysis of phytoplankton samples obtained from 1985 through 1990, a 1-liter subsample of each collection was fixed with Lugol's solution and concentrated by allowing the cells to settle for 72 hr. After decanting the supernatant water, a concentrated subsample of 50 ml was transferred to an acrylic plastic settling chamber, and the contents were allowed to settle for 24 hr. The chamber then was mounted on an inverted microscope (Wild M40), and 300 algal units were identified and counted at a magnification of 1750X (Lund et al. 1958). An algal unit was defined as an individual cell or diatom valve, if the taxon was a unicellular form, or an individual filament in the case of multicellular taxa. The counting procedure allowed the inclusion of organisms with a minimum cell size of about 1 μm in diameter. Sample preparation during the preliminary study (1982-1984) was similar to the procedure described above with the following exceptions: (1) 10 ml of the concentrated sample was transferred to a settling chamber and allowed to settle for 4 hr/1 cm height in the chamber; and (2) counts of 100 algal units (instead of 300 units) were made using a Zeiss inverted microscope at a magnification of 1250X. The increases in sample size from 100 to 300 algal units in 1985 provided better estimates of the abundances of dominant taxa and allowed the inclusion of more of the rarer taxa.

Data obtained from the counting procedure were used to estimate the relative abundances, cell densities, and cell biovolumes of taxa in the water samples. Estimates of cell densities were obtained from measurements of the counting chamber, the field lengths and widths of the observed transects, and corresponding dilution factors. Biovolume conversion factors were determined for each taxon using appropriate geometric formulae (Debacon and McIntire, 1990; Table 2). Cell densities were multiplied by these factors to obtain estimates of cell biovolumes. Cell biovolume estimates for each sample were used to calculate total phytoplankton biovolume integrated to a depth of 200 m. It was assumed that these values were representative of cell concentrations at the corresponding depths, and that a linear interpolation between depths provided satisfactory estimates of integrated cell biovolume and density.

The carbon-14 method was used to estimate primary production in the water column (Goldman 1965). One 125-ml light bottle and one 125-ml dark bottle were suspended at each depth. After the bottles were filled with water, each bottle was inoculated with 1 ml of radioactive (C-14) $NaHCO_3$. The dark bottles were covered with plastic tape and painted with black paint. At the end of a 4-hr incubation period, the bottles were retrieved from the lake and placed in a dark wooden box which was refrigerated with snow or ice. The samples were transported to the park laboratory for processing, which typically began within 2 hrs after incubation. Water from each bottle was filtered through a 0.45 um Millipore filter using a vacuum of less than 10 in. of Hg. In 1986 and 1987, the filters were transferred to empty scintilation vials and transported to the Radiation Center at Oregon State University. Aquasol II was added at the Center prior to counting the samples. After 1987, the filters were put into scintilation vials filled with 15 ml of Aquasol II at the park laboratory. Moreover, beginning in 1989, the filters were fumed for a short period over a solution of 0.2 N HCL for 10 sec before inserting them into the vials. All samples were counted in a Beckman Liquid Scintilation Counter (Model LS9000) at the OSU Radiation

Table 2. List of taxa found in phytoplankton samples from Crater Lake during the period from June 26, 1985 through September 5, 1990. The factor used for converting algal units per liter to biovolume, expressed as cubic micrometers per liter, is included for each taxon.

TAXON	FACTOR
DIVISION CHRYSOPHYTA	
Class Bacillariophyceae:	
Achnanthes lanceolata (Bréb.) Grun.	675
Achnanthes lanceolata var. *dubia* Grun.	294
Achnanthes minutissima Kütz.	276
Asterionella formosa Hass	920
Cocconeis rugosa Sov.	1021
Cyclotella kutzingiana Thwaites	339
Cymbella turgida Greg.	2160
Epithemia sorex Kütz.	7800
Fragilaria construens (Ehr.) Grun.	540
Fragilaria construens var. *veneta* (Ehr.) Grun.	260
Fragilaria crotenensis var. *oregona* Sov.	1229
Fragilaria leptostauron (Ehr.) Hust.	820
Fragilaria pinnata Ehr.	300
Fragilaria vaucheriae (Kütz.) Peters	640
Fragilaria vaucheriae var. *capitellata* (Grun.) Patr.	1100
Gomphonema heidinii Hust.	367
Gomphonema olivaceum var. *calcarea* (Cl.) Cl.	480
Gomphonema parvulum Kütz.	600
Gomphonema sp.	482
Navicula cryptocephala var. *veneta* (Kütz.) Rabh.	780
Navicula seminulum Grun.	176
Navicula sp.	749
Nitzschia acicularis W. Smith	144
Nitzschia acuta Hantzsch	1905
Nitzschia bacata Hust.	380
Nitzschia closterium (Ehr.) W. Smith	144
Nitzschia dissipata(Kütz.) Grun.	29
Nitzschia fonticola Grun.	120
Nitzschia frustulum Kütz.	276
Nitzschia gracilis Hantzsch	473
Nitzschia innominata Sov.	462
Nitzschia linearis W. Smith	9342
Nitzschia palea (Kütz.) W. Smith	1300

Table 2. (cont.)

TAXON	FACTOR
Nitzschia perminuta Grun.	315
Nitzschia serpenticula Arch.	2820
Nitzschia tryblionella Hantzsch	42000
Nitzschia tryblionella var. *levidensis* Hantzsch	857
Nitzschia vermicularis (Kütz.) Grun	4000
Rhoicosphenia curvata (Kütz.) Grun *ex* Rabh.	840
Stephanodiscus hantzschii Grun.	226
Synedra acus Kütz.	3114
Synedra delicatissima W. Smith	5000
Synedra mazamaensis Sov.	495
Synedra rumpens Kütz.	998
Synedra rumpens var. *familiaris* (Kütz.) Hust.	1460
Synedra tenera W. Smith	1050
Class Chrysophyceae:	
Bicoeca petiolatum (Stein) Pringsheim	137
Calycomonas sp.	73
Chromulina grandis Dolf.	268
Chromulina minor Pasch.	29
Chromulina parvula Conr.	17
Chromulina spectabilis Scherffel	72
Chrysocapsa planctonica Pascher	103
Chrysochromulina sp.	92
Chrysolykos planctonicus Mack.	50
Dinobryon bavaricum Imhoff.	77
Dinobryon sertularia Ehr.	399
Dinobryon sociale Ehr.	124
Diplomitella socialis (Kent) Silva	172
Kephyrion asper (Lack) Bourr.	36
Kephyrion cupriloforme Conr.	14
Kephyrion spirale (Lack.) Conr.	35
Ochromonas elegans Dolf.	226
Ochromonas granulosa H. Meyer	113
Ochromonas miniscula Conr.	33
Ochromonas ovalis Dolf.	100
Ochromonas verrucosa Skuja	29
Ophiocytium capitatum Wolle	146
Ophiocytium cochleare A. Br.	196
Ophiocytium parvulum (Perty) A. Br.	196
Pseudochromulina asymmetrica Dolf	9
Pseudokephyrion conicum (Schill) Schm.	65
Pseudopedinella sp.	924

Table 2. (cont.)

TAXON	FACTOR
Class Xanthophyceae:	
Tribonema affine G.S. West	1853
DIVISION CHLOROPHYTA	
Ankistrodesmus convolutus Corda	177
Ankistrodesmum falcatus (Corda) Ralfs.	177
Ankistrodesmus falcatus var. *acicularis* (A. Braun) G.S.	110
Ankistrodesmus spiralis (Turner) Lemm.	30
Crucigenia quadrata Morren	70
Dictyosphaerium pulchellum Wood	24
Kirchneriella contorta (Schmidle) Bohlin	9
Mougeotia parvula Hassel	424
Mougeotia sp.	33757
Oocystis pusilla Hansgrig	327
Planktosphaeria glatinosa G.M. Smith	144
Scenedesmus bijuga (Turp.) Lagerh.	88
Selenatrum minuta (Naeg.) Collins	22
DIVISION CRYPTOPHYTA	
Chroomonas acuta Uter.	34
Cryptochrysis polychrysis Pasher	963
Cryptomonas erosa Ehr.	339
Rhodomonas lacustris Pascher and Ruttner	1042
Rhodomonas minuta Skuja	823
Rhodomonas minuta var. *nannoplantica* Skuja	254
DIVISION CYANOPHYTA	
Nostoc sp.	72
Dactylococcopsis fascicularis Lemm.	12
Lyngbya sp.	4
Spirulina major Kütz.	9
Aphanocapsa delicatissima West & West	2
DIVISION PYRRHOPHYTA	
Amphidium lutum Skuja	346
Gymnodinium fuscum (Ehr.) Stein	33000
Gymnodinium inversum Nygaard	5440
Peridinium aciculiferum (Lemm.) lemm.	9425
Peridinium inconspicuum Lemm.	6750

Center. Beckman standards were used in each run of samples, and the counts were automatically corrected for quench and efficiency.

Concentrations of carbon-14 in the inoculum were determined for each set of vials produced from the stock solutions (New England Nuclear Company). This calibration was done by transferring 0.01 ml of the inoculum into scintilation vials filled with Aquasol II. Results from this procedure indicated that activities of the inoculum were not consistent among the stock solutions. In 1986 and 1987 through August, the inoculum had an average concentration of 2.68 μCi/ml, while in September 1987 and in January 1988, the concentration was 1.38 μCi/ml; the mean concentration in 1989 and 1990 was 4.0 μCi/ml. These activities were used in standard equations to estimate rates of primary production. The amount of carbon-12 available in each sample was estimated from the pH and alkalinity of water samples obtained concurrently with samples for carbon-14 inncubation. The factor used for converting total alkalinity to available carbon was 0.255, a value estimated by the procedure described by Saunders et al. (1962).

Water for chlorophyll determinations was transferred from Van Dorn bottles to 500 ml opaque polyethylene bottles. A few drops of a saturated solution of $MgCO_3$ were added to each sample, and the bottles were stored in the dark in boxes refrigerated with snow or ice. At the park laboratory, the samples were filtered (0.45 μm Millipore filters), usually within 3 to 5 hr after they were collected. During filtration, the vacuum was less than 10 inches of Hg, and five drops of $MgCO_3$ were added to each filter. After filtration, each filter was transferred to a scintilation vial and stored in a freezer.

Beginning in July 1990, a new study was undertaken to determine the relative contribution of picoplankton (i.e., autotrophic organisms less than 2 μm in diameter) to the total chlorophyll in the water column. To accomplish this, 1 l of water was first filtered through a 2.00 μm Millipore filter and then filtered again through a 0.22 μm filter. It was assumed that chlorophyll extracted from the material retained on the 0.22 μm filter was primarily associated with picoplankton and that the ratio between this fraction and the chlorophyll

extracted from both filters was indicative of the relative contributions of the two size classes.

Chlorophyll concentration in the samples was determined by the fluorometric procedure (Standard Methods, 1985). The frozen filters were placed into a 15 ml graduated glass tube to which 10 ml of 90% aqueous acetone was added. The filters were stored overnite in a cold room at 3° C. The following morning, the samples were centrifuged for 10 min and processed in a Turner Designs Model 10 Fluorometer. Chlorophyll standards provided by the Environmental Protection Agency were used to calculate chlorophyll concentrations from fluorometric units.

Data Analysis

Raw data obtained from the microscopic examination of plankton samples were recorded on computer coding sheets according to the standard format required by the programs selected for data analysis. Species diversity was expressed by Shannon's information measure:

$$H' = \Sigma(n_i/N)\log_e(n_i/N)$$

where n_i is the number of organisms belonging to the i-th taxon in a sample of N individuals, and S is the number of species in the sample. As an indicator of dominance in the phytoplankton samples, the infomation-based measure of redundancy was calculated from:

$$R = (H_{max} - H)/(H_{max} - H_{min}).$$

In this case, H_{max} and H_{min} represent the maximum and minimum possible values for a sample of size N and S species (McIntire and Overton 1971). Shannons index is a measure of heterogeneity (i.e., its value is determined by both species richness and relative abundance of each taxon). The redundancy index can vary from 0, when taxa are equally common, to 1, when there is one dominant taxon and all others are represented by a single individual.

Taxonomic resemblance between samples and groups of samples was expressed by SIMI, a similarity measure related to Simpson's measure of concentration and equal to the cosine of the angle between two vectors indicating the relative positions of two assemblages in species space (Stander 1970, McIntire and Moore 1977). The mathematical expression is

$$SIMI = (\Sigma p_{ai}p_{bi})/(\Sigma p^2_{ai} \times \Sigma p^2_{bi})^{1/2}.$$

SIMI is the degree of similarity between assemblages a and b; p_{ai} and p_{bi} are the proportions of individuals represented by the i-th taxon in assemblages a and b, respectively; and S is the total number of taxa in the assemblages. SIMI can vary between 0, when the assemblages have no taxa in common, to 1, when the relative abundances of the taxa are exactly the same in the assemblages.

Temporal and spatial variation in the phytoplankton assembages of Crater Lake was analyzed by Two-way Indicator Species Analysis using TWINSPAN, a computer program developed by M. O. Hill at Cornell University (Hill et al. 1975, Gauch 1982). TWINSPAN classifies samples (i.e., species-abundance data) and then uses this classification to obtain a corresponding classification of species according to their preferences. TWINSPAN is particularly well suited for the analysis of large data sets. After an interpretable cluster structure was found by this classification procedure, each sample in the data file was coded according to its cluster assignment, and the file was then reanalyzed by a canonical analysis of discriminance (Pimental 1979). The discriminant analysis provided variables that allowed a graphic display of the cluster structure generated by TWINSPAN. These variables also were correlated with selected environmental variables and with the original species variables to identify taxa that best separated the clusters.

For the TWINSPAN analysis, the data were partitioned into two separate files: (1) 1985 - 1988 data consisting of 254 samples, and (2) 1989 - 1990 data with 156 samples. Samples collected in January 1988 were included in the analysis of the 1989 - 1990 data, because these samples were counted by R. Truitt and included picoplankton down to 1 μm

in diameter. Taxa representing less than 1% of the total cell density and total cell biovolume in the data file were eliminated from the analysis. The numbers of taxa retained for the analyses were 25 (1985 - 1988) and 35 (1989 - 1990).

Results

Taxonomic Structure

The phytoplankton samples processed during the 10-year study contained a total of 157 taxa which included 55 diatoms (Bacillariophyceae), 53 chrysophytes (Chrysophyceae), 1 xanthophyte (Xanthophyceae), 21 chlorophytes (Chlorophyceae), 12 dinoflagellates (Pyrrhophyta) 6 cryptomonads (Cryptophyta), 7 cyanobacteria (Cyanophyta), and 2 unknown taxa. A list of 103 of the most prominant taxa, most of which were identified to the species or variety level, is presented in Table 2. When an organism could not be identified to species, it was given a unique number and a sketch was made so that it could be recognized and counted in other samples. Table 2 also includes the multiplier for each taxon that was used to convert estimates of cell density to biovolume.

Preliminary Study: 1982 - 1984. The preliminary study of the distribution and abundance of Crater Lake phytoplankton had three primary objectives: (1) to compare the taxonomic structures of assemblages in two deep-water basins (Station 13 and Station 23); (2) to obtain preliminary information concerning spatial and temporal variations in the phytoplankton during the summer and early fall; and (3) to obtain initial estimates of total phytoplankton biovolume at an intensive study site (Station 13). To accomplish these objectives, the 1982 - 1984 data set was analyzed by a simple measure of similarity (SIMI) after the data had been pooled into combinations compatible with the objective questions under consideration. In addition, cell densities were transformed into estimates of total cell biovolume using conversion factors worked out later in 1985 (Table 2).

Total cell biovolume in the water column between July 1982 and September 1984, integrated to a depth of 200 m, ranged from 23,380 $mm^3\ m^{-2}$ in September 1984 to 145,620

$mm^3\ m^{-2}$ in September 1983 (Fig. 2A). The value for September 7, 1983 was unusually high in comparison to values obtained throughout the program (also see Fig. 4A in the next section). The corresponding raw data indicated that this value was the result of the presence of two large dinoflagellates (*Peridinium inconspicuum* and *P. aciculiferum*) in relatively low densities. Considering the small sample size used during this period of the program (counts of 100 cells), estimates of cell biovolume were more vulnerable to sampling error than data obtained after 1984. With the exception of the samples taken on July 20, 1982 and September 7, 1983, the data also indicated that greater than 65% of the cell biovolume of netplankton and nannoplankton was concentrated below a depth of 20 m.

With the exception of samples taken on July 29, 1982, the species composition of phytoplankton assemblages at Station 13 and Station 23 was similar (SIMI > 0.74) at corresponding depths in the water column (Table 3). Data for 72 samples obtained in July or August of 1982, 1983, and 1984 from 12 depths in the water column were pooled into two samples (36 samples each) representing Station 13 and Station 23. The SIMI value for the comparison of the two pooled samples was 0.971, a value that indicated a very high overall similarity between the floras at the two sampling stations. Another comparison of 72 pooled samples obtained in September of 1982, 1983, and 1984 generated an even higher SIMI value (0.994).

SIMI values expressing overall resemblance between phytoplankton floras during the summers of 1982, 1983, and 1984 indicated that the floras in 1983 and 1984 were similar (SIMI > 0.8), whereas the flora in 1982 was less similar to the floras observed in 1983 and 1984 (Table 4), possibly because the date of sampling was earlier in 1984 than in either 1982 or 1983. This analysis was performed by pooling all samples obtained from 12 depths at Station 13 and Station 23 into three samples representing July 29, 1982, August 24, 1983, and July 12, 1984. A similar analysis of samples taken in September of 1982, 1983, and 1984 indicated that the floras for the three years were very similar (SIMI > 0.84) at that time of the year (Table 5). Consequently, the preliminary study suggested that, while the

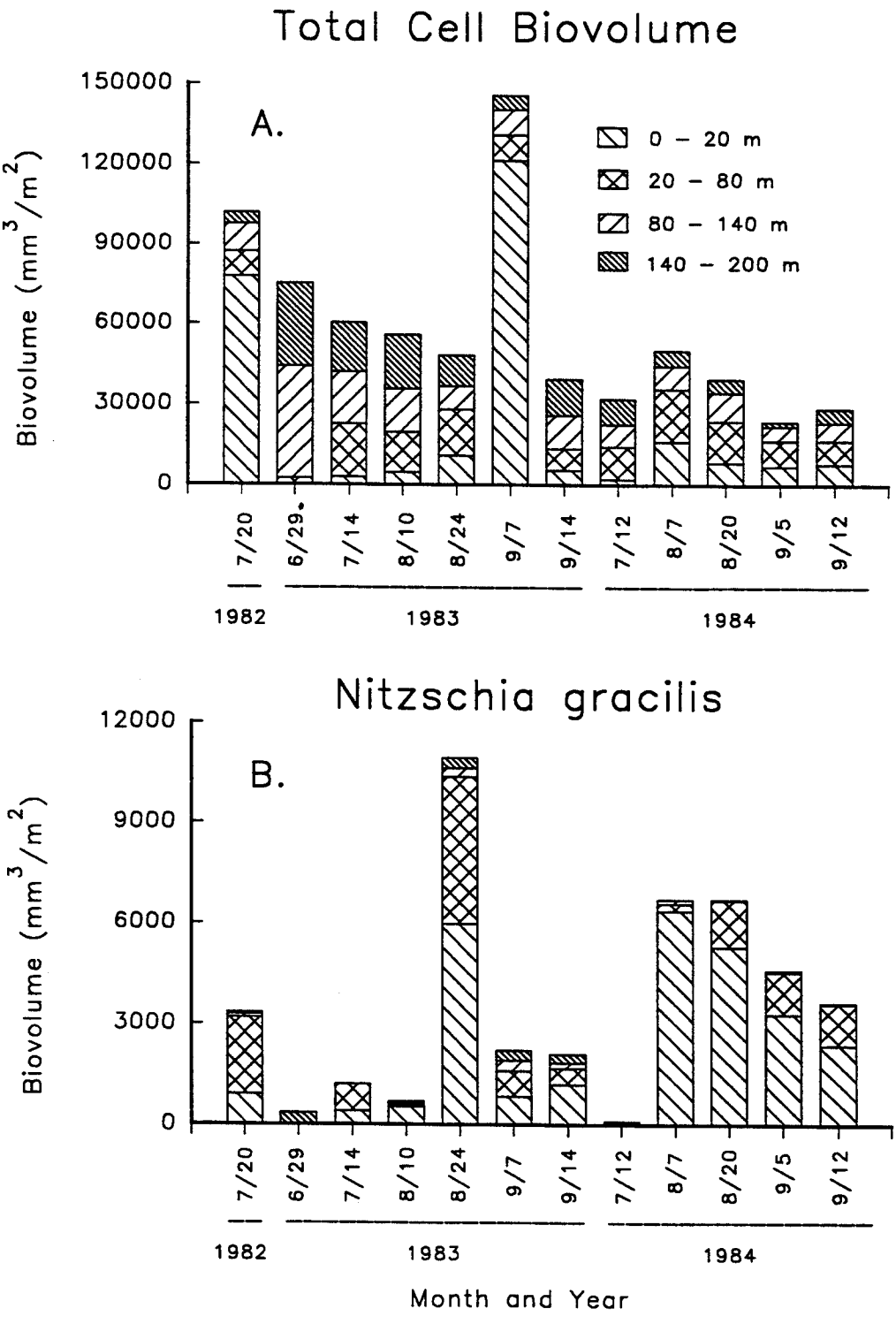


Figure 2. Vertical distribution of total phytoplankton cell biovolume (A) and biovolume of Nitzschia gracilis (B) in the water column at Station 13 between July 20, 1982, and September 12, 1984.

Table 3. Mean similarity values (SIMI) for the comparison of the species composition of the phytoplankton floras at Station 13 and Station 23. Each number represents the mean of 12 values comparing the floras at corresponding depths of 0, 10, 20, 40, 60, 80, 100, 120, 140, 160, 180, and 200 m.

Date	Mean Similarity (SIMI)	Standard Error
7/29/82	0.508	0.095
9/182	0.853	0.071
8/24/83	0.826	0.056
9/7/83	0.868	0.039
9/14/83	0.833	0.066
7/12/84	0.743	0.066
7/24/84	0.927	0.085
8/7/84	0.944	0.015
8/20/84	0.911	0.035
9/5/84	0.872	0.042
9/12/84	0.868	0.333
Mean	0.832	0.055

Table 4. Matrix of similarity values (SIMI) expressing resemblance between the phytoplankton floras in 1982, 1983, and 1984. The samples were obtained from 12 depths (0, 10, 20, 40, 40, 60, 80, 100, 120, 140, 160, 180, and 200 m) at Station 13 and Station 23 on July 29, 1982, August 24, 1983, and July 12, 1984. Data were pooled by year into three samples.

Year	1983	1984
1982	0.742	0.580
1983	--	0.832

Table 5. Matrix of similarity values (SIMI) expressing resemblance between the phytoplankton floras in 1982, 1983, and 1984. The samples were obtained from 12 depths (0, 10, 20, 40, 40, 60, 80, 100, 120, 140, 160, 180, and 200 m) at Station 13 and Station 23 on September 1, 1982, September 7, 1983, and September 5, 1984. Data were pooled by year into three samples.

Year	1983	1984
1982	0.896	0.848
1983	--	0.929

species composition of the phytoplankton in Crater Lake exhibits some variation from year to year, there were aspects of taxonomic structure that were potentially predictable on a seasonal basis, and that during the period from 1982 through 1984 the flora was more predictable in the early fall than in July and August. However, the SIMI value provided very little information about the rarer species, because it gave greatest weight to dominant taxa.

The 1982 - 1984 study also provided an opportunity for a preliminary examination of vertical distribution in the water column. For this analysis, all phytoplankton samples obtained on July 29, 1982, August 24, 1983, and July 12, 1984 at stations 13 and 23 were pooled by depth into 12 samples, and SIMI values were calculated for all possible pairs of pooled samples (Table 6, upper right triangle). A similar analysis was performed with data obtained from samples taken on September 1, 1982, September 7, 1983, and September 5, 1984 (Table 6, lower left triangle). Results of these analyses indicated that there was a discontinuity in the species composition of the flora between 10 m and 20 m during the summer (i.e., in July and August), and that the flora had a relatively uniform composition between 100 m and 200 m. In early fall, the discontinuity was deeper, between 20 m and 40 m, and the flora had a relatively uniform composition between 80 m and 200 m. The change in the position of the discontinuity with season corresponded to a gradual increase in the depth of the epilimnion, usually from about 10 m to 20 m, which occurs between July and September.

In general, spatial distributions of *Nitzschia gracilis*, *Stephanodiscus hantzschii*, and *Tribonema* sp. (=*Mougeotia* sp.) during the summer and early fall of 1982, 1983, and 1984 were similar to patterns found in 1978, 1979 and 1980 by Larson et al. (1987). Between 1982 and 1984, *Nitzschia gracilis* reached its maximum relative abundance in the epilimnion (i.e., between 0 m and 20 m) in August 1983 and in August and September of 1984; it also was prominent at depths between 20 m and 80 m (Fig. 2B). *Stephanodiscus hantzschii*

Table 6. Matrix of similarity values (SIMI X 1000) expressing the resemblance between the phytoplankton floras at different depths in the water column. The samples were obtained from 12 depths at Station 13 and Station 23 on July 29, 1982, August 24, 1983, and July 12, 1984 (upper right triangle), and on September 1, 1982, September 7, 1983, and September 5, 1984 (lower left triangle). Data were pooled by depth into 12 samples for each set of values.

Depth (m)	0	10	20	40	60	80	100	120	140	160	180	200
0	--	906	407	319	471	117	125	46	63	149	103	81
10	993	--	590	323	589	174	164	91	95	159	148	117
20	868	855	--	712	890	778	729	676	558	442	496	444
40	234	197	495	--	834	900	914	877	778	678	711	685
60	109	86	383	927	--	857	808	734	628	518	553	497
80	139	100	402	953	882	--	960	916	780	605	662	601
100	133	95	376	927	874	947	--	973	884	726	785	737
120	73	44	268	798	695	830	932	--	943	805	870	828
140	124	94	303	794	665	814	918	993	--	904	967	948
160	81	52	240	695	549	724	827	961	968	--	924	919
180	81	52	230	693	522	728	820	955	969	990	--	988
200	80	50	246	725	594	758	869	980	984	990	987	--

was found primarily at depths below 80 m in 1983 and 1984 (Fig. 3A), while *Mougeotia* sp. occurred in samples from all depths below 20 m (Fig. 3B).

In summary, the results of the preliminary study established that (1) the phytoplankton assemblages were similar in two of three major basins of Crater Lake during the summer months and in September; (2) the flora was variable from year to year with some predictable patterns; (3) the taxonomic structure of phytoplankton assemblages in the water column exhibited temporal and spatial discontinuities, possibly related to the physical process of thermal stratification; and (4) certain dominant taxa exhibited repeatable annual patterns between 1978 and 1984. Based on these results and careful consideration of the financial resources available for the program, it was decided that beginning in 1985 the sampling program would be concentrated at Station 13, the site of the deepest basin in the lake. This strategy provided a more complete analysis of vertical distribution and temporal patterns at the expense of a more detail analysis of horizontal distribution.

Netplankton and Nannoplankton: 1985 - 1988. With the exception of samples collected in January 1988, samples taken in 1985, 1986, 1987, and 1988 were processed by M. Debacon. Data from these samples were analyzed together, while data from the January 1988 samples, processed by R. Truitt, were included in the analysis of data from the 1989 and 1990 samples, also processed by R. Truitt. The major difference between the two data sets, i.e., between the 1985 - 1988 and the 1989 - 1990 data, was the inclusion of picoplankton down to a diameter of about 1 um in the 1989 - 1990 and January 1988 counts. The inclusion of picoplankton in the data provided the first indication of the relative contribution of the very small cyanobacteria (determined by fluorescent microscopy) to the production dynamics in the water column; greatly increased the value of the dominance measure (R) of community structure; and greatly increased estimates of total cell density in the water column, while having relatively little effect on estimates of total cell biovolume.

Total cell biovolume of netplankton and nannoplankton between June 1985 and August 1988, integrated to a depth of 200 m, ranged from 7,190 mm^3 m^{-2} in January 1987 to

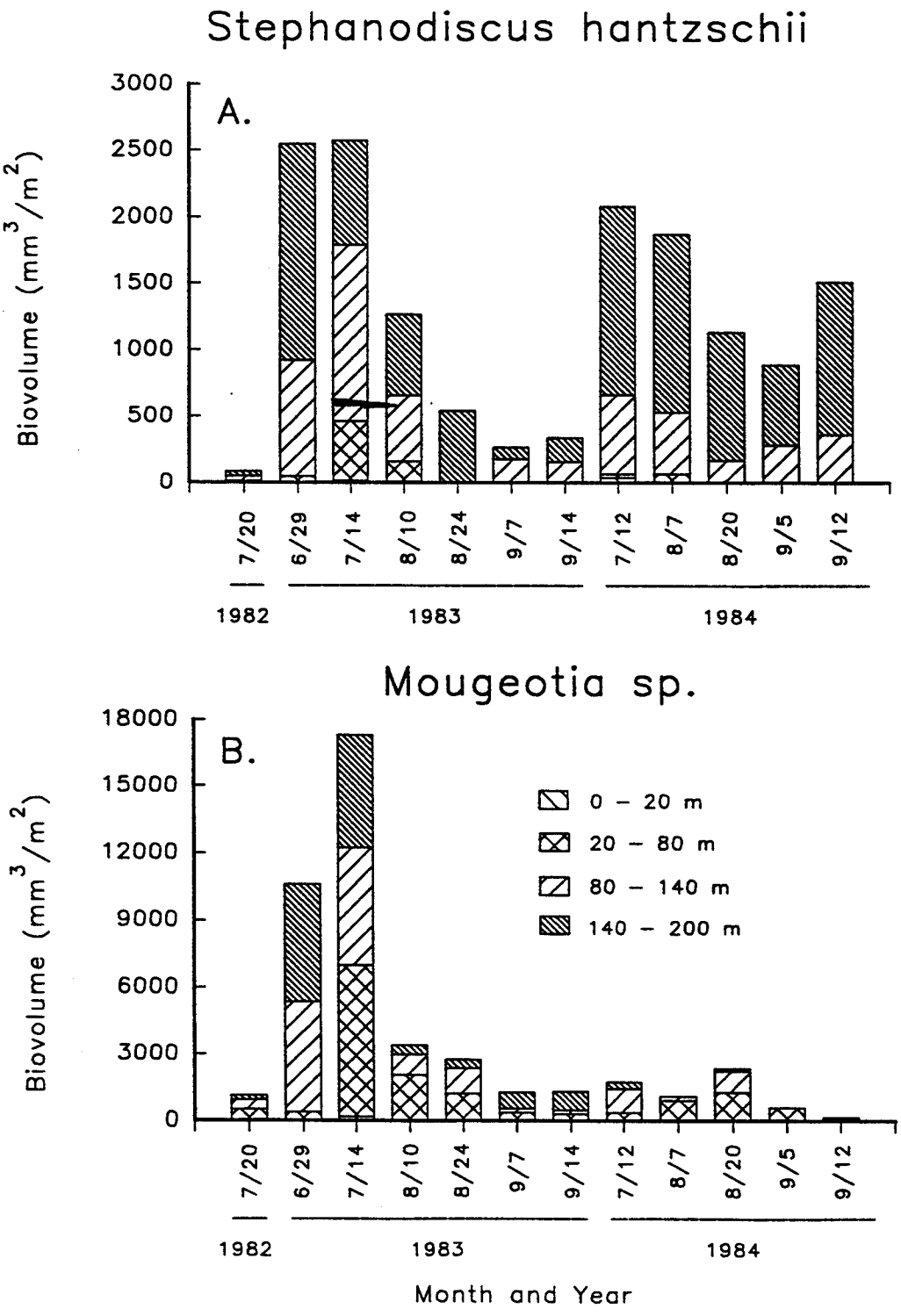


Figure 3. Vertical distribution of the cell biovolume of Stephanodiscus hantzschii (A) and Mougeotia sp. (B) in the water column at Station 13 between July 20, 1982, and September 12, 1984

a maximum of 55,190 mm^3 m^{-2} in July 1988 (Fig. 4A); the corresponding mean value for this period of time was 31,653 mm^3 m^{-2}. In general, total cell biovolume was higher in 1987 and 1988 than in 1985 and 1986. Estimates obtained during the preliminary study for 1983 and 1984 were more similar to values found for 1987 and 1988 than to the values for 1985 and 1986 (Figs. 2A and 4A). Moreover, the vertical distribution of cell biovolume varied seasonally, with concentrations in the upper 20 m of the water column reaching a maximum in either July or August of each year. These summer maxima corresponded to the formation of the epilimnion and the concurrent dominance of *Nitzschia gracilis*. However, regardless of season, over 70% of the total cell biovolume in the upper 200 m was distributed below a depth of 20 m.

Cell density of netplankton and nannoplankton between June 1985 and August 1988, excluding January 1988, was highest in July 1987 (1,070 cells/ml) and August 1988 (1,110 cells/ml) at the 5-m and 20-m depths, respectively; the minimum cell density found in the upper 200 m of the water column was 22 cells/ml at 200 m in September 1985. Total cell density integrated to a depth of 200 m for the same period, again excluding January 1988, ranged from 2.08 X 10^{10} cells/m^2 in January 1987 to 1.17 X 10^{11} cells/m^2 in May 1986 (Fig. 4b), with a mean value of 4.97 X 10^{10} cells/m^2. The vertical distribution of cells in the water column was similar to the distribution of cell biovolume, with more than 75% of the cells concentrated below a depth of 20 m on all sampling dates.

Cell biovolumes of eleven selected species also were integrated to a depth of 200 m (Figs. 5, 6, 7, 8, and 9). These species were among the 25 most abundant taxa found between June 1985 and August 1988, and were considered indicators of summer patterns, when the epilimnion was established, and at other times of the year, when thermal stratification was not present. Figures 5 - 9 also include a cell density factor (cdf), a constant that converts the integrated cell biovolumes to estimates of integrated cell density expressed as cells/m^2. In this case, a low cdf value (e.g., values for the dinoflagellates *Gymnodinium*

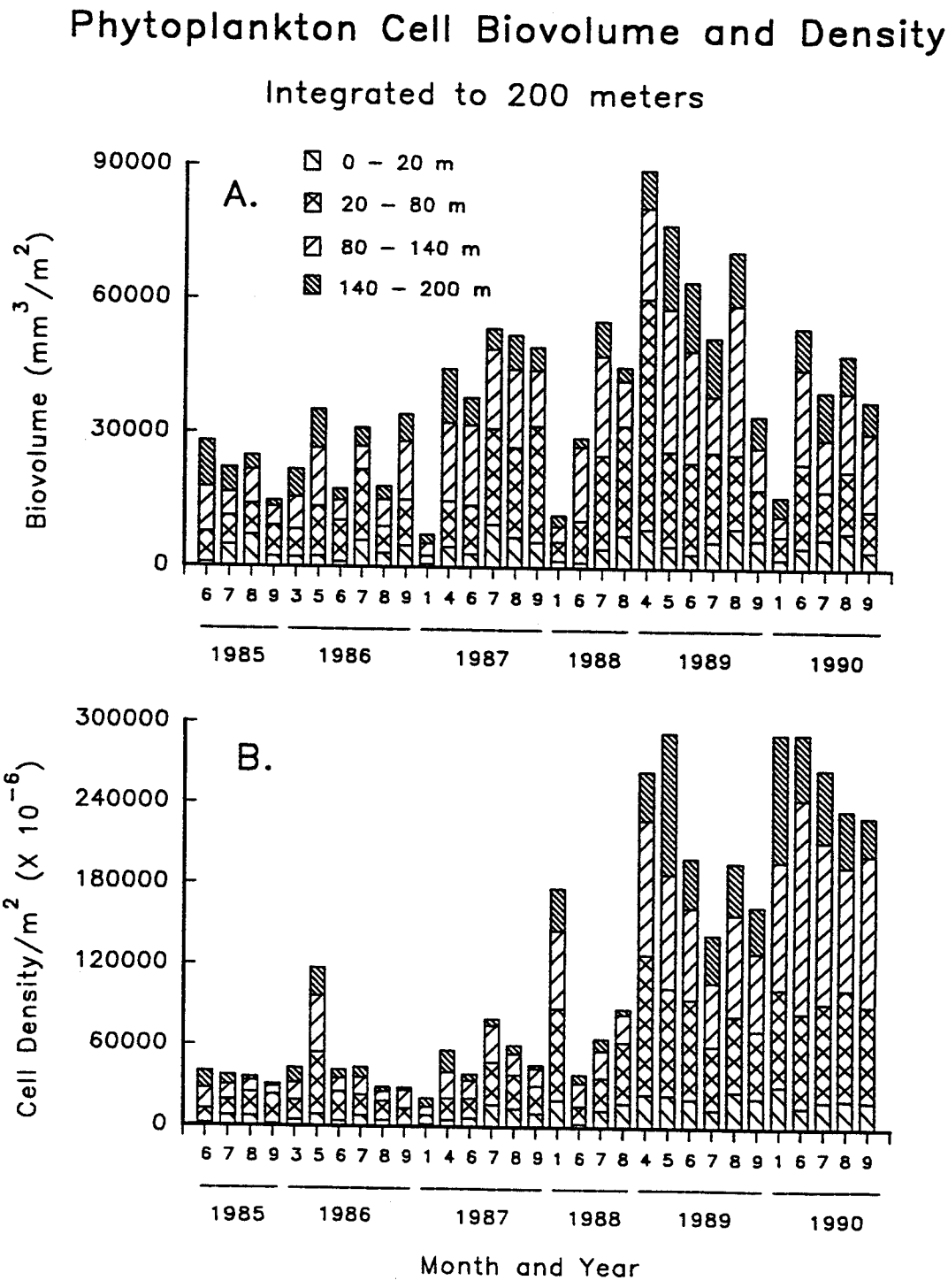


Figure 4. Vertical distribution of total phytoplankton cell biovolume (A) and cell density (B) in the water column at Station 13 between June 1985 and September 1990.

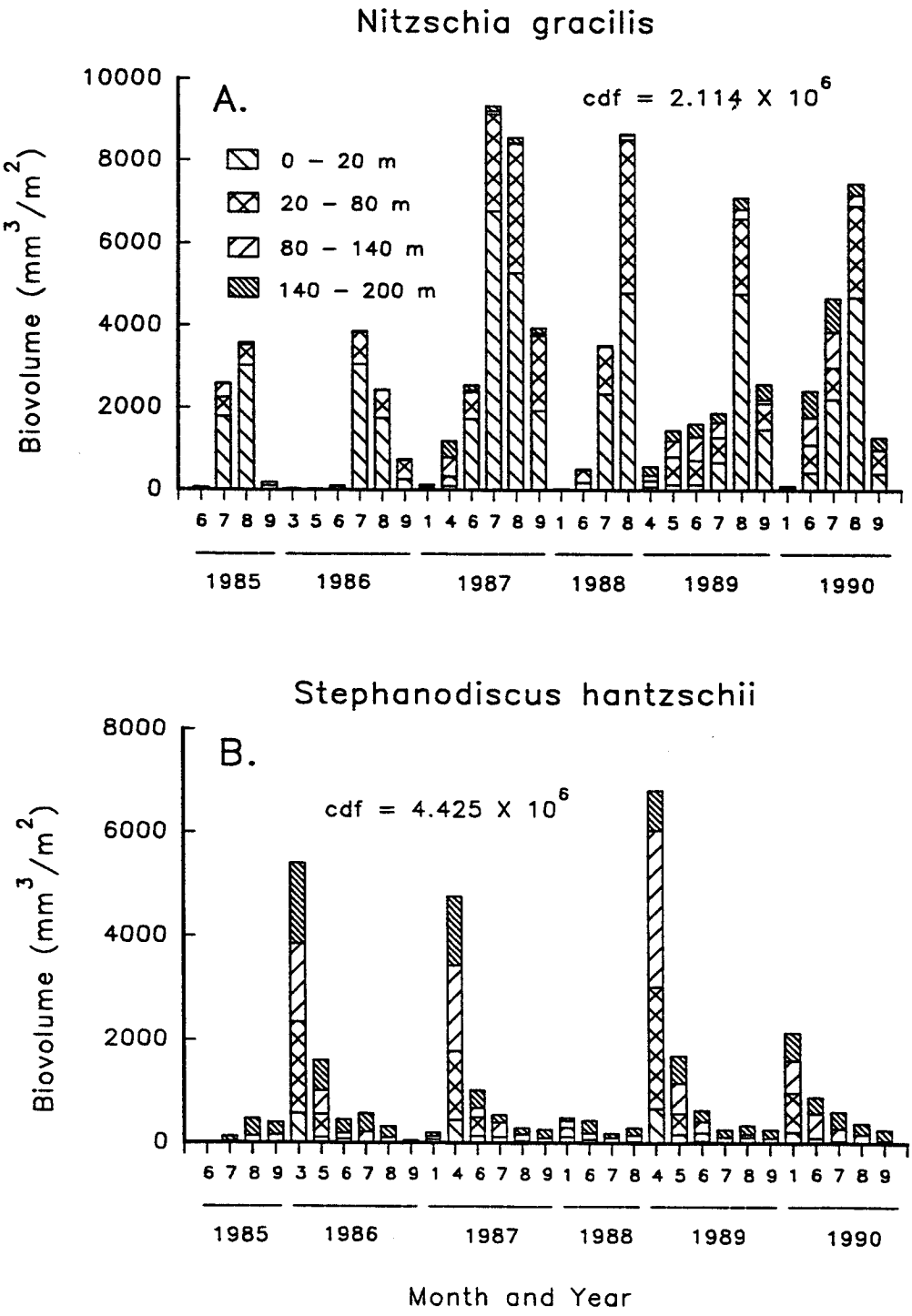


Figure 5. Vertical distribution of the cell biovolume of Nitzschia gracilis (A) and Stephanodiscus hantzschii (B) in the water column at Station 13 between June 1985 and September 1990.

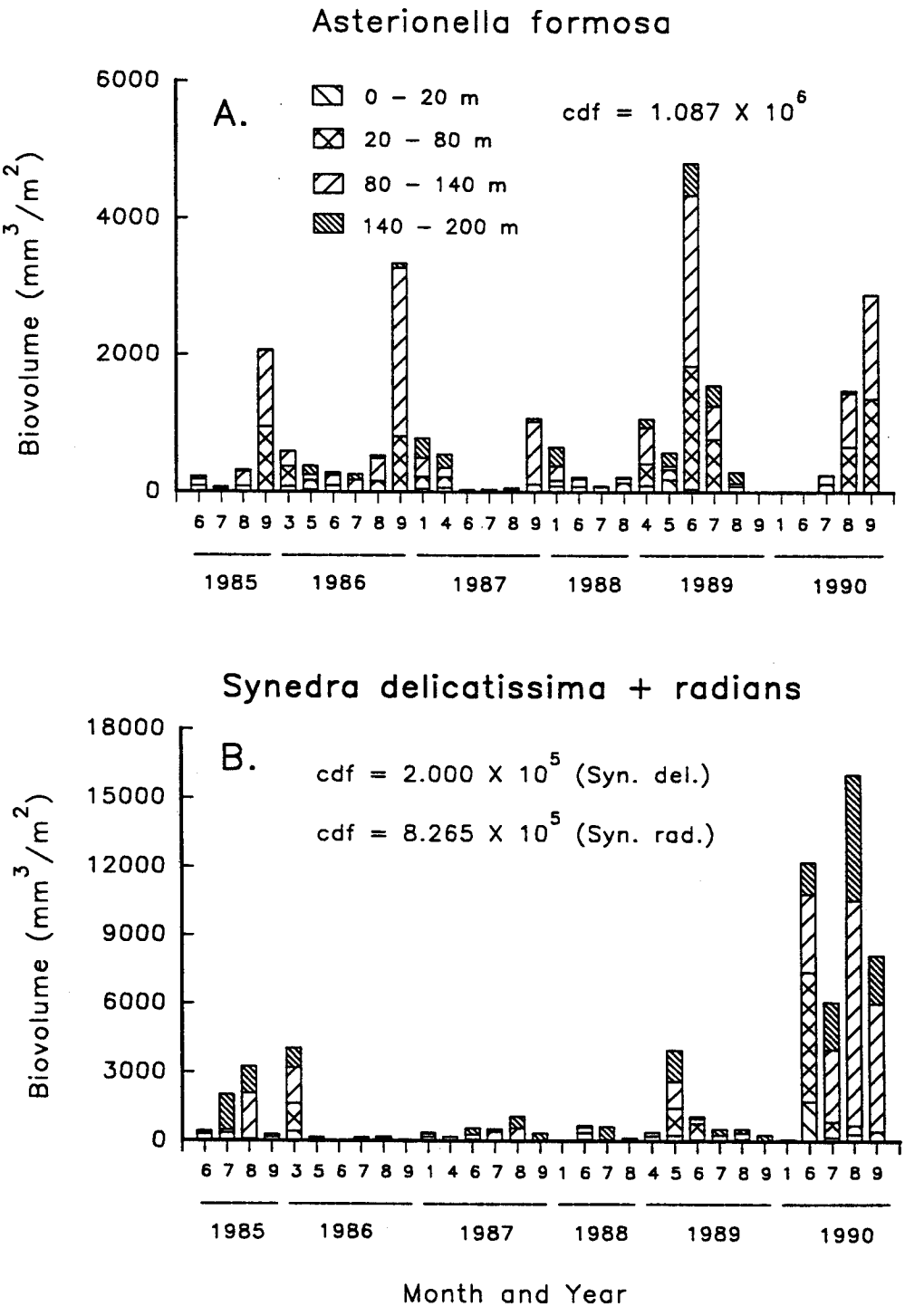


Figure 6. Vertical distribution of the cell biovolume of Asterionella formosa (A) and Synedra delicatissima + radians (B) in the water column at Station 13 between June 1985 and September 1990.

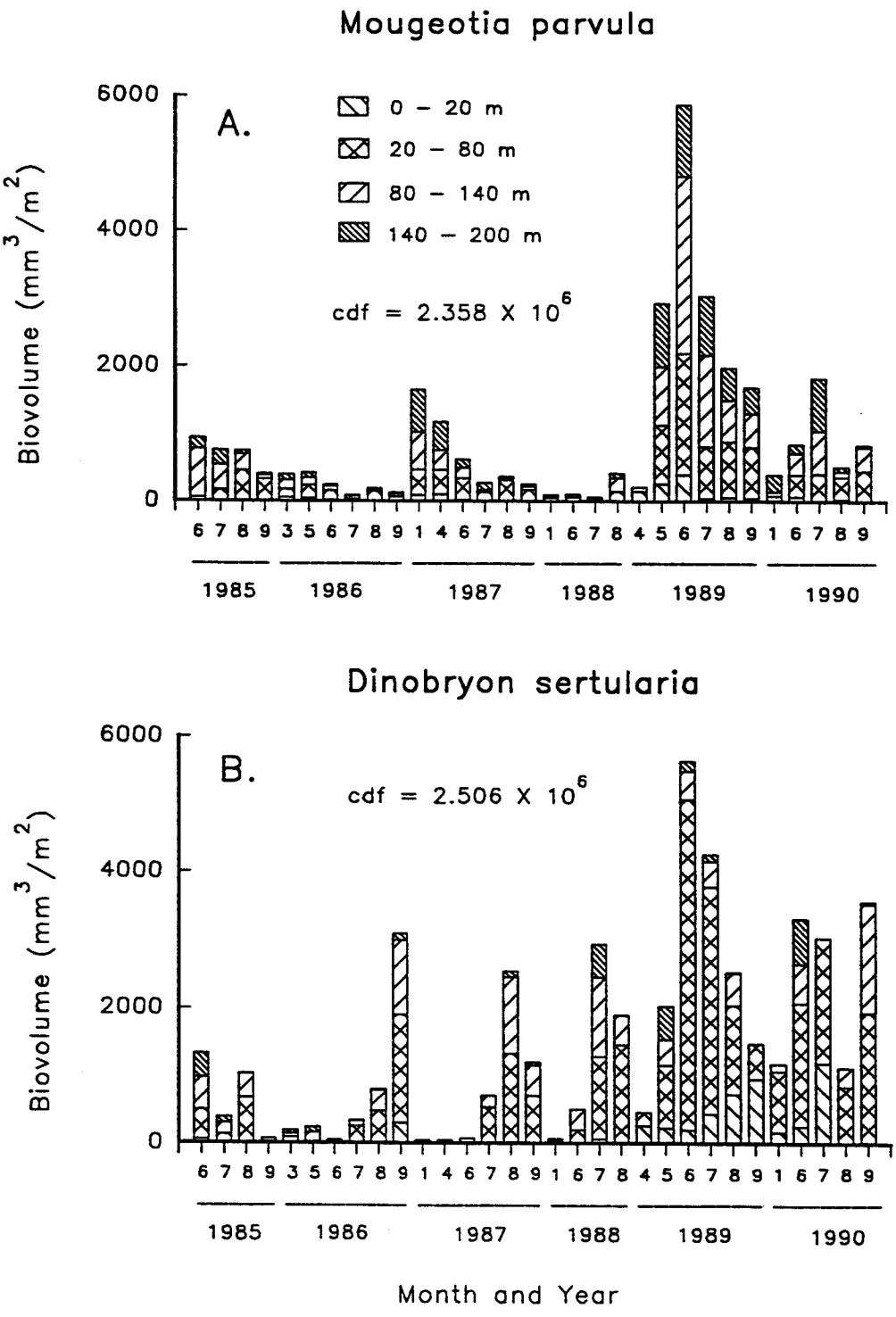


Figure 7. Vertical distribution of the cell biovolume of Mougeotia parvula (A) and Dinobryon sertularia (B) in the water column at Station 13 between June 1985 and September 1990.

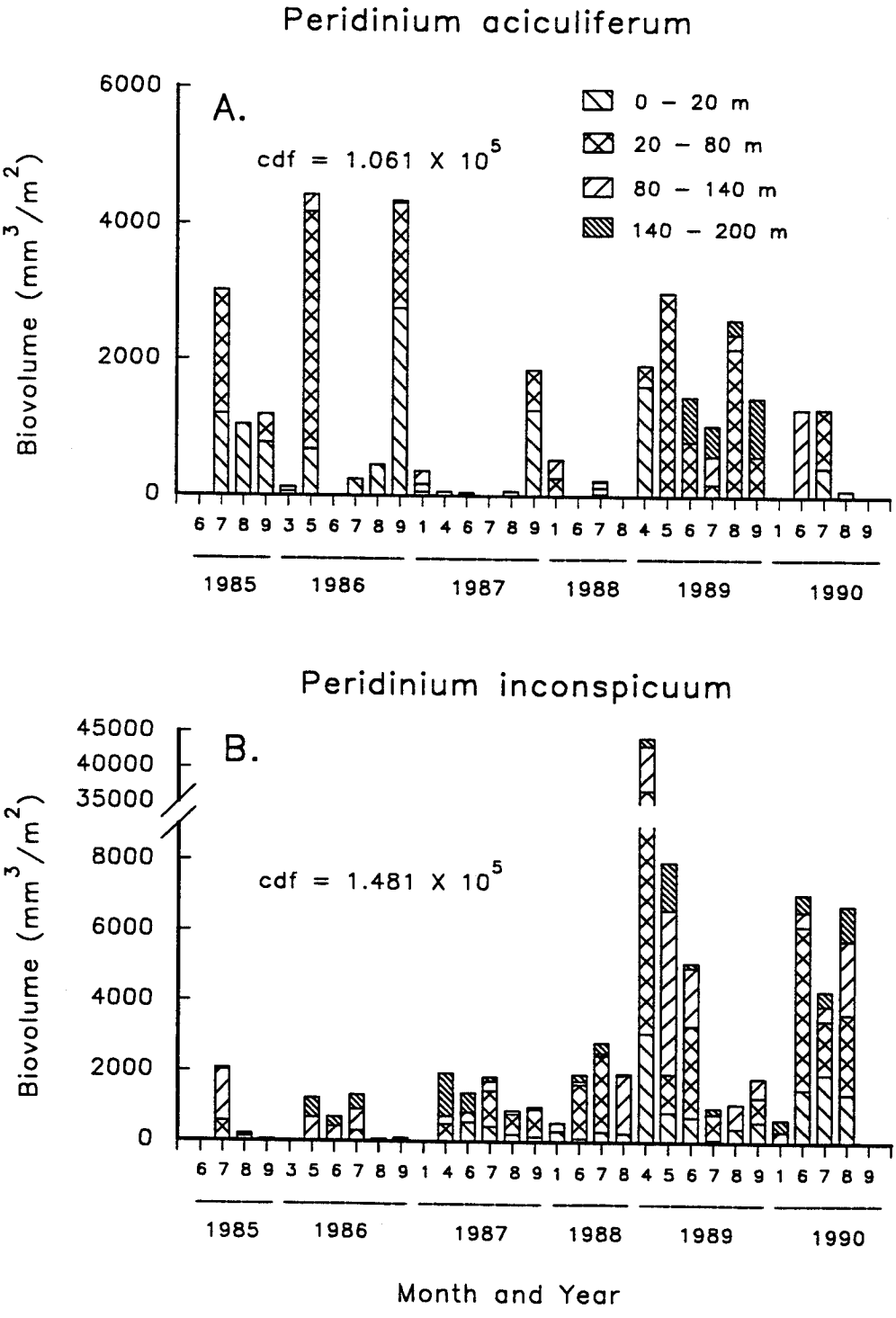


Figure 8. Vertical distribution of the cell biovolume of Peridinium aciculiferum (A) and Peridinium inconspicuum (B) in the water column at Station 13 between June 1985 and September 1990.

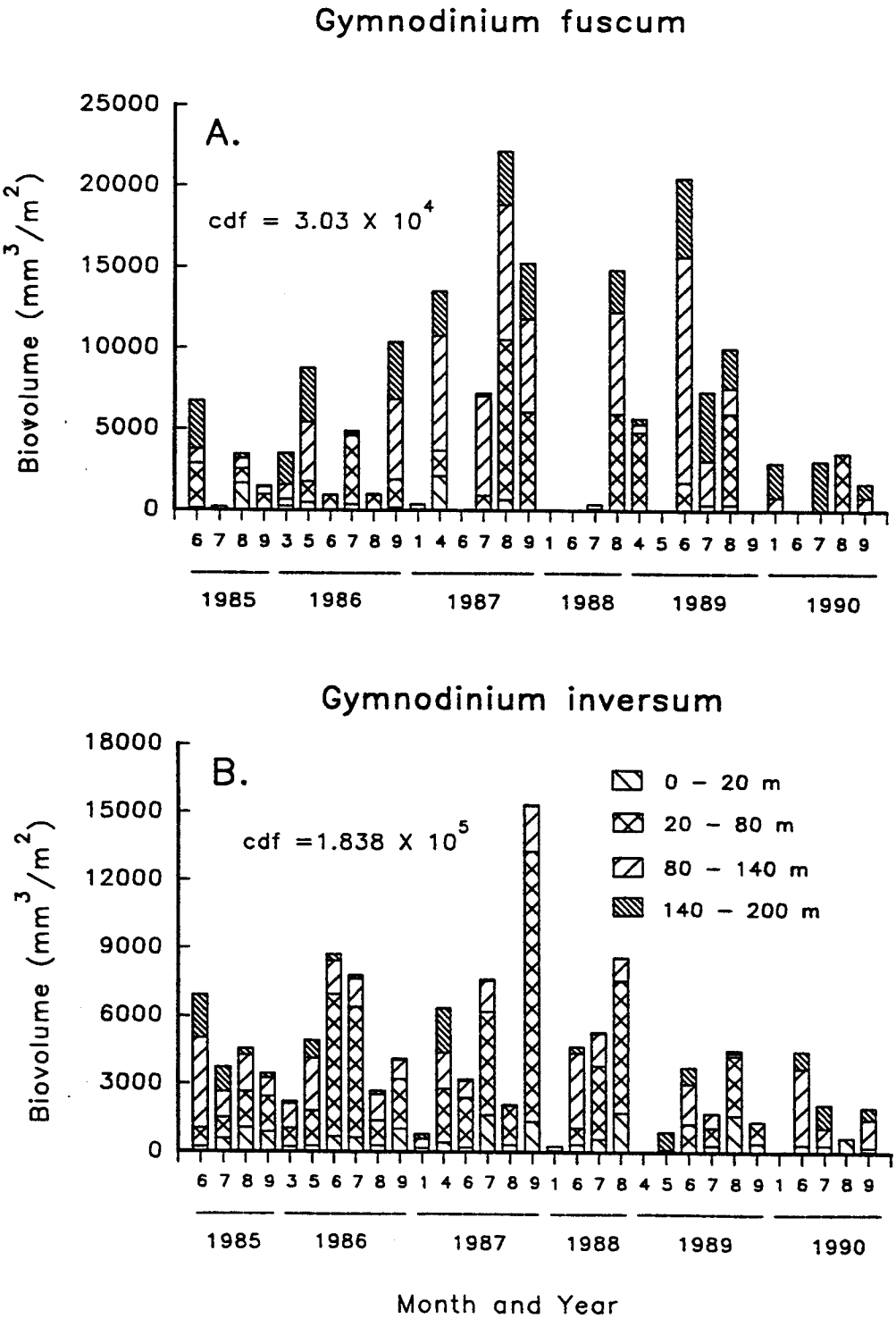


Figure 9. Vertical distribution of the cell biovolume of Gymnodinium fuscum (A) and Gymnodinium inversum (B) in the water column at Station 13 between June 1985 and September 1990.

fuscum, *G. inversum*, *Peridinium aciculiferum*, and *P. inconspicuum*) is indicative of a relatively large organism, whereas the larger values (e.g., values for *Stephanodiscus hantzschii*, *Nitzschia gracilis*, and *Dinobryon sertularia*) are associated with smaller taxa.

Nitzschia gracilis, *Stephanodiscus hantzschii*, *Asterionella formosa*, and to a lesser extent, *Dinobryon setularia* and *Mougeotia parvula* exhibited seasonal patterns of distribution between June 1985 and August 1988 (Figs. 5A, 5B, 6A, 7A, and 7B). *N. gracilis* was particularly abundant in the upper 20 m of the water column in July and August (Fig. 5A), while *S. hantzschii* reached its maximum biovolume in the winter or spring of the year (Fig. 5B). Cell biovolume of *S. hantzschii* was concentrated at depths below 80 m from midsummer through September, whereas in the spring when circulation occurred to a depth of 200 m, it was more uniformly distributed in the water column, a pattern that was consistent with the results of the preliminary study (Figs. 5B and 3A). *A. formosa* was abundant in September of 1985, 1986, and 1987 when most of its biovolume was concentrated at depths between 20 m and 140 m (Fig. 6A). *D. sertularia* reached relatively high biovolumes during the summer or in September at depths below 20 m, although it occasionally was found in the epilimnion (Fig. 7B). *M. parvula* was more abundant earlier in the year, particularly in the spring or in June (Fig. 7A). Of the taxa that exhibited recurring temporal patterns, only *N. gracilis* was dominant in the upper 20 m of the water column after the formation of the epilimnion, with mean relative abundances of 70% of the cell density and 59% of the cell biovolume during the months of July and August.

Temporal distributions of four dinoflagellates and two species of *Synedra* from June 1985 through August 1988 were less predictable than patterns associated with *N. gracilis*, *S. hantzschii*, *A. formosa*, *D. sertularia*, and *M. parvula* (Figs. 6B, 8, and 9). The dinoflagellates were usually present in low densities, but because of their relatively large size, they often represented a large proportion of the total cell biovolume. *Peridinium aciculiferum* was found mostly in the top 80 m of the water column at all seasons of the year, whereas *P. inconspicuum* was more abundant at depths between 20 m and 200 m (Fig. 8). Two species

of *Gymnodinium* (*G. fuscum* and *G. inversum*) were collected from all depths at most seasons of the year; they were least abundant in the January samples (Fig. 9). The genus *Synedra* was abundant only in the summer of 1985, in March 1986, and near the end of the program in May 1989 and the summer of 1990 (Fig. 6B).

The species-abundance data (cell biovolume and cell density) also were pooled by major taxonomic division, or in the case of the Chrysophyta, by class (Figs. 10 - 15). At this taxonomic level, distributional patterns were not distinct. In general, taxa representing the Bacillariophyceae, Chlorophyta, and Pyrrhophyta were abundant in the spring and summer, and relatively rare in January; temporal patterns of the chrysophytes and cryptomonads were less predictable, with maxima occurring at different times each year. The graph for the Cyanobacteria (Fig. 15) simply indicates the samples in which picoplankton down to 1 um in diameter were counted along with the netplankton and nannoplankton, as blue-green algae larger than 2 um were rare in the water column.

The netplankton and nannoplankton exhibited two patterns of species diversity between June 1985 and August 1988 (Figs. 16 and 17). In August, when the epilimnion was established, species diversity (H') was relatively low in the upper 20 m of the water column, usually less than 1.0 (Fig. 16). Whereas at other times of the year, when thermal stratification was not present, diversity was more uniform between the water surface and a depth of 200 m (Fig. 17). Patterns of dominance, as expressed by the redundancy index (R), also were related to thermal stratification (Figs. 18 and 19). In August the R value was relatively high for samples obtained from the epilimnion, usually greater than 0.7, a pattern clearly related to the dominance of *Nitzschia gracilis*. This same pattern also was observed during the preliminary study and in data reported by Larson et al. (1987) for 1978, 1979, and 1980. Although the shape of curves representing the vertical profiles of species diversity were indicative of either stratified or unstratified conditions, mean species diversity in the water column (i.e., the mean H' value for the 13 samples taken on a particular date) varied seasonally and from year to year at the same season. For example, there was a

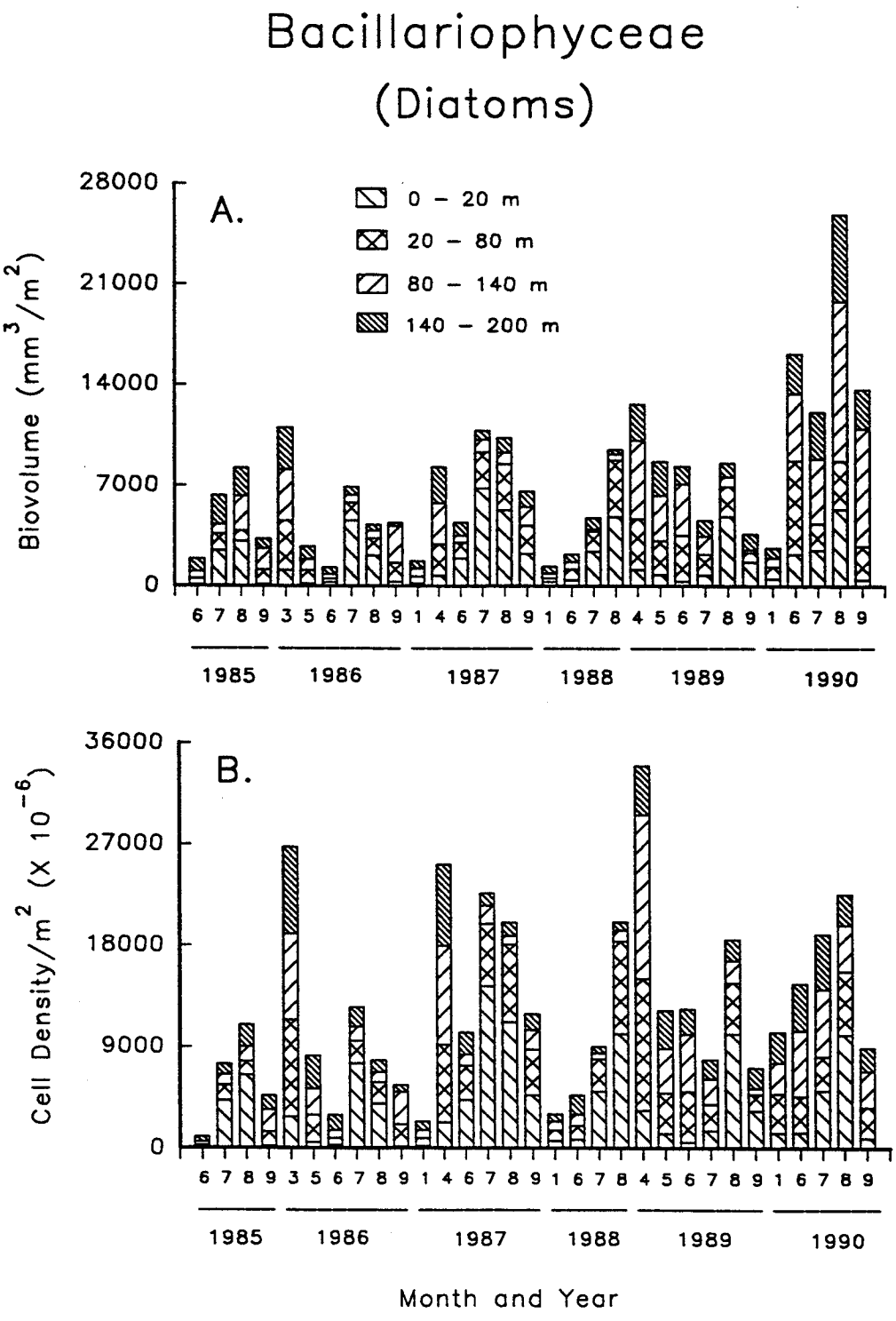


Figure 10. Vertical distribution of the cell biovolume (A) and cell density (B) of the Bacillariophyceae (diatoms) in the water column at Station 13 between June 1985 and September 1990.

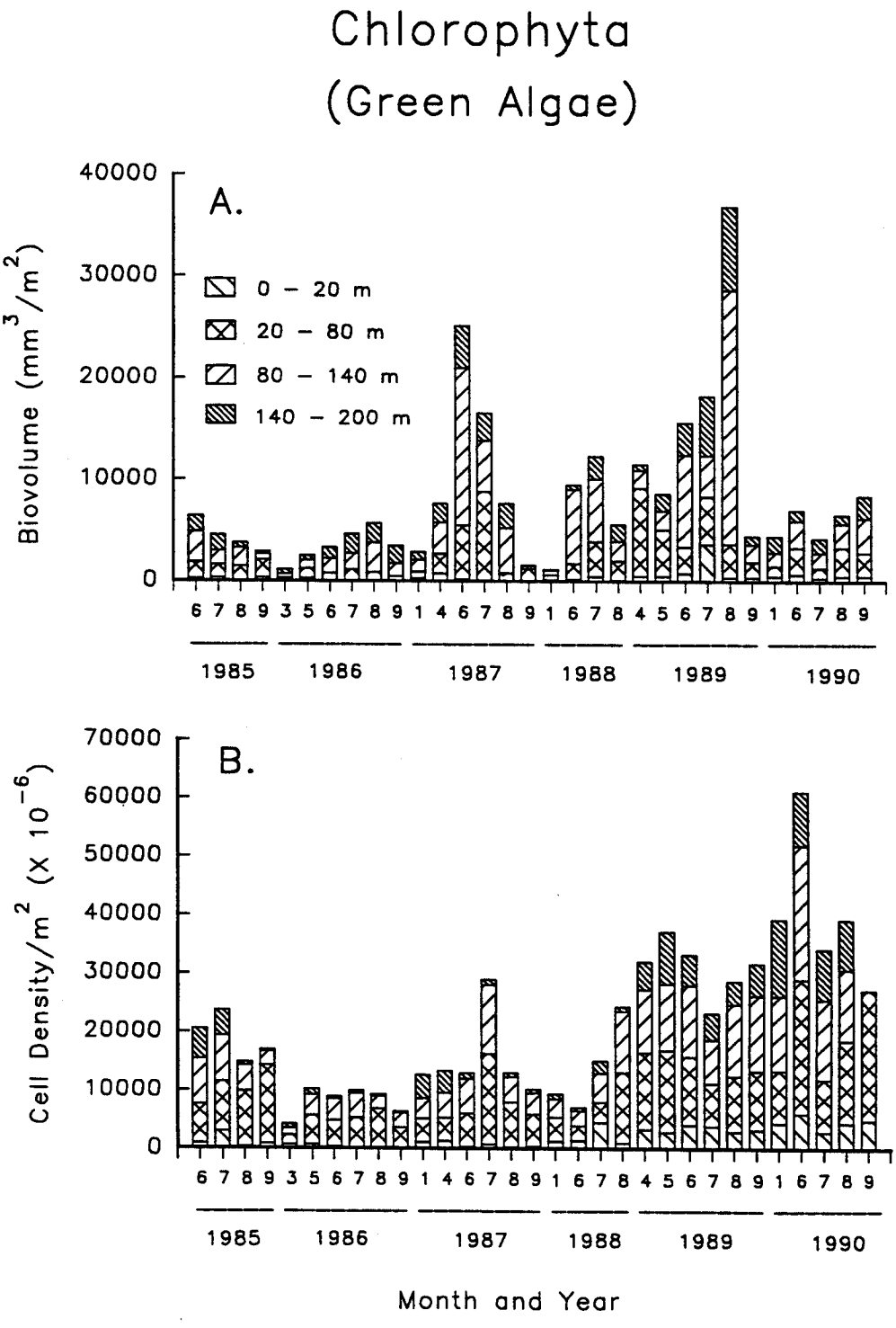


Figure 11. Vertical distribution of the cell biovolume (A) and cell density (B) of the Chlorophyta (green algae) in the water column at Station 13 between June 1985 and September 1990.

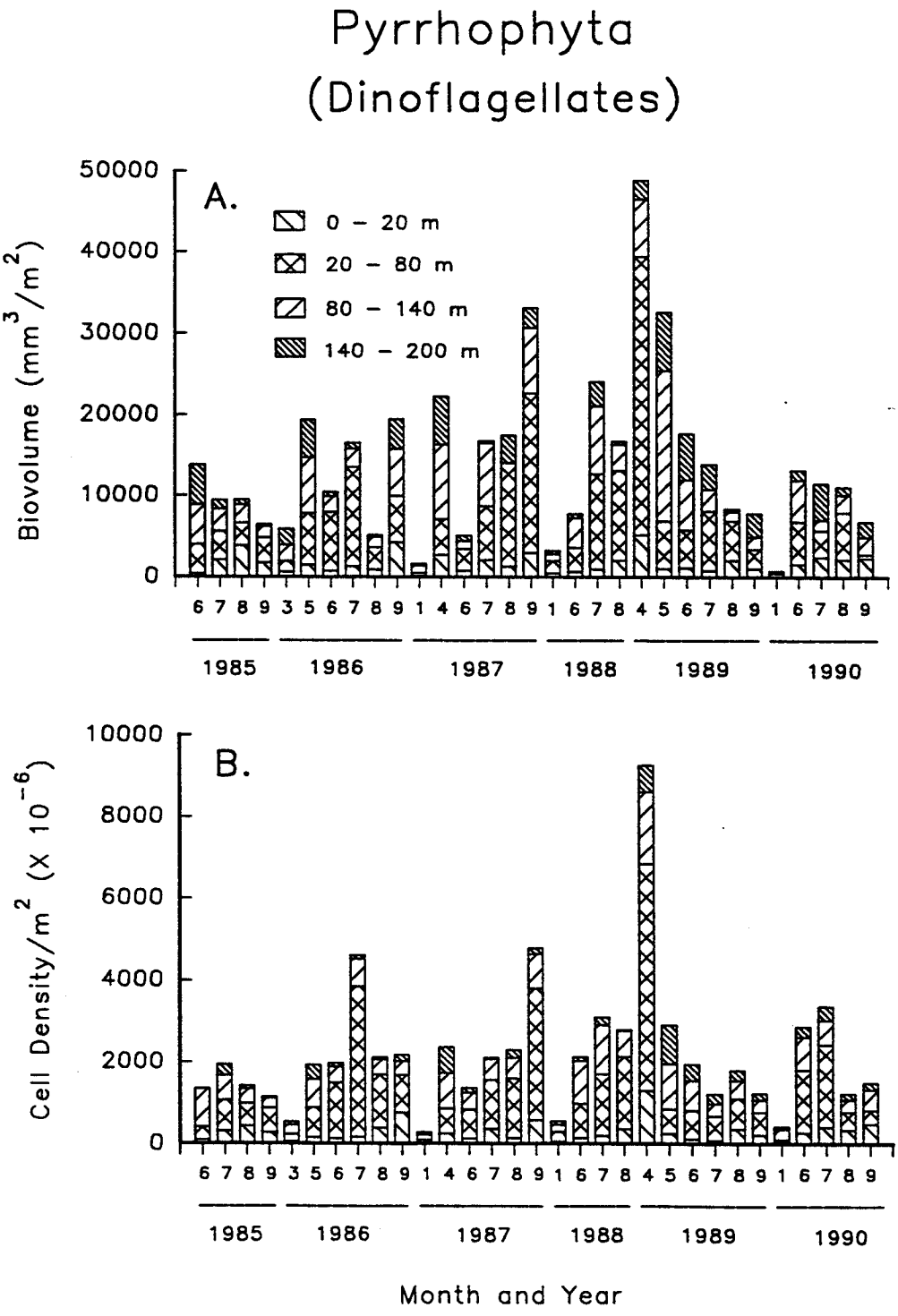


Figure 12. Vertical distribution of the cell biovolume (A) and cell density (B) of the Pyrrhophyta (dinoflagellates) in the water column at Station 13 between June 1985 and September 1990.

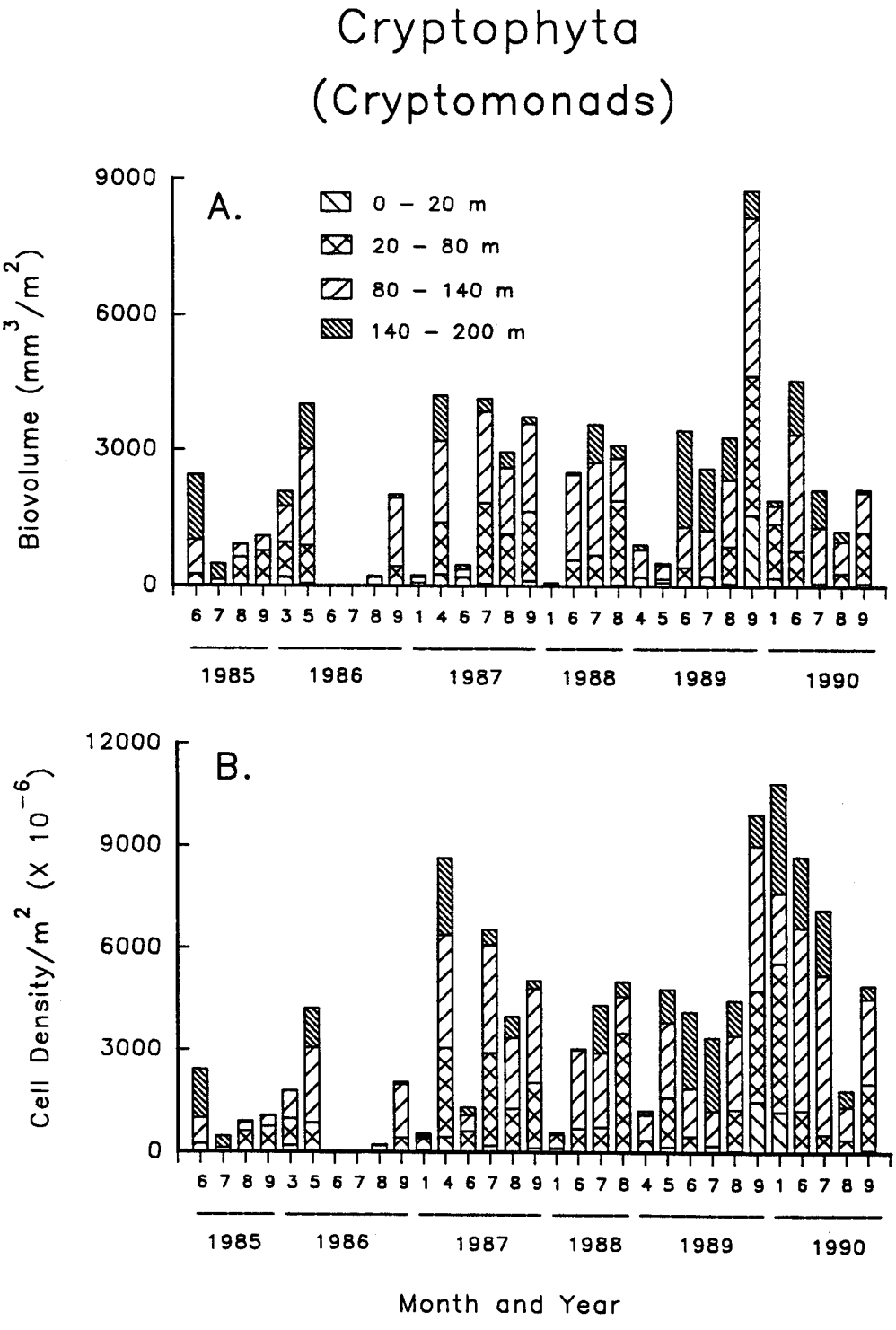


Figure 13. Vertical distribution of the cell biovolume (A) and cell density (B) of the Cryptophyta (cryptomonads) in the water column at Station 13 between June 1985 and September 1990.

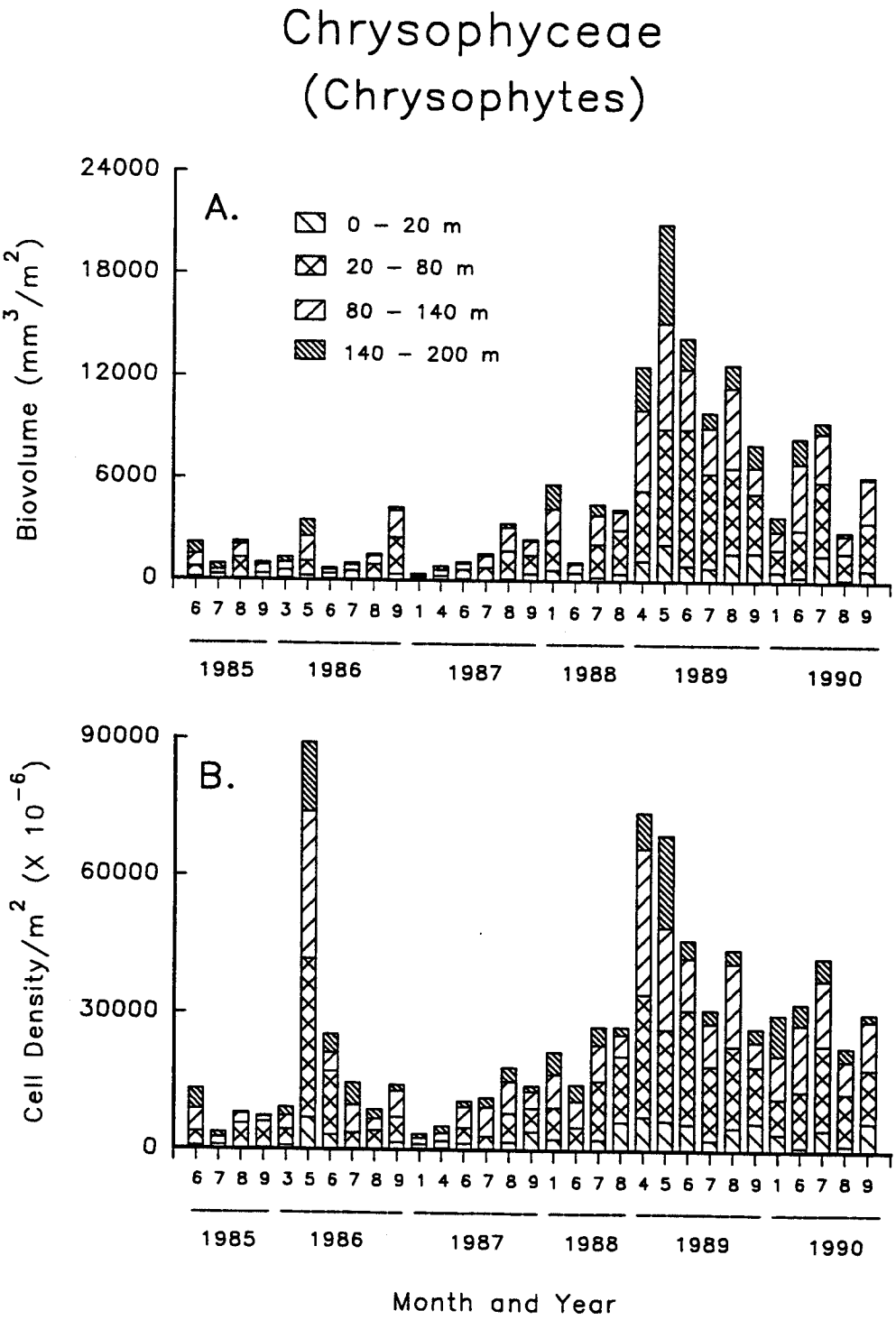


Figure 14. Vertical distribution of the cell biovolume (A) and cell density (B) of the Chrysophyceae (chrysophytes) in the water column at Station 13 between June 1985 and September 1990.

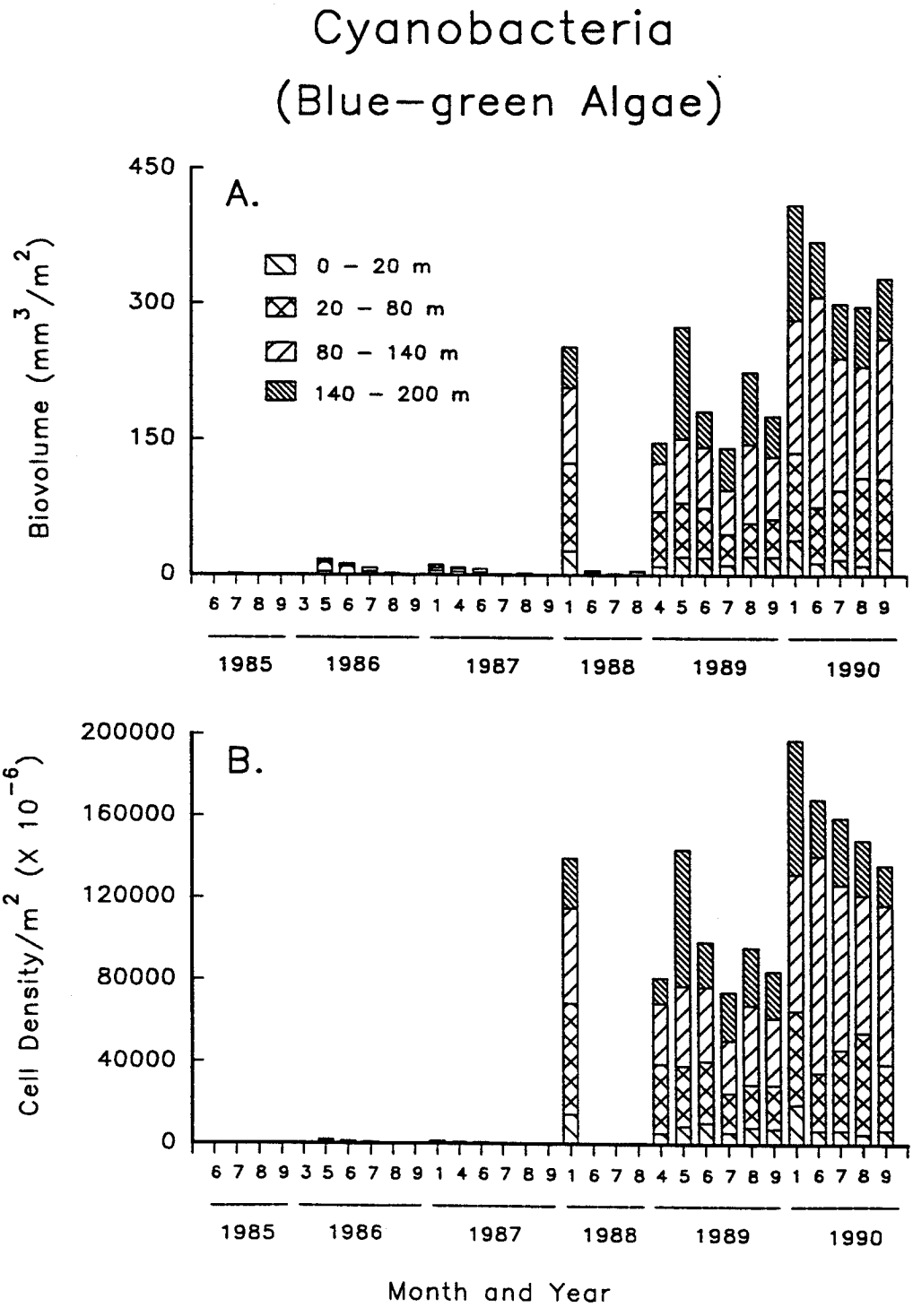


Figure 15. Vertical distribution of the cell biovolume (A) and cell density (B) of the Cyanobacteria (blue-green algae) in the water column at Station 13 between June 1985 and September 1990.

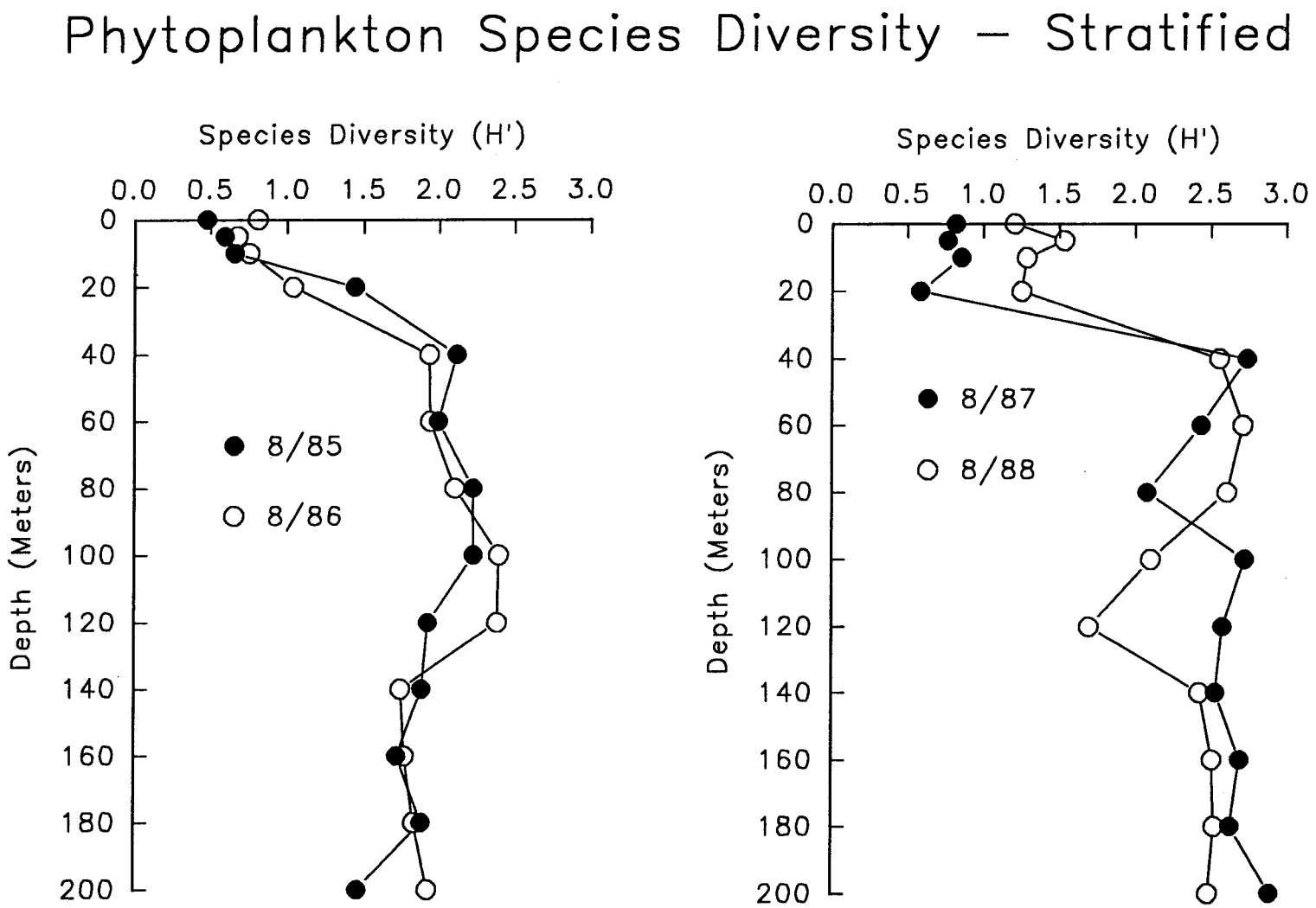


Figure 16. Vertical patterns of species diversity (H′) in phytoplankton assemblages at Station 13 during thermal stratification. Samples were taken in August 1985, 1986, 1987, and 1988.

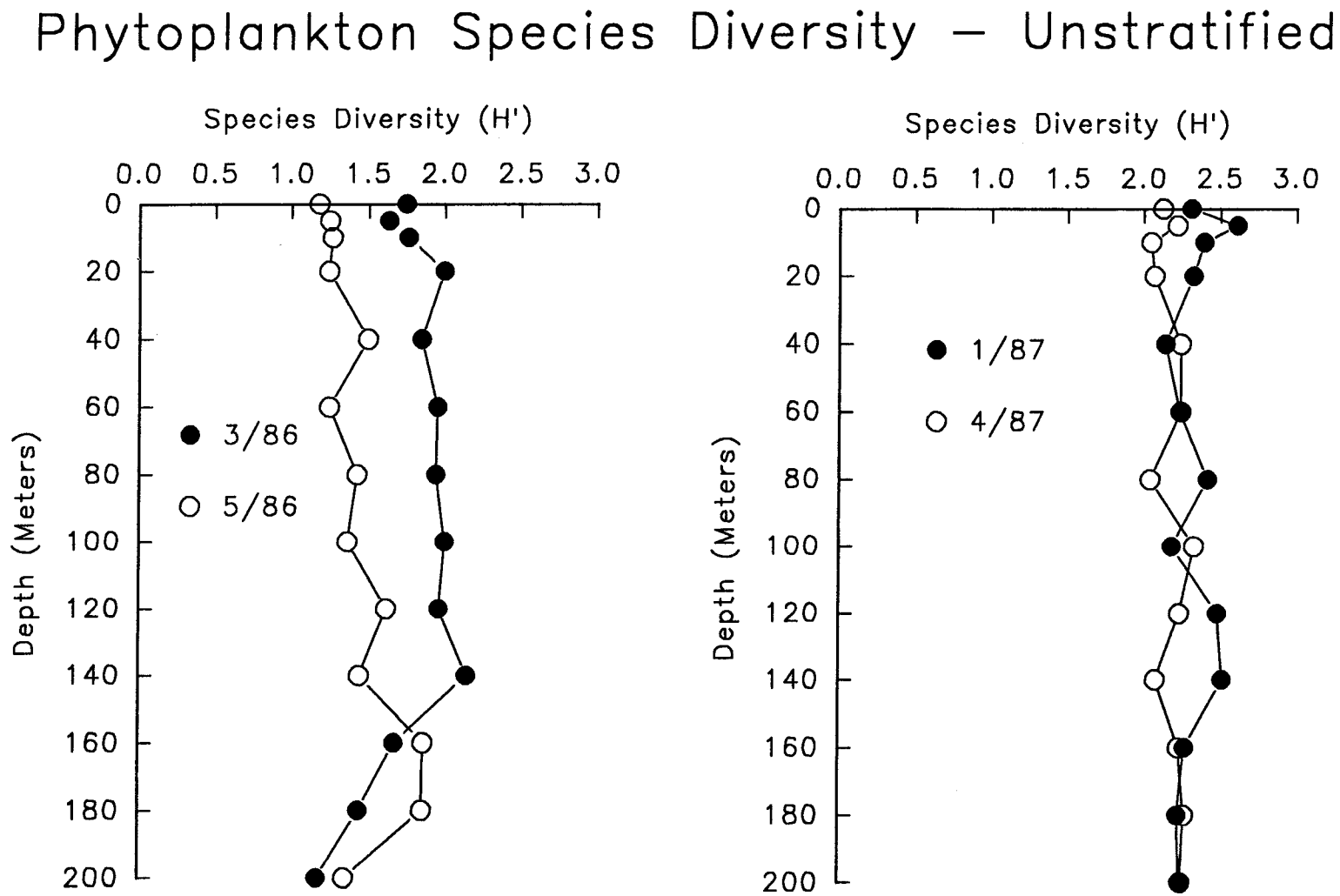


Figure 17. Vertical patterns of species diversity (H′) in phytoplankton assemblages at Station 13 in the absence of thermal stratification. Samples were taken in March and May 1986, and in January and April 1987.

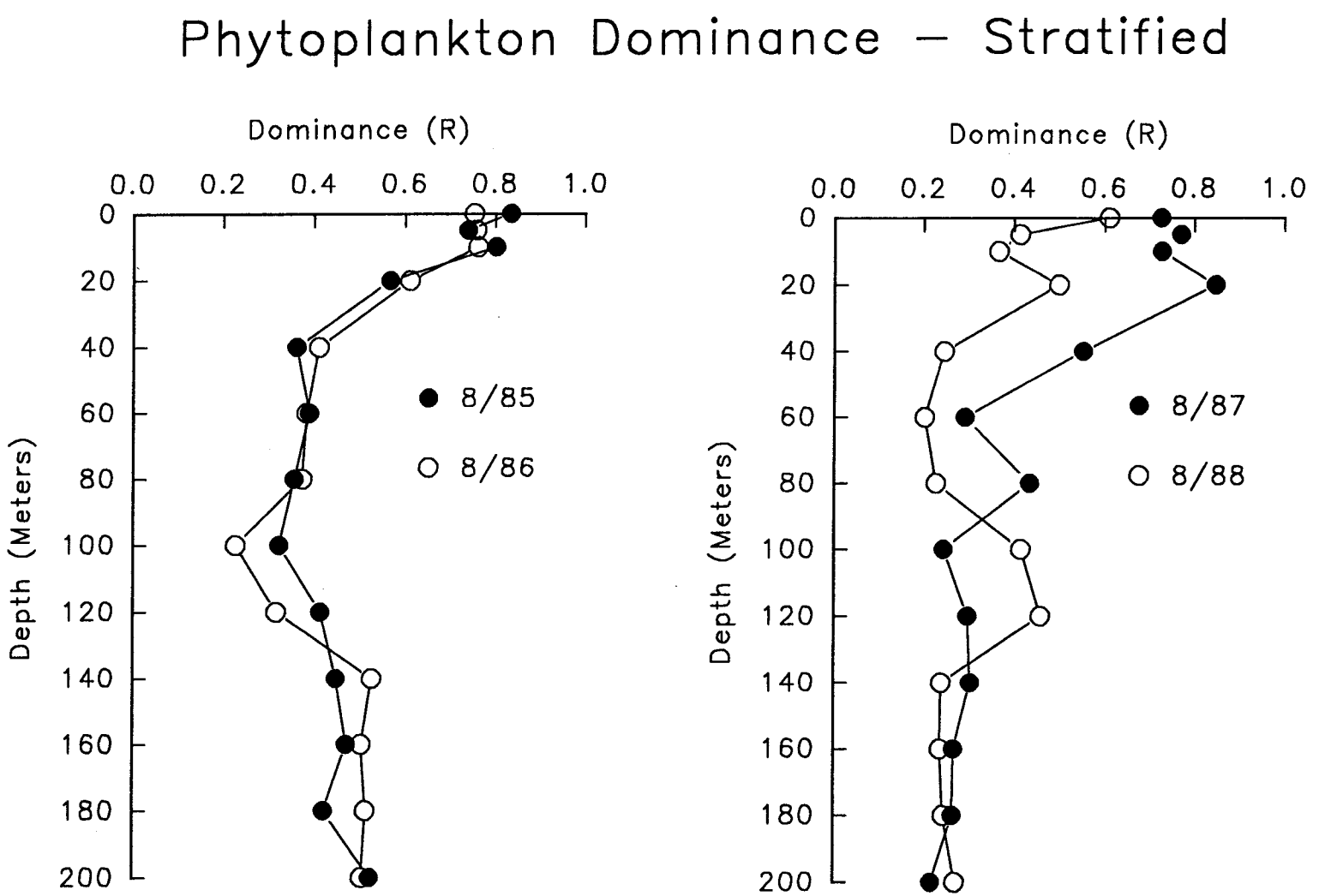


Figure 18. Vertical patterns of taxonomic dominance (R) in phytoplankton assemblages at Station 13 during thermal stratification. Samples were taken in August 1985, 1986, 1987, and 1988.

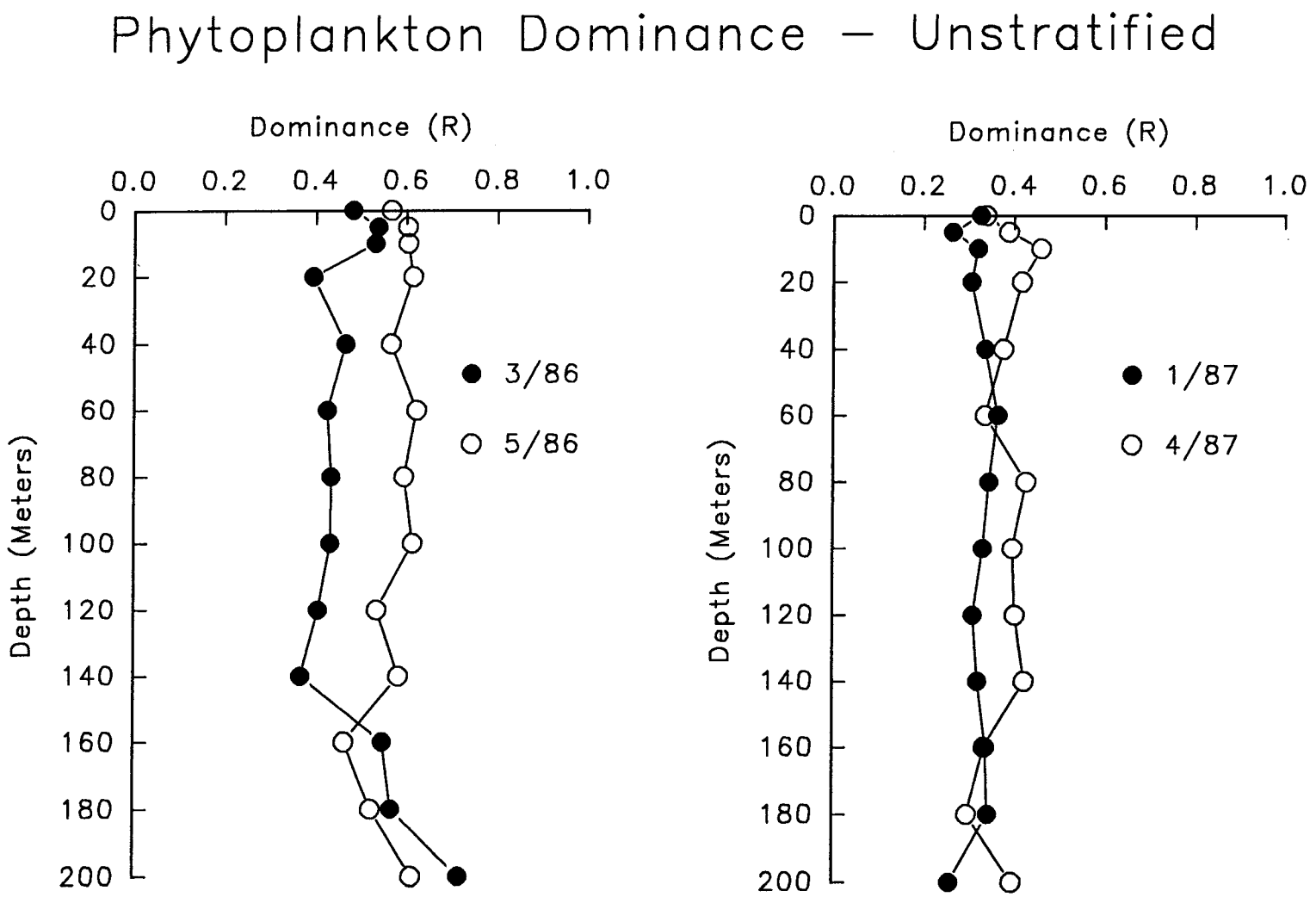


Figure 19. Vertical patterns of taxonomic dominance (R) in phytoplankton assemblages at Station 13 in the absence of thermal stratification. Samples were taken in March and May 1986, and in January and April 1987.

greater difference in mean species diversity between samples taken in March and May 1986 (mean H' = 1.79 and 1.43, respectively) than between samples taken between January and April 1987 (mean H' = 2.34 and 2.19, respectively); also, mean species diversity in the spring (March or April) was greater in 1987 than in 1986 (Fig. 17).

Results of the TWINSPAN analysis of the 1985 - 1988 species-abundance data indicated that a five-cluster structure was the most interpretable configuration (Fig. 20). The number of sample units in the clusters were 56 (cluster E), 76 (cluster A), 16 (cluster AA), 24 (cluster S), and 82 (cluster SS).

Samples in clusters S and SS contained a flora with a relatively low mean cell biovolume (Table 7). Collectively, these samples represented a sparse flora that was found throughout the water column in the spring, but was confined to depths below 100 m in the summer when thermal stratification was present (Fig. 20). Mean species diversity (H') was

Table 7. Mean species richness, species diversity (H'), dominance (R), and cell biovolume in the five clusters partitioned by a TWINSPAN analysis of the 1985-1988 phytoplankton data.

Cluster	Cluster Size	Mean Species Richness	Mean Species Diversity (H')	Mean Dominance (R)	Mean Cell Biovolume (μm^3/ml)
E	56	14.1	1.289	0.568	240,715
A	76	23.8	2.177	0.358	143,099
AA	16	23.8	2.595	0.214	369,821
S	24	19.1	1.821	0.430	85,210
SS	82	23.3	1.977	0.434	113,875

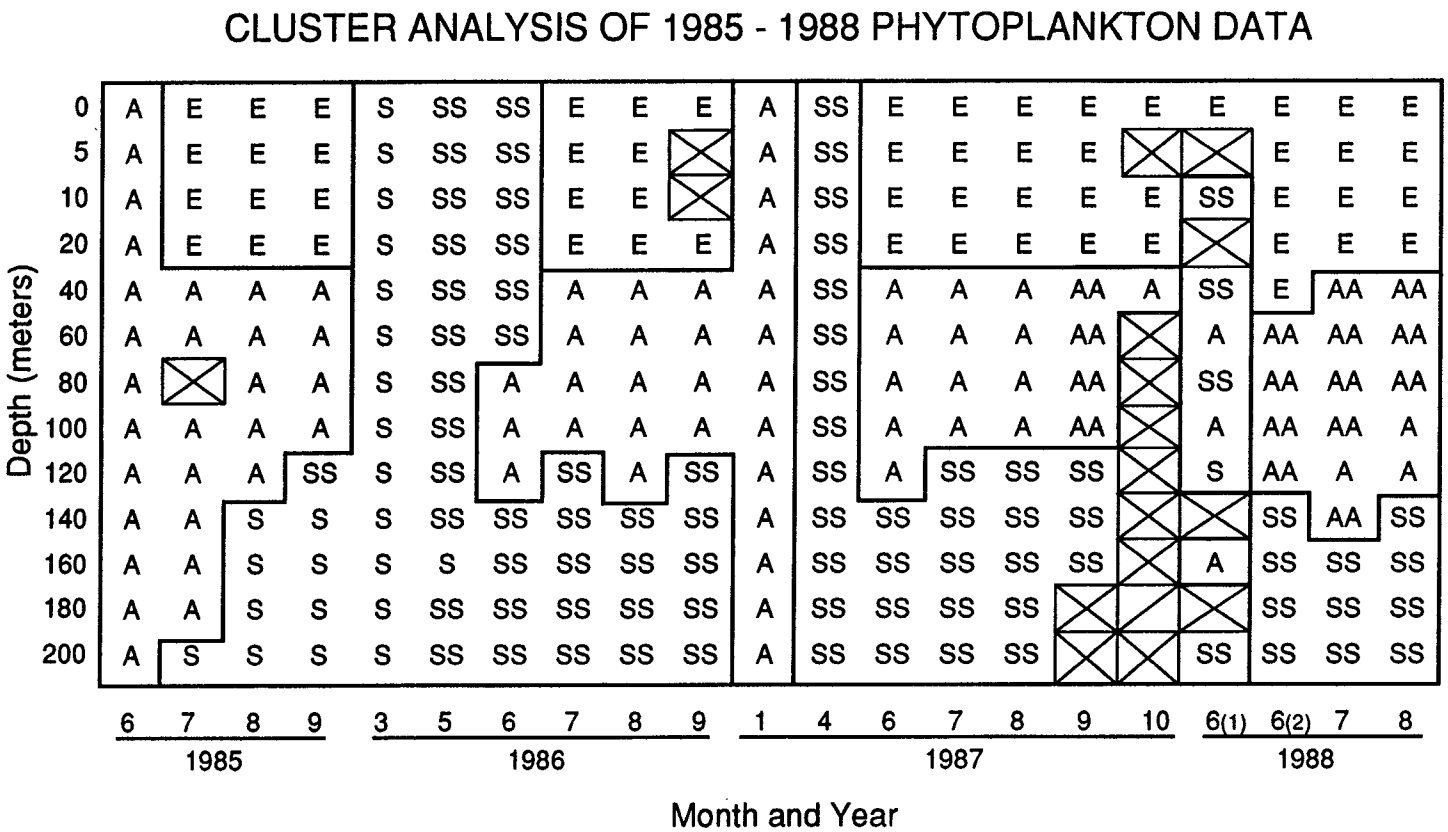


Figure 20. Five-cluster structure of 1985-1988 phytoplankton data. X-marks indicate missing observations.

1.821 for the 24 samples in cluster S and 1.977 for the 82 samples in cluster SS; corresponding values for mean dominance (R) were 0.430 and 0.434, respectively (Table 7). Prominent taxa associated with clusters S and SS included *Stephanodiscus hantzschii*, *Ankistrodesmus spiralis*, and a small, unidentified chrysophyte (Fig. 21). Clusters S and SS separated mainly on the basis of the relative abundances of *S. hantzschii* and the small chrysophyte, with *S. hantzschii* more strongly associated with cluster S and the latter taxon with a higher relative abundance in samples belonging to cluster SS.

Clusters A and AA were made up primarily of samples obtained at depths between 40 m and 120 m, the zone of maximum primary production (see Figs. 40 - 42 below). Samples representing these clusters had a high mean species diversity ($H' > 2.0$) and relatively low mean dominance ($R < 0.4$). However, mean cell biovolume for samples in cluster AA was higher than the means for the other clusters (Table 7), indicating that netplankton and nannoplankton were particularly abundant between 40 m and 120 m in September 1987 and in the summer of 1988. The species compositions of the flora associated with clusters A and AA were similar, as samples in both clusters contained *Ankistrodesmus spiralis*, *Dinobryon sertularia*, and an unidentified chrysophyte as dominant taxa (Fig. 21). In addition, *Tribonema* sp., *Rhodomonas lacustris*, and *Gymnodinium inversum* were abundant in cluster AA samples, while *Mougeotia parvula* and an unidentified chlorophyte had high relative abundances in cluster A samples.

Cluster E represented a discrete phytoplankton assemblage that occupied the epilimnion of Crater Lake during the summer and early fall (Fig. 20). Samples in this cluster had a relatively high mean cell biovolume, the lowest mean species diversity, and the highest mean dominance value (Table 7). *Nitzschia gracilis* was dominant in these samples with a mean relative abundance of 58.7% of the cell biovolume.

Euclidean distance values and a plot of the cluster centroids in discriminant space indicated that cluster E had the highest mean centroid distance in relation to the other

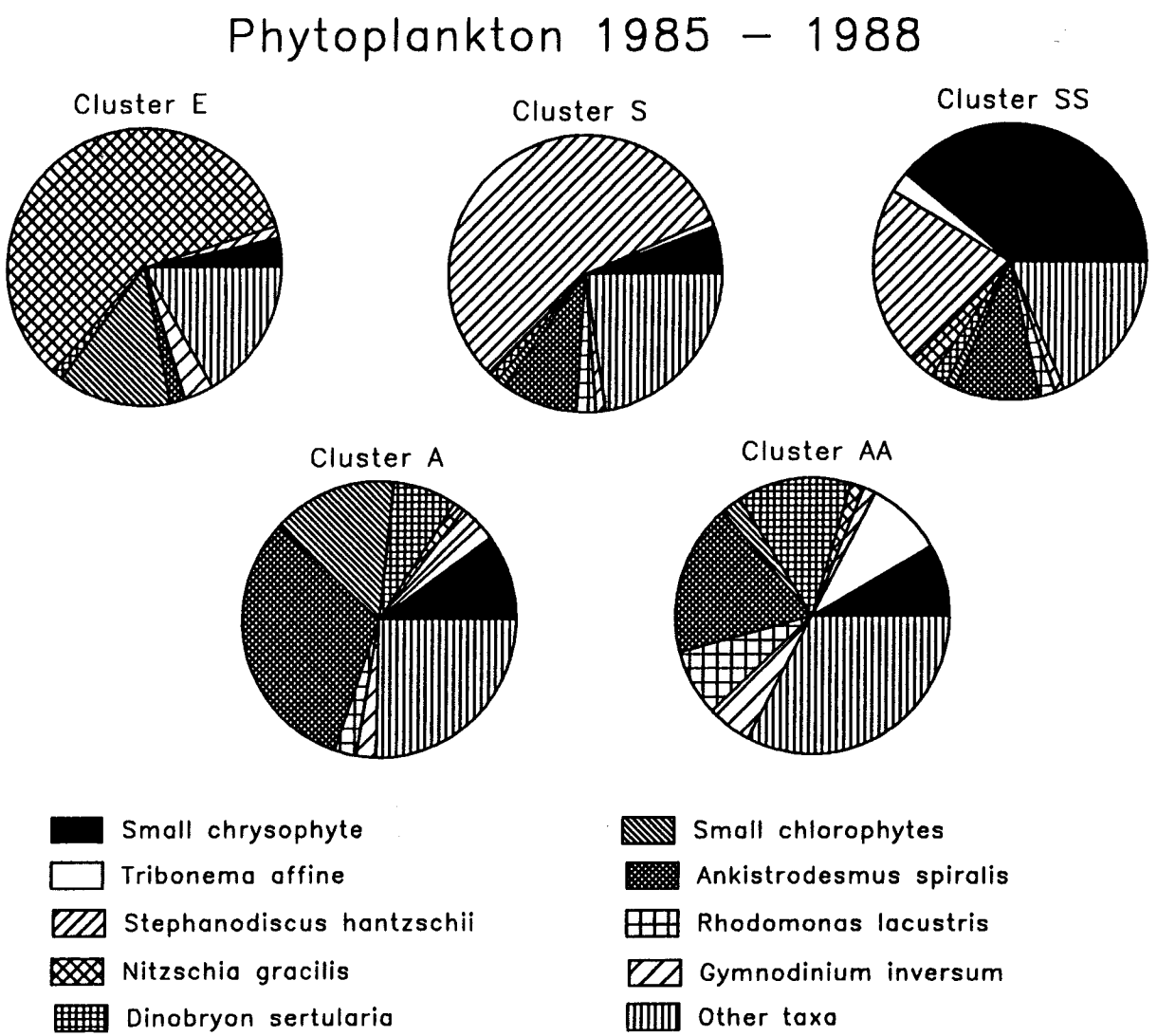


Figure 21. Mean relative abundance of nine phytoplankton taxa in the samples of clusters E, S, SS, A, and AA. Data represent netplankton and nannoplankton samples between June 1985 and September 1988 at Station 13.

clusters (Table 8 and Fig. 22). Apparently, physical processes associated with the formation of the epilimnion accounted for this discontinuity. Samples in clusters A and AA were most similar taxonomically (distance = 0.254), while clusters E and S were least similar (distance = 0.817).

Netplankton, Nannoplankton, and Picoplankton: 1989 - 1990. The effect of including small organisms down to a cell diameter of 1 um in the counts of samples taken in 1989, 1990, and January 1988 is illustrated by the bar graphs representing cell biovolume and cell density of the Cyanobacteria (Fig. 15). Small cyanobacteria occurred at all depths sampled and at all seasons of the year. Their presence also was confirmed by flourescent microscopy and by differential filtration of samples obtained for the analysis of carbon-14 primary production and chlorophyll concentration. The abundance of the small cyanobacteria in the upper 200 m of the water column (mostly *Aphanocapsa delicatissima*) reached a maxi-

Table 8. A matrix of Euclidean distance values comparing the centroids of five clusters derived from the TWINSPAN analysis of the 1985-1988 phytoplankton data. Mean distances between each centroid and the centroids of the other four clusters are listed at the bottom of the table.

Cluster	E	A	AA	S	SS
E	--				
A	0.679	--			
AA	0.636	0.254	--		
S	0.817	0.607	0.592	--	
SS	0.710	0.435	0.412	0.491	--
Mean Distance	0.711	0.494	0.474	0.627	0.512

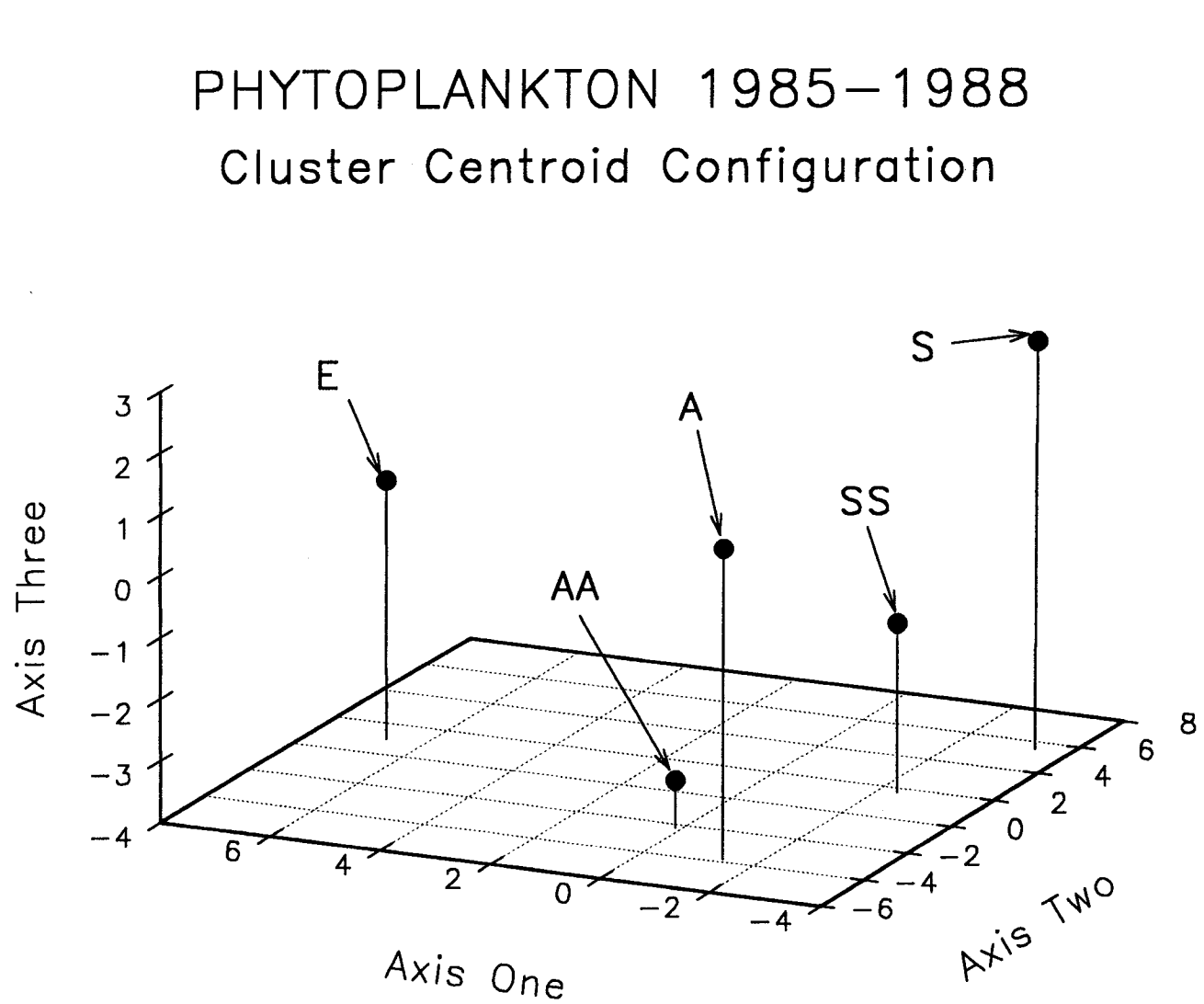


Figure 22. Relative positions of cluster centroids in discriminant space. Data from phytoplankton samples obtained between June 1985 and September 1988 at Station 13.

mum of about 2 X 10^{11} cells/m^2 in January 1990 (Fig. 15). However, because of their small size, the inclusion of these organisms had relatively little impact on estimates of total phytoplankton cell biovolume (Fig. 4).

For the period between June 1985 and September 1990, total phytoplankton cell biovolume integrated to a depth of 200 m reached its maximum value of about 90,000 mm^3/m^2 in April 1989 (Fig. 4). Values in 1990 were lower and more similar to those recorded for 1987 and 1988. If the results of the preliminary study are examined in relation to patterns found for 1985-1990, the data suggest a cyclic behavior in the variations of cell biovolume, with high years in 1982, 1983, and 1989, and low years in 1984, 1985, and 1986.

The temporal and spatial distributions of *Nitzschia gracilis* and *Stephanodiscus hantzschii* in 1989 and 1990 were similar to patterns observed in the 1985-1988 data (Fig. 5). However, *Mougeotia parvula*, *Dinobryon sertularia*, *Peridinium inconspicuum*, and species of *Synedra* were more abundant in 1989 and 1990 than at corresponding times in 1985, 1986, 1987, and 1988 (Figs. 6B, 7, and 8B). *Asterionella formosa* reached its annual maximum cell biovolume in June of 1989 in contrast to the maxima that this taxon exhibited in September of 1985, 1986, 1987, and 1990 (Fig. 6A). The TWINSPAN analysis of the 1989-1990 species-abundance data generated a four-cluster structure (Fig. 23). This analysis, which was based on 35 of the most abundant taxa, partitioned out groups of 22 samples (cluster E), 41 samples (cluster A), 43 samples (cluster B), and 50 samples (cluster C). Based on cell density, the most abundant taxon in samples from all four groups was *Aphanocapsa delicatissima*, one of the cyanobacteria with a cell diameter of 1-2 um. Mean relative abundances of this taxon for the four groups of samples were 33.4% (cluster E), 49.2% (cluster A), 56.3% (cluster B), and 61.8% (cluster C). Therefore, the inclusion of *A. delicatissima* in the 1989-1990 data had a pronounced effect on the results of the cluster analysis, and cluster separation was determined to a great degree by the relative abundance of this taxon and a few subdominant taxa from the nannoplankton and netplankton size categories.

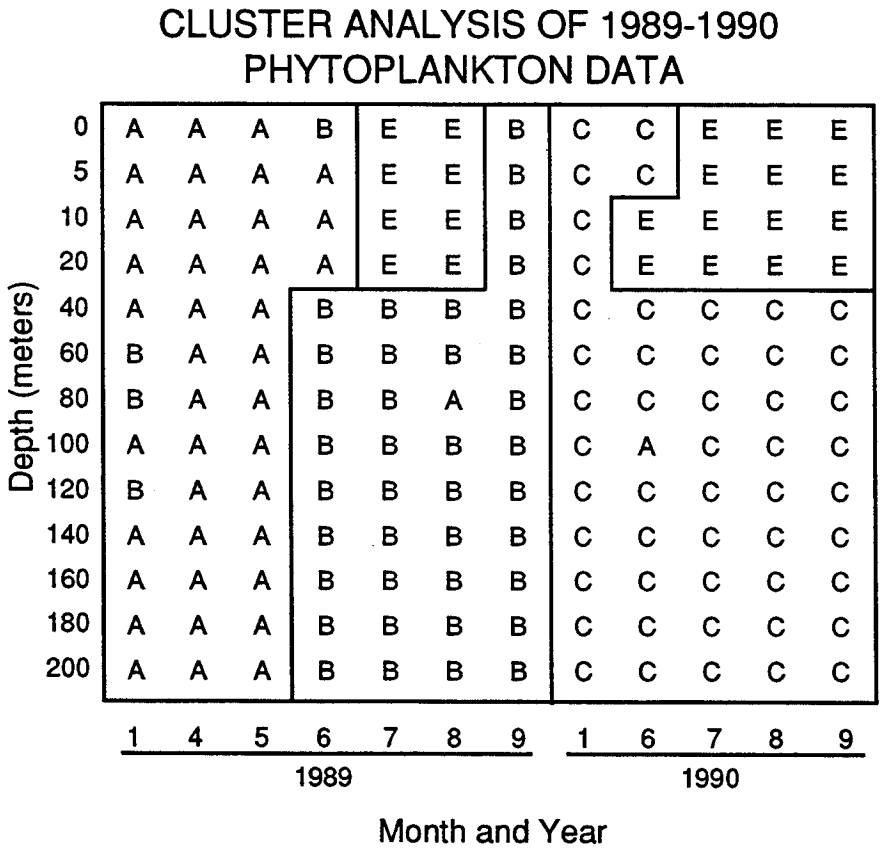


Figure 23. Four-cluster structure of 1989-1990 phytoplankton data.

Cluster E included 22 samples from the epilimnion in the summers of 1989 and 1990 (Fig. 23). Mean cell biovolume of these samples was relatively high (Table 9), whereas mean species richness was low (14 taxa in a count of 300 cells). In addition to *Aphanocapsa delicatissima*, other dominant taxa in the samples of cluster E were *Nitzschia gracilis* (23.8%), *Dinobryon sertularia* (5.1%), and an unidentified species of *Chlorella* (Fig. 24). In general, cluster E, with its high relative abundance of *N. gracilis*, represented the same pattern found for the epilimnion in the 1985-1988 data (see cluster E in Fig. 21).

In the 1989-1990 data, clusters A, B, and C partitioned out on the basis of temporal changes in the flora (Fig. 23). Because of the ubiquitous distribution and dominance of *Aphanocapsa delicatissima*, the three-tier structure revealed for netplankton and nanno-plankton by the analysis of the 1985-1988 data (Fig. 20) was not apparent in the 1989-1990 data, when picoplankton down to 1 μm in diameter were included in the counts. Samples in cluster A were collected mostly in January 1988 and in April and May 1989, while

Table 9. Mean species richness, species diversity (H'), dominance (R), and cell biovolume in the four clusters partitioned by a TWINSPAN analysis of the 1989-1990 phyto-plankton data.

Cluster	Cluster Size	Mean Species Richness	Mean Species Diversity (H')	Mean Dominance (R)	Mean Cell Biovolume (μm^3/ml)
E	22	14.3	1.633	0.431	321,355
A	41	21.7	1.853	0.468	287,531
B	43	20.0	1.707	0.501	255,574
C	50	15.9	1.450	0.537	165,363

samples in cluster B were taken below the epilimnion in the summer of 1989 and throughout the water column in September 1989; samples associated with cluster C were distributed throughout the water column in January 1990 and below the epilimnion in July, August, and September 1990. The relatively low mean cell biovolume for samples in cluster C (Table 9) was related to a decrease in total cell biovolume in the water column between 1989 and 1990 (Fig. 4A). This decrease occurred mostly below a depth of 20 m, as the mean cell biovolume for the eight 1989 samples in cluster E (348,931 um^3/ml) was similar to the corresponding value for the 14 1990 samples in cluster E (305,596 um^3/ml). Numerically, dominant taxa other than *A. delicatissima* associated with cluster A (Fig. 24) were *Stephanodiscus hantzschii* (4.9%), *Chromulina* sp. (5.1%), *Chlorella* sp. (8.6%), and *Ophiocytium parvulum* (6.9%); whereas dominants in samples from cluster B were *Mougeotia parvula* (4.2%) and *Chlorella* sp. (9.3%). In addition to *A. delicatissima*, the dominant taxon associated with cluster C was *Chlorella* sp. (14.4%).

Distances between the 1989-1990 cluster centroids and their relative positions in discriminant space are presented in Table 10 and Figure 25. Euclidean distance values were relatively small, with the centroid for cluster E exhibiting the greatest mean distance from the centroids of its neighboring clusters. A similar discontinuity between samples from the epilimnion and the other samples was found for the 1985-1988 data (Table 8). The relatively small distances among the 1989-1990 cluster centroids was related to the high relative abundance of *Aphanocapsa delicatissima* in samples from all clusters.

Distribution of Chlorophyll

Measurements of chlorophyll in the water column extended to a depth of at least 200 m on all sampling dates, and in some years to 300 m (1987, 1989, and 1990) and 550 m (1986). This variable provided a useful index to the distribution of planktonic autotrophs and their capacity to synthesize organic materials. Data obtained during the 10-year study represented a period from 1984 through 1990. In addition, data collected between 1979

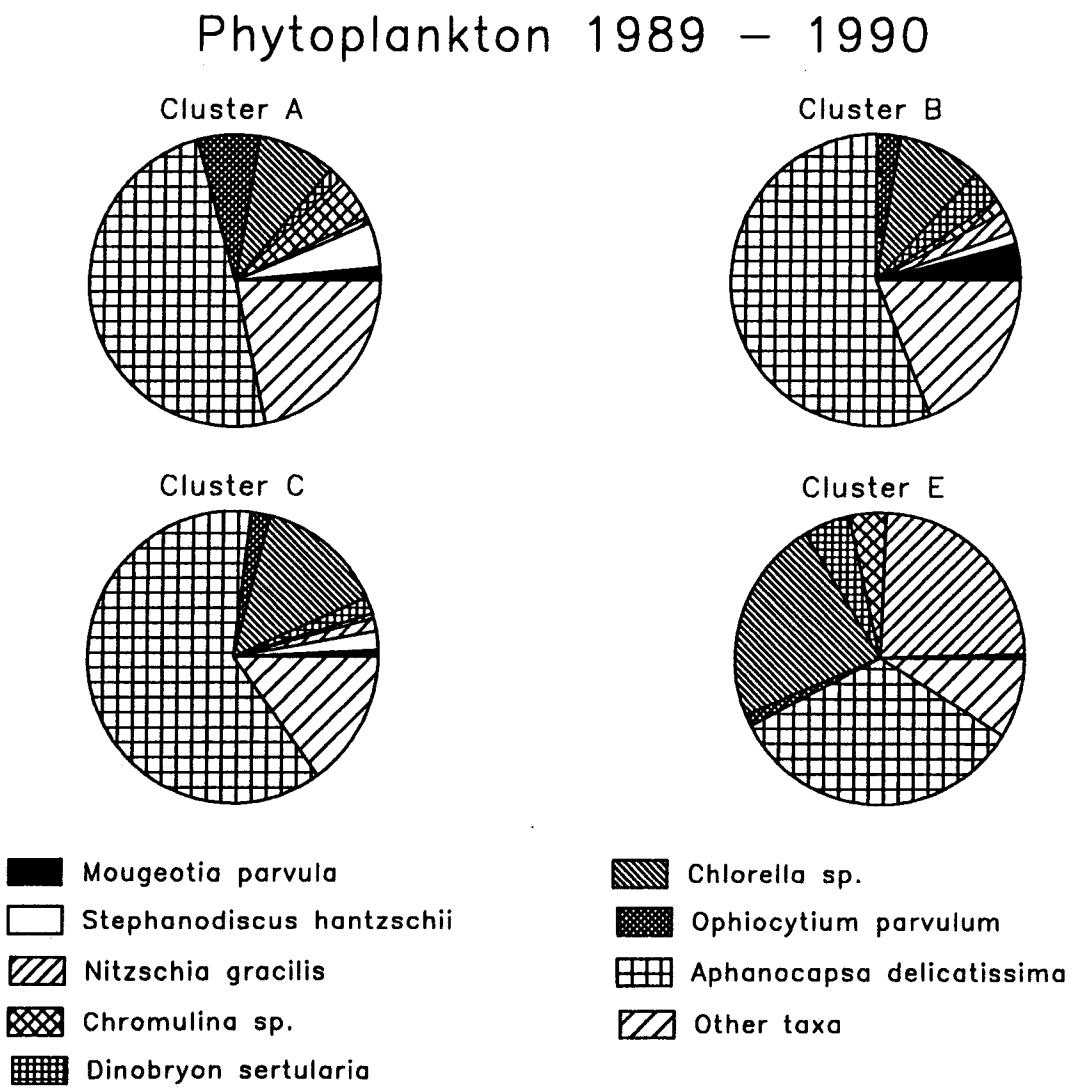


Figure 24. Mean relative abundance of eight phytoplankton taxa in the samples of clusters A, B, C, an E. Data represent phytoplankton sampled between January 1989 and September 1990 at Station 13.

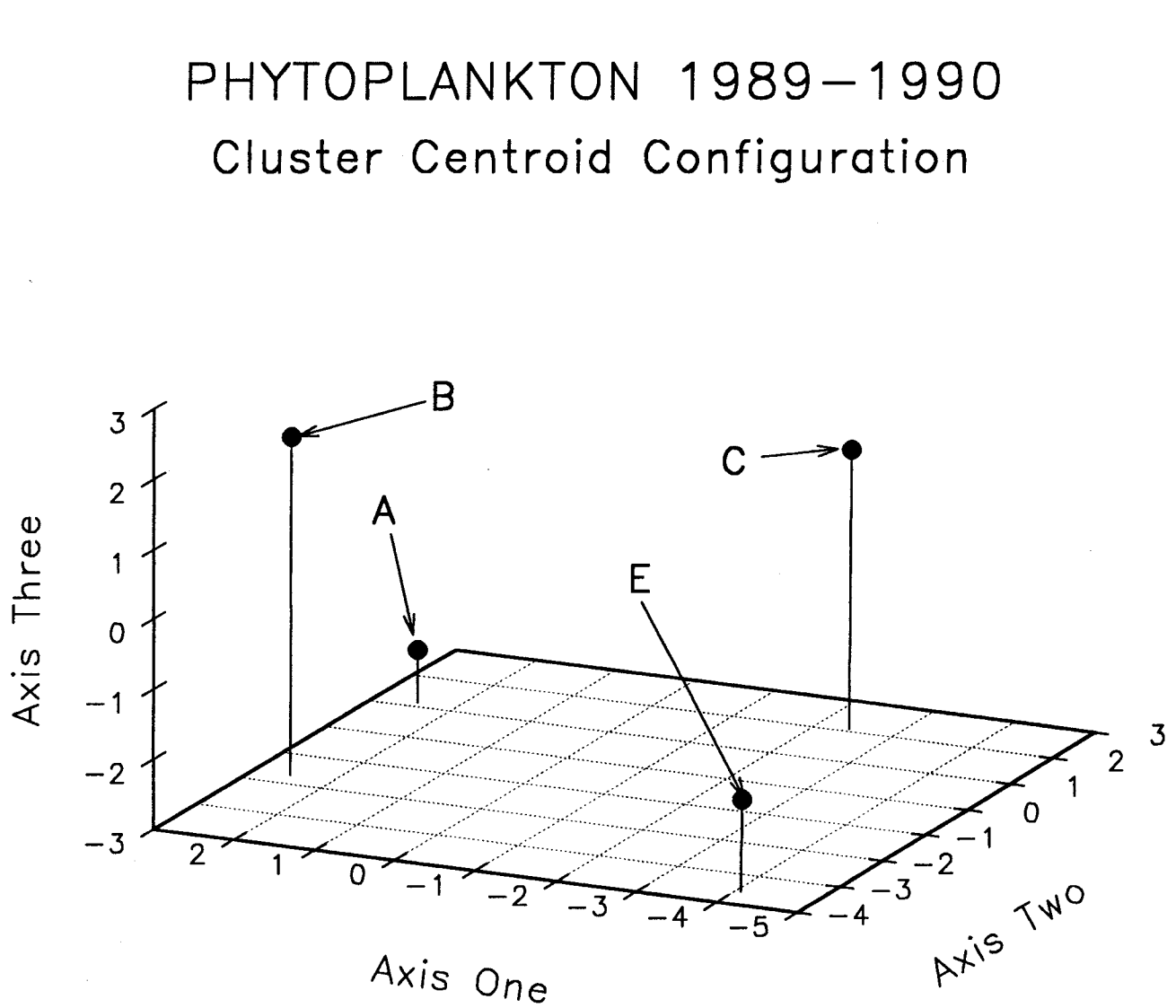


Figure 25. Relative positions of cluster centroids in discriminant space. Data from phytoplankton samples obtained between January 1989 and September 1990 at Station 13.

Table 10. A matrix of Euclidean distance values comparing the centroids of four clusters derived from the TWINSPAN analysis of the 1989-1990 phytoplankton data. Mean distances between each centroid and the centroids of the other three clusters are listed at the bottom of the table.

Cluster	E	A	B	C
E	--			
A	0.335	--		
B	0.347	0.133	--	
C	0.376	0.180	0.104	--
Mean Distance	0.353	0.216	0.195	0.220

and 1983 were made available to us by D. W. Larson and are included in this section for comparative purposes. Analytical methods used by Dr. Larson were similar to methods used for the 10-year study with the exception that he measured absorbance by pigment extracts with a Bausch and Lomb Spectronic 70 spectrophotometer instead of using the flurometric procedure.

Depth Profiles. The vertical distribution of chlorophyll in the water column of Crater Lake exhibited patterns that were related to seasonal changes in the chemical and physical properties of the water mass. Such patterns were evident in both the 1984 - 1990 data and in data obtained by Dr. Larson between 1979 and 1983. Between late June and September, the maximum concentration of chlorophyll usually occurred between 100 m and 140 m below the water surface (Figs. 26 - 28). This pattern was coincident with the onset of thermal stratification and the gradual development of a well-defined epilimnion, a

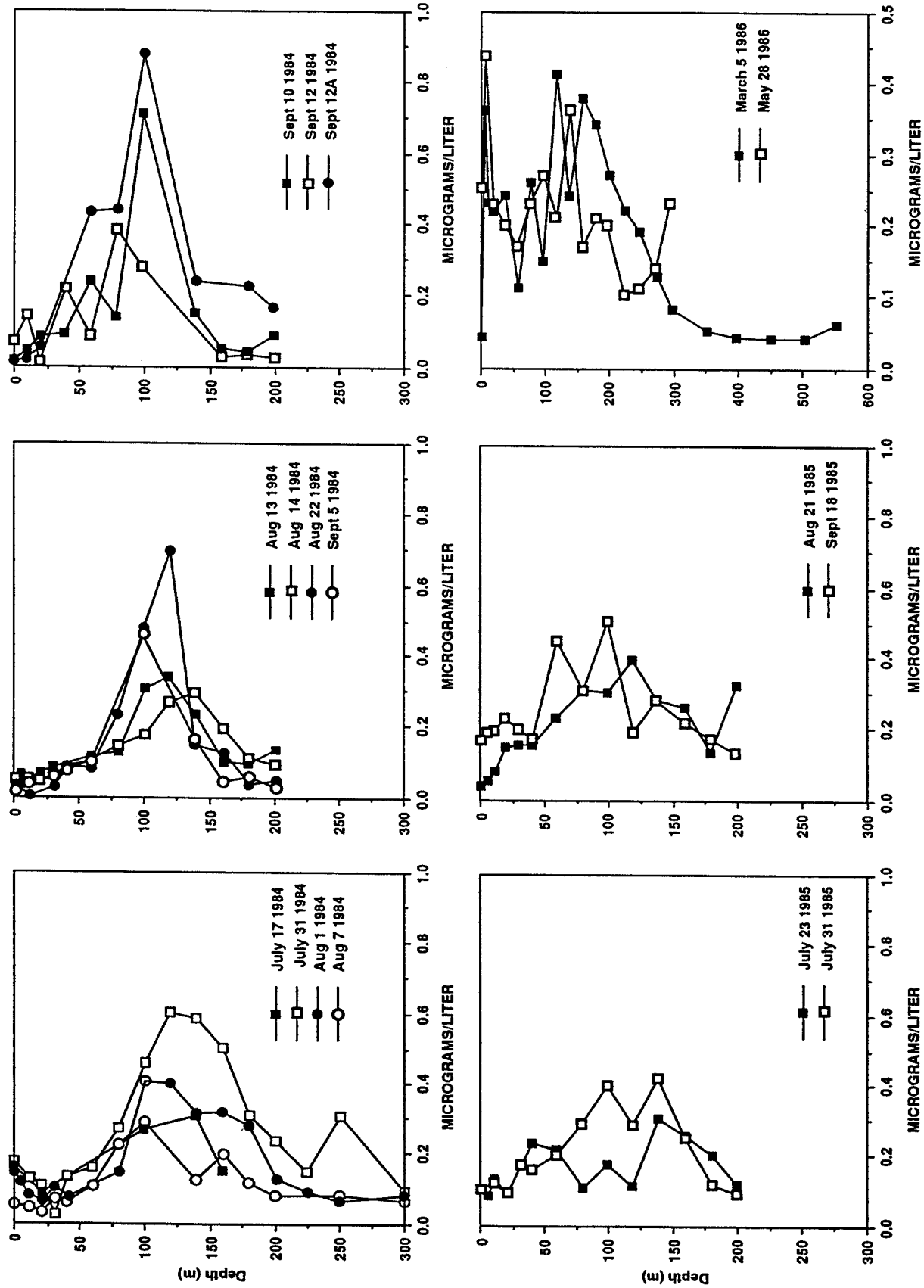


Figure 26. Vertical distribution of chlorophyll in the water column at Station 13 between July 17, 1984, and May 28, 1986.

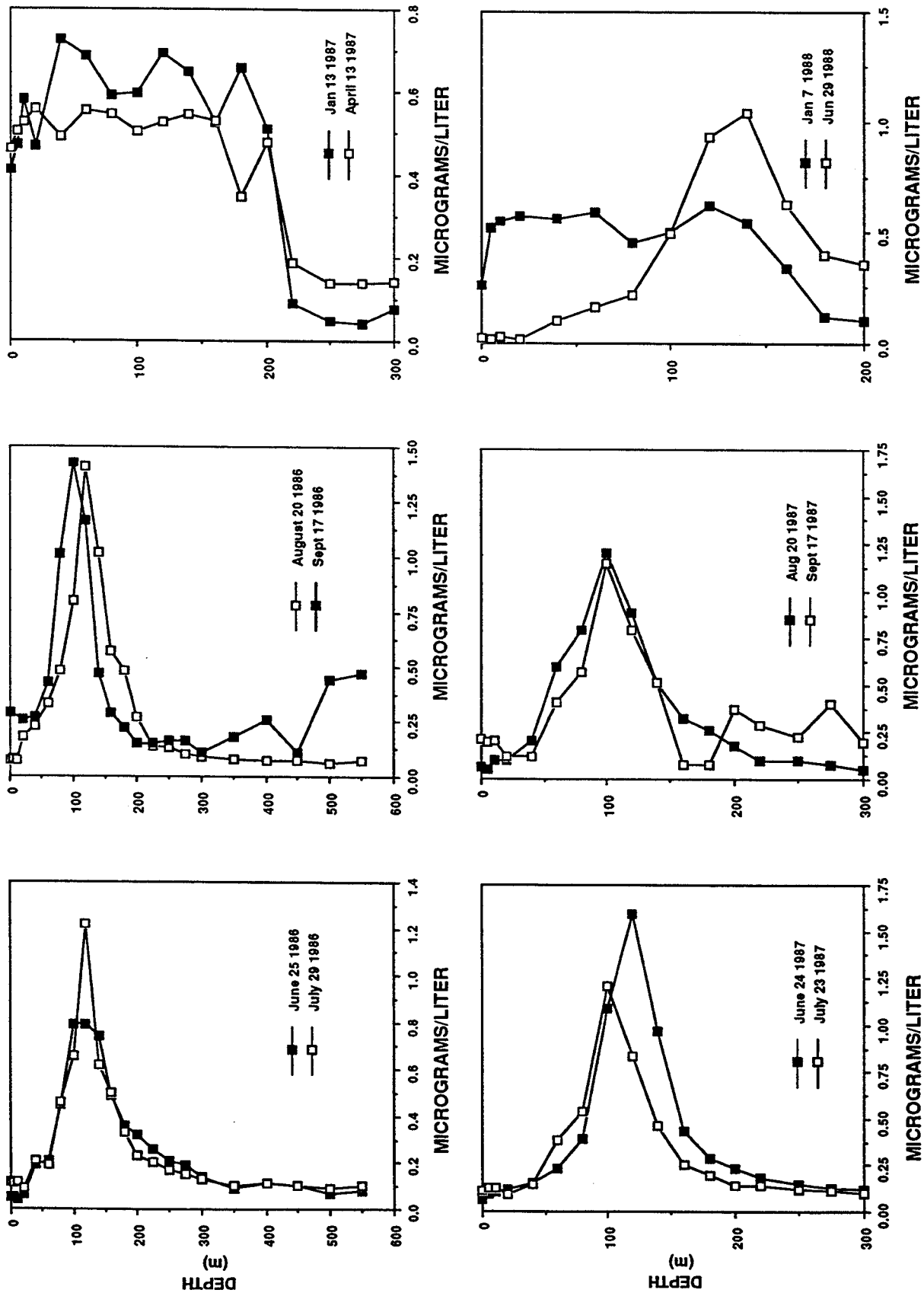


Figure 27. Vertical distribution of chlorophyll in the water column at Station 13 between June 25, 1986, and June 29, 1988.

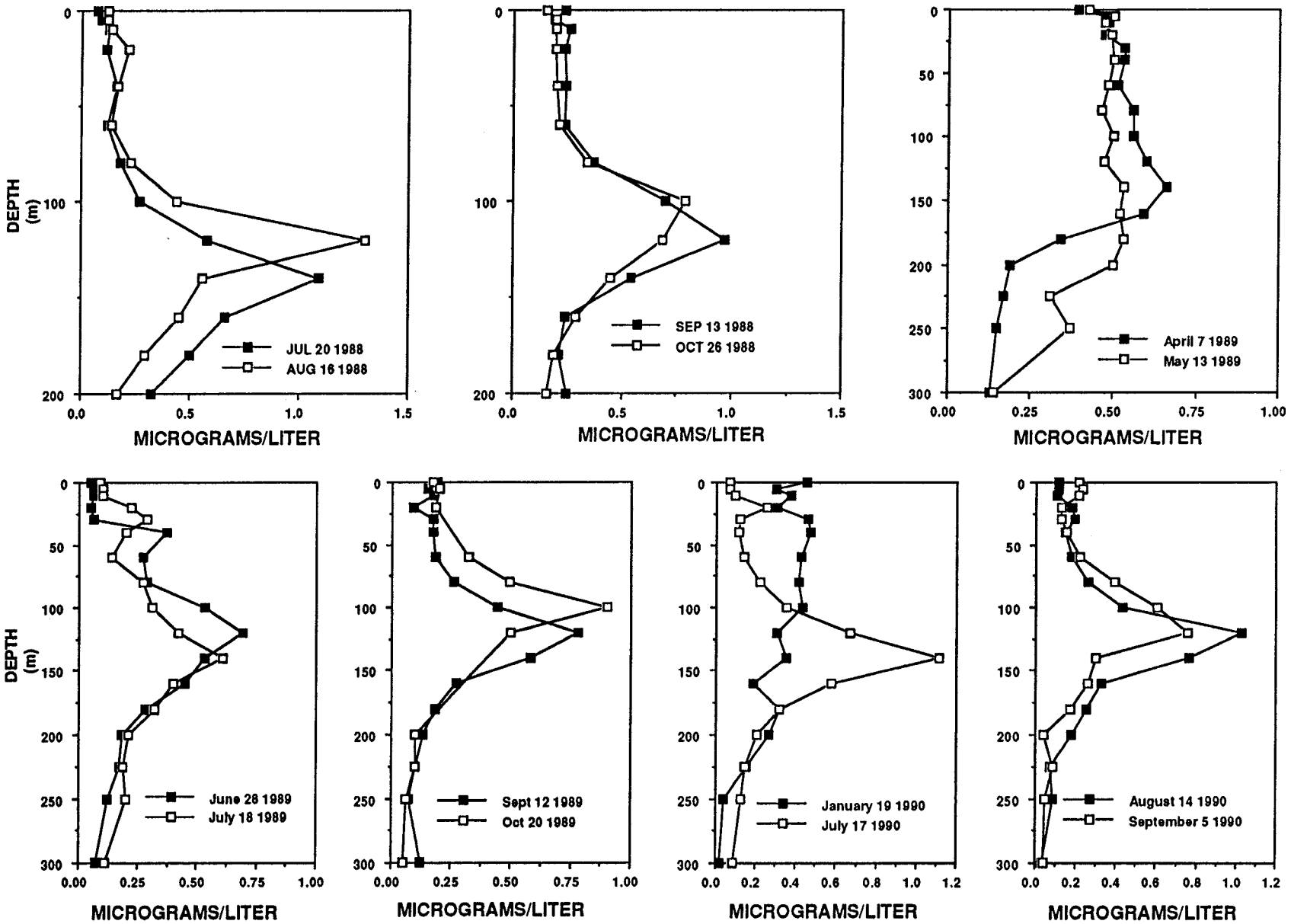


Figure 28. Vertical distribution of chlorophyll in the water column at Station 13 between July 20, 1988, and September 5, 1990.

process that was usually complete by late August. The highest concentration of chlorophyll measured between 1979 and 1990 was 1.595 μg/l, a value found for a water sample collected from a depth of 120 m on June 24, 1987 (Fig. 27). In the winter and spring, when vertical mixing occurred, chlorophyll was more uniformly distributed in the water column than in the summer. At this time of year, concentrations usually ranged from 0.3 to 0.8 μg/l in the upper 150 m, while below 200 m the concentration was often less than 0.2 μg/l (Figs. 26 - 28).

Further indication of seasonal shifts in the distribution of chlorophyll is evident in plots of mean concentrations for upper and lower segments of the water column, specifically between 0 and 40 m and between 100 and 140 m, respectively (Fig. 29). During January and the spring months when the water column was mixing to a depth of about 200 m, mean chlorophyll concentrations in the two water segments were similar, varying between 0.2 and 0.6 μg/l. However, in the summer and early fall when thermal stratification was present, mean chlorophyll concentration was high between depths of 100 m and 140 m and relatively low in the epilimnion. The unweighted average concentration for the months of June, July, August, and September was 0.675 μg/l between 100 and 140 m and 0.168 μg/l for the segment between the surface and a depth of 40 m.

The relationship between the depth profiles of chlorophyll and cell biovolume was unclear, particularly in the upper 100 m of the water column when thermal stratification was present. Data obtained in August for an eight-year period (1983-1990) indicated that maximum correspondence occurred in 1989, when the maximum for both variables was found between 100 m and 140 m below the surface; in other years, the patterns were dissimilar above the depth of 100 m (Figs. 30 and 31). In the epilimnion and metalimnion, relative cell biovolume, expressed as a proportion of the maximum value, was usually higher than the corresponding relative chlorophyll concentration. Therefore, phytoplankton isolated above the hypolimnion during thermal stratification had relatively low concentrations of chlorophyll at a time of year when nutrient inputs and concentrations were low

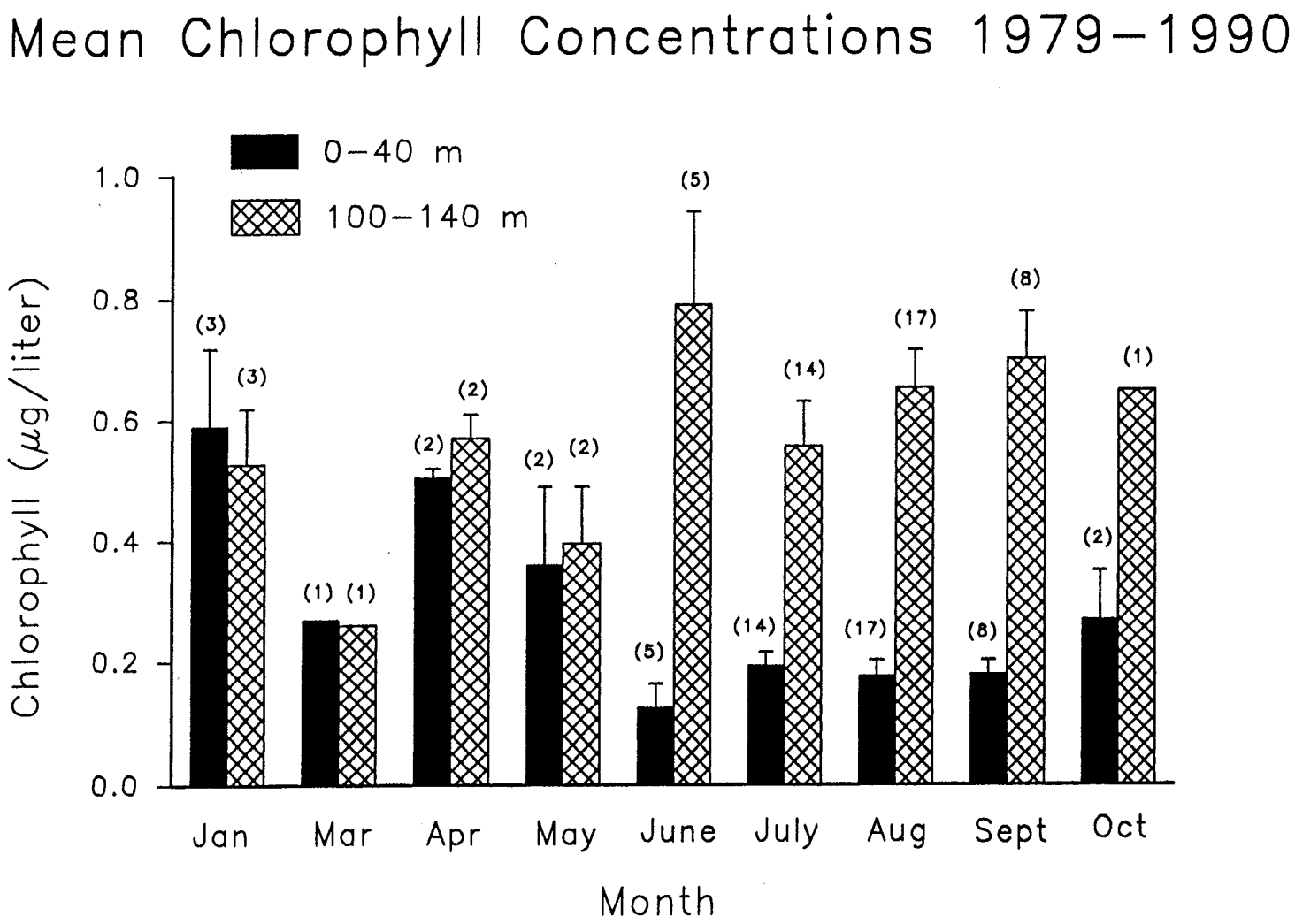


Figure 29. Seasonal variation in the mean concentrations of chlorophyll in the 0-40 m and 100-140 m depth segments of the water column at Station 13. Numbers above each bar indicate the number of sampling dates represented by each mean, and variation for each month is the standard error of the mean.

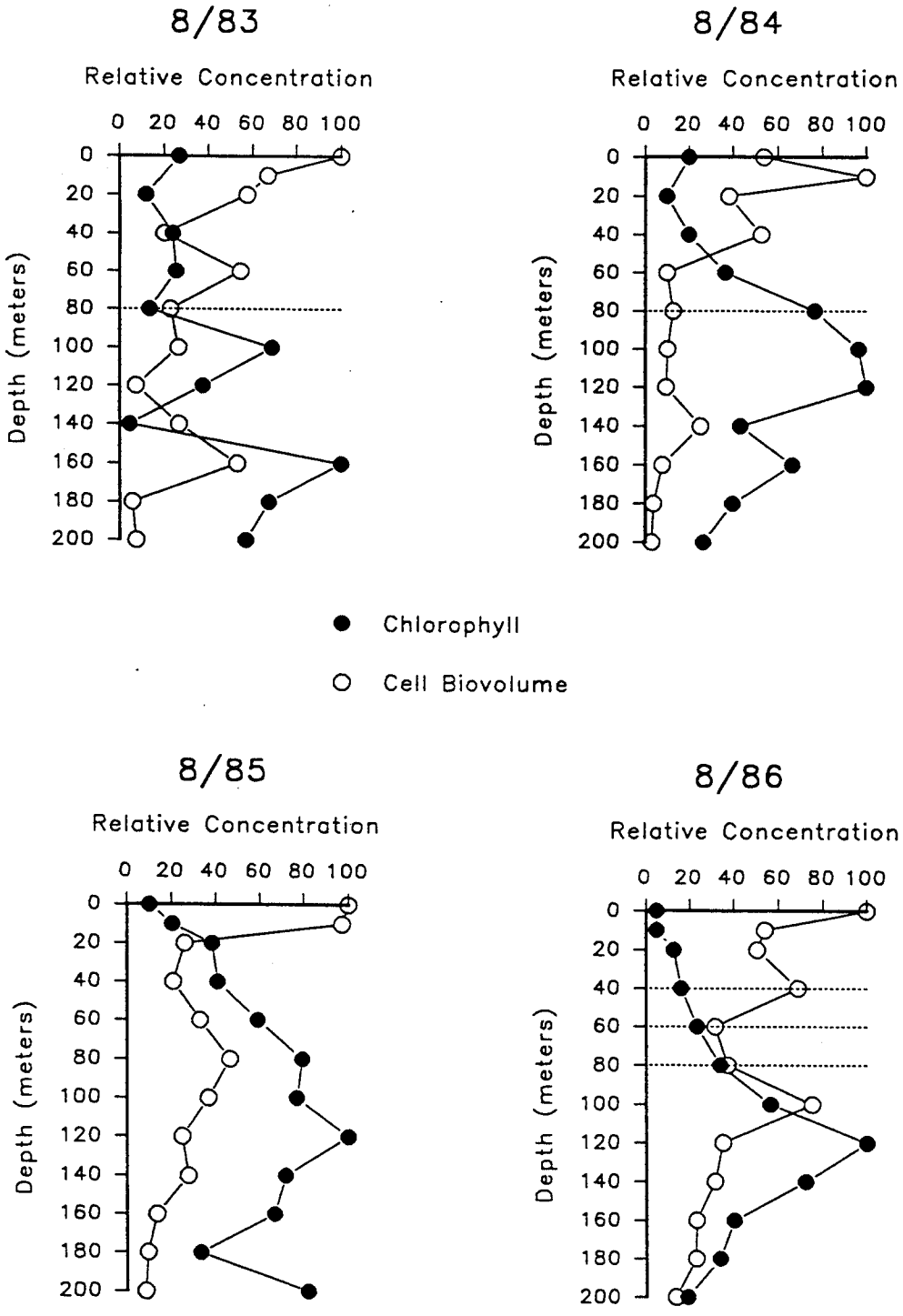


Figure 30. Relative concentrations of chlorophyll and cell biovolume at various depths at Station 13 in August 1983, 1984, 1985, and 1986. Data are expressed as percentage of the maximum value. Dotted lines represent the depth(s) of maximum C-14 primary production.

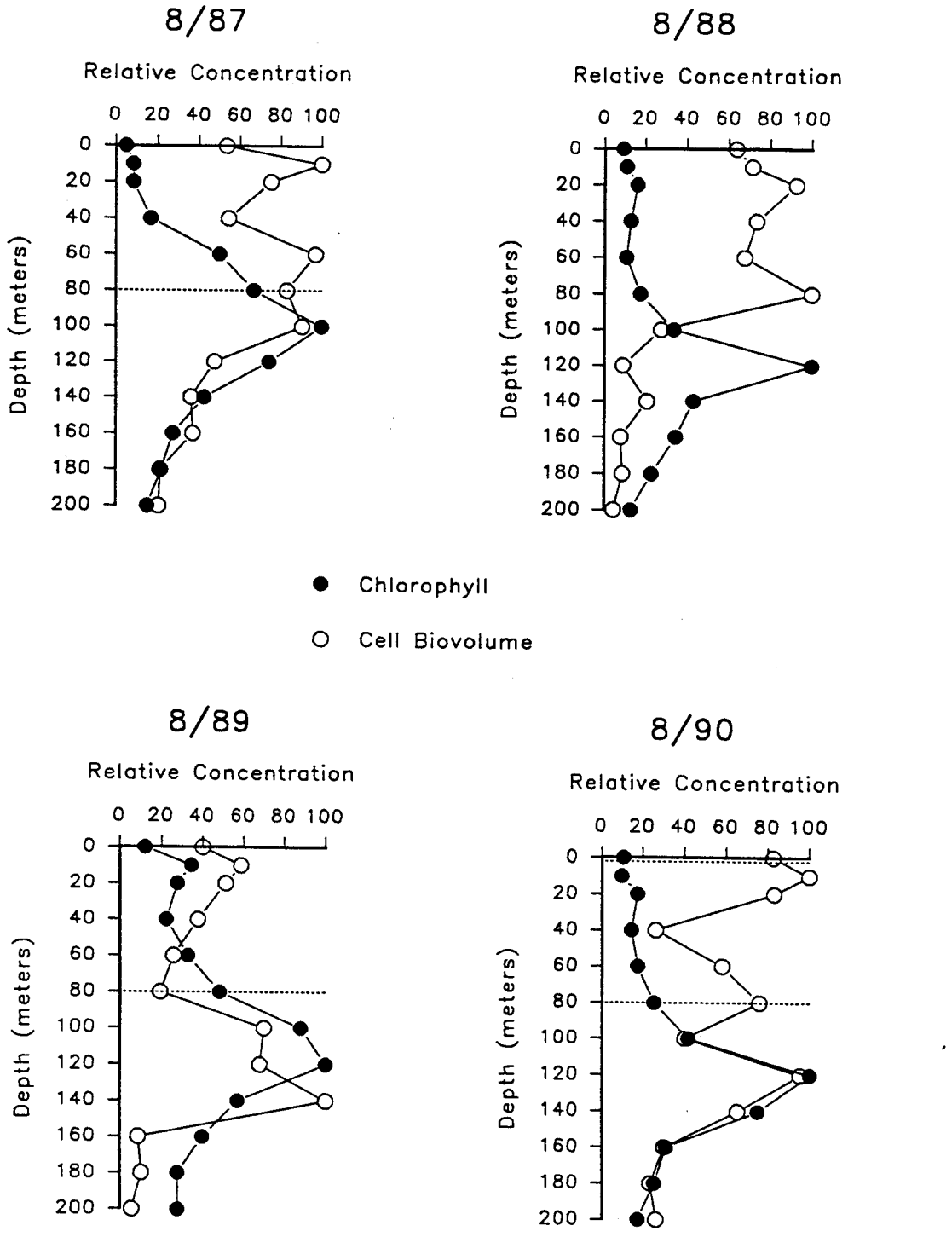


Figure 31. Relative concentrations of chlorophyll and cell biovolume at various depths at Station 13 in August 1987, 1988, 1989, and 1990. Data are expressed as a percentage of the maximum value. Dotted lines represent the depth of maximum C-14 primary production.

in the upper strata of the water column. In most years the ratio of chlorophyll concentration to cell biovolume, expressed as mg chlorophyll per ml, reached a summer minimum value (< 1) in the epilimnion and a summer maximum value (usually > 5) at a depth between 120 and 160 m (Figs. 32 - 34).

Patterns of Total Chlorophyll. Chlorophyll data for the period between 1969 and 1990 were integrated to obtain estimates of total chlorophyll in the upper 200 m of the water column. In this case, the values were expressed as milligrams of chlorophyll below one square meter of surface area to a depth of 200 m. Seasonal trends were determined by plotting mean values, over all years, for the nine months when samples were taken (Fig. 35).

The highest mean concentration of chlorophyll in the upper 200 m of the water column was 103 mg/m^2, a value representing two sets of samples obtained in April of 1987 and 1989. Moreover, the data indicated a gradual decrease in total chlorophyll during the development of the epilimnion in the summer, in this case, from 86.6 mg/m^2 in June to 66.1 mg/m^2 in August. Therefore, with the exception of the one low value for March 1986, the concentration of chlorophyll in the upper 200 m was higher in the winter, spring, and early summer than during thermal stratification in the late summer and early fall.

An examination of the pattern of total chlorophyll for the period from 1969 through 1990 indicated cyclic variation (Fig. 36). A curve fitted to the data revealed chlorophyll maxima in 1981 and 1987, and years of minimum concentrations in 1984 and sometime between 1969 and 1979. Also, there was a rough correspondence between annual variations in total chlorophyll and total C-14 primary production when both variables were expressed as integrated values in the water column to a depth of 200 m (Fig. 36).

Although the data in Figure 36 indicated the possibility of cyclic patterns of autotrophy in the water column, seasonal variations tend to obscure temporal patterns at an annual resolution. To eliminate seasonal effects, data representing integrated estimates of total chlorophyll were plotted for all samples obtained in August during the period from

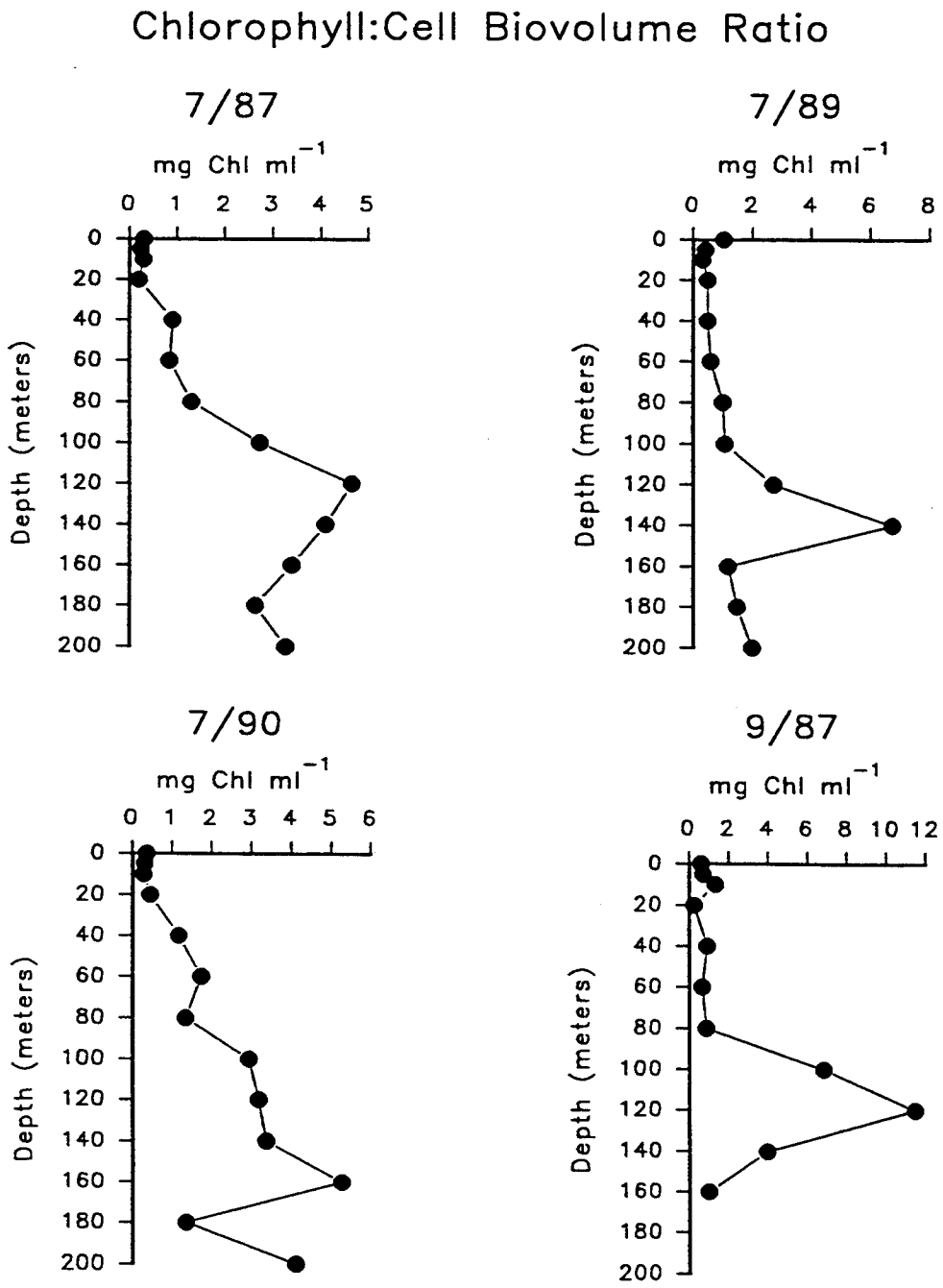


Figure 32. Ratio of the concentration of chlorophyll to the concentration of phytoplankton cell biovolume (mg/ml) at various depths at Station 13 in July 1987, 1989, and 1990, and in September 1987.

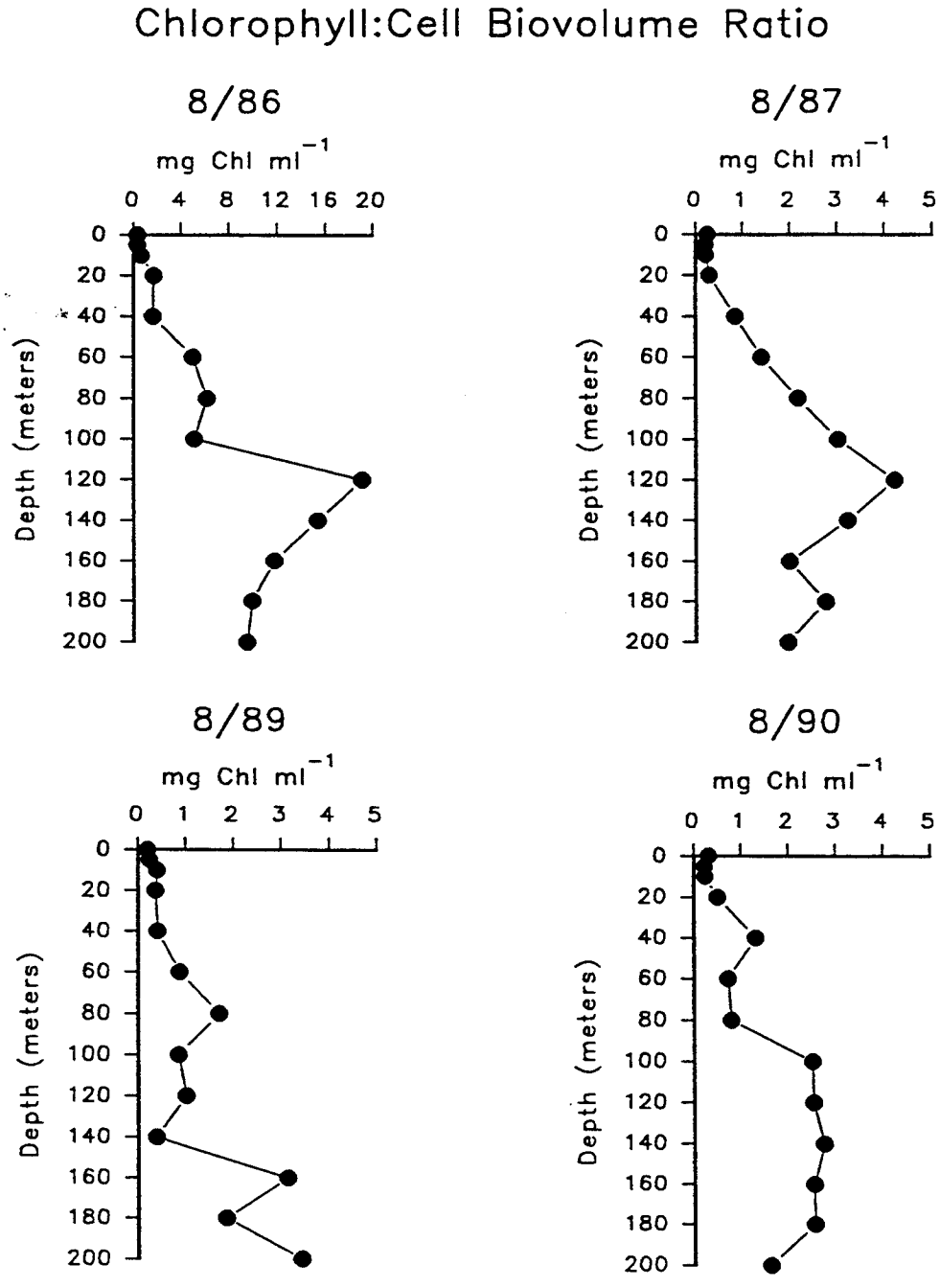


Figure 33. Ratio of the concentration of chlorophyll to the concentration of phytoplankton cell biovolume (mg/ml) at various depths at Station 13 in August 1986, 1987, 1989, and 1990.

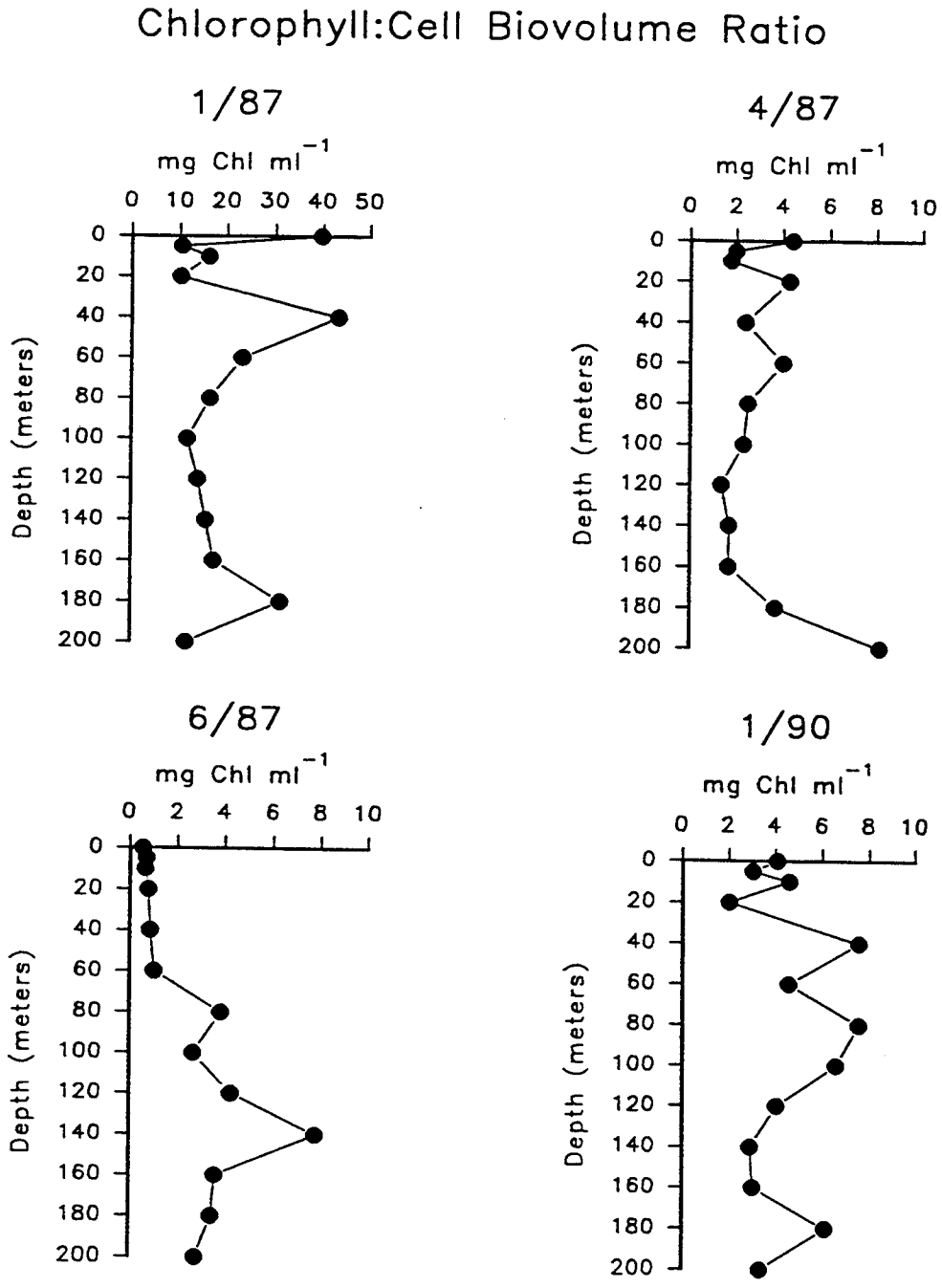


Figure 34. Ratio of the concentration of chlorophyll to the concentration of phytoplankton cell biovolume (mg/ml) at various depths at Station 13 in January 1987 and 1990, April 1987, and June 1987.

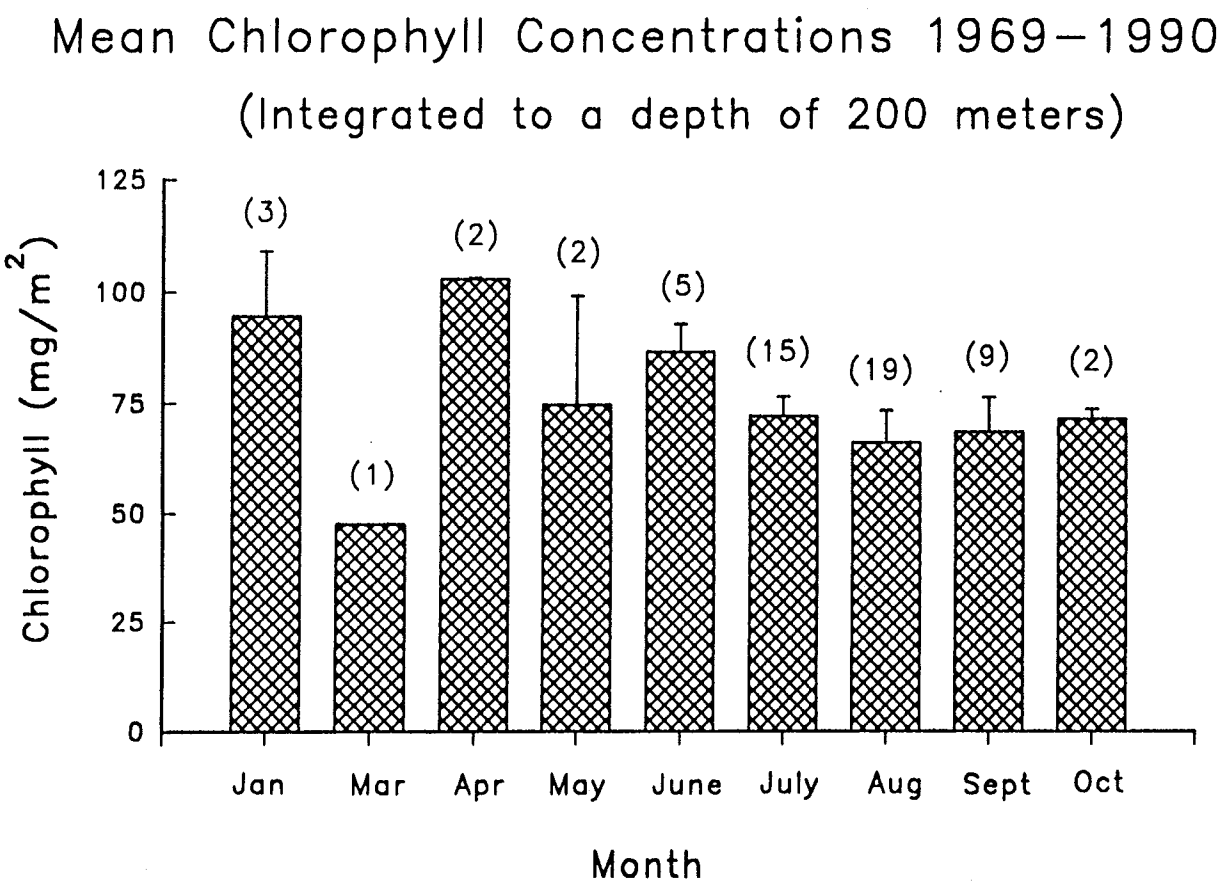


Figure 35. Seasonal variation in mean chlorophyll concentration at Station 13, integrated to a depth of 200 m for the period between 1969 and 1990. Numbers above each bar indicate the number of sampling dates represented, and variation for each month is the standard error of the mean.

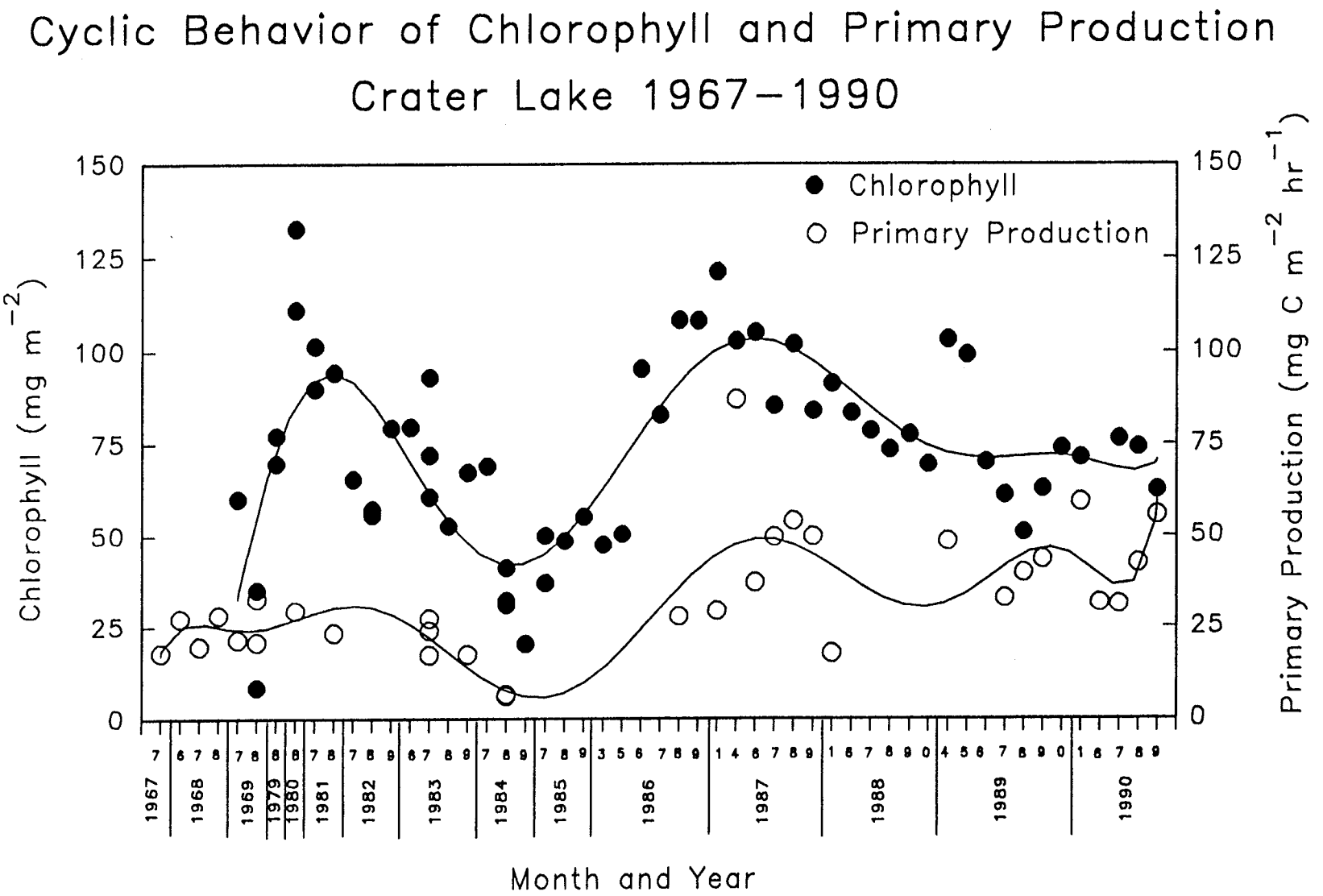


Figure 36. Cyclic behavior of chlorophyll concentration and the rate of C-14 primary production at Station 13 for the period from July 1967 to September 1990. All data represent integrated values for the upper 200 m of the water column. 1967-1984 data were made available by Douglas Larson and Cliff Dahm.

1979 through 1990 (Fig. 37). The month of August was chosen for this analysis because, by late summer, thermal stratification was complete and the physical and chemical characteristics of the lake were similar and predictable from year to year. Based on the August data, curve fitting again identified cyclic changes in the temporal pattern of total chlorophyll. In this case, the high years were 1980-81 and 1986-87 and the low years were 1983-84 and 1989, suggesting a period of about 6 to 7 years. By using the August data, it was possible to demonstrate close correspondence between temporal changes in chlorophyll and C-14 primary production (Fig. 37). However, relationships between these variables and total cell biovolume, integrated to a depth of 200 m, were not clear (Fig. 37).

Picoplankton Chlorophyll. Picoplankton chlorophyll reached a maximum of 0.2 μg/l in September 1990 at a depth of 120 m (Fig. 38). Another relatively high value (0.16 μg/l) was found in July 1990 at the same depth. Both of these maxima represented approximately 30% of the total chlorophyll at 120 m, assuming the summation of chlorophyll extracted from both filters was a satisfactory estimate of the total (Fig. 39). In general, picoplankton chlorophyll was relatively low in August 1990 at all depths (< 0.08 μg/l). On all three dates in 1990, the concentration was highest between the depths of 60 m and 160 m and lowest (< 0.04 μg/l) between the water surface and 60 m and below the depth of 180 m. The depth segment between 60 m and 160 m also included the zone of maximum primary production (60 m to 80 m) and the zone of maximum nannoplankton/ netplankton chlorophyll (100 m to 140 m).

C-14 Primary Production

Data representing depth profiles of C-14 primary production in Crater Lake were collected as early as July 1967 (Hoffman and Donaldson 1968). Subsequent studies were conducted by D. Larson and associates during the summers of 1968, 1969, 1980, 1981, 1983, and 1984 (Larson 1972, Larson et al. 1987). For the 10-year study, C-14 primary production was measured in 1986 (August), 1987 (January, April, June, July, August, and Septem-

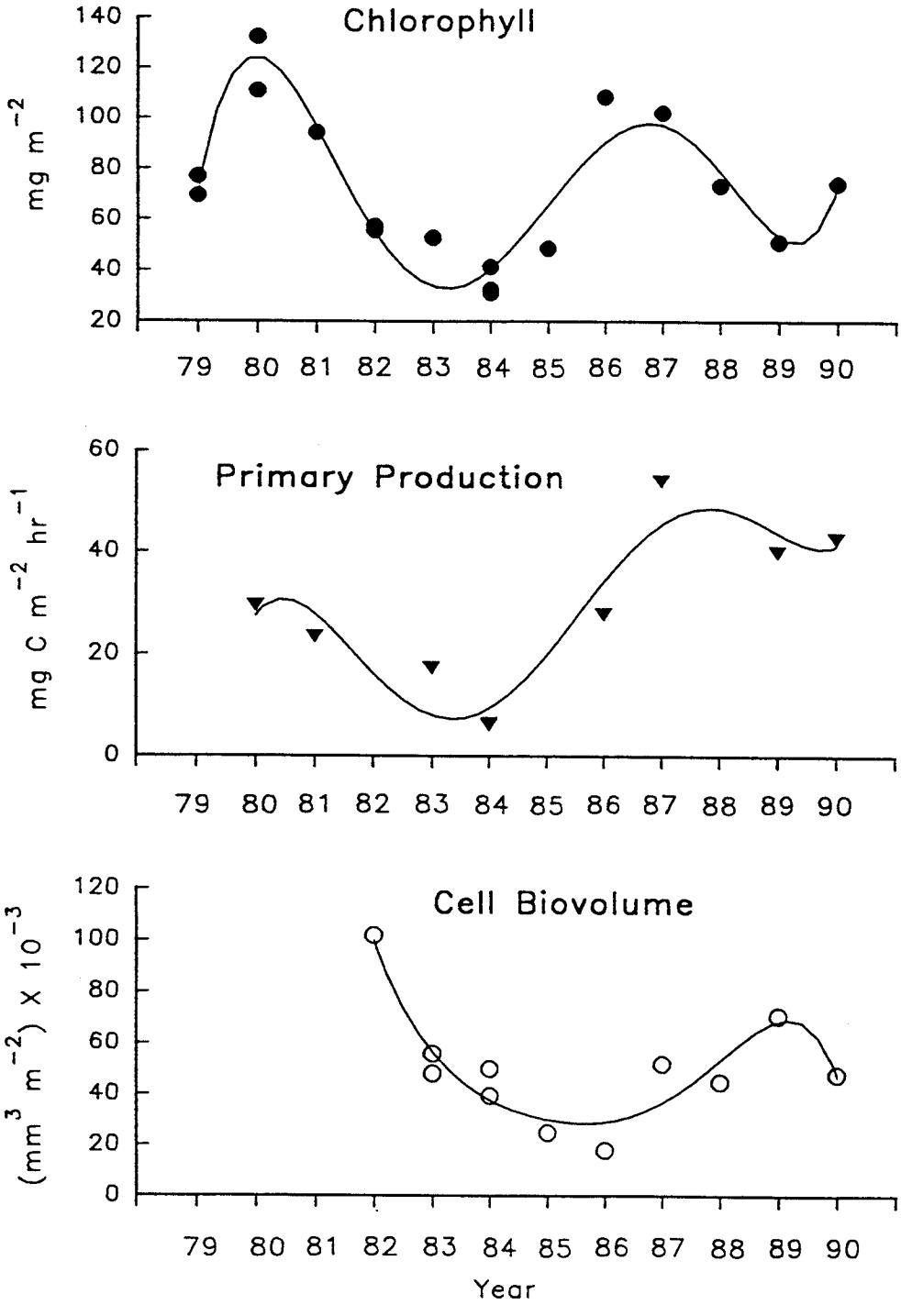


Figure 37. Cyclic behavior of chlorophyll concentration, C-14 primary production, and phytoplankton cell biovolume during thermal stratification in August between 1979 and 1990. All data represent integrated values for the upper 200 m of the water column.

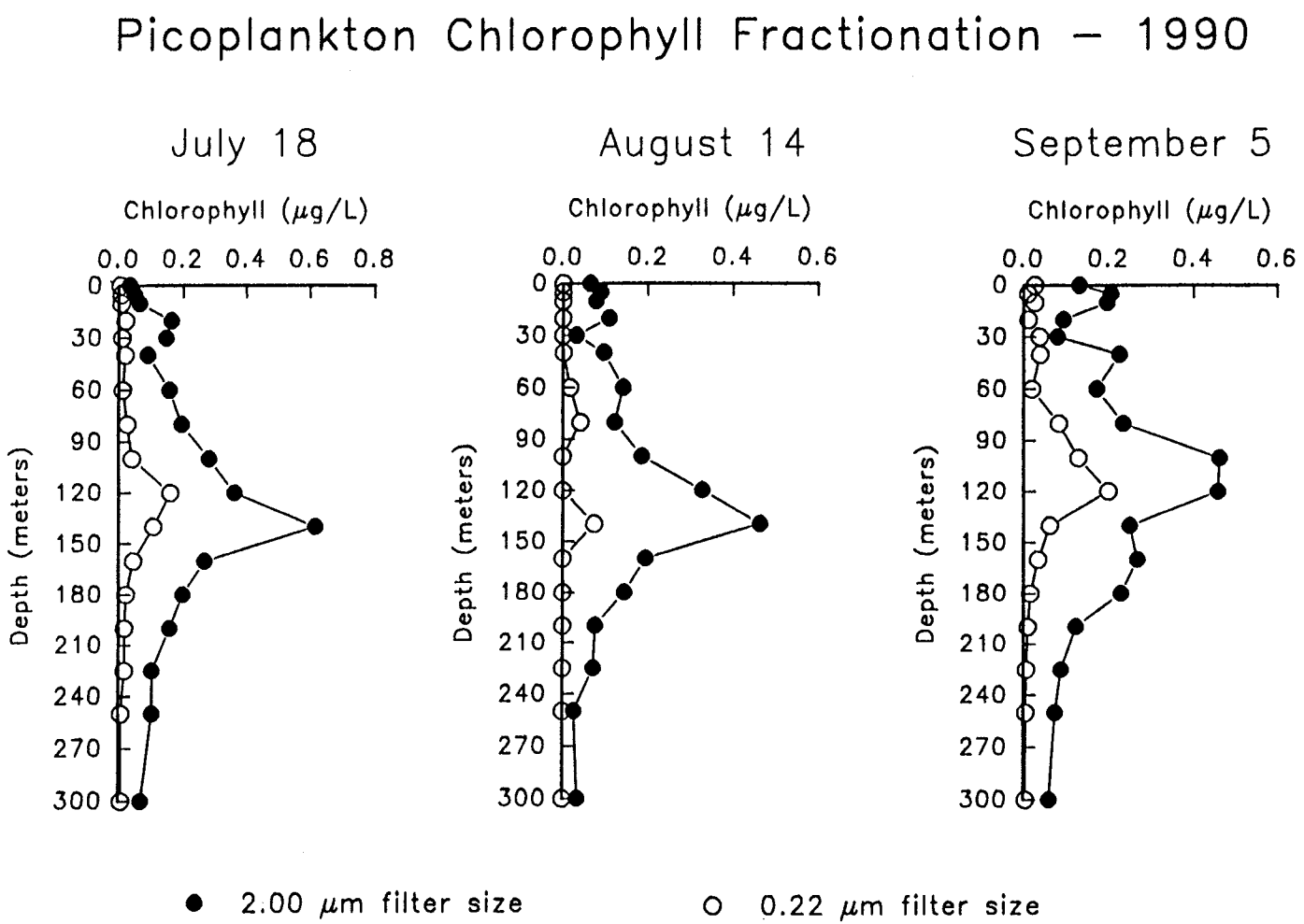


Figure 38. Vertical distribution of chlorophyll concentration partitioned into netplankton-nannoplankton (2.00 um filter) and picoplankton (0.22 um filter) size fractions for July, August, and September 1990.

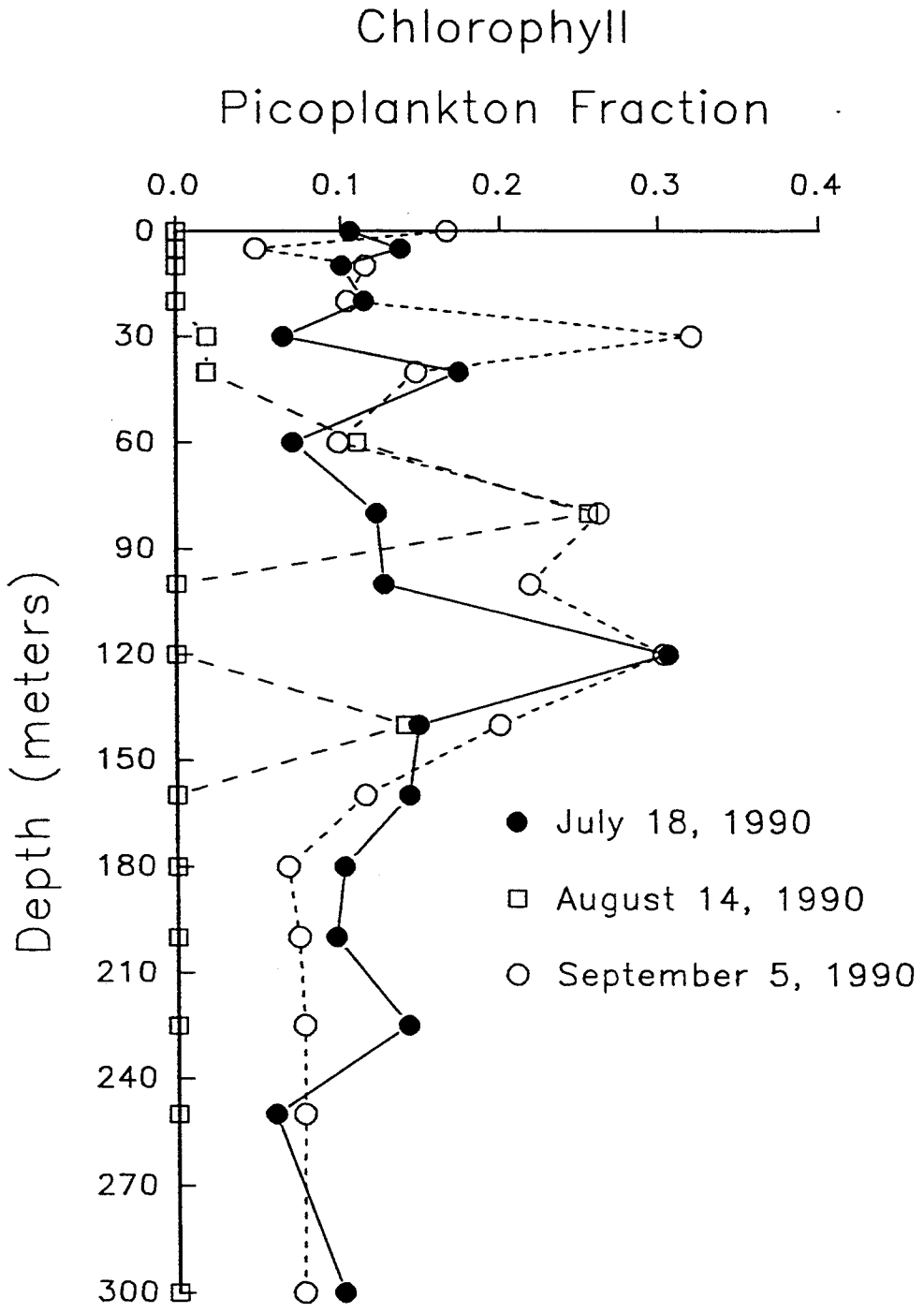


Figure 39. The proportion of the total chlorophyll concentration attributable to picoplankton at various depths at Station 13 in July, August, and September 1990.

ber), 1988 (January), 1989 (April, May, July, August, and September), and 1990 (January, June, July, August, and September). In this report, we include all C-14 primary production data and present the results as depth profiles and as estimates of rates of primary production in the water column integrated to a depth of the deepest measurement, usually 180 m. The earlier data (i.e., before 1986) was kindly supplied by D. Larson or obtained from the literature.

Depth Profiles. Highest rates of C-14 primary production were measured at depths of 40 and 60 m in April 1987 when the values were between 1.2 and 1.3 mg C m^{-3} hr^{-1} (Fig. 40); maximum rates in other years were usually between 0.2 and 0.8 mg C m^{-3} hr^{-1} (Figs. 40 - 42). An examination of all C-14 primary production data indicated that the maximum rate of carbon assimilation during thermal stratification in the summer usually occurred at a depth between 60 and 100 m. Notable exceptions to this pattern were observed on July 23, 1968, August 24, 1981, August 13, 1984, July 23, 1987 (Fig. 40), and July 18, 1989 (Fig. 41). The relatively uniform pattern of primary production on July 23, 1968 was attributed to sampling error (Larson 1972), whereas profiles on August 24, 1981, August 13, 1984, and July 18, 1989 exhibited a prominent maximum in the upper 10 m of the water column. Production maxima in the epilimnion also were found in July and August of 1968, 1969, 1980, 1983, 1986, 1987, and 1990 (Figs. 40 - 42). These maxima were associated with the dominance of *Nitzschia gracilis* in the near-surface water and were less than the deep-water maximum between 60 and 100 m. In winter and spring, maximum rates of primary production usually were found at depths between 20 and 60 m.

The ratio of C-14 primary production to chlorophyll concentration (assimilation number) expressed as mgC $mgChl^{-1}$ hr^{-1} ranged from values near zero at depths below 120 m to a maximum of 12.1 in the epilimnion. The usual pattern of variation for this variable is illustrated by seasonal changes between January and September 1987 (Figs. 43 - 45). In the winter and spring of 1987, the assimilation number reached a maximum value of 1 to 3 mgC $mgChl^{-1}$ hr^{-1} at depths between 20 and 60 m. However, with the onset of thermal

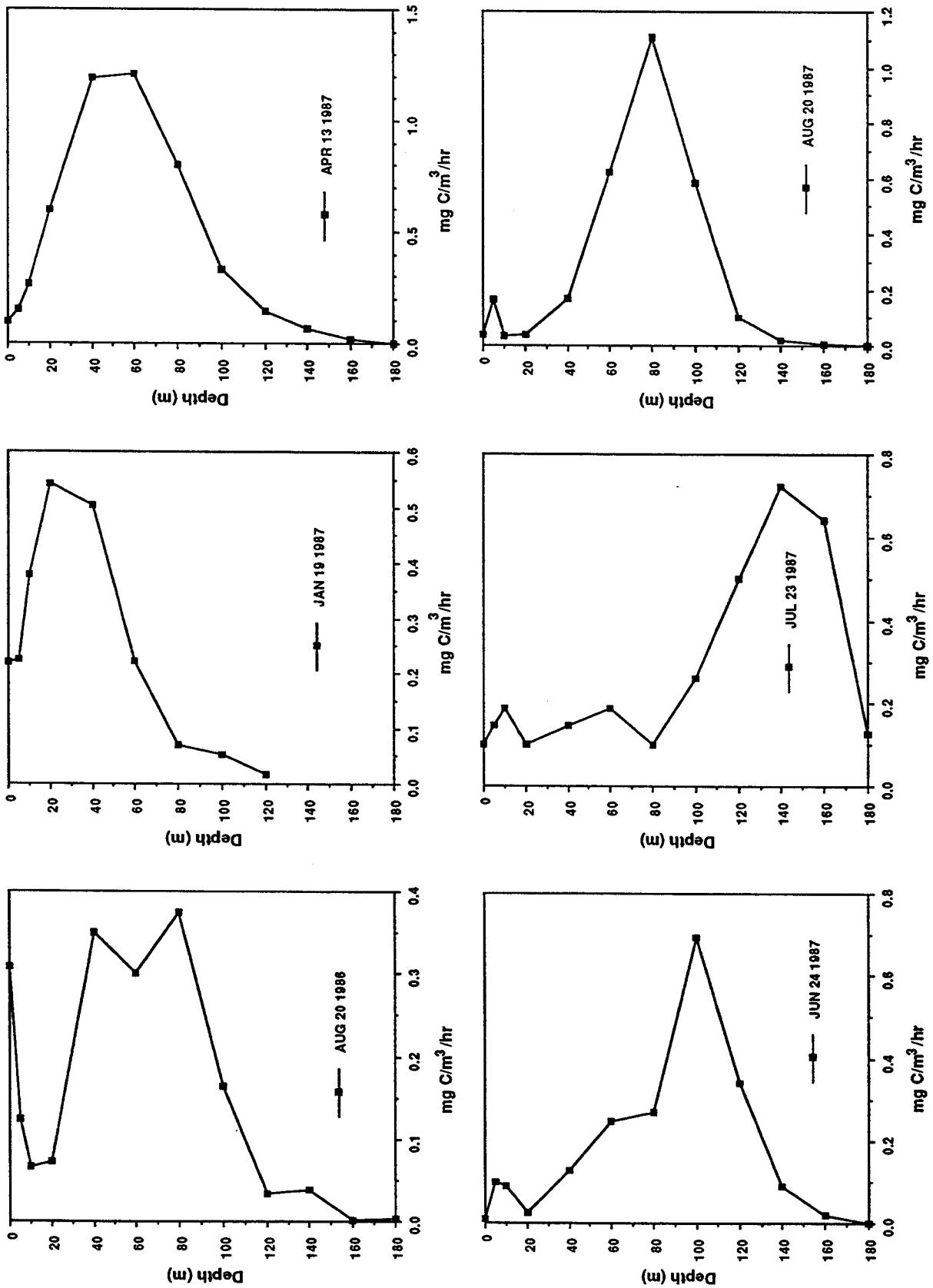


Figure 40. Vertical distribution of C-14 primary production in the water column at Station 13 between August 1986 and August 1987.

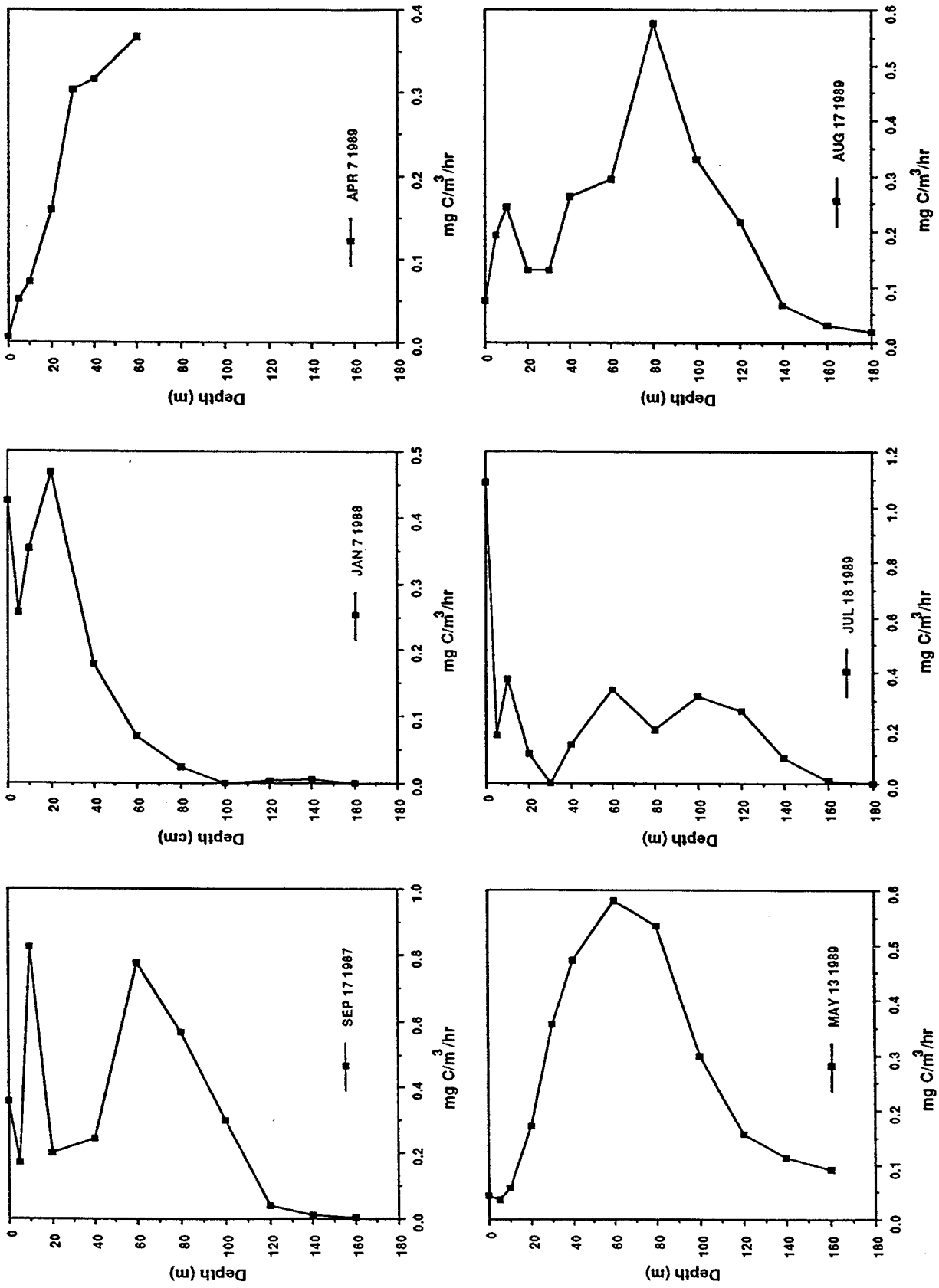


Figure 41. Vertical distribution of C-14 primary production in the water column at Station 13 between September 1987 and August 1989.

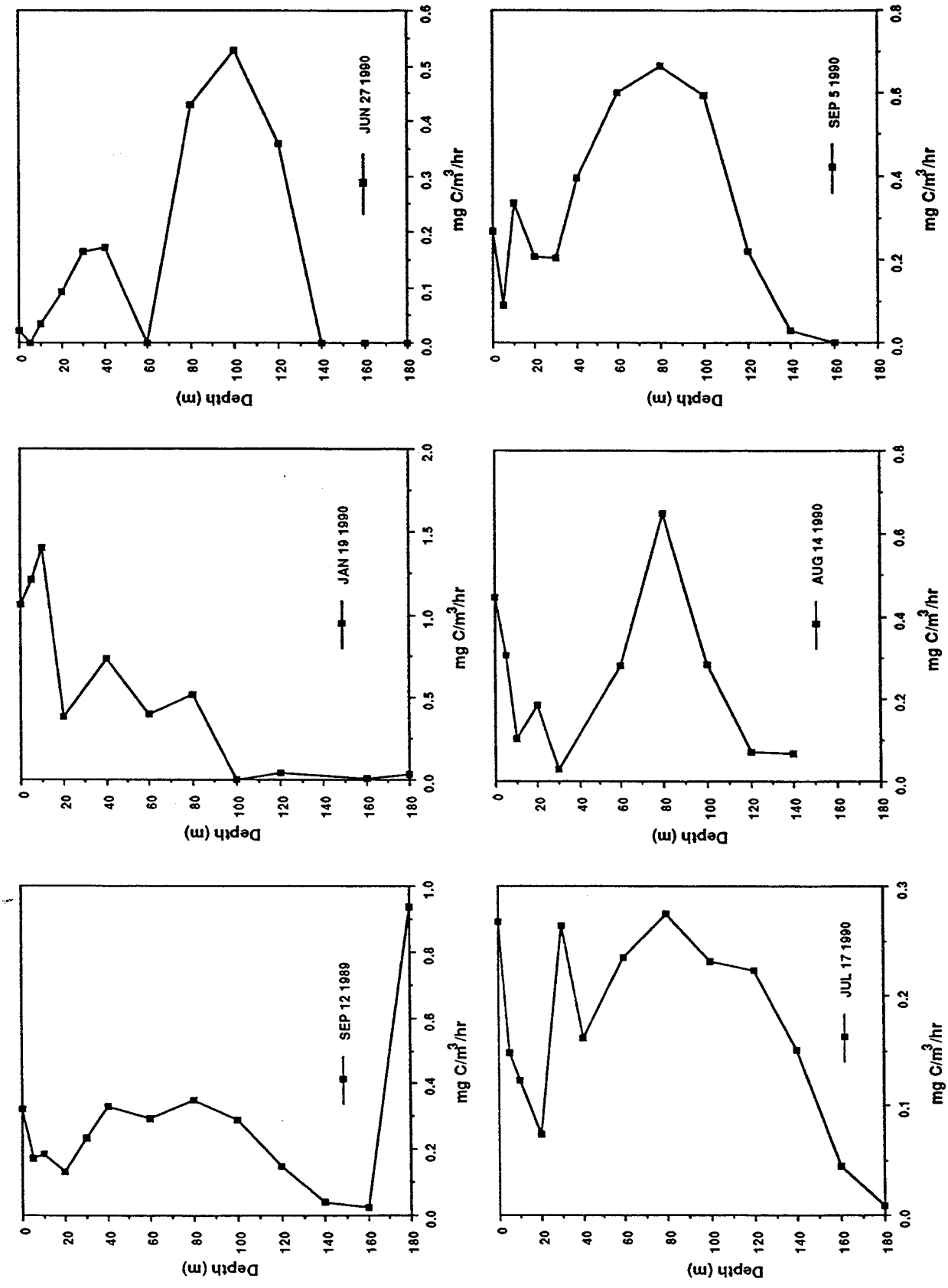


Figure 42. Vertical distribution of C-14 primary production in the water column at Station 13 between September 1989 and September 1990.

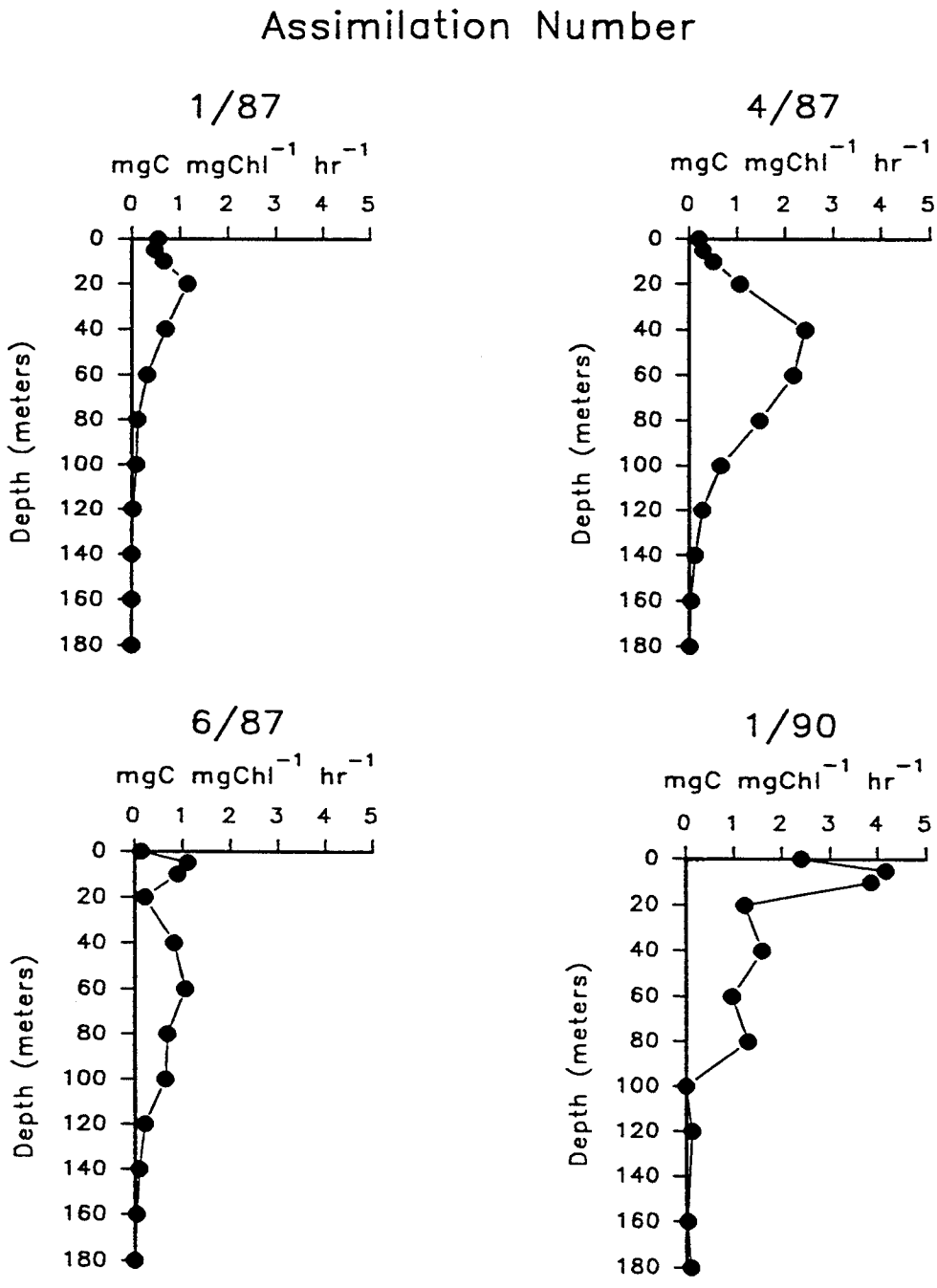


Figure 43. Ratio of C-14 primary production to chlorophyll concentration (assimilation ratio) at various depths at Station 13 in January 1987 and 1990, April 1987, and June 1987.

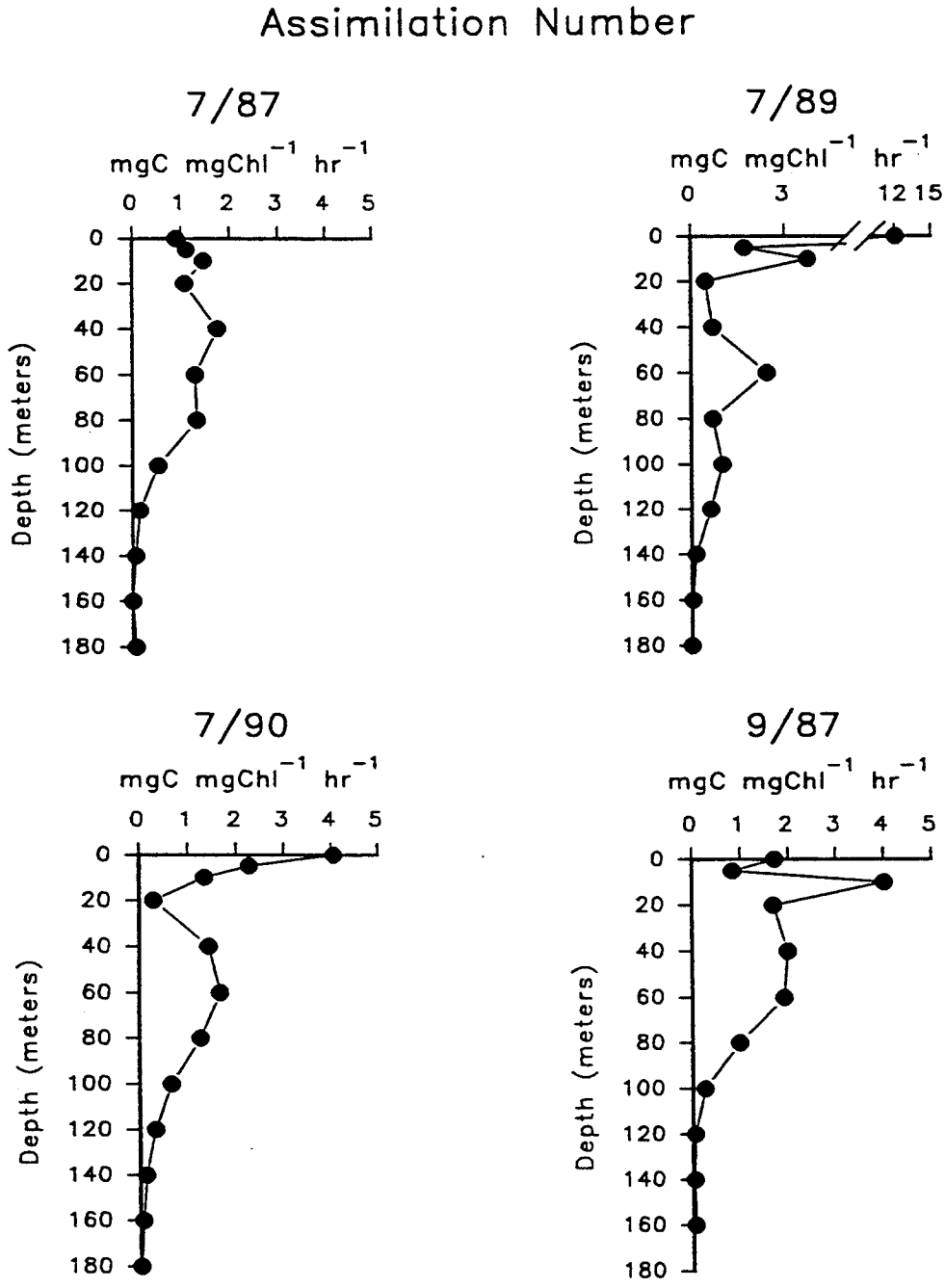


Figure 44. Ratio of C-14 primary production to chlorophyll concentration (assimilation ratio) at various depths at Station 13 in July 1987, 1989, and 1990, and in September 1987.

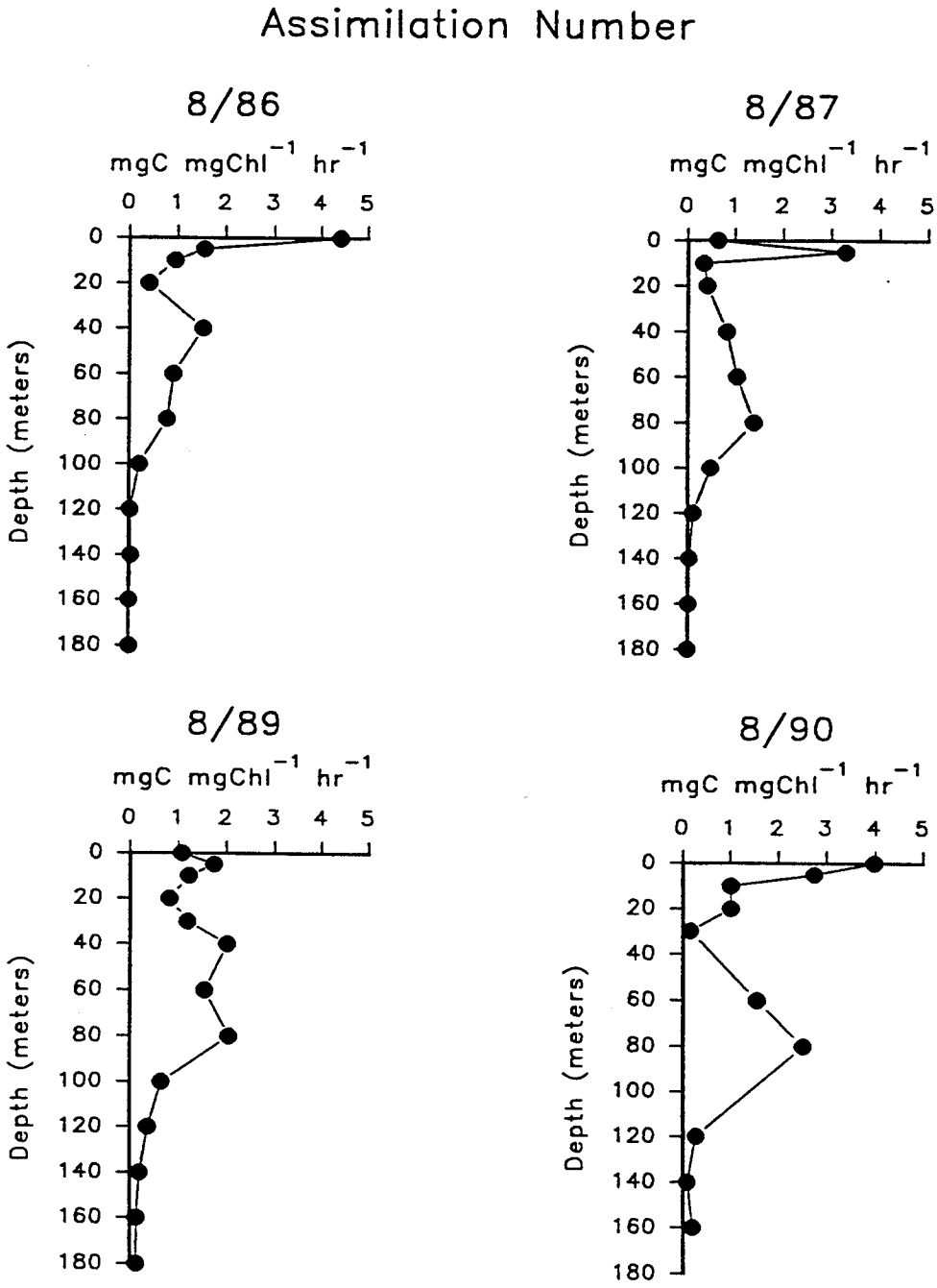


Figure 45. Ratio of C-14 primary production to chlorophyll concentration (assimilation ratio) at various depths at Station 13 in August 1986, 1987, 1989, and 1990.

stratification, a second maximum appeared concurrently with an increase in the abundance of *Nitzschia gracilis* in the upper 10 m of the water column. In 1987 this near surface maximum (ca. 4 mgC $mgChl^{-1}$ hr^{-1}) was observed in August and September, whereas in some years (e.g., 1989 and 1990) it was present as early as July.

Patterns of Total Primary Production. During the 10-year study, the rate of C-14 primary production integrated to a depth of 180 m ranged from 17.7 mg C m^{-2} hr^{-1} in January 1988 to 87.1 mg C m^{-2} hr^{-1} in April 1987 (Table 11). Earlier data obtained between 1967 and 1984 by Hoffman and Donaldson (1968) and D. Larson et al. (Table 12) generated integrated rates from 6.1 mg C m^{-2} hr^{-1} (August 1984) to 32.7 mg C m^{-2} hr^{-1} (August 1969). The mean rate of C-14 primary production per cubic meter in the water column for all studies varied between 0.03 mg C/hr (August 1984) and 0.48 mg C/hr (April 1987) with an overall mean and standard error for all data of 0.18 and 0.017 mg C/hr, respectively.

Cyclic behavior in the primary production data was less obvious than in the pattern found for the chlorophyll data (Fig. 36). However, primary production data for the month of August followed a distinct cyclic pattern with high years in 1980 and 1987 and a low year in 1984 (Fig. 37). Moreover, cycles in primary production corresponded more closely to the cycle for chlorophyll concentration than to the cycle for total cell biovolume. The latter variable had relatively low years in 1985 and 1986, but did not reach a maximum value until 1989, two years after maxima found for chlorophyll and primary production.

Picoplankton Primary Production. Measurements of picoplankton primary production began in July 1990 and were concurrent with measurements of picoplankton chlorophyll. Water samples were collected and incubated while following the procedure described in the sampling section of this paper. After retrieval each sample was filtered first through a 2.00 μm Millipore filter and then through another filter with a pore size of 0.22 μm. The C-14 activity of each filter was determined at the Oregon State University Radiation Center. Interpretation of the results was based on the assumption that the radioactivity of material on the 0.22 μm filter was indicative of picoplankton primary production,

Table 11. Estimates of C-14 primary production at Station 13 for the period from 1986 through 1990. Values are expressed as the mean rate per cubic meter throughout the water column to a depth of 180 m and the rate under a square meter of water surface integrated to a depth of 180 m. Estimates of carbon fixation were based on the measured activity of the inoculum, and on the assumed inoculum activity of 5 μCi/ml for comparisons with the 1967-84 data.

Date	Measured Activity of Inoculum		Assumed Activity of 5 μCi/ml	
	(mg C m^{-3} hr^{-1})	(mg C m^{-2} hr^{-1})	(mg C m^{-3} hr^{-1})	(mg C m^{-2} hr^{-1})
8/86	0.15	27.8	0.08	15.2
1/87	0.16	29.4	0.09	16.0
4/87	0.48	87.1	0.26	46.8
6/87	0.21	37.2	0.11	20.0
7/87	0.28	49.6	0.15	26.6
8/87	0.30	54.0	0.16	29.0
9/87	0.28	49.8	0.08	13.5
1/88	0.10	17.7	0.03	4.8
5/89	0.27	48.5	0.22	38.9
7/89	0.18	32.9	0.15	26.9
8/89	0.22	39.9	0.18	32.0
9/89	0.24	43.6	0.20	35.1
1/90	0.33	59.3	0.26	47.4
6/90	0.18	31.7	0.15	26.4
7/90	0.17	31.2	0.15	26.1
8/90	0.24	42.5	0.19	34.8
9/90	0.31	55.7	0.26	45.9

Table 12. Estimates of C-14 primary production at Station 13 for the period from 1967 through 1984. Values are expressed as the mean rate per cubic meter throughout the water column for the indicated depth interval and the rate under a square meter of water surface integrated to the maximum depth of the interval. Data for this table were made available for comparative purposes by Douglas Larson and Cliff Dahm. Estimates of carbon fixation were based on an assumed inoculum activity of 5 μCi/ml.

Date	Depth Interval	Mean Rate	Integrated Rate
	(meters)	(mg C m^{-3} hr^{-1})	(mg C m^{-2} hr^{-1})
7/26/67	0 - 200	0.09	18.2
6/14/68	0 - 140	0.20	27.3
7/23/68	0 - 130	0.14	19.7
8/27/68	0 - 140	0.20	28.1
7/16/69	0 - 200	0.11	21.4
8/5/69	0 - 200	0.10	20.7
8/31/69	0 - 200	0.16	32.7
8/27/80	0 - 200	0.15	29.4
8/24/81	0 - 200	0.12	23.2
7/15/83*	0 - 200	0.14	27.2
7/28/83*	0 - 200	0.12	23.8
7/29/83*	0 - 200	0.09	17.3
9/14/83*	0 - 200	0.09	17.5
8/13/84*	0 - 200	0.03	6.4
8/23/84*	0 - 200	0.03	6.1

while activity associated with the 2.00 μm filter was related to netplankton and nanno-plankton primary production.

Two patterns of picoplankton primary production were found in 1990 (Fig. 46). In July differential filtration indicated that rates of pico-plankton primary production exceeded corresponding rates for the larger size classes of phytoplankton at depths between 0 and 60 m and between 140 and 180 m. In particular, picoplankton primary production was relatively high at the water surface and at a depth of 40 m; between 60 and 120 m rates were low and less than corresponding values for netplankton and nannoplankton. In September, picoplankton primary production was either less than or approximately equal to the primary production associated with the larger organisms. The greatest differences between the two size classes occurred in the epilimnion and at depths between 40 and 100 m. Moreover, vertical profiles of primary production for September closely resembled vertical patterns found for the chlorophyll data, whereas there was virtually no correspondence in the July data (Figs. 38 and 46). Mechanisms accounting for the discrepency between primary production and chlorophyll in July are still unclear.

Discussion

Taxonomic Structure

The use of individual species of phytoplankton as indicators of lake trophic status has generated inconsistencies and confusion. Some of these problems are undoubtedly related to differences in taxonomic interpretation, and to weak correspondences between the morphological criteria used for taxonomic separation and the physiological characteristics of different populations. A list of oligotrophic indicator species given by Hutchinson (1967) from the work of Jarnefelt (1952) included *Nitzschia gracilis* and species of *Dinobryon*, *Crucigenia*, and *Kephyrion*, taxa that were prominent at times in Crater Lake.

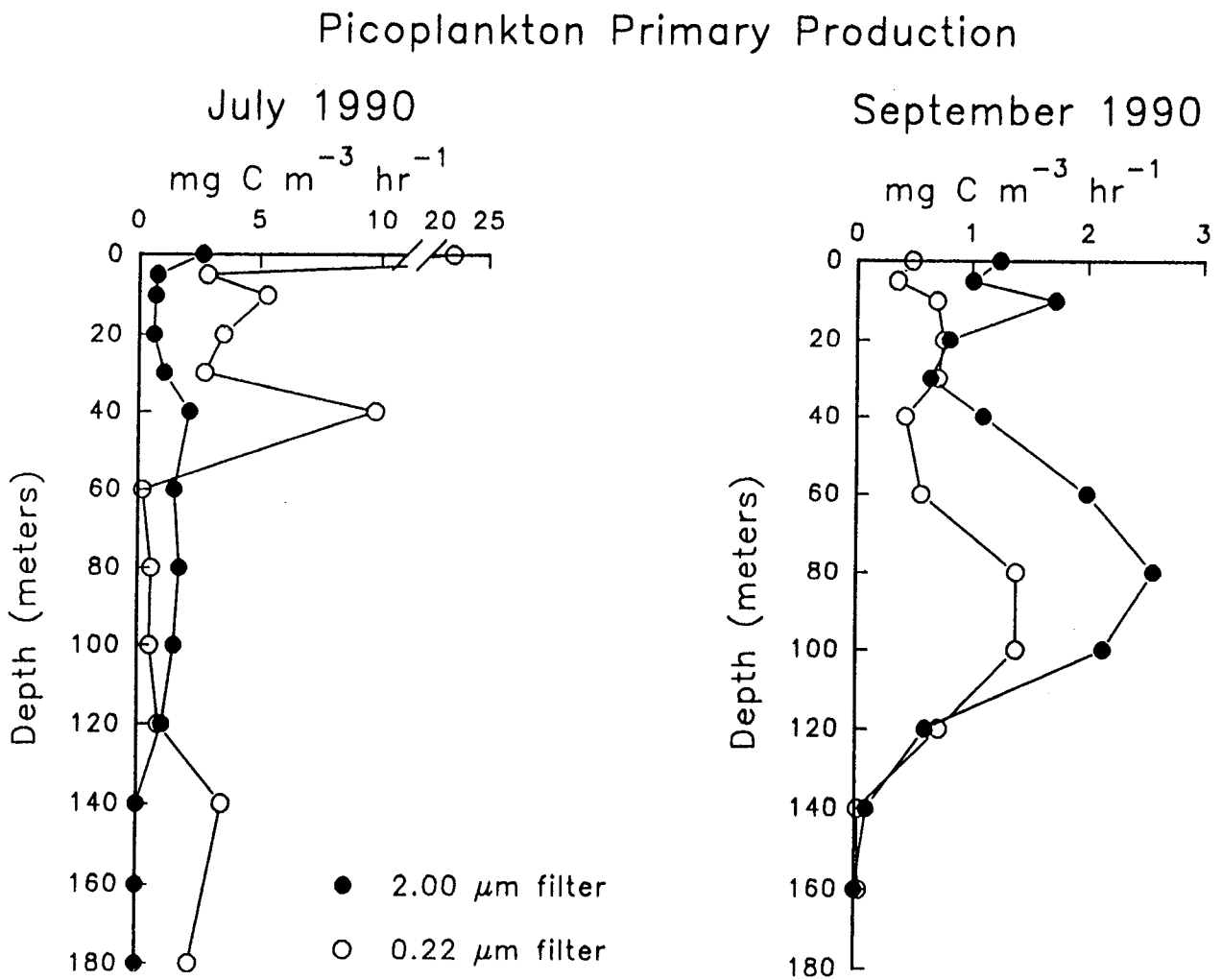


Figure 46. Vertical distribution of C-14 primary production partitioned into netplankton-nannoplankton (2.00 um filter) and picoplankton (0.22 um filter) size fractions for July and September 1990.

However, the ecological properties of *Asterionella formosa* apparently are more complex, as this taxon is known to have eurythermal and stenothermal ecotypes which exhibit different spatial distributions (Ruttner 1937). In Crater Lake, *A. formosa* was most prominent in the autumn at depths between 20 and 140 m, a pattern that was different than the spring maxima found in other studies (Hutchinson 1967, Patrick and Reimer 1966). Although *A. formosa* has been reported to have a high nutrient requirement (Pearsall 1932, Lowe 1974), Rawson (1956) lists this taxon as a strong indicator of oligotrophic conditions in the lakes of Western Canada. The organism identified in the Crater Lake samples as *Stephanodiscus hantzschii* may in fact be more closely related to the coarsely structured form of *S. parvus* Stoermer and Hakansson (Stoermer & Hakansson 1984). Such taxonomic uncertainties make ecological interpretations difficult. While the spring maximum of *S. hantzschii* in Crater Lake corresponds with temporal patterns reported in the literature (Hutchinson 1967), its abundance and that of *S. parvus* in natural waters have been more closely associated with eutrophic conditions and silicon limitation than with an oligotrophic environment (Lowe 1974, Stoermer & Hakansson 1984, Hakansson & Stoermer 1984). In any case, cell densities of the dominant planktonic algae (> 2 um in diameter) in Crater Lake were always low (< 200 cells ml^{-1}), with the notable exception of *N. gracilis* which reached a maximum density of 765 cells ml^{-1} in August 1980 (Larson et al. 1987).

There have been attempts to introduce generalizations concerning broad distributional patterns in the major taxonomic divisions and classes of planktonic algae (e.g., see review articles in Sandgren 1988). In the Crater Lake data, very little pattern emerged at the division and class taxonomic levels, whereas at the level of genus and species some assemblages representing one or more divisions and classes were identified. Chrysophytes were distributed throughout the water column during all seasons of the year, and were particularly abundant below a depth of 20 m. Sandgren (1988) suggested that phagotrophic nutrition by chrysophytes may allow active ingestion of bacterial cells and other algae, thereby providing these consumers with the advantages of 24-hour feeding, a source of

large concentrations of nutrients quickly, and a source of micrometals in a utilizable form. Moreover, high rates of organic molecule leakage from chrysophyte cells in combination with bactivory may represent a chrysophyte-bacterial nutritional loop that makes these algae particularly adapted for persistence in deep water where the supply of light energy is low. In many lakes, cryptomonads exhibit permanent presence throughout the year, have their maximal population development at depths well below the lake surface, and are capable of surviving at low light levels (Klaveness 1988). These generalizations also apply to Crater Lake where cryptomonads are present at all seasons of the year and are particularly abundant at depths between 20 m and 200 m. With the exception of the genus *Mougeotia*, planktonic green algae (chlorophytes) in Crater Lake are relatively small organisms (nannoplankton) with a high surface to volume ratio; they exhibit maximum abundance during the spring and summer months. Happey-Wood (1988) found that small-celled green algae, both motile and nonmotile taxa, often persist throughout the year and form a major component of the nannoplankton and picoplankton in lakes of low productivity. Dinoflagellates in Crater Lake occur in relatively low densities in comparison to chrysophytes, chlorophytes, and diatoms. However, because of their relatively large cell size, members of the Pyrrhophyta represented a significant proportion of the total phytoplankton cell biovolume, especially in the spring at depths between 20 m and 140 m. According to Pollingher (1988), motility in dinoflagellates enhances nutrient uptake and minimizes sedimentation, although these organisms are not considered to be strong competitors with other nannoplanktonic species at times of high turbulence in the water column. The very low abundance of dinoflagellates in the January samples from Crater Lake supports the hypothesis that conditions of short daylengths and mixing in the water column are unfavorable for growth and survival of this division. The most abundant diatoms in Crater Lake include *Nitzschia gracilis*, *Stephanodiscus hantzschii*, *Asterionella formosa*, and species of *Synedra*, taxa that have a relatively high surface to volume ratio. Some research has indicated that diatoms often become abundant in the spring and again in the fall, and that

there is sometimes a predictable successional sequence of taxa related to nutrient dynamics (Hutchinson 1967, Patrick 1977). However, such patterns were not evident in Crater Lake, as the only predictable diatom bloom was related to the rapid increase in the density of *Nitzschia gracilis* in July and August when thermal stratification was present. Planktonic cyanobacteria in Crater Lake were almost entirely unicellular, coccoid picoplanktonic species less than 3 μm in diameter. A few specimens of filamentous forms were observed in the samples, but these were probably of benthic origin. The ecological significance of picoplanktonic cyanobacteria in the lake is poorly understood and needs further investigation.

The three-tier model for the summertime phytoplankton of Crater Lake (Larson et al. 1987) predicts three zones in the water column, each with low species diversity and a high degree of dominance by a single taxon. Therefore, conformity to this structure would require that the assemblages exhibit low species diversity throughout the water column to a depth of 200 m. Data from the 1985-88 samples clearly identified an upper zone which supported an assemblage with very low species diversity ($H < 1.0$) and a high dominance by *Nitzschia gracilis*. However, the data also revealed a conspicuous discontinuity in the pattern of species diversity in the metalimnion (between 10 and 40 m below the surface), and a relatively high mean species diversity ($H > 1.8$) for assemblages collected below the metalimnion. Consequently, we conclude that the structure of phytoplankton assemblages at mid depth (40 - 140 m) and in the deeper zone (140 - 200 m) is much more complex and less predictable than the pattern described by the three-tier model. The discrepency between the 1985-88 data and the model is due to our failure to find dominance by *Tribonema* sp. and *Stephanodiscus hantzschii* at any depth below the epilimnion. Whether or not there has been a decrease in dominance since the 1978-80 study, or instead, the lack of correspondence is related to differences in sampling and counting procedures is uncertain.

The summer distributions of *Nitzschia gracilis* and *Stephanodiscus hantzschii* during the 10-year study corresponded to vertical distributions reported by Larson et al. (1987) for

1978, 1979, and 1980. Of these species, *N. gracilis* exhibited the most predictable pattern in both studies with relatively high cell biovolumes confined to the upper 80 m of the water column during July and August. This taxon was particularly abundant in all samples obtained from the epilimnion since 1978. Concentrations of *S. hantzschii* in the water column between 80 and 200 m also corresponded roughly to the distribution reported in the earlier study. However, this taxon usually accounted for less than 5% of the total cell biovolume in the July and August samples from this depth segment.

The discovery of relatively high phytoplankton cell biovolumes between 80 and 200 m in Crater Lake is consistent with patterns reported for oligotrophic lakes (Tilzer et al., 1977). Kiefer et al. (1972) recorded a maximum cell biovolume of 200×10^6 μm^3 l^{-1} at a depth of 100 m in Lake Tahoe and concluded that deep-water maxima are a characteristic feature of oligotrophic lakes. In data obtained between June 1985 and September 1990, deep-water maxima as high as 854×10^6 and 842×10^6 μm^3 l^{-1} were found at depths of 120 m (May 1989) and 140 m (August 1989), respectively. In addition, the sampling strategy revealed a periodicity associated with the cell biovolume in the upper 20 m of the water column and a relatively uniform distribution of cell biovolume to a depth of 200 m during the winter and spring months. In the upper 20 m, summer biovolume maxima, which ranged between a mean of 304×10^6 (July 1986) and 469×10^6 μm^3 l^{-1} (July 1987), were related to an unusual growth potential of *Nitzschia gracilis* under conditions of high temperature (14 - 16°C), high light intensity, and very low nutrient concentrations. Integrated cell biovolume (to 200 m) also reached maxima in the spring (e.g., May 1986 and April 1989), presumably due to increases in daylength and nutrient input from the deep lake and melting snow.

The multivariate analysis of the 1985-1988 data clearly indicated that assembages of netplankton and nannoplankton in Crater Lake exhibited recurring patterns over a four-year period. Although the clustering algorithm forced samples into discrete groups, an examination of distances between cluster centroids and mean abundances of the prominent

taxa in the samples for each cluster indicated considerable overlap in the species compositions of the five assemblages identified by the analysis. The five-cluster structure is interpreted as a manifestation of periodic shifts in the spatial and temporal patterns of dominance by one or more species. These surges of dominance by individual taxa accounted for periodic increases in cell biovolume and generated the pronounced taxonomic discontinuity between the floras in the epilimnion and hypolimnion during July and August.

The greatest variation in the taxonomic structure of the Crater Lake phytoplankton occurred between 40 and 80 m below the water surface, a depth range which corresponded to the zone of maximum primary productivity during the summer and early autumn. Variations in community structure associated with this depth segment usually were related to temporal changes in the relative abundances of *Asterionella formosa*, *Dinobryon sertularia*, and three dinoflagellates from June through September. Apparently, the zone of maximum primary productivity provides an environment that allows more rapid changes in population growth rates than conditions in the deeper, lower regions of the photic zone. Karnaugh (1988) also found both seasonal and annual variation in the distribution and abundance of zooplankton below the metalimnion, changes that may account for some of the temporal fluctuation in the phytoplankton assemblage.

All chemical data obtained since 1983 indicate that the phytoplankton assemblage in Crater Lake exists under conditions of severe nitrogen limitation (Larson, 1985, 1987, 1989). Also, recent data from sediment collection chambers (Dymond & Collier, 1987) suggest that about 95% of the primary productivity in the euphotic zone is supported by recycled nutrients rather than by the input of new nutrients. Consequently, thermal stratification in the summer may temporarily isolate the upper 20 m of the water column from some of the benefits of recycling, thereby creating an impoverished environment that is unsuitable for the maintenance of high species diversity. The fact that *Nitzschia gracilis* generates high cell densities under such conditions is interesting and merits further investigation. An exhaustive search of the distributional records for this taxon at the Philadelphia

Academy of Natural Sciences (Charles Reimer, personal communication) revealed that morphological entities interpreted as *N. gracilis* have been reported from a wide range of habitats (e.g., the plankton of lakes and ponds, on mud, epiphytic on moss, in bogs, and in streams and rivers). In any case, the population of *N. gracilis* in Crater Lake is extremely efficient in its utilization of the very meager allochthonous input of nutrients, apparently resulting in low species richness and high dominance in the epilimnion. Moreover, this species has greater than twice the surface to volume ratio of a spherical shaped cell with the same volume, a morphological adaptation that may enhance nutrient uptake when concentrations are low. Since *N. gracilis* also occurs in low densities in deeper water, we conclude that it is a combination of high light energy, relatively high temperature, and an efficient pattern of nutrient utilization that results in the abundance and dominance of this species in the upper 20 m of the water column during the summer months.

Chlorophyll and Primary Production

In winter and spring, the distribution of chlorophyll in Crater Lake is relatively uniform to a depth of 200 m, the apparent maximum depth of active mixing in the water column. In addition, the ratio of chlorophyll concentration to phytoplankton cell biovolume is relatively high at that time of year. The period of mixing in winter and early spring is characterized by low inputs of light energy and relatively high nutrient inputs from precipitation, snowmelt run-off (Reilly 1989), and upwelling from the deep lake (McManus 1993). During the initial stage of thermal stratification mixing and nutrient inputs decrease, and the chlorophyll to cell biovolume ratio decreases while a deep-water chlorophyll maximum (DCM) begins to form. With the period of high light energy input and thermal stratification in July and August, the input of nutrients into the euphotic zone from the caldera walls and the deep-water zone (depths > 200 m) is low, although the deposition of atmospheric dry fall may provide significant inputs at this time (Goldman et al. 1990). By August, the DCM is usually located at a depth between 100 m and 140 m, a

stratum characterized by low nutrient concentrations and very low inputs of light energy. The chlorophyll to biovolume ratio is usually relatively high in the region of the DCM and low elsewhere in the water column. These conditions persist throughout the month of September, although the DCM may shift upward in the water column slightly with a decrease in the availability of light energy. The DCM presumably erodes later in the fall or early winter after the thermocline disappears. Spatial and temporal characteristics of the DCM in Crater Lake are very similar to those in Lake Tahoe, with the exceptions that in the latter case the DCM occurs at shallower depths (ca. 100 m) and is associated with a nitracline (Goldman and de Amezaga 1975, Abbott et al. 1984, Coon et al. 1987).

The location of primary production maxima and corresponding ratios of primary production to chlorophyll concentration in the water column change with season in Crater Lake. In the spring, the deep-water primary production maximum (DPM) occurs between 40 m and 60 m below the water surface, and the ratio of primary production to chlorophyll concentration begins to increase. During the summer months, the primary production depth profile is usually bimodal, with one maximum in the epilimnion and the DPM shifting down the water column to a depth range of 40 m to 80 m by August. At this time of year, the primary production to chlorophyll concentration ratio is highest in the DPM, and epilimnion maxima are often associated with high cell densities of *Nitzschia gracilis*. By September, the location of the DPM may be similar to its position in August or it may shift slightly upward in the water column. Primary production to chlorophyll ratios are low in the deep-water chlorophyll maximum, but are always greater than zero. Moreover, limited data for January, indicate that the DPM is higher in the water column and primary production to chlorophyll concentration ratios are lower in the winter than during the summer months. In general, patterns of primary production in Crater Lake are similar to those reported for Lake Tahoe, at least to the degree that deep-water maxima can occur at depths below 30 m (Goldman and de Amezaga, 1975; Coon et al., 1987). However,

primary production maxima in Lake Tahoe are usually located higher in the water column than the maxima in Crater Lake.

In winter and spring, *Stephanodiscus hantzschii* was uniformly distributed in the nannoplankton from the lake surface to a depth of 200 m (Fig. 5). However, during thermal stratification, this taxon was much less abundant, and approximately 60% of its biovolume was distributed just below the DCM. Also, at this time dinoflagellates and the genus *Ankistrodesmus* were prominent in the water column between a depth of 40 m and the DCM. Therefore, the flora in the DCM was not a relict of the winter flora (Cullen 1982).

Although processes responsible for the formation and maintenance of the DCM in Crater Lake are poorly understood, it is clear that thermal stratification is a prerequisite for its formation. Furthermore, the DCM in Crater Lake apparently is more stable than the DCM in either Lake Tahoe (Abbott et al. 1984) or the Great Lakes (Brooks and Torke 1977, Moll et al. 1984). The small fetch in Crater Lake probably minimizes deterioration of the thermocline during summer storms and periods of mixing by large internal seiches, mechanisms that account for instability in lakes with relatively large surface areas.

Deep-water chlorphyll maxima and primary production maxima have been reported from a variety of oligotrophic lakes and locations in the oceans, where the euphotic zone extends below the thermocline (Anderson 1969, Kiefer et al. 1972, Venrick et al. 1973, Moll and Stoermer 1982, Abbott et al 1984, and Coon et al. 1987). DCM typically occur within or directly below the metalimnion, near the light compensation depth and in association with sharp nutrient gradients (Kerekes 1974, Abbott et al. 1984, Coon et al. 1987), whereas DPM often occur at depths above the DCM (Cullen 1982). However, DCM also have been found associated with sharp nutrient gradients well below the thermocline, where the photon flux density is only 0.1 to 1.0% of the surface irradiance (Moll and Stoermer 1982, Cullen 1982). In such cases, DCM are often interpreted as an indication of transition zones between nutrient limitation and light energy limitation for autotrophic

organisms (Coon et al. 1987). The locations of DPM in the water column of Crater Lake are consistent with this interpretation, as DPM usually occur at depths above the associated DCM, while the DCM are positioned well below the thermocline where light energy is less than 1% of the surface irradiance. Furthermore, the high chlorophyll to cell biovolume ratios in the DCM of Crater Lake are similar to ratios found in the DCM of Lake Tahoe (Abbott et al. 1984), indicating that the algal cells are physiologically adapted to low irradiance (Tilzer and Goldman 1978). Phytoplankton in the DCM of Crater Lake are photosynthetically active, especially during July (e.g., 1987) when the DPM sometimes corresponds in position to the DCM. However, it is still not known whether or not sinking cells (Steele and Yentsch 1960) accumulate in the DCM of Crater Lake or the degree to which heterotrophy (Vincent and Goldman 1980) is involved in the deep-water production dynamics.

In contrast to other oligotrophic lakes described in the literature, the DCM in Crater Lake is not closely associated with the nitracline, a discontinuity located approximately 100 m below the maximum concentration of chlorophyll. Hypotheses that help explain the position of the DCM in Crater Lake include (1) upwelling of nutrients from depths below the DCM (McManus 1992); (2) sinking of organic material above the DCM (see Particle Flux section); and (3) nutrient recycling associated with zooplankton feeding (Bergquist and Carpenter 1986). Although some research has suggested that the DCM is maintained by zooplankton grazing above the chlorophyll maximum (Venrick et al. 1973), Cullen (1982) argued that the occurrence and position of the DCM can be explained without considering the activities of zooplankton populations. In Crater Lake, *Bosmina longirostris* and *Daphnia pulicaria* exhibit diel vertical migration between a depth of about 120 m and the upper surface, whereas most species of rotifers attain their maximum abundances between the depths of 80 m and 120 m (Karnaugh 1990). Therefore, it is possible that grazing and detrital feeding by rotifers may enhance nutrient cycling at depths above and adjacent to the DCM. Consequently, we hypothesize that a zone of nutrient recycling

between the depths of 80 m and 120 m helps maintain the DCM and provides the nutrients required to sustain the position of the DPM (at a depth of 80 m) in August.

While mechanisms accounting for the long-term cyclic patterns in chlorophyll, primary production and phytoplankton cell biovolumes are unclear, such cycles may be related to fish predation (see Ecology of Kokanee Salmon and Rainbow Trout section) and variations in nutrient inputs. Our data indicate that pronounced decreases in the density of *Daphnia pulicaria* are associated with increases in size of the kokanee population, while the abundance of *Daphnia* is inversely related to the density of rotifers (Karnaugh 1990). Therefore, effects of fish predation on the density of zooplankton populations could have a cyclic impact on the distribution and abundance of phytoplankton (Kerfoot 1987). Although our data base is limited, the decline in the concentration of chlorophyll between 1986 and 1989 coincided with an increase in the abundance of *Daphnia* when the abundance of kokanee over one year old was low. Moreover, an increase in the concentration of chlorophyll in 1990 corresponded to an abundance of kokanee older than one year and a very low density of *Daphnia*. While these observations do suggest relationships between functional groups of organisms in the water column of Crater Lake, they do not confirm or explain the presence of biological cycles with predictable periodicities.

Seasonal patterns of chlorophyll concentration, primary production, and phytoplankton cell biovolume in Crater Lake are controlled in part by changes in nutrient supply. In particular, nitrogen and some trace elements (e.g., iron) may be limiting primary production in the water column. Bulk precipitation provides over 90% of the nitrogen input to the lake each year (Reilly 1989), and about 78% of the percipitation that falls into the caldera is deposited directly into the lake, most of which occurs during the winter as snow. In the winter, nutrient inputs can be mixed to a depth of about 200 m (see Temperature and Water Quality section). Also, the relatively dense water in the upper 200 m can sink under certain climatic conditions, which in turn causes water in the deep lake to upwell in the winter and early spring (McManus 1992). While the occurrence and extent of

the upwelling varies annually, the input of nitrogen from the deep lake to the euphotic zone is several orders of magnitude greater than inputs from bulk precipitation and run-off (see Mass Balance section). Therefore, upwelling of nitrogen rich water from the deep lake is probably a very important process regulating the cyclic patterns of primary production and associated variables in Crater Lake.

Kokanee may also contribute to the process of nutrient recycling in Crater Lake. Kokanee are found from near the lake surface to a depth of about 80 m, and are cyclic in density and biomass (see Ecology of Kokanee Salmon and Rainbow Trout section). Although predation on zooplankton by the kokanee population undoubtedly accounts for some nutrient regeneration, cyclic patterns in the distribution and abundance of kokanee did not correspond to the observed patterns of primary production and cell biovolume between 1986 and 1990. Consequently, the influence, if any, of the kokanee population on cyclic patterns of primary production remains unclear.

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Zooplankton

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A preliminary investigation of the distribution and abundance of zooplankton was initiated in 1985 as part of the 10-year study of Crater Lake. Before this study, relatively little was known about the species composition and production dynamics of zooplankton assemblages in the lake. Evermann (1897) found that *Daphnia pulex pulicaria* was the most abundant crustacean in net samples from the near-surface water and littoral zone. Kemmerer et al. (1924) collected two species of crustaceans and three species of rotifers in August and September 1913 using a closing net of No. 20 mesh silk (75 μm holes). Numerically, *Asplanchna* was dominant, and *Daphnia pulex* was second in abundance, with greatest densities between 40 m and 80 m below the water surface. No zooplankton were found in samples between the surface and a depth of 30 m, or below a depth of 200 m. Brode (1938) reported that zooplankton were not present in samples obtained above the depth of 15 m, whereas *Daphnia* reached its maximum abundance in samples between depths of 38 m and 53 m. In 1937 Hasler (1938) found the maximum numbers of pelagic *Daphnia* between 50 m and 122 m and also noted the presence of *Daphnia* in the bays of Wizard Island. In contrast, Hasler and Farner (1942) reported that in 1940 *Daphnia* was not observed around Wizard Island or collected by vertical net tows between 100 m and the water surface. In a more recent study, Hoffman (1969) investigated horizontal distributions and vertical migrations of limnetic *Daphnia pulicaria* and *Bosmina longirostris* from June to August in 1967 and 1968. In the 1967 samples, *Bosmina* and *Daphnia* accounted for 98% and 2% of the their combined densities, respectively, whereas in 1968 corresponding relative abundances were 59% and 41%. However, in 1969 Malick (1971) found that *Bosmina* represented only 2% of the density, whereas the relative abundance of *Daphnia* had increased to 98%. The sampling procedure followed by both Hoffman (1969) and Malick (1971) involved 100-m vertical tows with a 0.5-m No. 20 mesh net. In summary, early

studies of zooplankton in Crater Lake, which focused on cladocerans, revealed that relative abundances of *Daphnia* and *Bosmina* were variable from year to year, and that these genera were rare in the summer at depths corresponding to the position of the epilimnion.

One of the primary objectives of the 10-year study of Crater Lake was to describe the taxonomic structure of zooplankton assemblages in the water column and to generate hypotheses that help explain the vertical and seasonal distribution and abundance of the constituent populations. Relationships between the distribution and abundance of zooplankton populations and related chemical and physical variables were of particular interest, as well as effects of other biotic components of the ecosystem (e.g., phytoplankton and fish) on the structure and function of the zooplankton assemblage. Because of recent concern about decreases in the clarity of Crater Lake, spatial and temporal changes in the zooplankton assemblage also were investigated relative to the optical properties of the water column. For example, Hrbacek et al. (1961) found that, in the presence of planktivorous fish, the zooplankton assemblage in back-water areas of the river Elbe consisted of small cladocerans and rotifers, while water transparency was relatively low because of an abundance of nannoplankton. However, when fish were removed from the system, the species composition of the zooplankton shifted to large cladocerans, and the phytoplankton composition changed to lower densities of the larger algal species, a change that increased the depth of light penetration. This work suggested that trophic interactions within Crater Lake may account, in part, for the observed fluctuations in lake clarity.

For the 10-year study of Crater Lake, data related to the distribution and abundance of zooplankton populations represented a time period from July 1985 to September 1990. Results of this investigation are reported in two sections: (1) a preliminary study including samples obtained between July 23, 1985 and June 16, 1988; and (2) a more recent study representing the period between June 30, 1988 and September 6, 1990. During the preliminary study it was necessary to explore a variety of sampling methods and strategies, because of a lack of historical information and the difficulties inherent in sampling a system such as

Crater Lake. Therefore, this data set was analyzed separately from data obtained between June 1988 and September 1990, while using approaches dictated by variations in the pattern of sampling. Beginning with samples taken on June 30, 1988, the depth intervals for the vertical net tows were standardized, a sampling strategy that provided a consistent and comparable set of samples between summer 1988 and fall 1990.

Sampling

All zooplankton samples described in this report were obtained by vertical net tows through selected segments of the water column at Station 13, the site selected for intensive sampling of phytoplankton populations and associated variables (see Study Area and Facilities section). In addition, samples were taken from the littoral zone of the lake in August 1986, and field experiments were conducted to compare sampling methods and test equipment performance. Results of this work were reported by Karnaugh (1988) and are not included in this report. Sampling dates and corresponding depth intervals sampled during the 10-year study of Crater Lake are summarized in Table 1.

Beginning in September 1988, zooplankton samples were obtained during the day, and then again at night, between 12:00 p.m. and 2:00 a.m. Sampling procedures and depths for day and night tows were identical. The purpose of the day/night series of samples was to investigate diurnal changes in the vertical distribution of dominant zooplankton taxa. Day/night samples were obtained in June (1989), July (1989 and 1990), August (1990), and September (1988, 1989, and 1990).

Two zooplankton nets were used during the 10-year study, a 0.75-m diameter net with a closing apparatus and mesh size of 64 um, and a 0.50-m diameter net with a mesh size of 64 um. The latter net was not equipped with a closing apparatus until summer 1986. Both nets were designed by Karl Banse of the University of Washington and built by Research Nets, Inc., in Bothell, Washington. Most water column samples were obtained with the 0.75-m net. The smaller net was used to sample the littoral zone and during winter

Table 1. Summary of zooplankton samples obtained from Crater Lake at Station 13 between July 23, 1985 and September 6, 1990. Depth ranges represent depth intervals sampled by a vertical net tow through the corresponding segment of the water column.

Date	Net Characteristics	Depth Interval (meters)
7/23/85	0.75 m, closing, 64 micrometer mesh	20 - 40
		40 - 80
		80 - 120
		120 - 160
		160 - 200
		200 - 300
		300 - 400
8/14/85	0.75 m, closing, 64 micrometer mesh	0 - 20
		20 - 40
		40 - 80
		80 - 120
		120 - 160
		160 - 200
		200 - 300
		300 - 400
		400 - 500
3/5/86	0.50 m, 64 micrometer mesh	0 - 50
5/29/86		0 - 100
		0 - 300
6/24/86		0 - 40
7/22/86		20 - 80
8/19/86		80 - 120
9/16/86		120 - 200
		200 - 500

Table 1. (continued)

Date	Net Characteristics	Depth Interval (meters)
1/19/87	0.50 m, 64 micrometer mesh	0 - 50
4/14/87		0 - 100
		0 - 200
6/22/87	0.75 m, closing, 64 micrometer mesh	0 - 40
7/21/87		40 - 80
8/18/87		80 -100
9/15/87		100 - 120
		120 - 160
		160 - 200
1/11/88	0.75 m, closing, 64 micrometer mesh	0 - 120
6/16/88		
6/30/88	0.75 m, closing, 64 micrometer mesh	0 - 20
7/19/88		20 - 40
8/15/88		40 - 60
9/15/88*		60 - 80
10/27/88		80 - 100
4/12/89		100 - 120
6/26/89*		120 - 160
7/19/89*		160 - 200
8/18/89		
9/13/89*		
1/20/90		
7/2/90*		
7/18/90*		
8/15/90*		
9/6/90*		

* Night tows also taken on these dates at the same depth intervals.

cruises when sampling was difficult. The nets were towed vertically in the water column with a gasoline-powered winch at a speed of 0.75 m sec^{-1}. A net filtration factor was obtained for each net by comparing a reading from a Tsurumi Seiki Kosakusho flowmeter mounted mid-way between the net center and the rim with a corresponding reading from a similar flowmeter mounted 0.3 m outside the rim (Karnaugh 1988). Filtration factors for the 0.50 m and 0.75 m nets were 0.926 and 0.703, respectively.

Sample Processing and Analysis

Zooplankton samples were preserved in the field with a 4% sucrose-formaldehyde solution. In the laboratory, the samples were diluted to acceptable concentrations, and two 2-ml subsamples were removed from each sample and counted. Tests were run to check this procedure for random dispersion and sampling error (See Karnaugh 1988, for details). Specimens were stained with Eosin Y to facilitate counting. All subsamples were counted in a rectangular chamber using a dissecting microscope at 40X magnification. Counts from subsamples were used to estimate the number of organisms per cubic meter of lake water filtered:

$$N = (nV_s)/(SV_f),$$

where N = number of organisms per cubic meter;

n = average number of organisms per subsample;

V_s = concentrated volume (ml) of sample;

S = subsample size (ml);

V_f = volume (m^3) of lake water filtered.

Here, V_f = net opening area (m^2) X length of tow (m) X filter factor. Biomass estimates for each taxon were obtained by multipling the corresponding density (N) by the weight conversion factors listed in Table 2.

Table 2. Species list and corresponding acronyms and weight conversion factors of dominant pelagic zooplankton found in samples from Crater Lake, 1985 - 1990. Conversion factors are expressed as micrograms per individual.

Phylum or Order	Taxon	Acronym	Factor
Cladocera	*Daphnia pulicaria (Forbs) (emend. Hrbacek)*	DAPPUL	9.930
	Bosmina longirostris (sensu latu)	BOSLON	1.470
Rotifera	*Keratella cochlearis (Gosse) morph macracantha (Lauterborn)*	KERCOC	0.108
	Keratella quadrata var. dispersa (Carlin)	KERQUA	0.770
	Kellicottia longispina (Kellicott)	KELLON	0.840
	Polyarthra dolichoptera (Idelson)	POLDOL	0.388
	Philodina cf. acuticornis (Murray)	PHIACU	0.348
	Filinia terminalis (Plate)	FILTER	0.840
	Synchaeta oblonga (Ehrenberg)	SYNOBL	0.200
	Synchaeta lakowitziana (Lucks)	SYNOBL	0.200
	Conochilus unicornis (Rousselet)	CONUNI	0.840
	Collotheca pelagica (Rousselet)	COLPEL	0.840
	Asplanchna sp.	ASPLAN	--

Data Analysis

In general, the approach to the analysis of the zooplankton data was the same as the approach described for the phytoplankton (see Phytoplankton section). Briefly, species diversity and dominance were expressed by the Shannon information measure and its related measure of redundancy. Temporal and spatial variations in the zooplankton assemblage were analyzed by a cluster analysis using the program CLUSB. When relatively few

species are represented in the data file, only 13 in this case, CLUSB sometimes provides a more interpretable cluster structure than TWINSPAN, a program that works well when a data file has many variables and is relatively large. The algorithm used in CLUSB is a divisive procedure that provides a minimum variance partition of the data (McIntire 1973). Because of the different patterns of sampling, it was necessary to partition the data into three files for the cluster analysis: (1) summer 1986; (2) summer 1987; and (3) all data obtained from June 30, 1988 through September 6, 1990. Each file was analyzed separately, and results were reported in cluster diagrams similar to diagrams presented for the phytoplankton (see Phytoplankton section). Similarity in species composition between clusters was expressed by the SIMI measure of community resemblance (see Phytoplankton section).

Results

Species Composition

Zooplankton counts were made by Elena Karnaugh (1985 - 1987 samples) and Robert Truitt (1988 - 1990 samples). Rotifer species from the 1985 and 1986 samples were identified by Dr. Walter Koste of West Germany, and specimens of Cladocera from 1985, 1986, and some early samples (1968 and 1969) were idendified by Dr. Vladimir Korinek of the Katedra Parasitologie a Hydrobiologie, Czechoslovakia. Cladocera from the 1960's samples were identified as *Daphnia pulicaria* and *Bosmina longirostris*, not as *Daphnia pulex* and *Bosmina longispina* as reported by Hoffman (1969) and Malick (1971). Dr. Edward S. Deevey, Jr. of the University of Florida also confirmed the identification of *Bosmina longirostris*.

Data obtained from the counting procedure represented the abundances of 2 cladocerans and 11 rotifers (Table 2). In this study it was not possible to distinquish *Synchaeta lakowitziana* from *S. oblonga* when counting preserved samples. Consequently, count data for these taxa were combined and reported as *S. oblonga*. The feeding method, feeding

mode, temperature tolerance, and trophi (rotifers only) of each of the zooplankton taxa are summarized in Table 3 (for more information, see Karnaugh 1988). *Bosmina longirostris*, *Keratella cochlearis*, *Polyarthra dolichoptera*, *Synchaeta oblonga*, and *Filina terminalis* were the most commonly observed and abundant species in samples taken at Station 13 between July 1985 and September 1990 (Table 4). *Philodina acuticornis* was abundant in deep-water samples (depth interval of 160 m to 200 m) obtained in the summer and fall of 1988, whereas *Daphnia pulicaria* and *Collotheca pelagica* had high relative abundances in samples collected from the upper 20 m of the water column in 1988 and 1989, respectively. *Kellicottia longispina* was present in 84.6% of the samples, but its relative abundance was usually less than 5% of the total density. Even rarer taxa included an unidentified species of *Asplanchna* which was found in samples at depths between 20 m and 160 m in August and September 1990, and cyclopoid nauplii which were identified in only one sample (July 2, 1990; 160 m - 200 m tow).

Distribution and Abundance

Preliminary Study: July 23, 1985 - June 16, 1988. Because of variations in sampling stategy, plots of zooplankton biomass and density for the preliminary study were separated into six graphs representing groups of sampling dates which shared the same pattern of sampling. From these data, it was apparent that total zooplankton biomass integrated to various depths in the water column reached maximum values in August 1985 (Figs. 1 and 2). Estimated biomasses at this time integrated to depths of 200 m and 500 m were 3,981 mg m^{-2} and 3,994 mg m^{-2}, respectively; corresponding densities were 10.741 X 10^6 and 10.764 X 10^6 organisms m^{-2} (Figs. 3 and 4). In the water column down to a depth of 500 m, 93.4% of the total zooplankton density and 92.9% of the total biomass were distributed between the depths of 40 m and 160 m (Figs. 1 and 3). In August 1987, zooplankton biomass integrated to a depth of 200 m was 1,454 mg m^{-2}, less than half of that found in August 1985 (Figs. 1 and 2). The decline in total density of zooplankton also was pronounced,

Table 3. Feeding method, feeding mode, temperature tolerance, and trophi (rotifers only) of zooplankton taxa collected in Crater Lake between 1985 and 1990 (see Karnaugh, 1988).

Feeding Method/Taxon	Feeding Mode	Trophi	Temperature Tolerance
Filtering:			
Keratella cochlearis	polyphagous	malleate	eurythermal
Keratella quadrata	polyphagous	malleate	eurythermal
Philodina acuticornis	polyphagous	ramate	unknown
Kellicottia longispina	phytophagous	malleate	eurythermal
Filinia terminalis	triptophagous	malleorama	cold stenothermal
Daphnia pulicaria	polyphagous	N/A	eurythermal
Conochilus unicornis	triptophagous	malleorama	eurythermal
Trapping:			
Collotheca pelagica	phytophagous	uncinate	warm stenothermal
Filtering/Grasping:			
Bosmina longirostris	polyphagous	N/A	eurythermal
Grasping/Piercing/Sucking			
Polyarthra dolichoptera	phytophagous	virgate	cold stenothermal
Synchaeta oblonga	phytophagous	virgate	warm stenothermal
Synchaeta lakowitziana	phytophagous	virgate	cold stenothermal
Grasping:			
Asplanchna sp.	omnivorous	incudate	unknown

Table 4. Frequency of occurrence and proportional abundances of zooplankton taxa in 298 samples obtained between July 23, 1985 and September 6, 1990.

Taxon	Occurrence (% of samples)	Proportional Abundance
Daphnia pulicaria	70.0	0.015
Bosmina longirostris	88.6	0.045
Keratella cochlearis	89.9	0.475
Keratella quadrata	51.0	0.015
Filinia terminalis	64.4	0.035
Kellicottia longispina	84.6	0.042
Polyarthra dolichoptera	90.9	0.151
Synchaeta oblonga - lakowitziana	88.3	0.183
Philodina acuticornis	25.5	0.037
Conochilus unicornis	6.4	0.001
Collotheca pelagica	15.1	<0.000
Asplanchna sp.	2.3	<0.000

changing from 10.741 X 10^6 organisms m^{-2} in August 1985 to 3.685 X 10^6 organisms m^{-2} in August 1987 (Figs. 3 and 4).

Although 77.5% of the crustacean biomass was found below a depth of 80 m in July 1985, after that time, crustaceans were concentrated in the upper 100 m of the water column (Figs. 5 and 6). In contrast, rotifers were distributed throughout the water column between the depths of 20 m and 200 m, and usually over one-half of the rotifer biomass waschanging from 10.741 X 10^6 organisms m^{-2} in August 1985 to 3.685 X 10^6 organisms m^{-2} in August 1987 (Figs. 3 and 4).

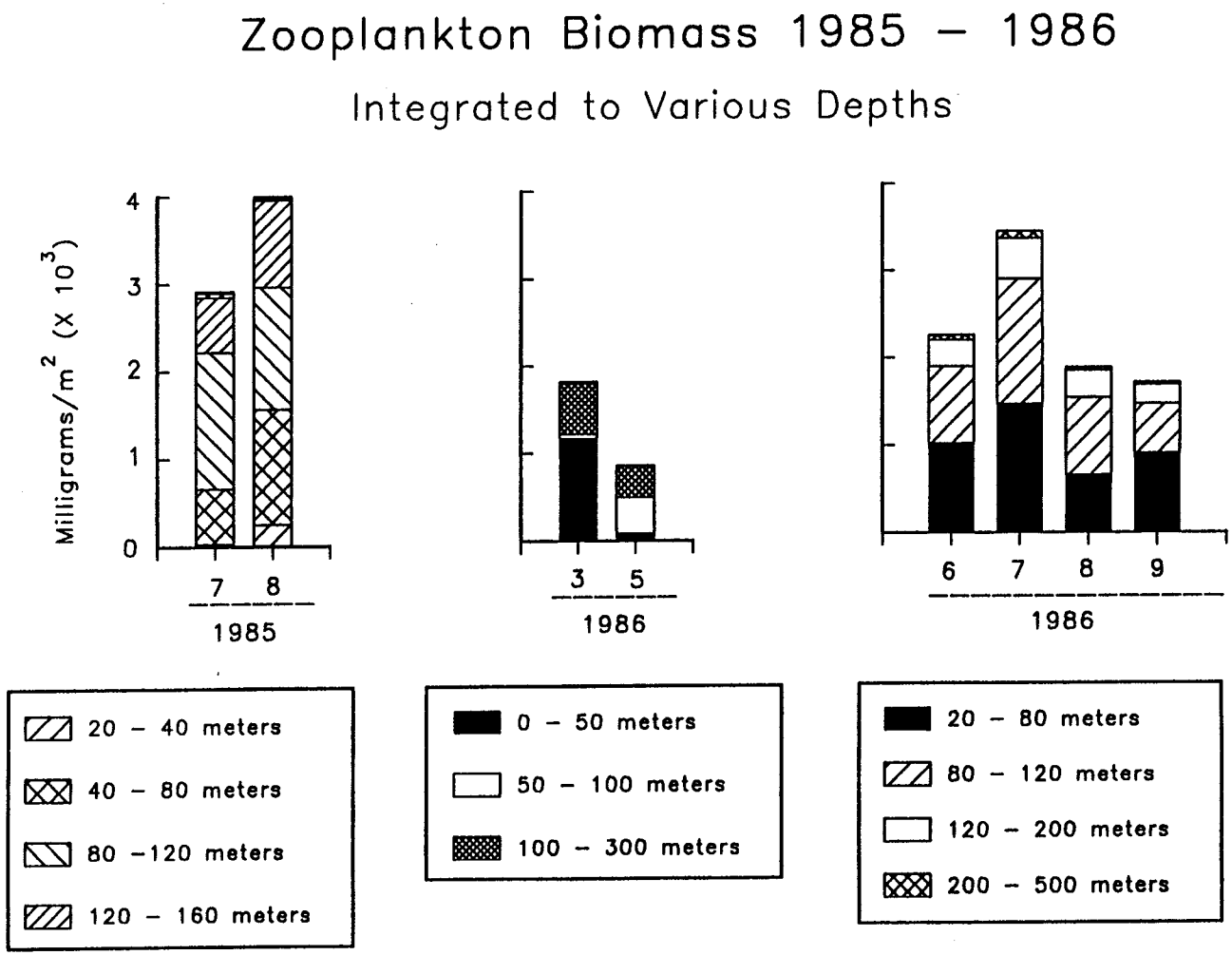


Figure 1. Zooplankton at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

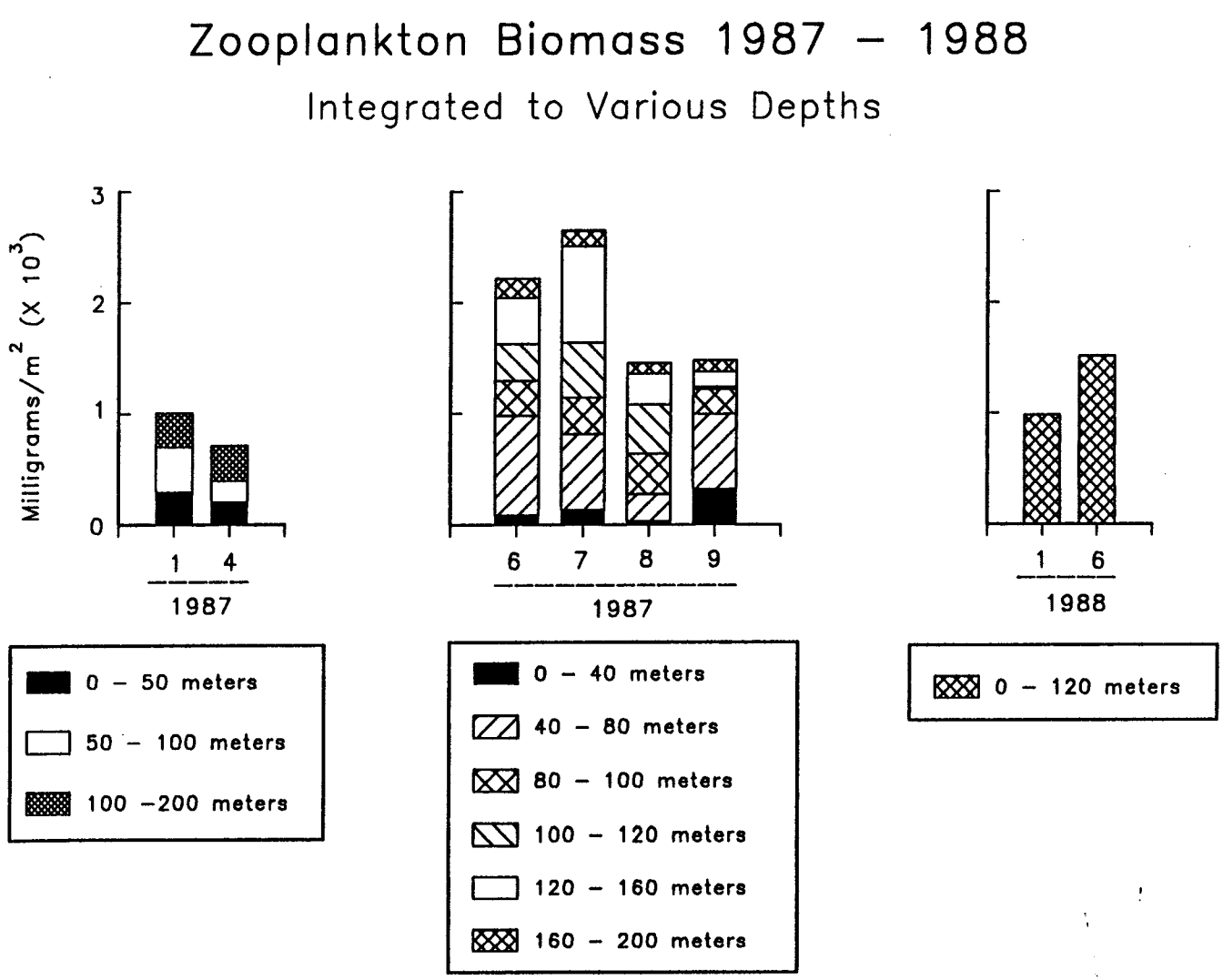


Figure 2. Zooplankton biomass at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

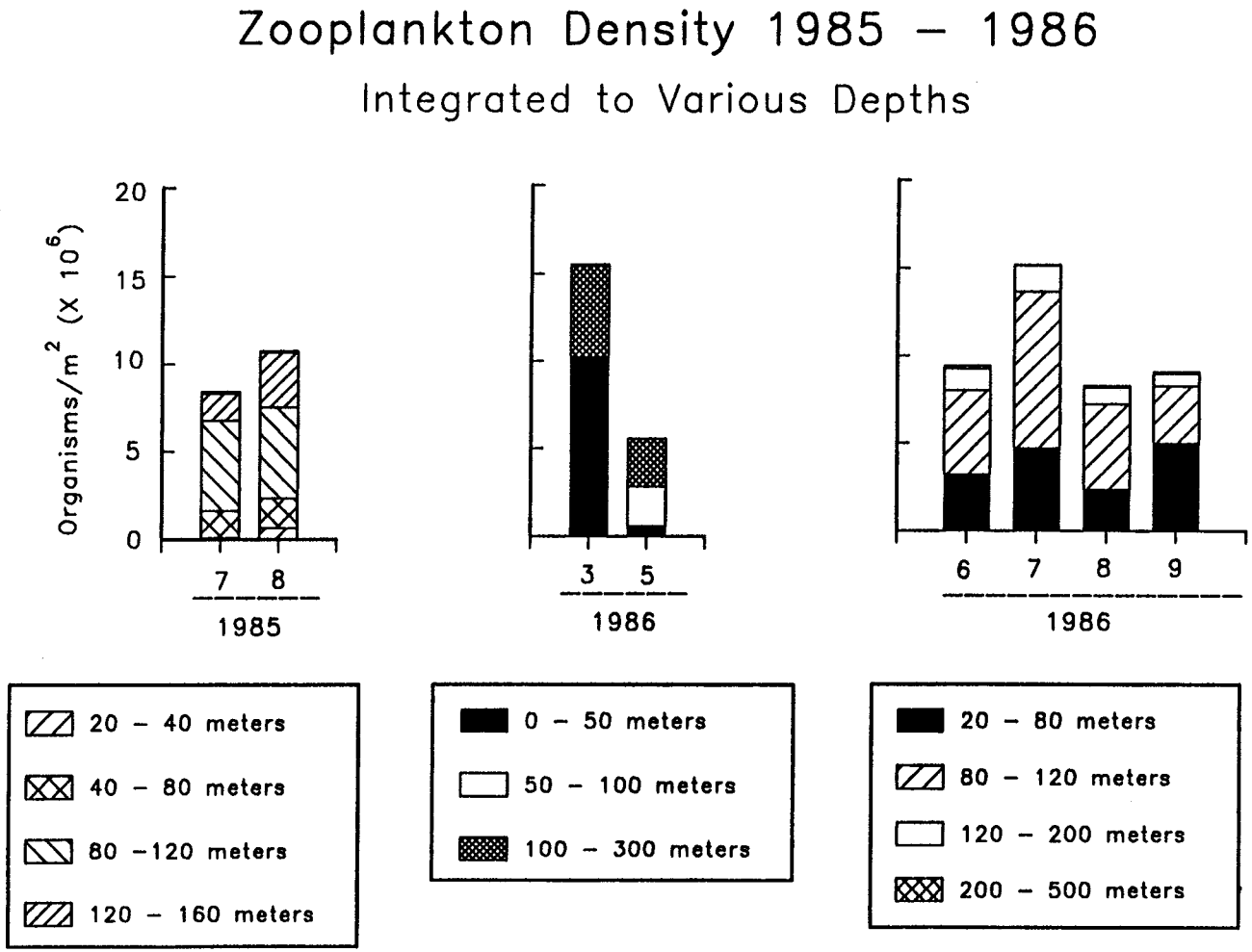


Figure 3. Zooplankton density at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

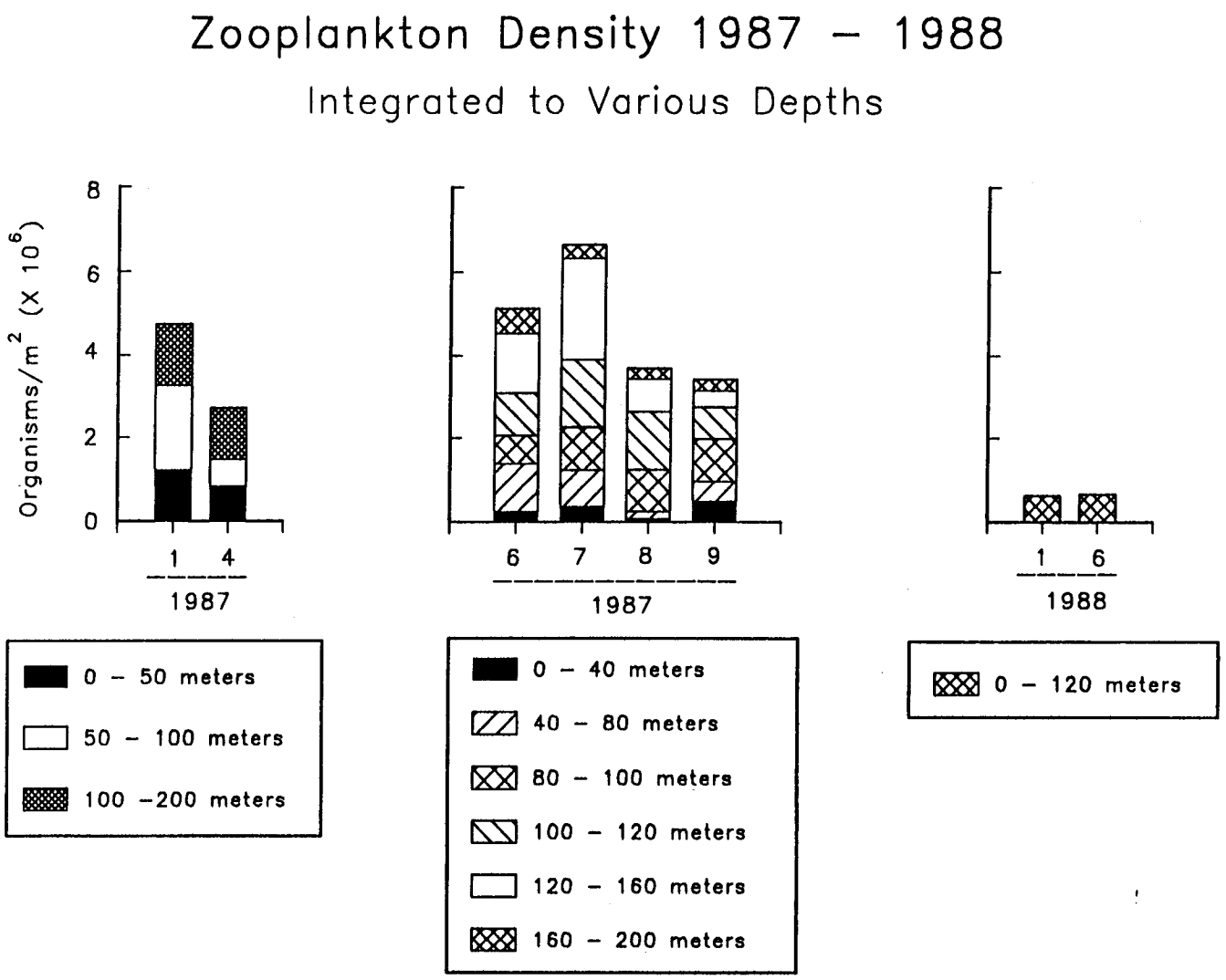


Figure 4. Zooplankton density at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

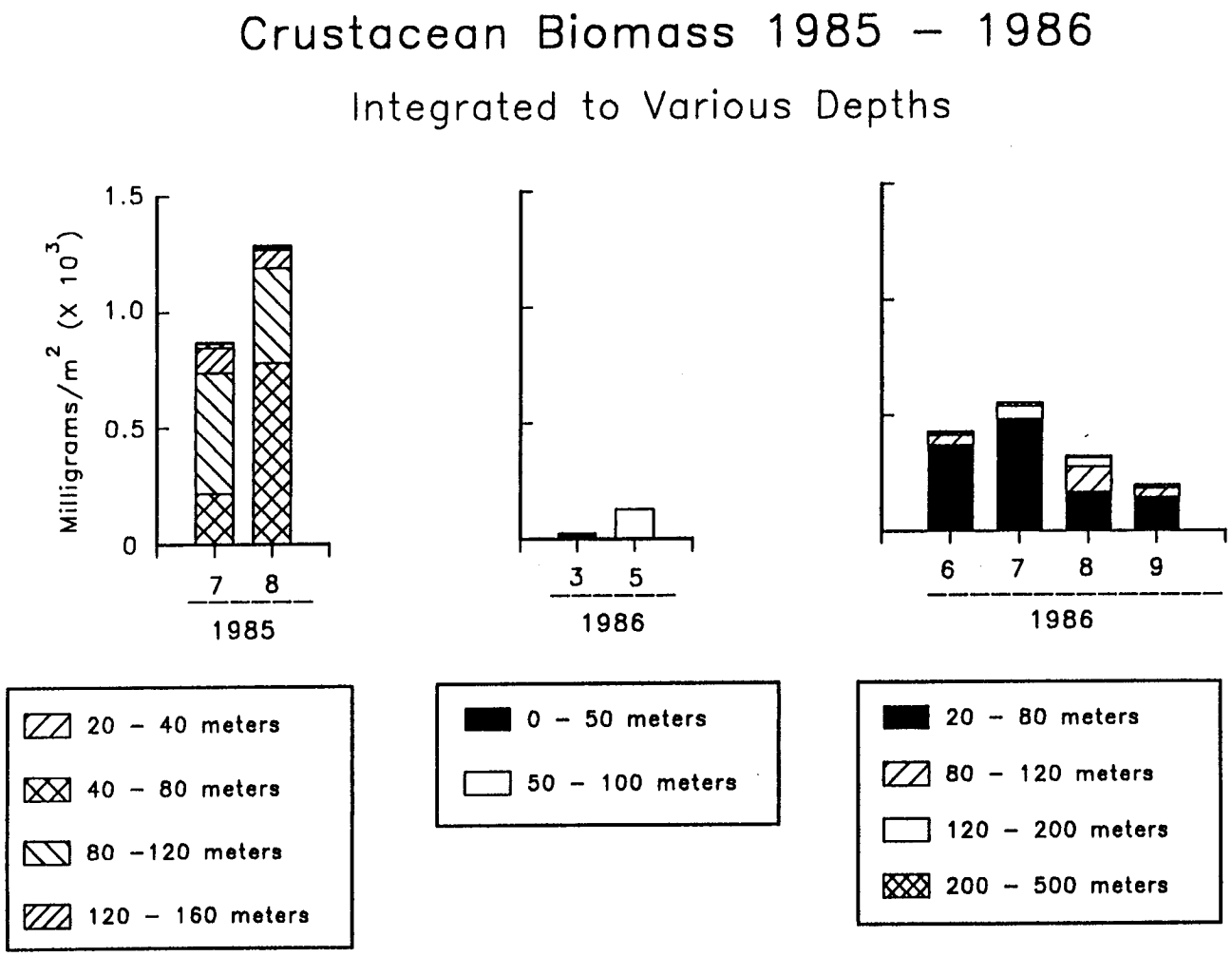


Figure 5. Crustacean biomass at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

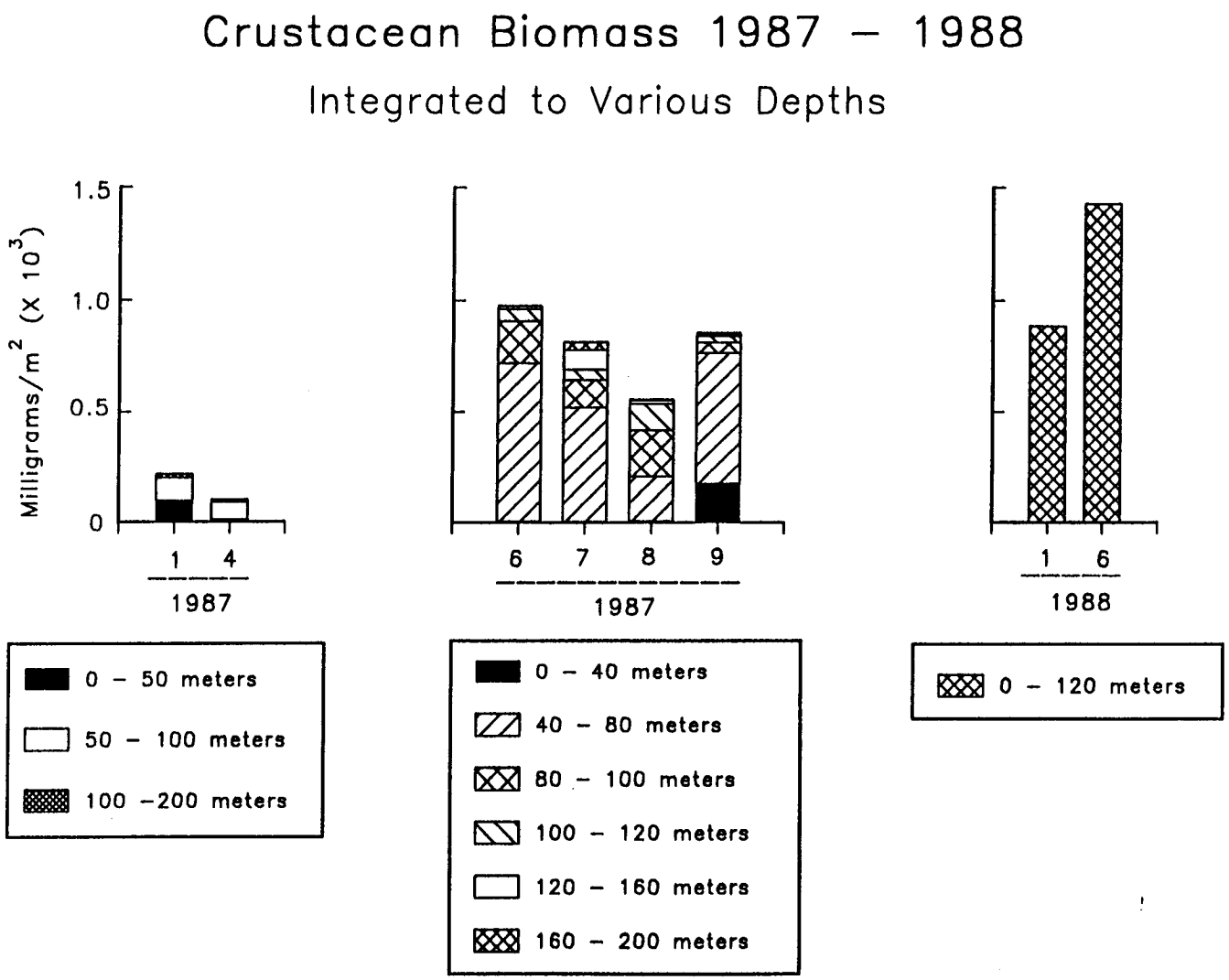


Figure 6. Crustacean biomass at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

Although 77.5% of the crustacean biomass was found below a depth of 80 m in July 1985, after that time, crustaceans were concentrated in the upper 100 m of the water column (Figs. 5 and 6). In contrast, rotifers were distributed throughout the water column between the depths of 20 m and 200 m, and usually over one-half of the rotifer biomass was located below a depth of 80 m (Figs. 7 and 8). During the preliminary study, crustacean biomass integrated to 200 m was relatively high in August 1985 (1,279 mg m^{-2}), decreased to 315 mg m^{-2} in August 1986, and was 557 mg m^{-2} in August 1987; by June 1988 crustacean biomass had increased to a maximum of 1429 mg m^{-2}. Maximum rotifer biomass was found in the summer, during either July or August. In the summers of 1985, 1986, and 1987, rotifer biomass integrated to a depth of 200 m varied between 897 mg m^{-2} (August 1987) and 2,893 mg m^{-2} (July 1986).

The distribution and abundance of *Bosmina longirostris* and *Daphnia pulicaria*, the only crustaceans found in the water column of Crater Lake, are illustrated in Figures 9 - 12. Of these two taxa, *B. longirostris* had the highest densities in all samples collected between July 1985 and June 1988. During this period, *B. longirostris* reached a maximum density in August 1985 when 92% of the population was distributed between depths of 40 m and 120 m, a zone corresponding to the region of maximum primary production and phytoplankton biomass (Fig. 9). The density of this taxon in June and July 1986 was approximately one-half that found in 1985 and 1987 at the same time of year. Densities of *B. longirostris* during the summers of 1985, 1986, and 1987, integrated to a depth of 200 m, varied between 1.926 X 10^5 organisms m^{-2} (August 1986) and 8.703 X 10^5 organisms m^{-2} (August 1985). *Daphnia pulicaria* was not found in samples taken in July and August 1985 (Fig. 11). The density of this taxon integrated to a depth of 120 m increased from 802 organisms m^{-2} in July 1986 to a maximum of 1.196 X 10^5 organisms m^{-2} in June 1988. *D. pulicaria* was concentrated in the upper 100 m of the water column on most sampling dates. Densities of *B. longirostris* and *D. pulicaria* for all samples from 1985, 1986, and 1987 were not correlated ($r = 0.082$).

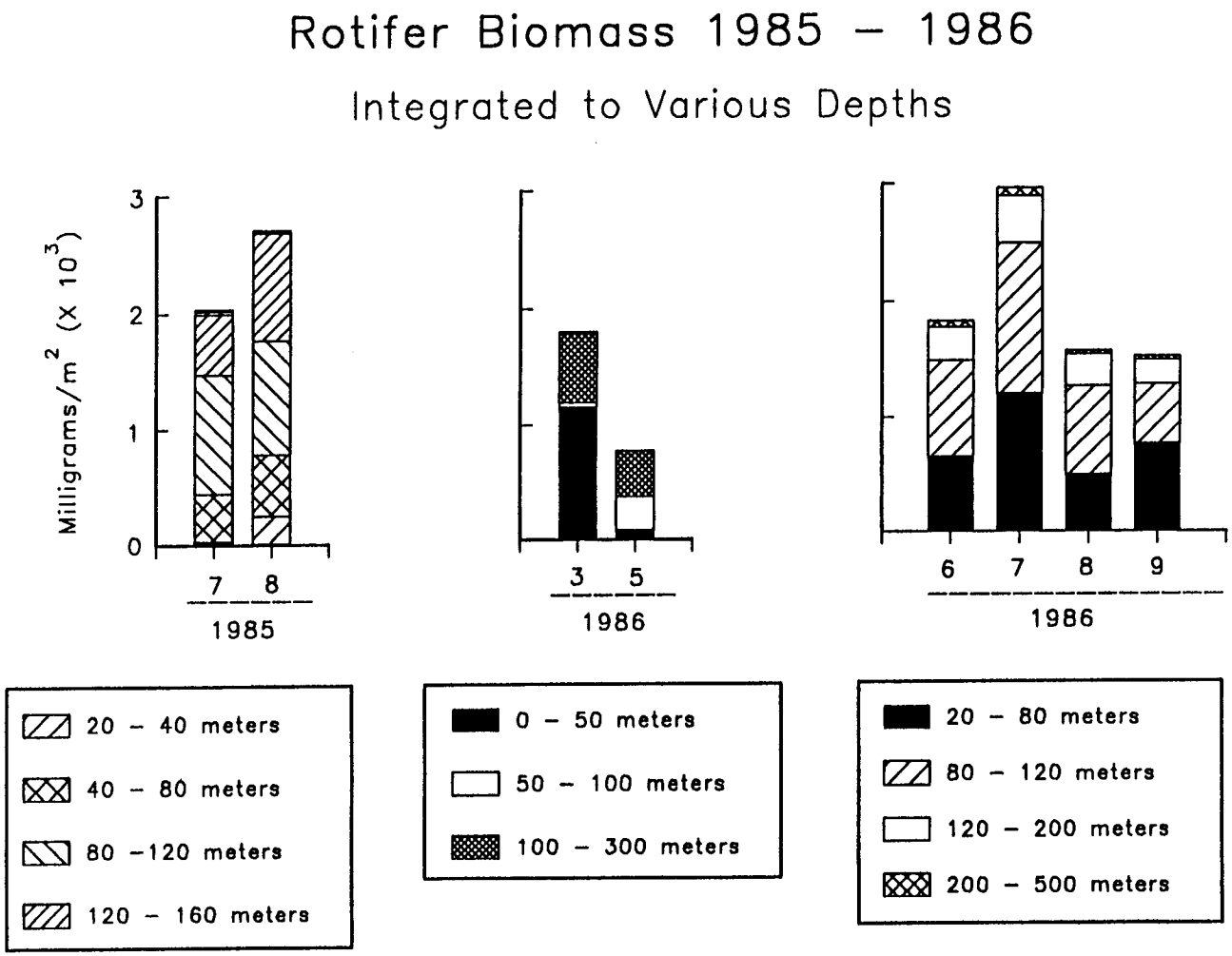


Figure 7. Rotifer biomass at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

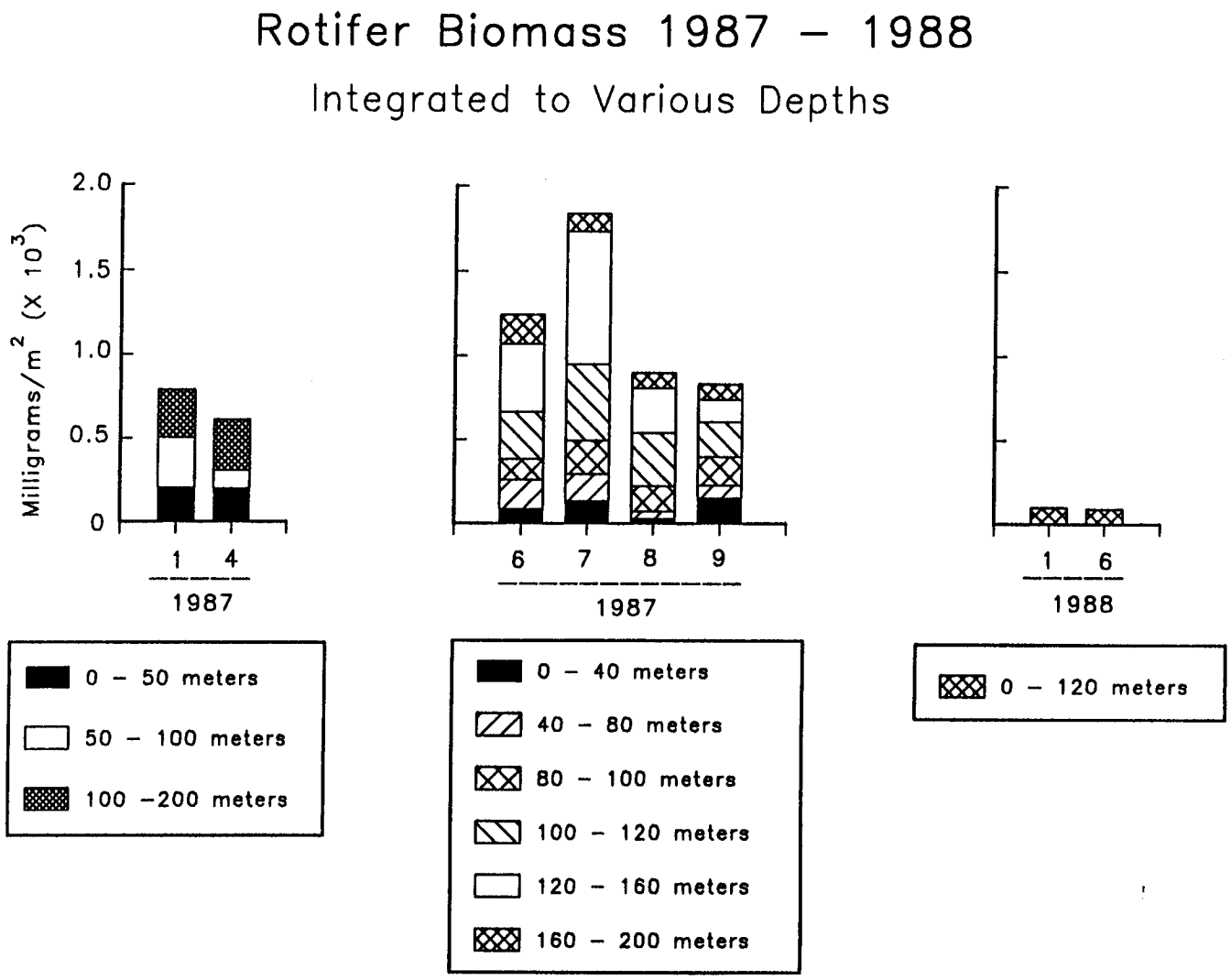


Figure 8. Rotifer biomass at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

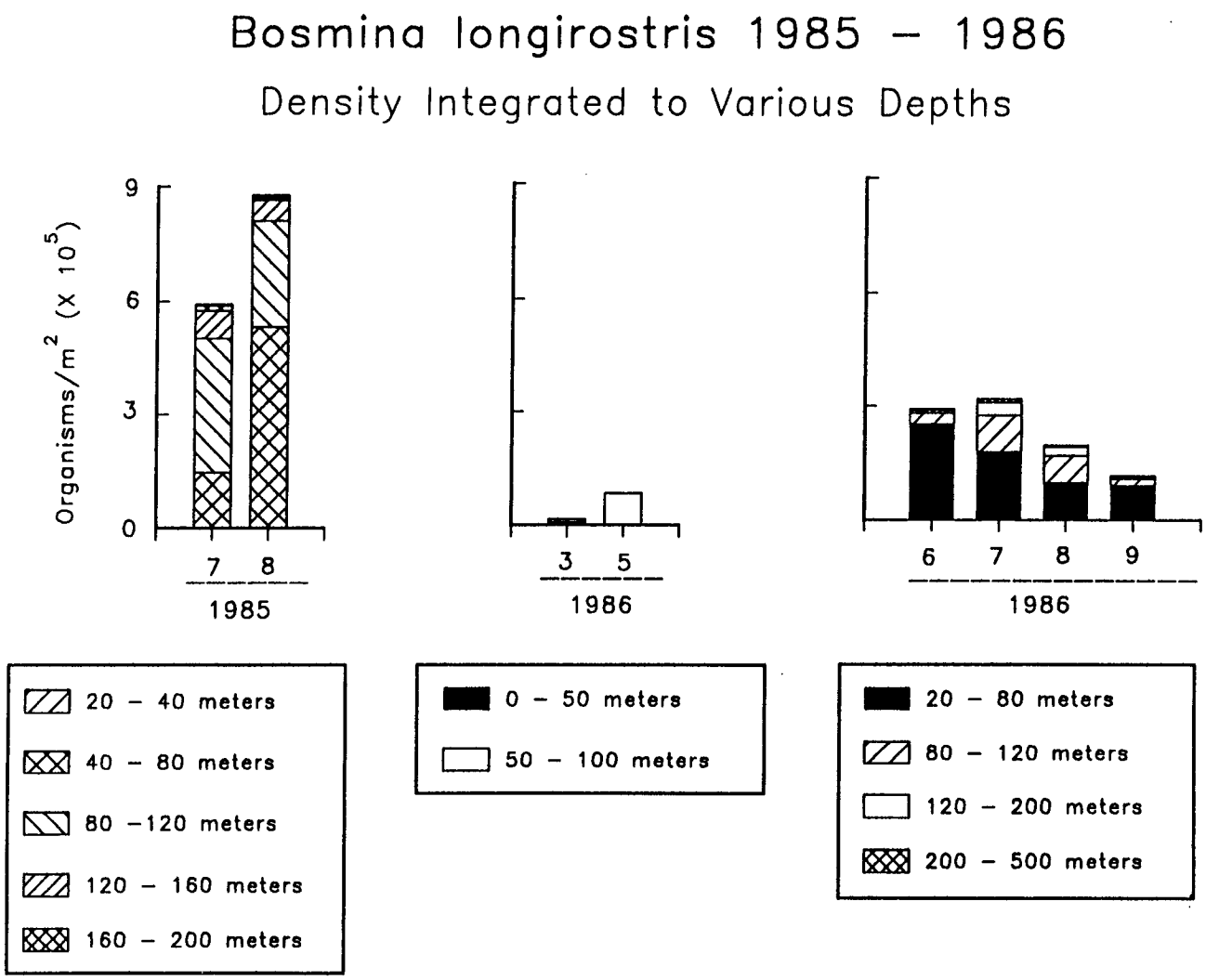


Figure 9. Density of Bosmina longirostris at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

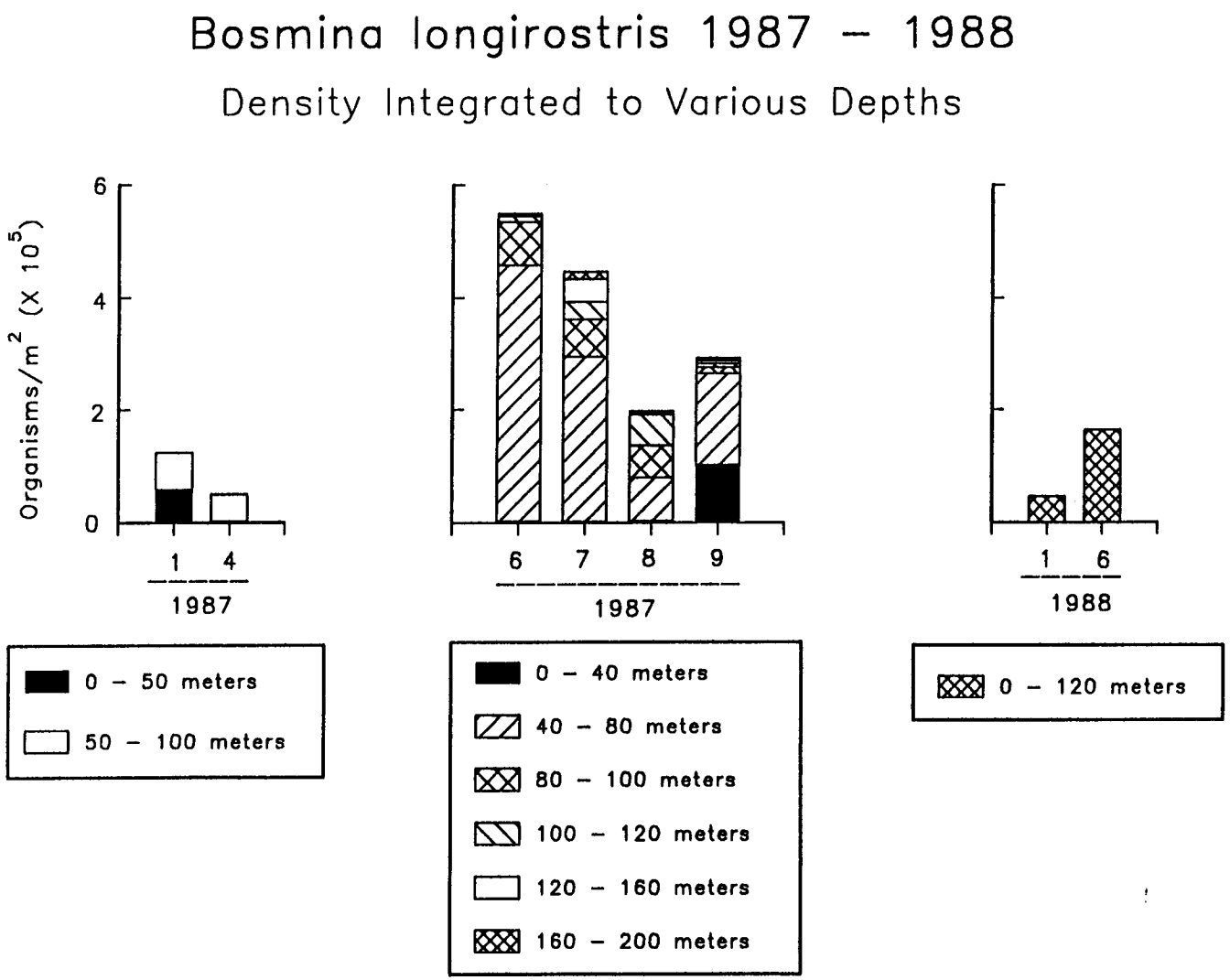


Figure 10. Density of Bosmina longirostris at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

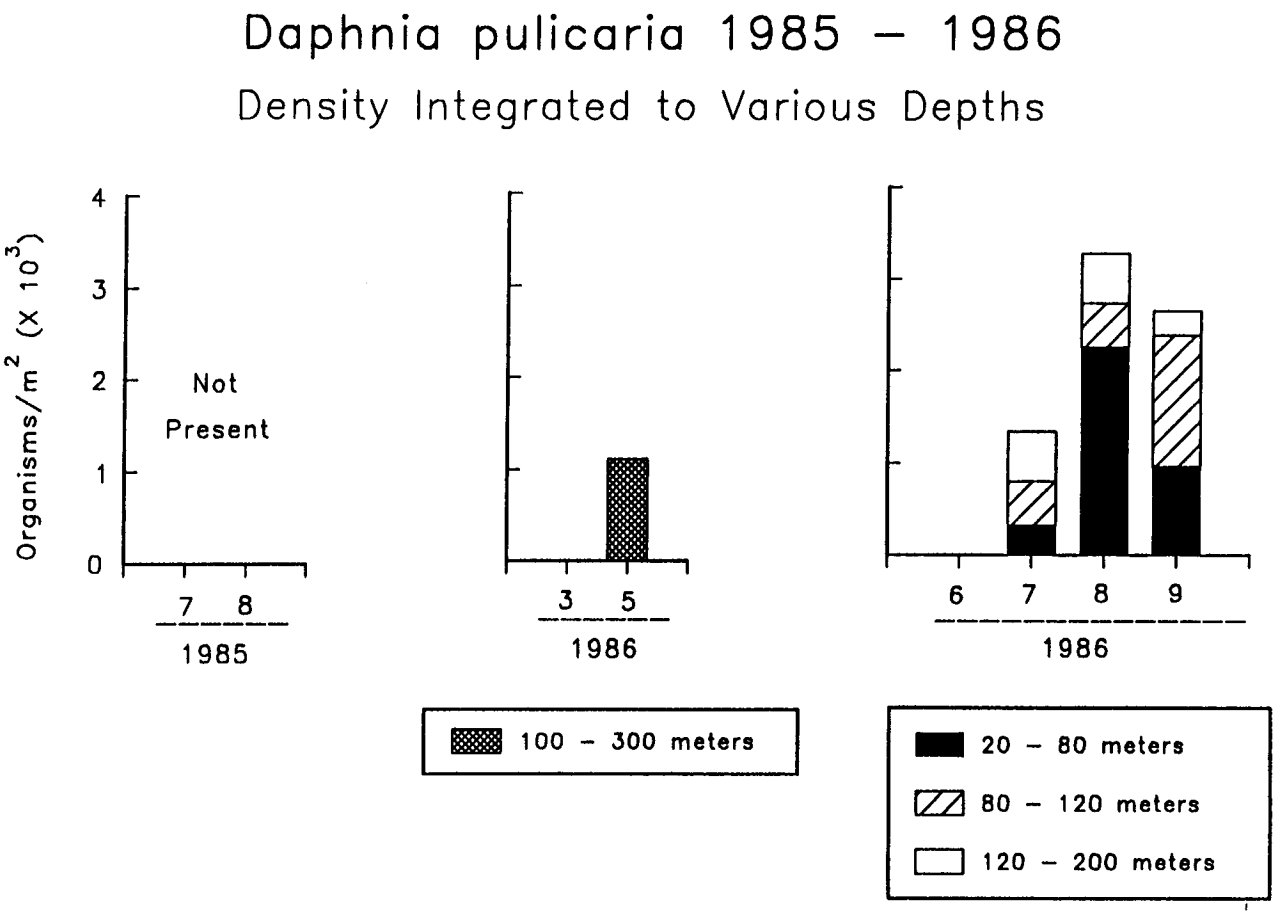


Figure 11. Density of Daphnia pulicaria at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

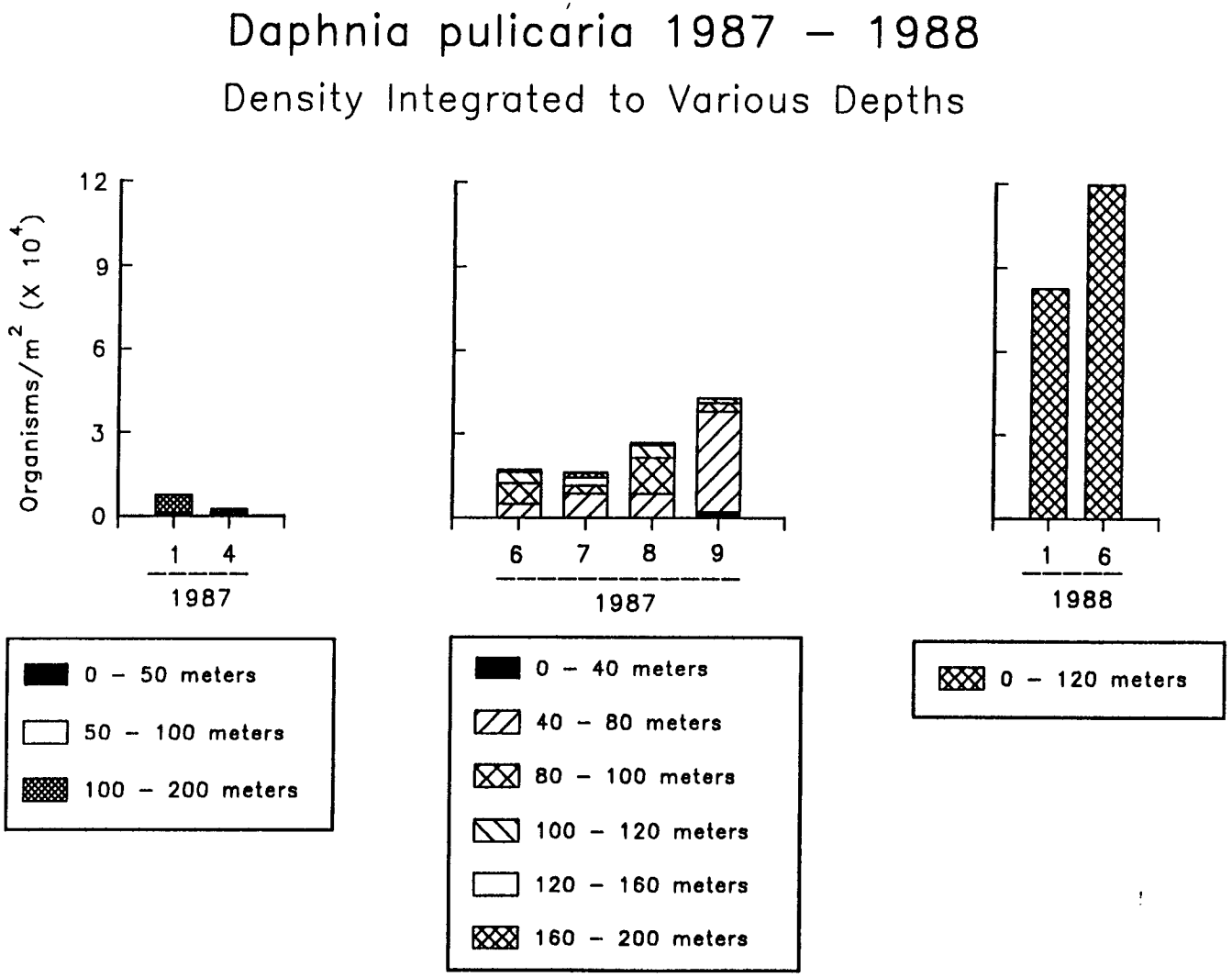


Figure 12. Density of Daphnia pulicaria at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

While many rotifer taxa observed during the preliminary study had overlapping distributions, an analysis of density patterns indicated some spatial and temporal separation of maximum concentrations. *Keratella cochlearis* was the most abundant rotifer in the lake between July 1985 and June 1988 (Figs. 13 and 14). This species reached a maximum density (integrated to a depth of 300 m) of 15.229 X 10^6 organisms m^{-2} in March 1986. In general, it was more abundant in 1986 than in 1985 and 1987. In summer months when thermal stratification was present, *K. cochlearis* was concentrated between the depth of maximum primary production (80 m) and the chlorophyll maximum at 120 m. *Polyarthra dolichoptera* also was more abundant in 1986 than in 1985 or 1987, but in contrast to *K. cochlearis*, its density was highest in the upper 80 m of the water column (Figs. 15 and 16). *Synchaeta oblonga* was abundant in the summers of 1985, 1986, and 1987, and was more evenly distributed in the water column than *K. cochlearis* and *P. dolichoptera*; it reached a maximum density (integrated to 200 m) of 1.605 X 10^6 organisms m^{-2} in June 1987 (Figs. 17 and 18). *Philodina acuticornis* was rare in the 1985 samples, but was abundant in the summers of 1986 and 1987, reaching a maximum density (integrated to 200 m) of 3.014 X 10^6 organisms m^{-2} in July 1987 (Figs. 19 and 20). This species was distributed lower in the water column than *K. cochlearis*, *P. dolichoptera*, and *S. oblonga*, usually concentrated at depths below 120 m. Other rotifers abundant enough to be found in all samples taken between July 1985 and June 1988 included *Keratella quadrata*, *Kellicottia longispina*, and *Filinia terminalis* (Figs. 21 - 26). Maximum densities of these taxa were usually found below a depth of 80 m. *Conochilus unicornis* was collected in July 1985, August 1985, and January 1987, but was not present in samples obtained in spring 1986, summer 1986, and summer 1987 (Figs. 27 and 28).

Zooplankton: June 30, 1988 - September 6, 1990. Zooplankton assemblages were sampled from the same eight segments of the water column to a depth of 200 m at Station 13 from June 30, 1988 to September 6, 1990 (Table 1). Consequently, this data set provided a good basis for a detailed analysis of distribution and abundance.

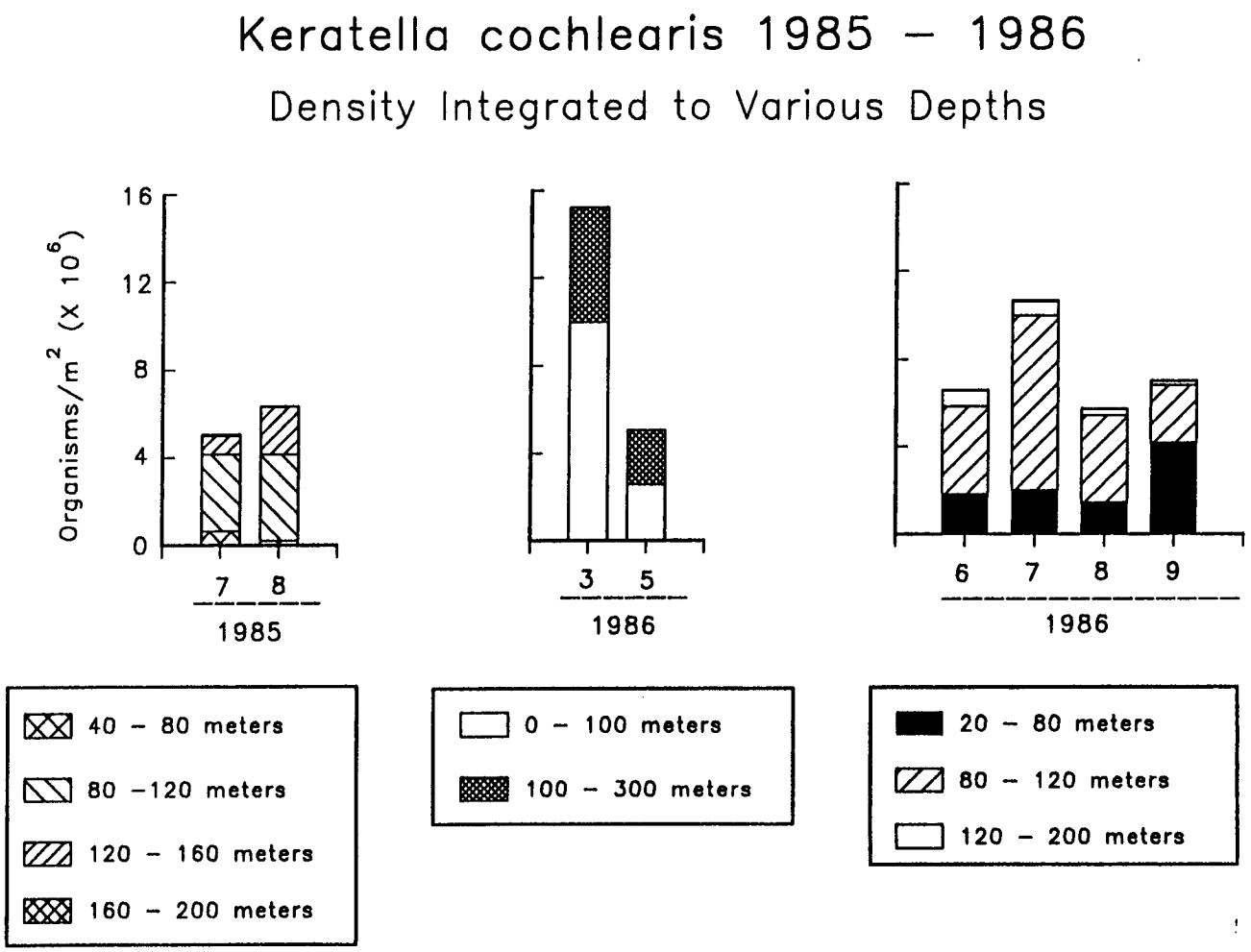


Figure 13. Density of Keratella cochlearis at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

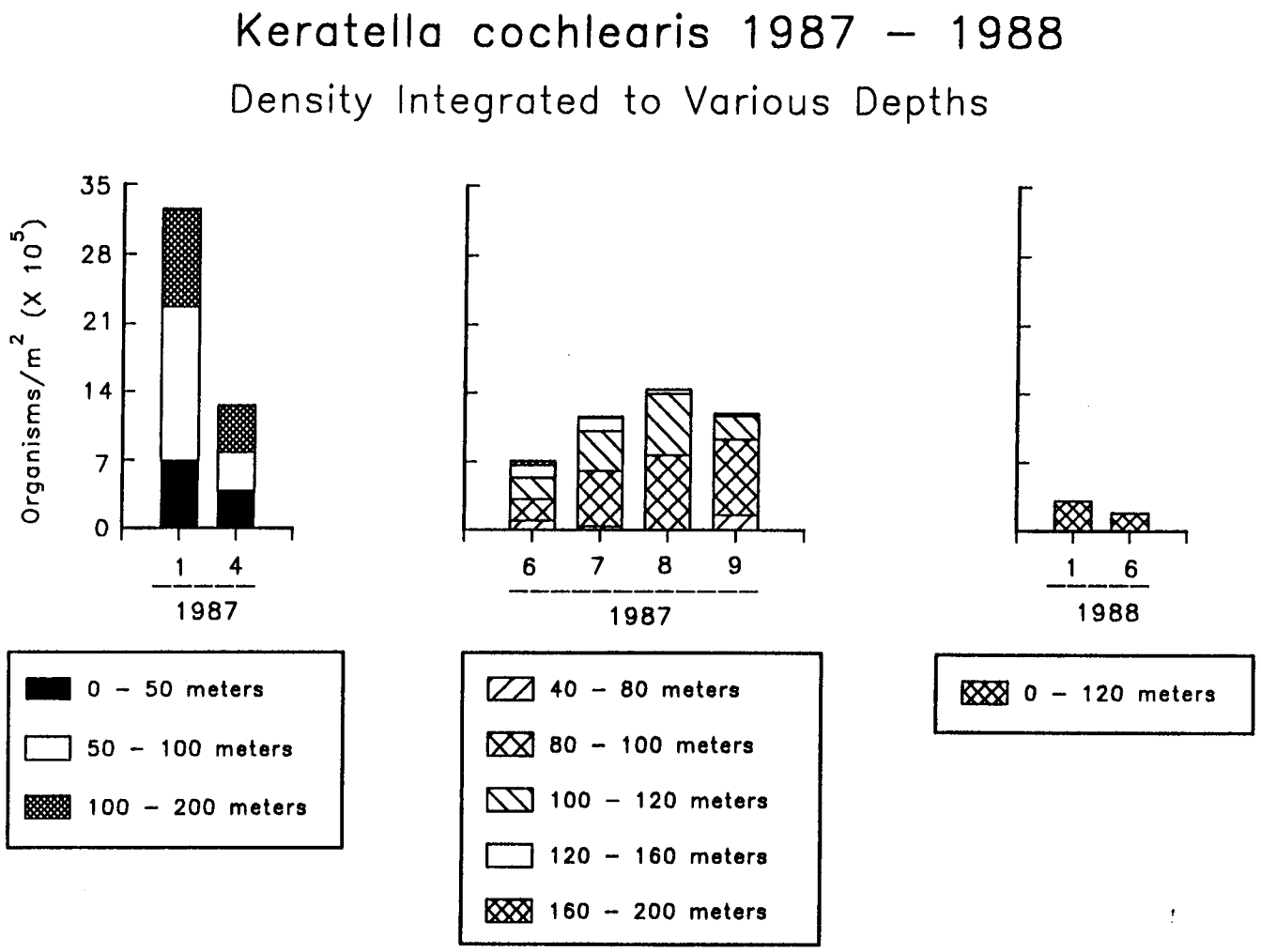


Figure 14. Density of Keratella cochlearis at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

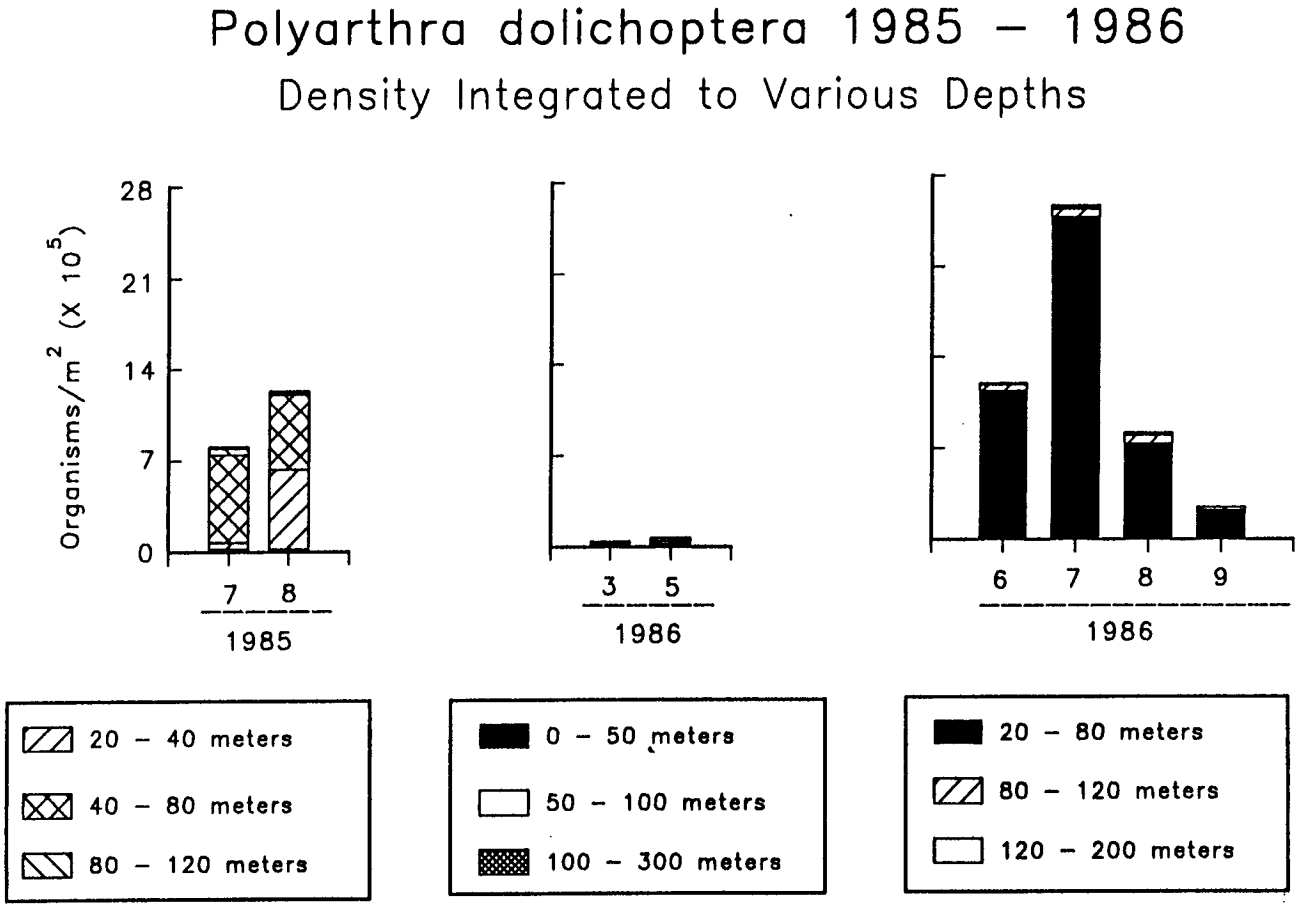


Figure 15. Density of Polyarthra dolichoptera at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

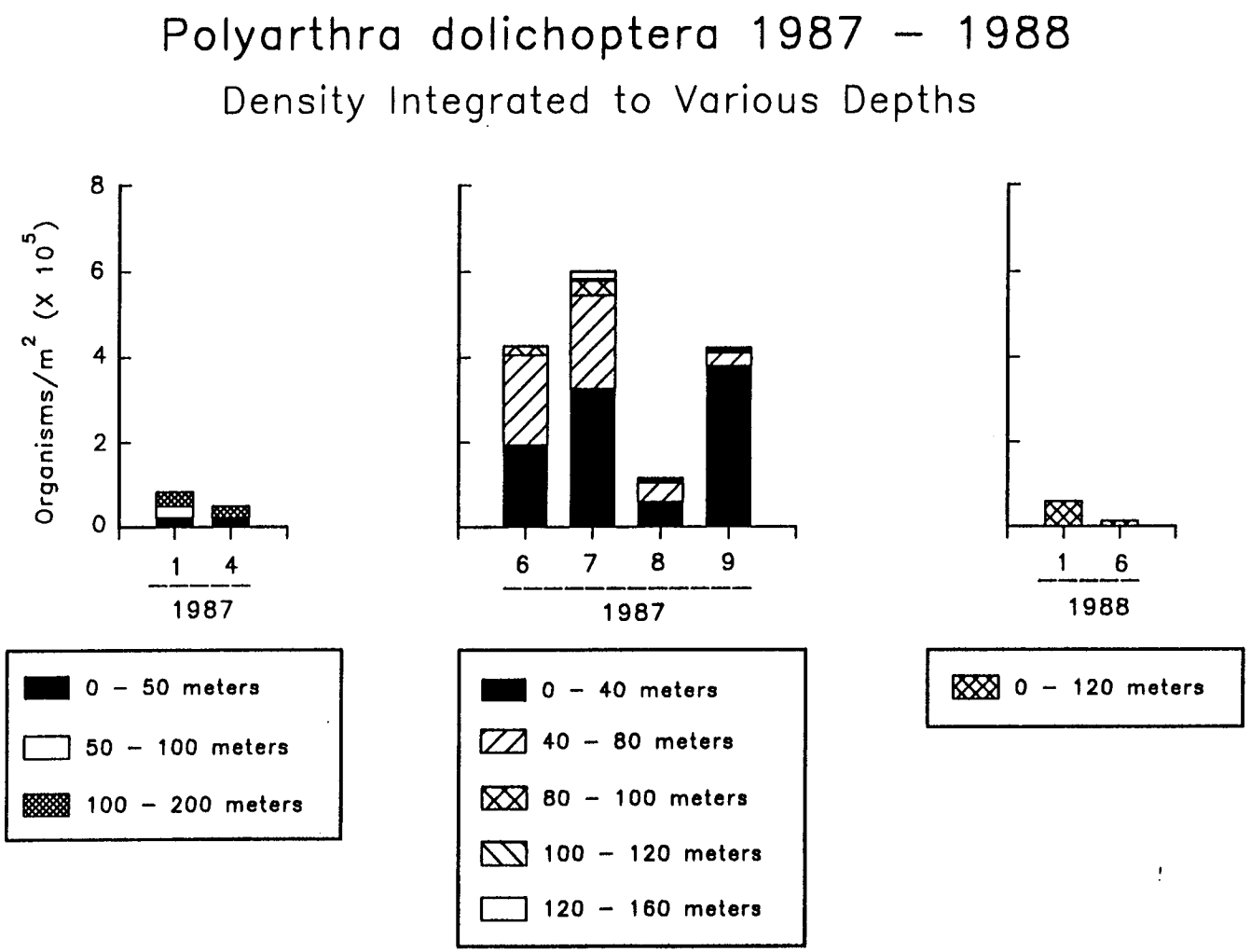


Figure 16. Density of Polyarthra dolichopter at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

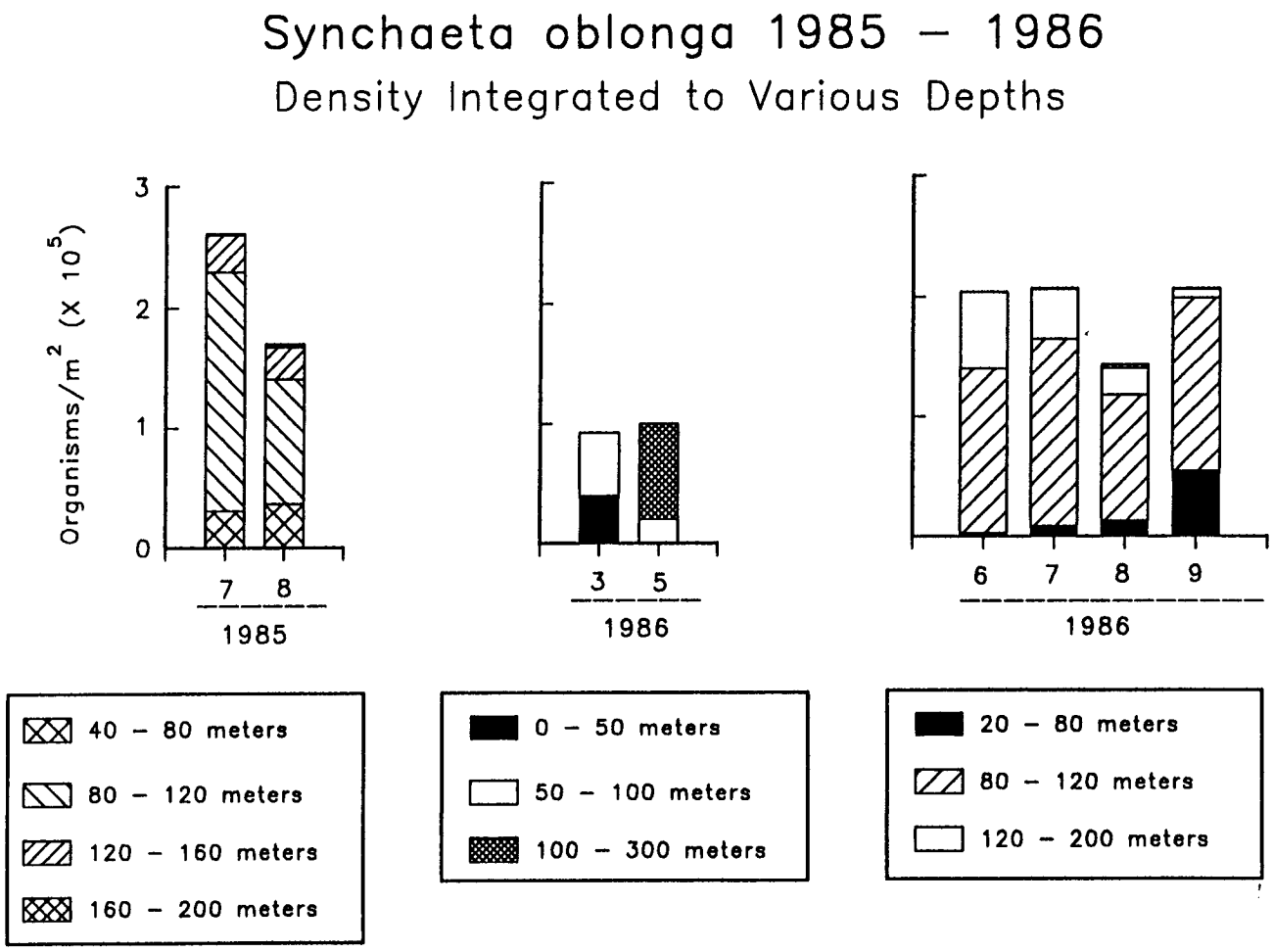


Figure 17. Density of Synchaeta oblonga at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

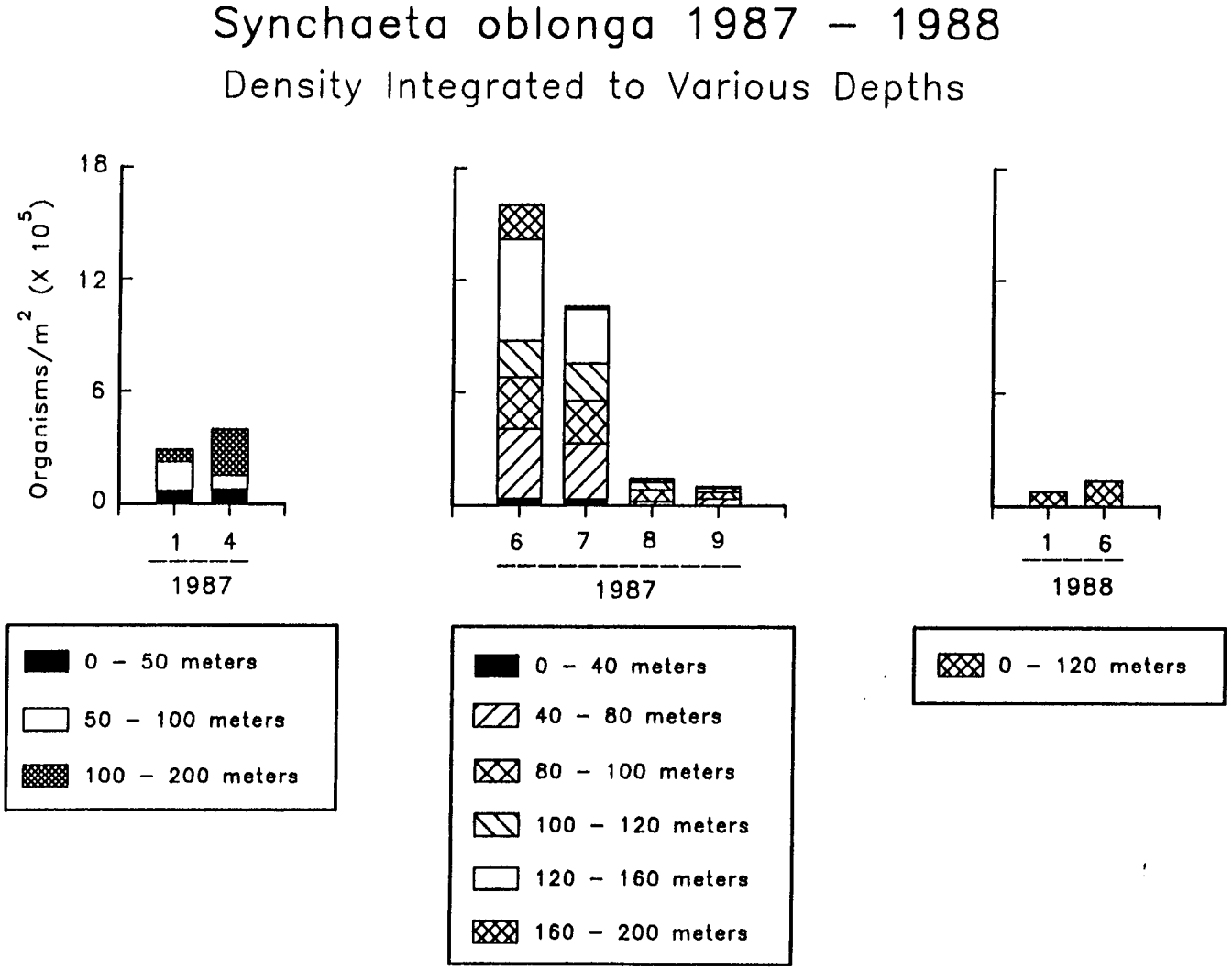


Figure 18. Density of Synchaeta oblonga at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

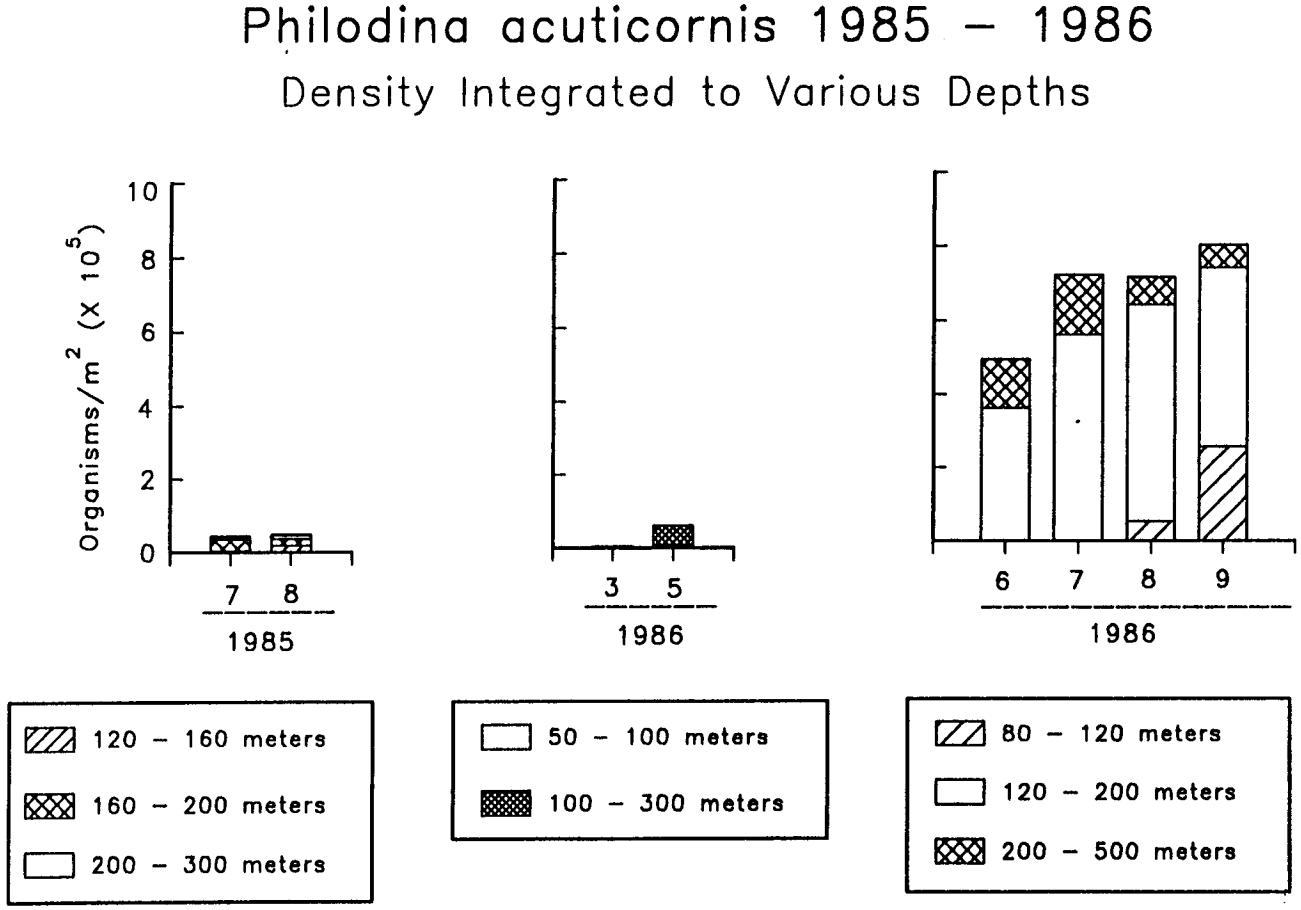


Figure 19. Density of Philodina acuticornis at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

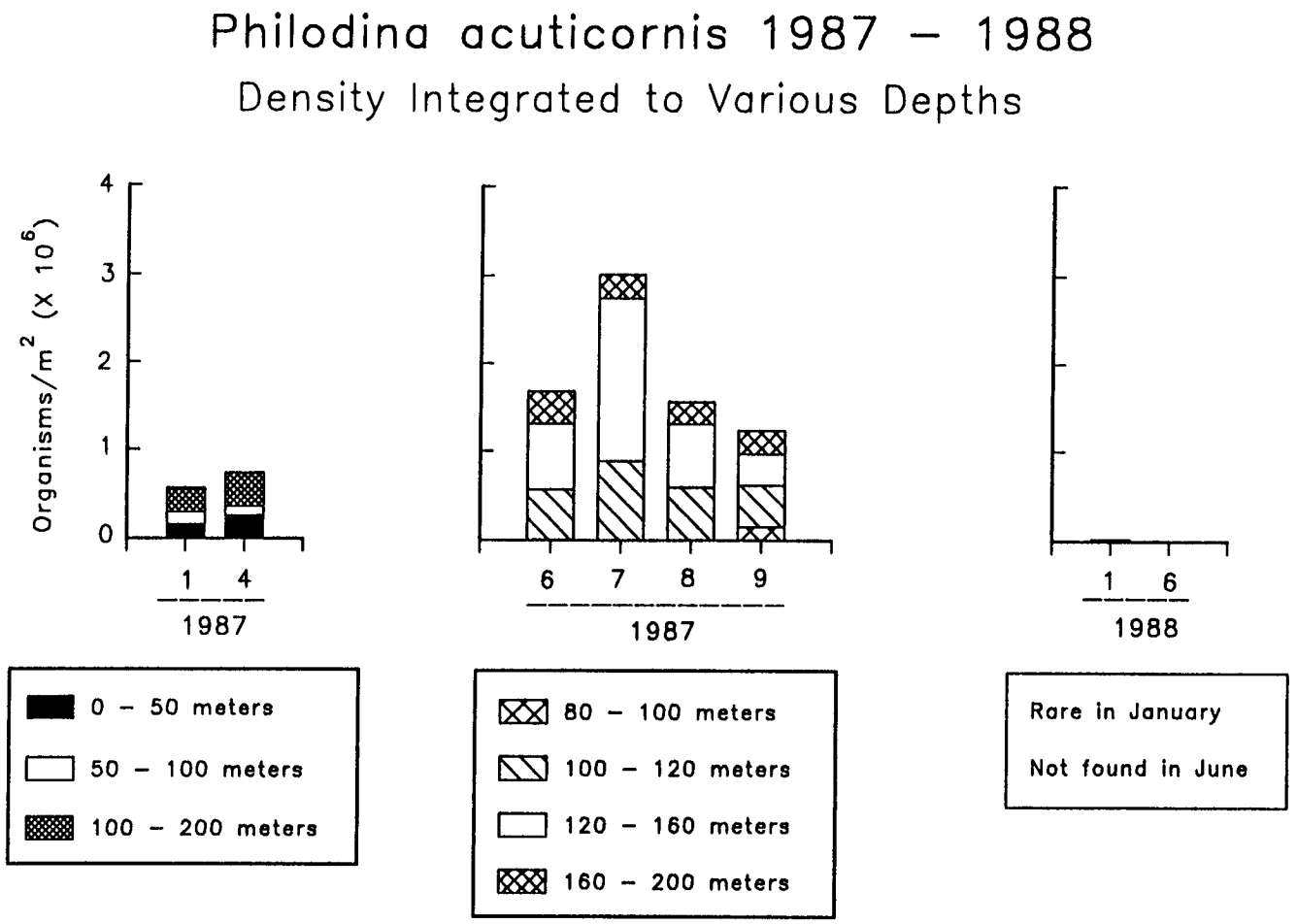


Figure 20. Density of Philodina acuticornis at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

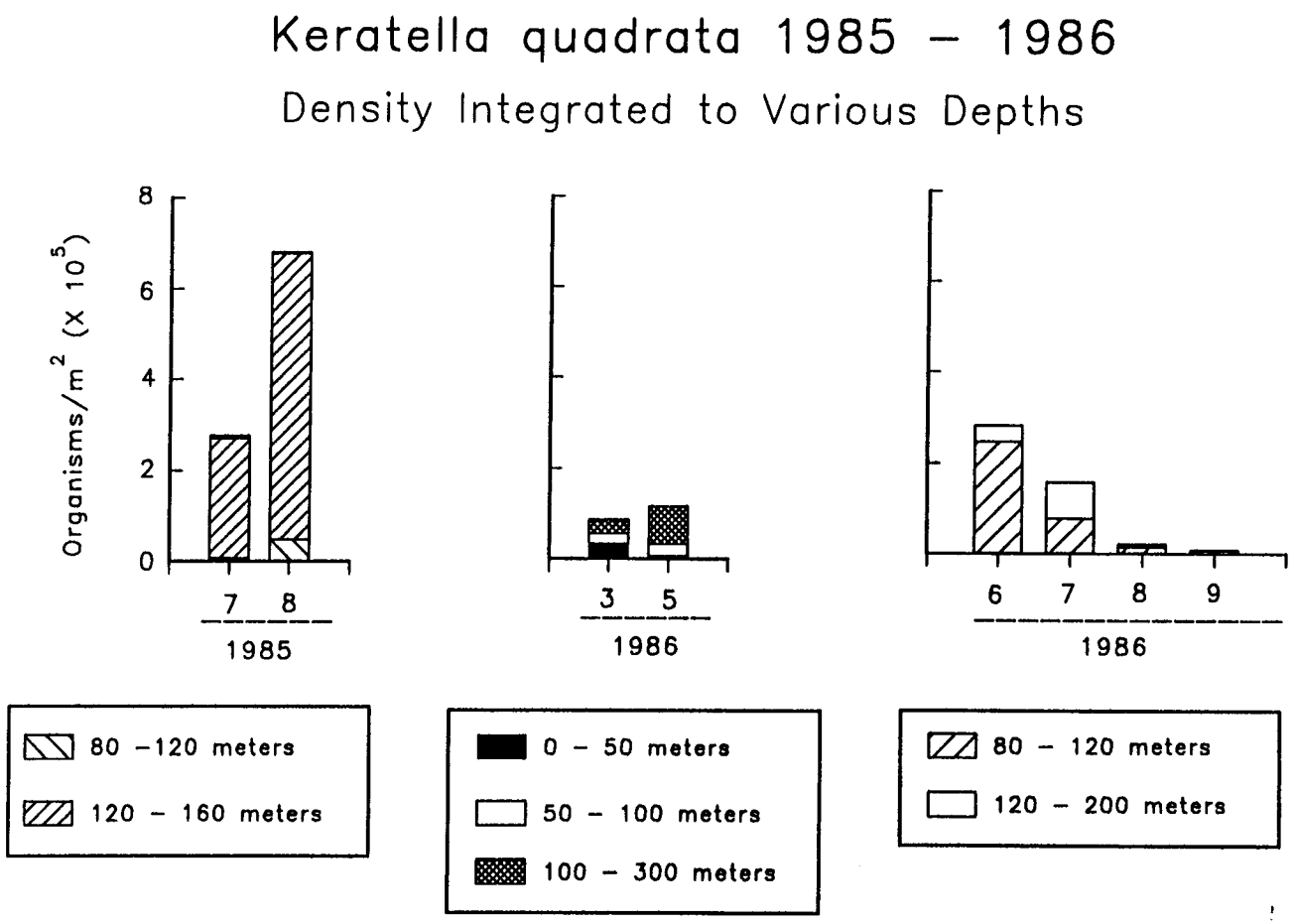


Figure 21. Density of Keratella quadrata at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

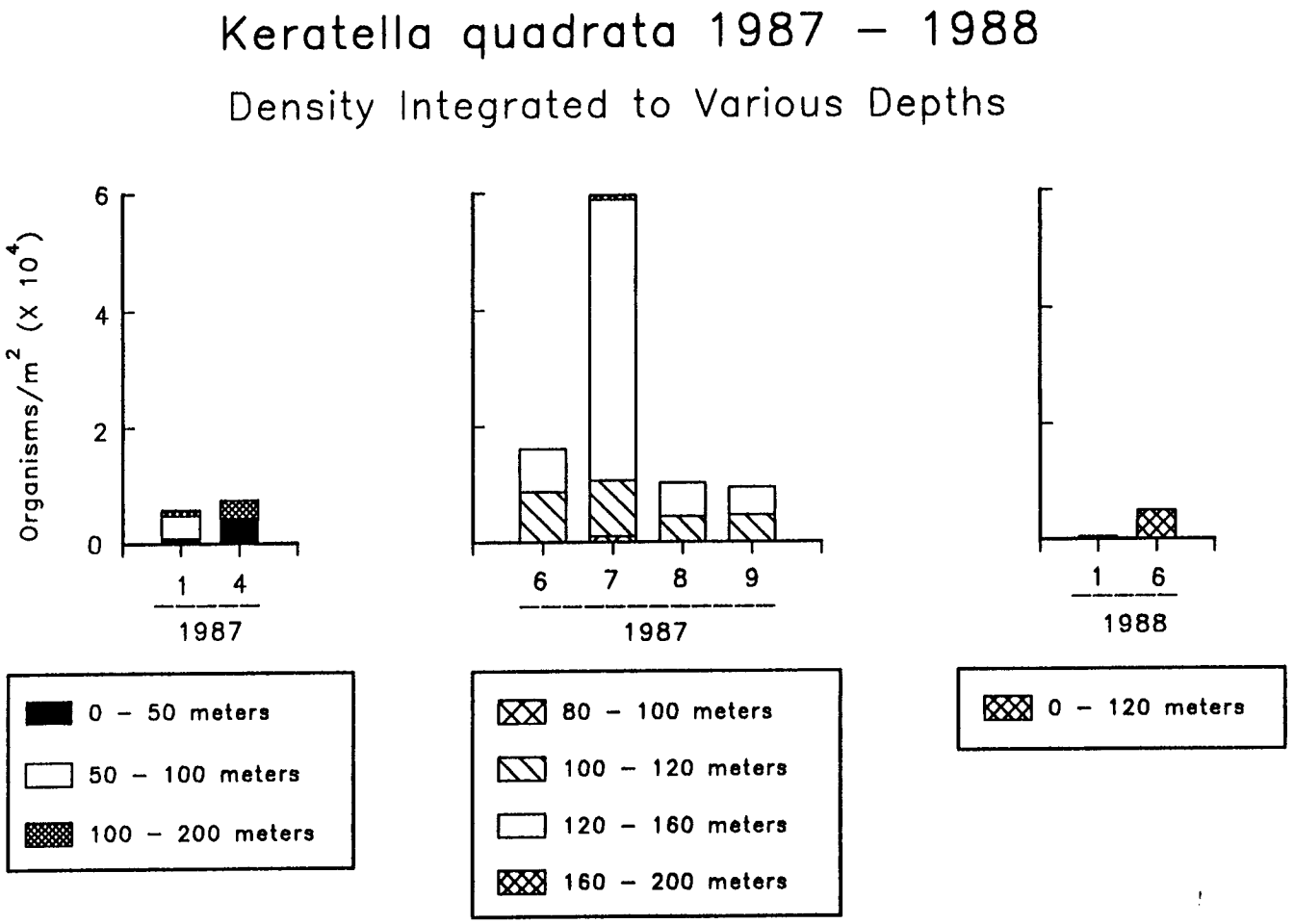


Figure 22. Density of Keratella quadrata at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

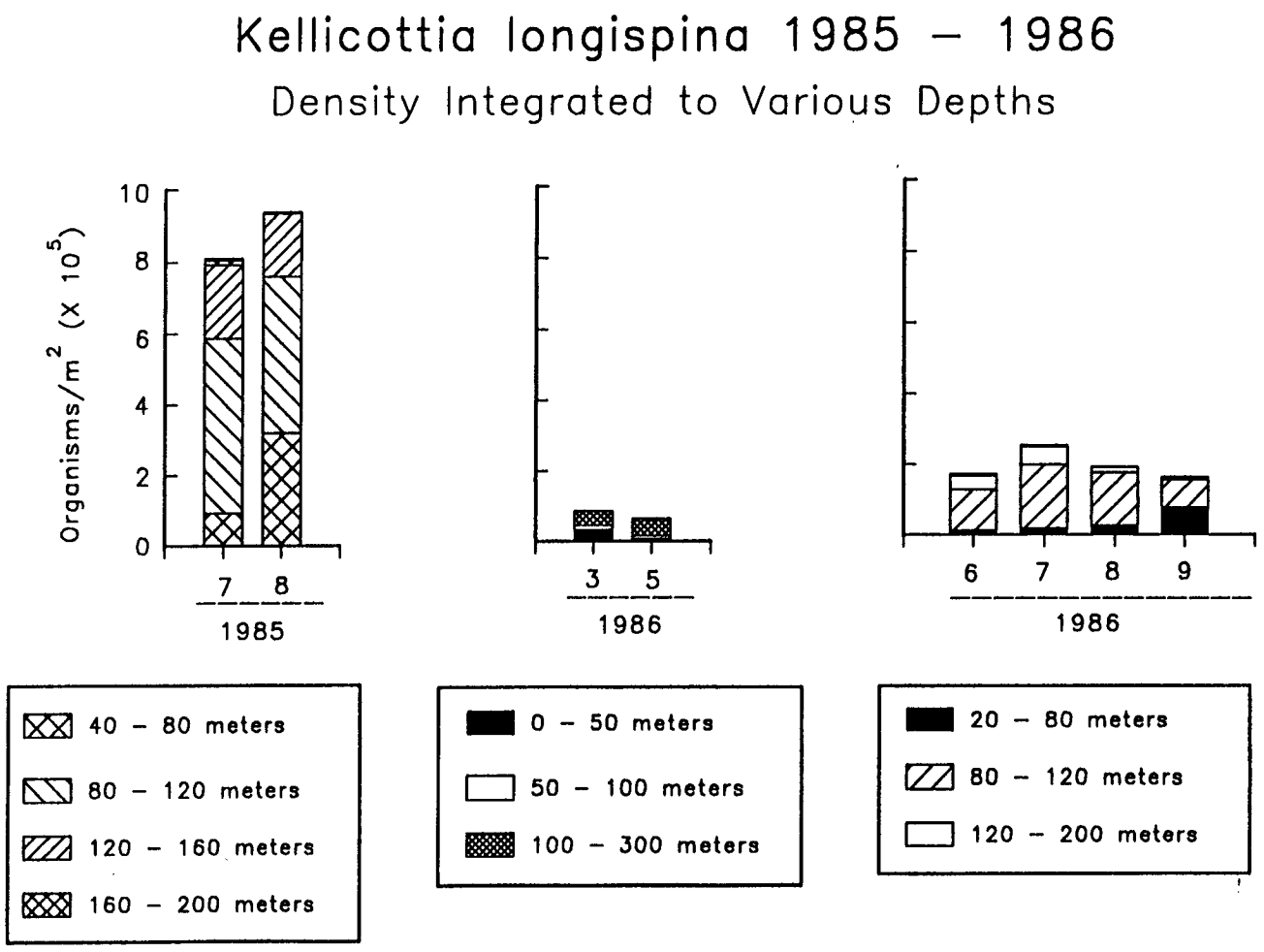


Figure 23. Density of Kellicottia longispina at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

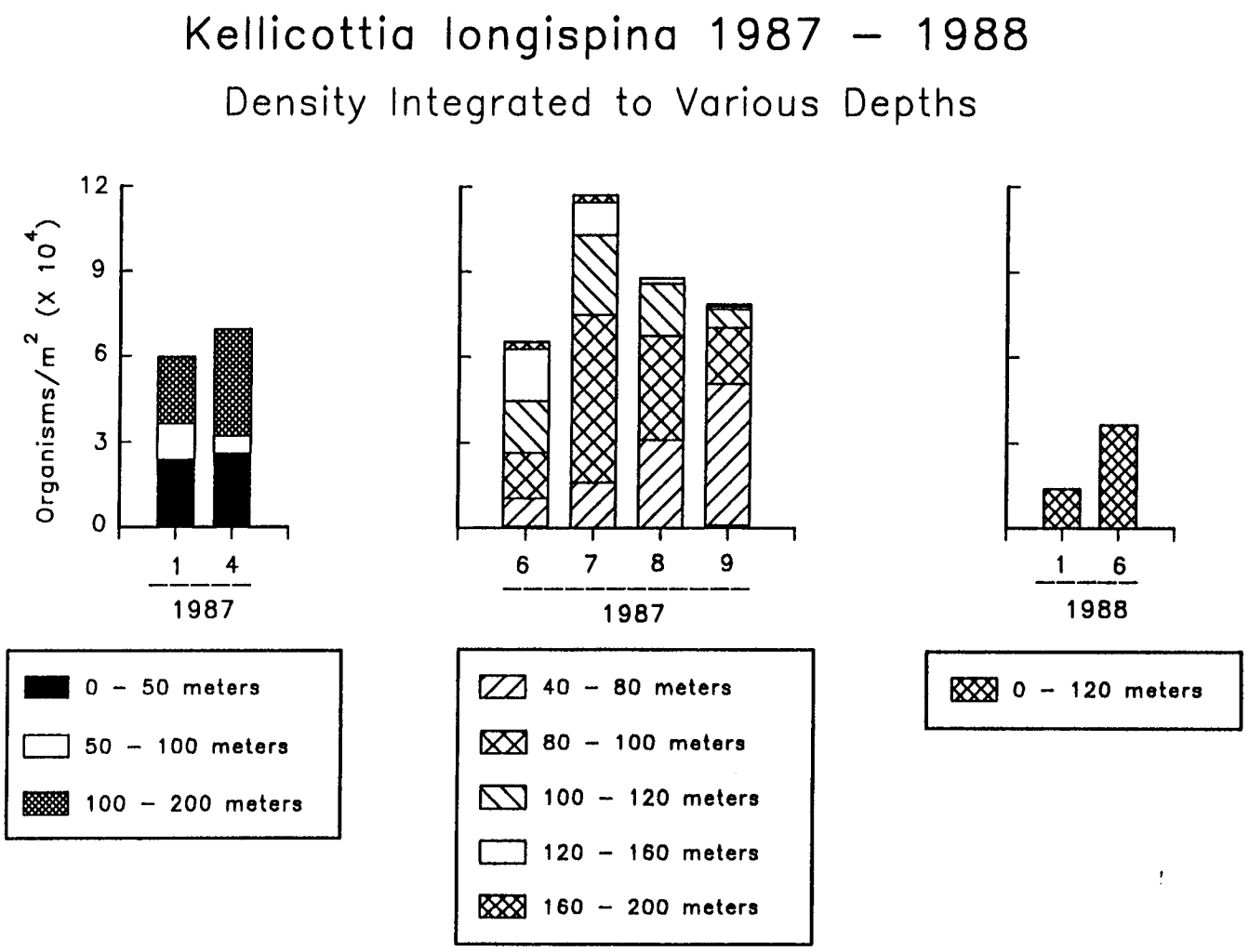


Figure 24. Density of Kellicottia longispina at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

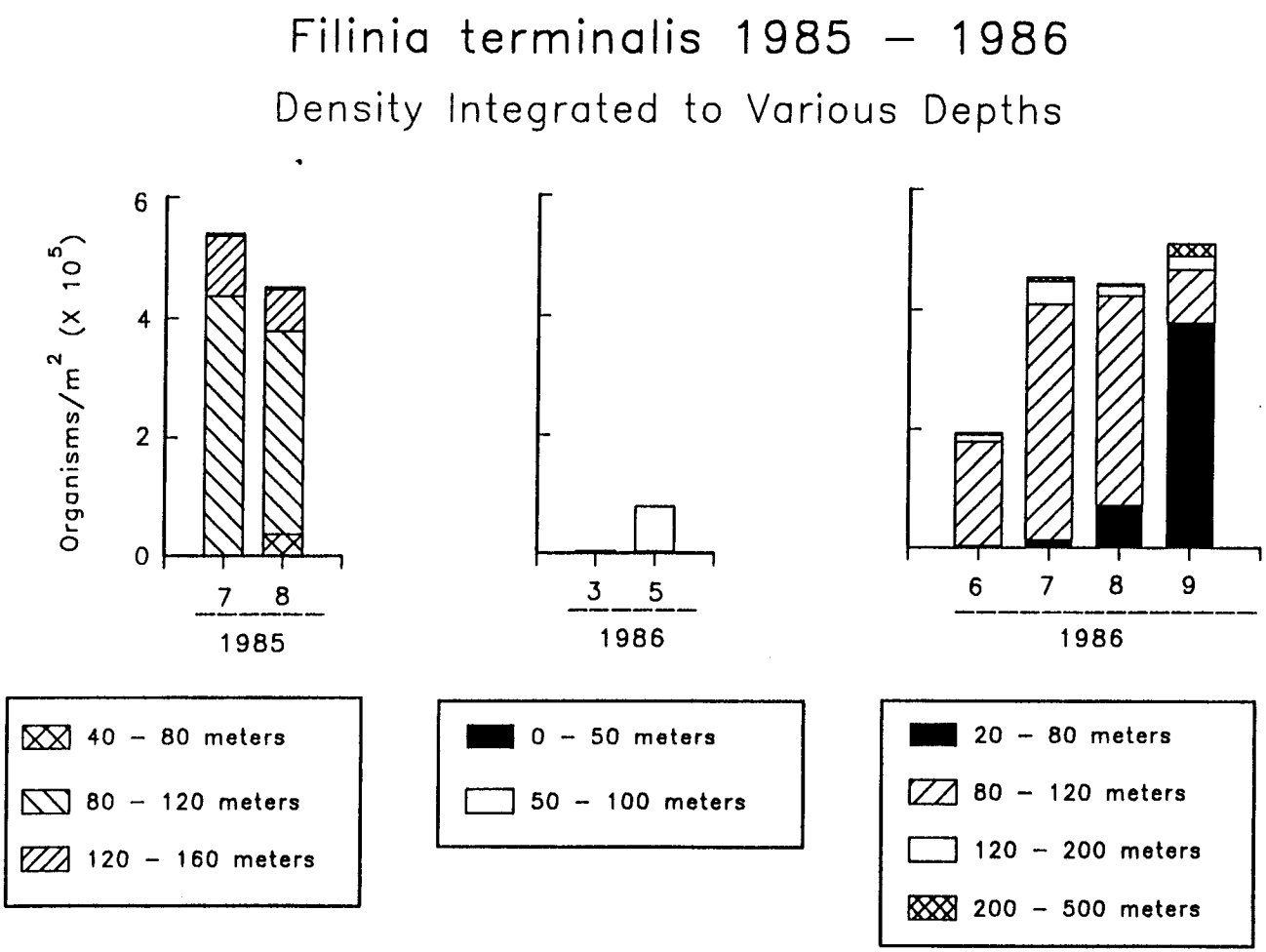


Figure 25. Density of Filinia terminalis at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

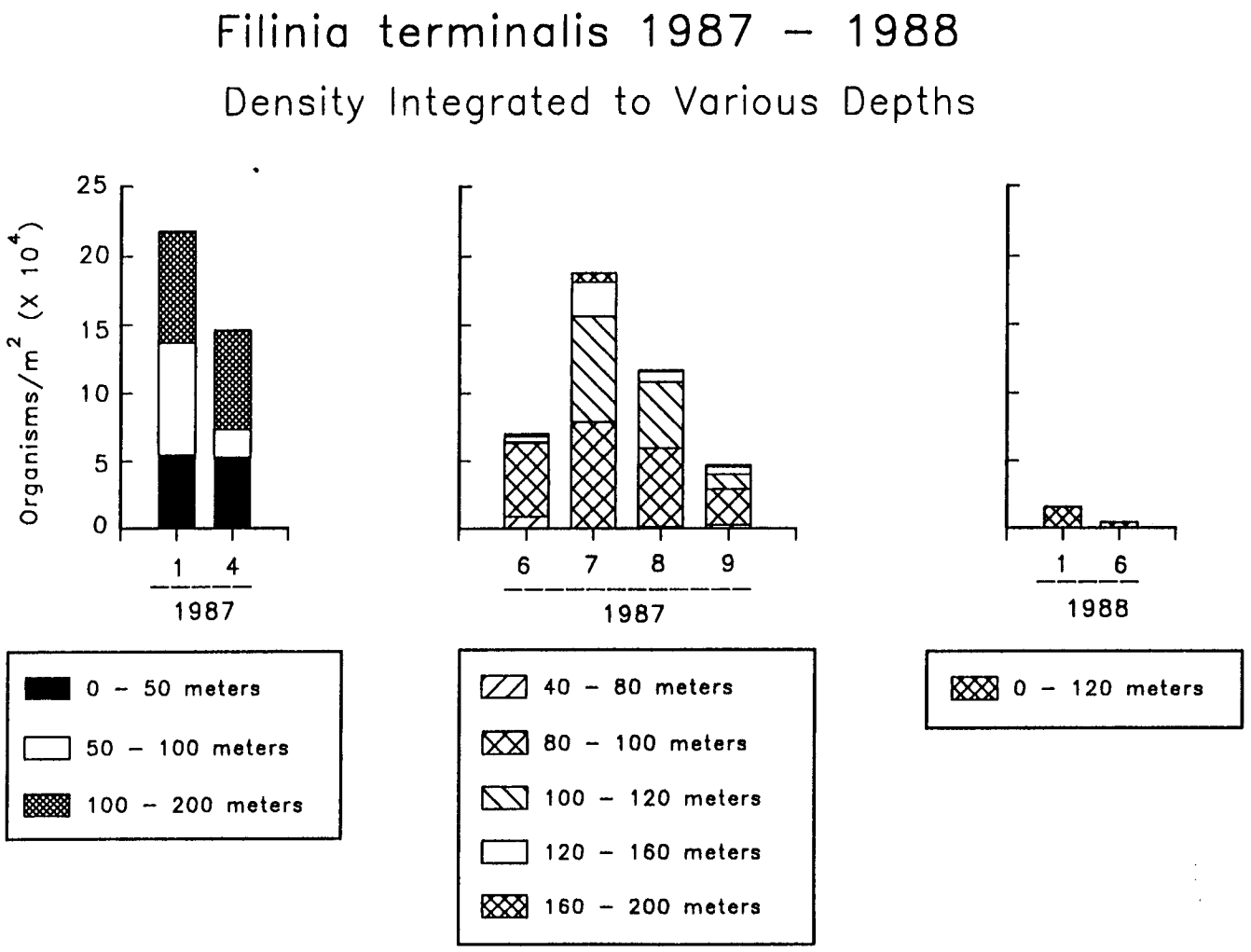


Figure 26. Density of Filinia terminalis at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

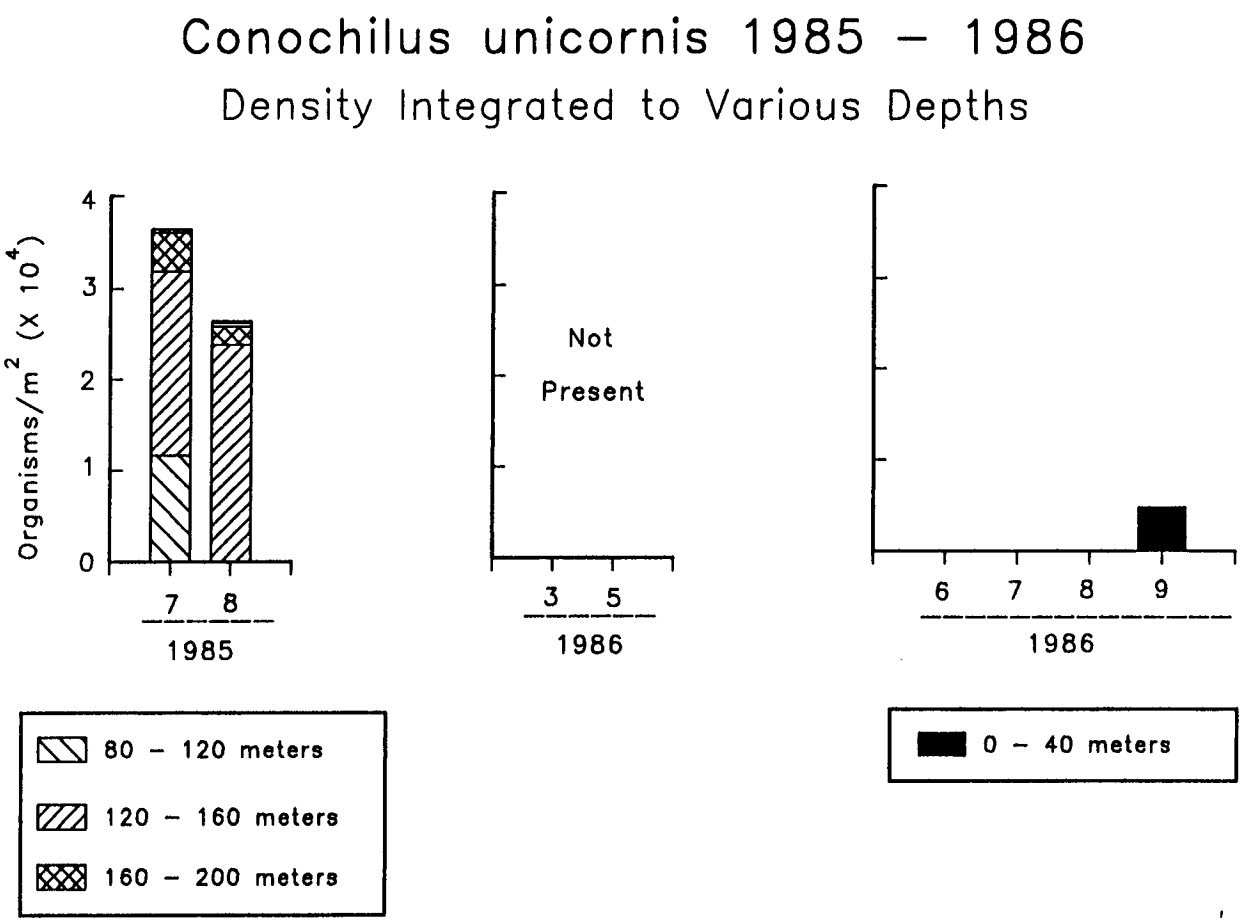


Figure 27. Density of Conochilus unicornis at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1985 and 1986.

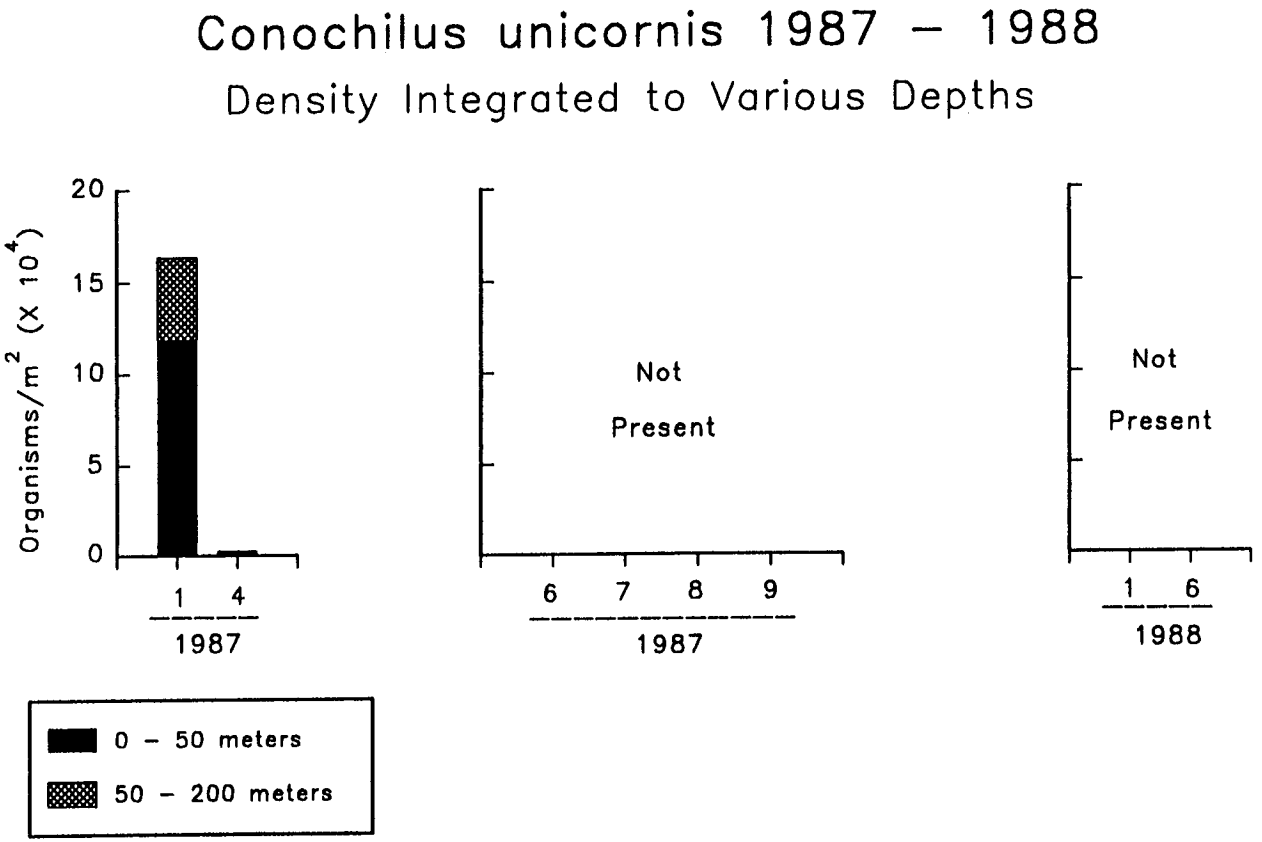


Figure 28. Density of Conochilus unicornis at Station 13 integrated to various depths in the water column. Data represent samples obtained from vertical net tows in 1987 and 1988.

Total zooplankton biomass integrated to a depth of 200 m was higher in 1988 and 1989 than in 1990 (Fig. 29). Corresponding mean biomasses for the months of June, July, August, and September were 2,167 mg m^{-2} (1988), 2,303 mg m^{-2} (1989), and 1,365 mg m^{-2} (1990). The pattern of total density integrated to a depth of 200 m was different than that found for total biomass, indicating variations in taxonomic composition and mean sizes of individual species (Fig. 30). Mean densities for the summer months and September were 2.427 X 10^6 organisms m^{-2} (1988), 13.190 X 10^6 organisms m^{-2} (1989), and 4.196 X 10^6 organisms m^{-2} (1990). Although rotifer biomass was higher in 1990 than in 1988, crustacean biomass was relatively low in 1990, a pattern that accounted for a decrease in total zooplankton biomass between September 1989 and July 1990 (Figs. 31 and 32). During the summers of 1988, 1989, and 1990, most of the zooplankton biomass and density was distributed between depths of 40 m and 160 m, whereas in April 1989 and January 1990 biomass was more evenly distributed between the water surface and a depth of 200 m.

Densities of the two dominant crustaceans, *Bosmina longirostris* and *Daphnia pulicaria*, exhibited different temporal patterns and a low correlation (r = 0.131) for the period from June 30, 1988 to September 6, 1990 (Figs. 33 and 34). *B. longirostris* had its maximum densities integrated to 200 m in September 1989 and 1990 (4.878 X 10^5 and 4.726 X 10^5 organisms m^{-2}, respectively), whereas *D. pulicaria* was most abundant in June 1988 (1.690 X 10^5 organisms m^{-2}) and July 1988 (1.616 X 10^5 organisms m^{-2}). *D. pulicaria* was rare in all samples obtained in summer and early fall 1990. Therefore, the pronounced difference in total zooplankton biomass between 1988 and 1990 (Fig. 29) was closely related to the decline in the density of this taxon between January and July 1990.

Correlation coefficients comparing densities among dominant rotifers for the period June 30, 1988 to September 6, 1990, varied from values near zero to 0.615 (Table 5). In general, *Keratella cochlearis*, *Filinia terminalis*, *Kellicottia longispina*, *Synchaeta oblonga*, and to a lesser degree *Keratella quadrata*, had a greater tendency to co-occur with other rotifer taxa than either *Polyarthra dolichoptera* or *Collotheca pelagica*. *P. dolichoptera* was distrib-

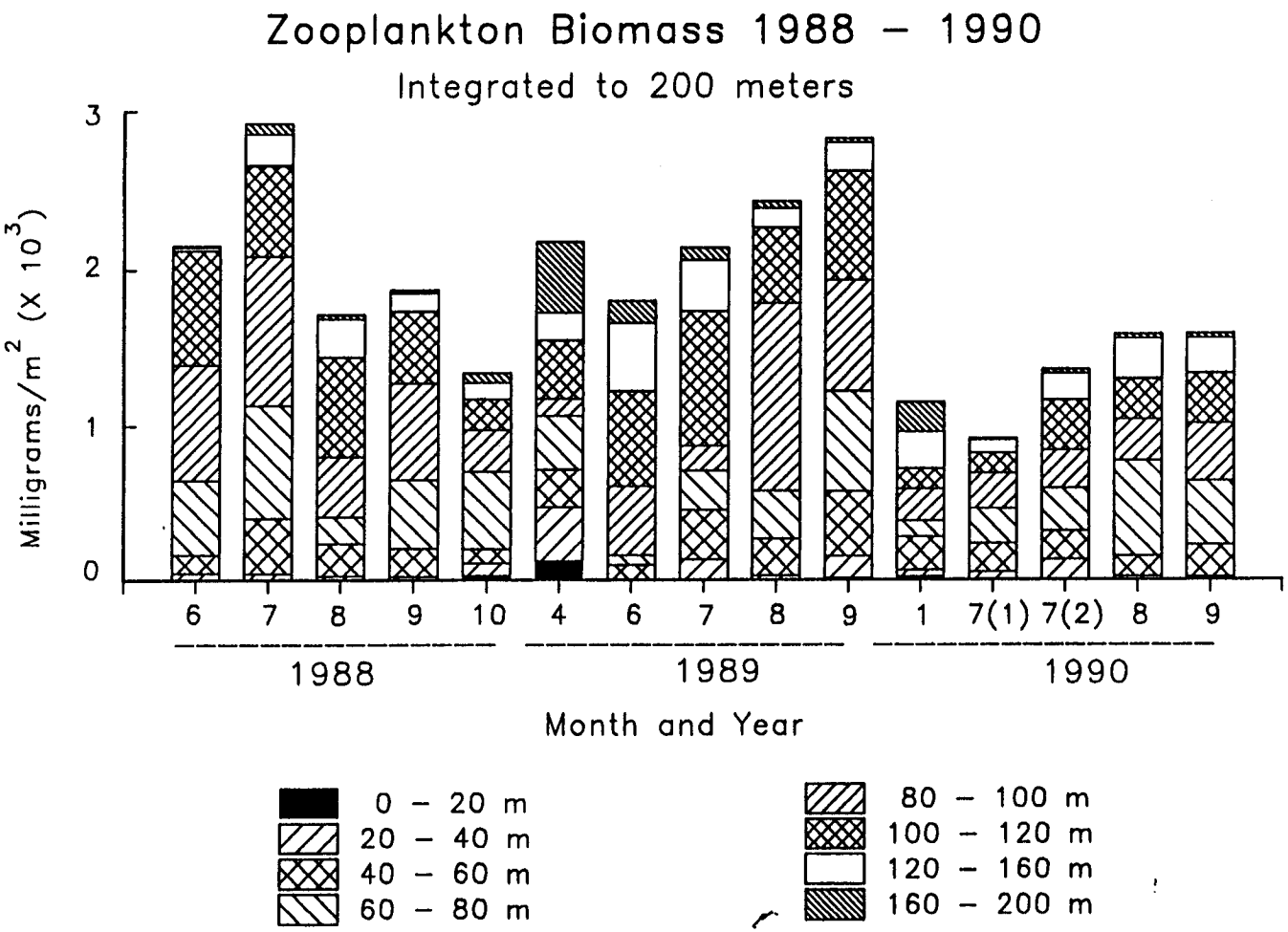


Figure 29. Zooplankton biomass at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

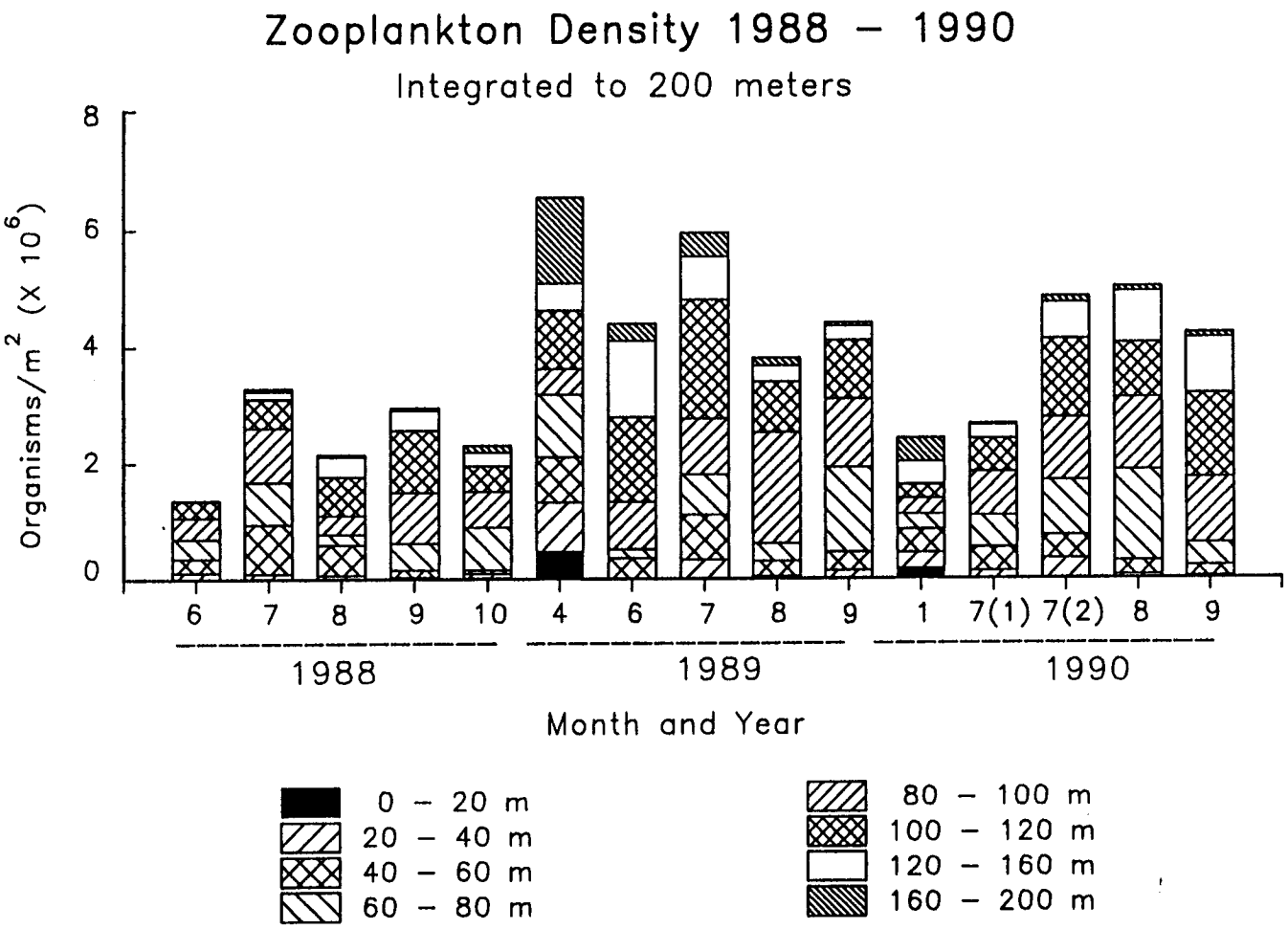


Figure 30. Zooplankton density at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

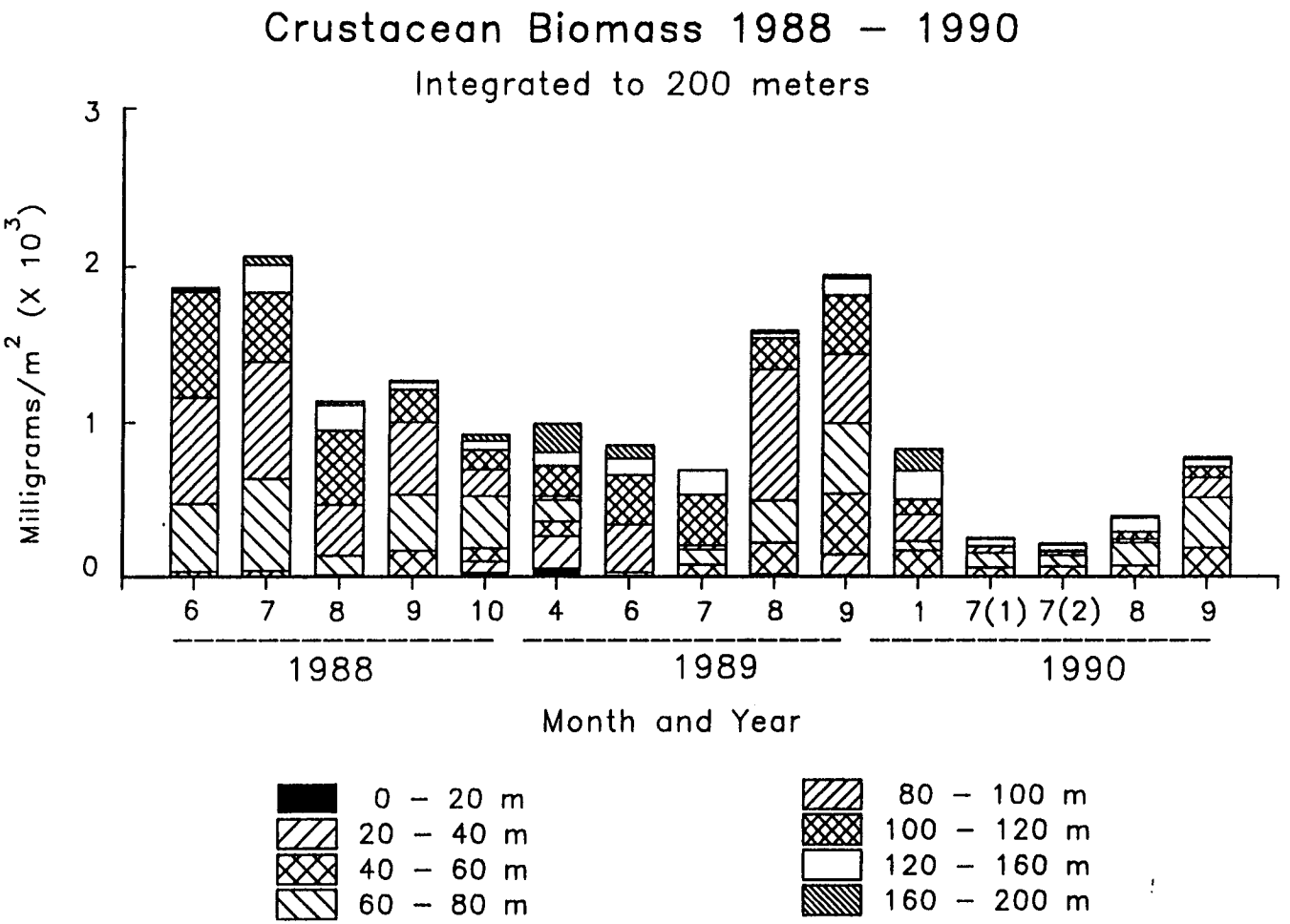


Figure 31. Crustacean biomass at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

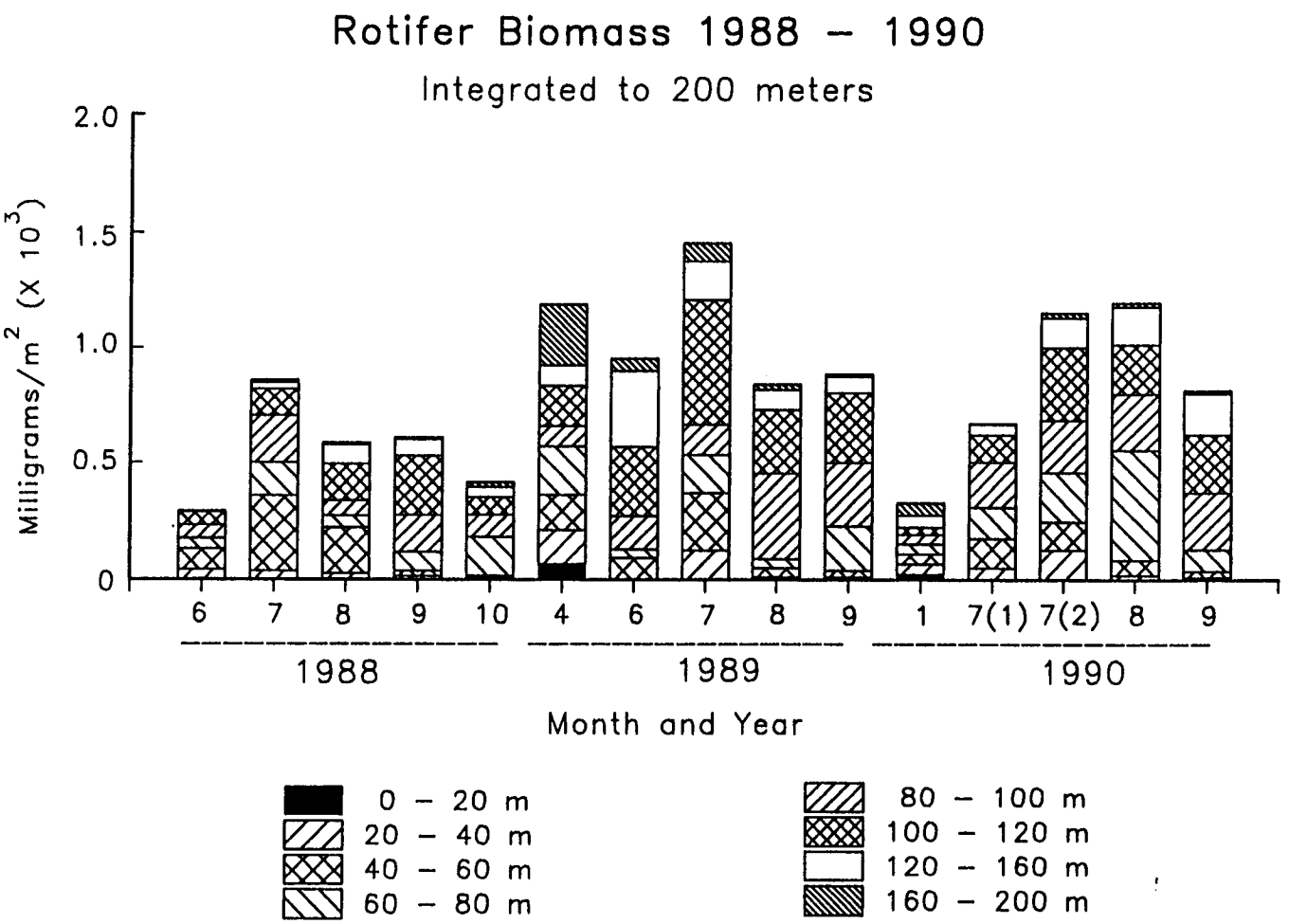


Figure 32. Rotifer biomass at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

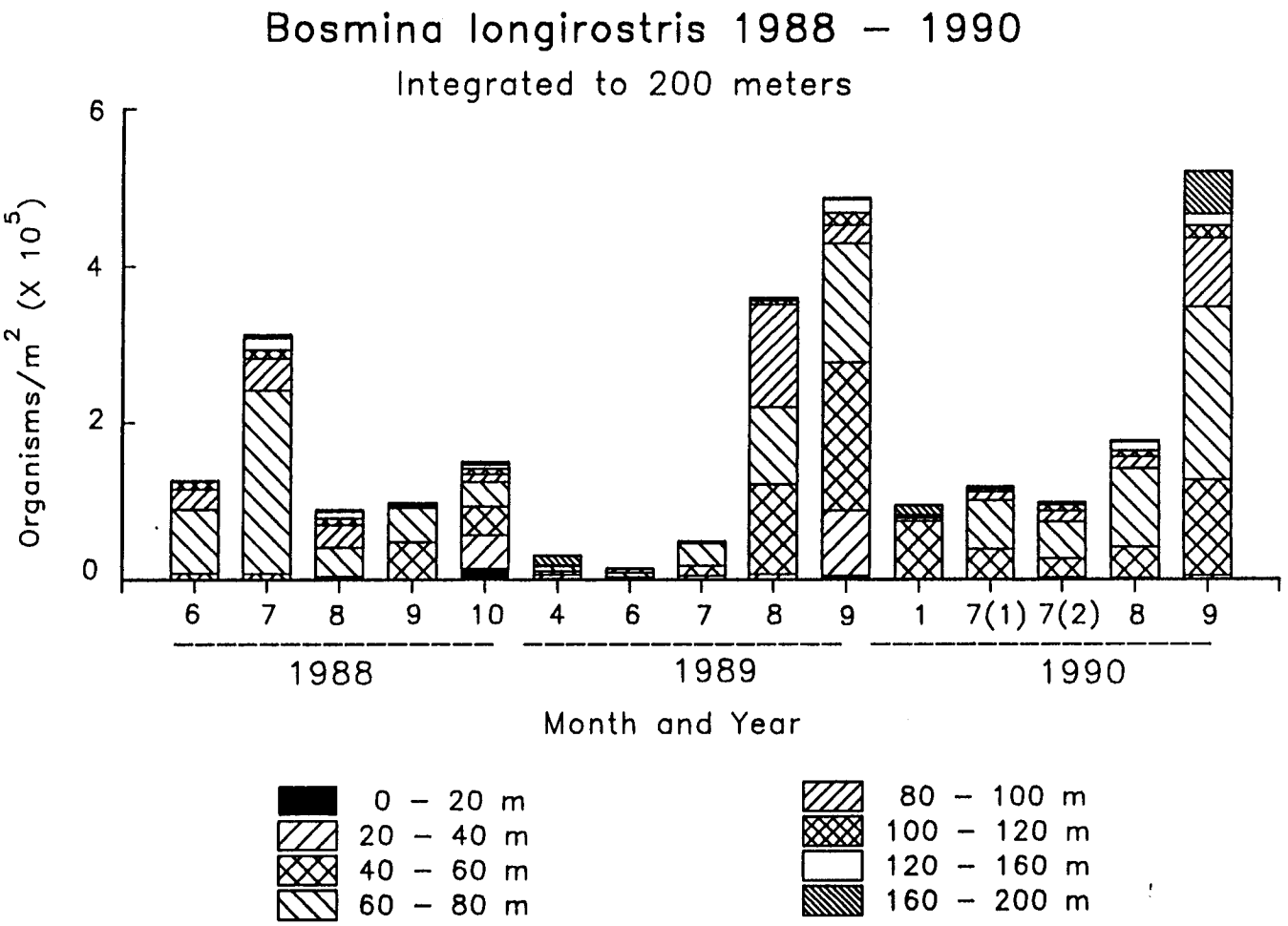


Figure 33. Density of Bosmina longirostris at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

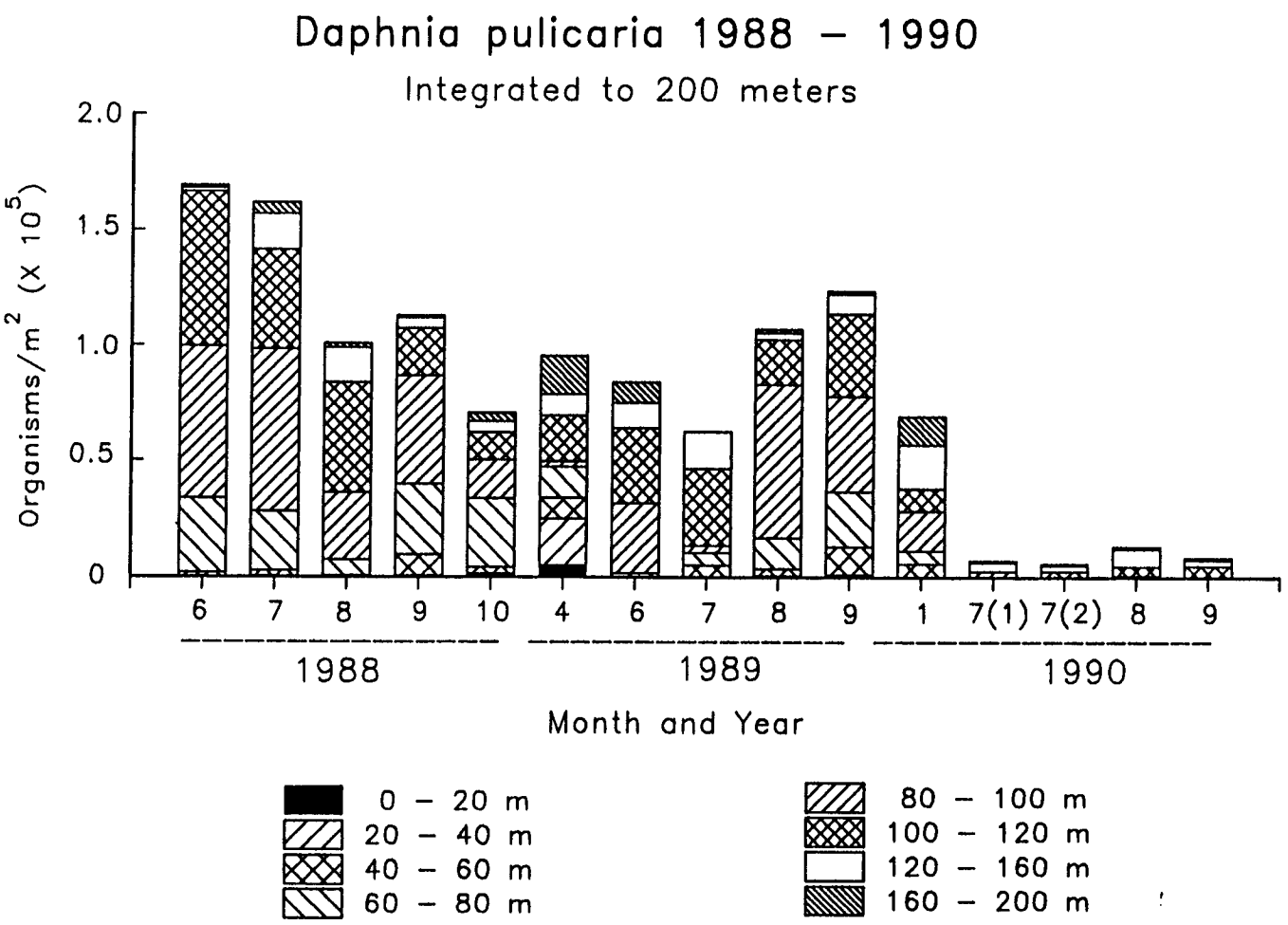


Figure 34. Density of Daphnia pulicaria at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

Table 5. Correlation coefficients comparing densities of dominant rotifer taxa in Crater Lake for the period from June 30, 1988 to September 6, 1990. Values are based on 184 samples taken at Station 13 from various depths between the water surface and 200 m below the surface.

Taxon	KERCOC	KERQUA	FILTER	KELLON	POLDOL	SYNOBL
KERQUA	.256**					
FILTER	.595**	.466**				
KELLON	.584**	.217*	.391**			
POLDOL	.081	-.057	-.003	.099		
SYNOBL	.565**	.280**	.451**	.615**	.301**	
COLPEL	.097	.051	-.024	-.103	-.082	-.042

1-tailed significance: * = $P < 0.01$ and ** = $P < 0.001$

uted higher in the water column than other rotifer taxa, whereas *C. pelagica* was relatively rare in 1988 and 1989. Most of the correlation coefficients for comparisons between rotifer taxa and the two dominant crustaceans (Table 6) were negative and relatively low ($r < 0.5$) Highest negative correlations were between *Bosmina longirostris* and *K. cochlearis* ($r = -.425$), *Filinia terminalis* ($r = -.243$), and *Synchaeta oblonga* ($r = -.300$).

Keratella cochlearis, *Polyarthra dolichoptera*, and *Synchaeta oblonga* were the dominant rotifers found in the lake between June 30, 1988 and September 6, 1990. *K. cochlearis* was more abundant in 1989 and 1990 than in 1988, with mean total densities (integrated to 200 m) for the summer months of 0.457×10^6 organisms m^{-2} (1988), 1.971×10^6 organisms m^{-2} (1989), and 1.666×10^6 organisms m^{-2} (1990). This species reached a maximum integrated density of 3.927×10^6 organisms m^{-2} in April 1989 (Fig. 35). *K. cochlearis* was uni-

Table 6. Correlation coefficients comparing densities of dominant rotifer taxa with densities of the the two dominant crustaceans in Crater Lake for the period from June 30, 1988 to September 6, 1990. Data set and symbols for significance are the same as in Table 5.

Taxon	KERCOC	KERQUA	FILTER	KELLON	POLDOL	SYNOBL	COLPEL
BOSLON	-.425**	-.155	-.243**	.031	-.086	-.300**	-.030
DAPPUL	-.100	-.026	-.085	.024	-.180*	-.152	-.046

formly distributed throughout the water column to a depth of 200 m in April 1989 and January 1990, whereas in the summers of 1988, 1989, and 1990, when thermal stratification was present, it reached maximum densities at depths below 60 m. *P. dolichoptera* was more abundant in the summer than at other seasons (Fig. 36), reaching its maximum integrated density in either July (1988 and 1989) or August (1990); mean integrated densities for the summer months were 0.751 X 10^6 organisms m^{-2} (1988), 0.757 X 10^6 organisms m^{-2} (1989), and 1.073 X 10^6 organisms m^{-2} (1990). Concentrations of *P. dolichoptera* usually occurred between 20 m and 80 m below the water surface, although it also was abundant between depths of 100 m and 120 m in 1989 and 1990. *S. oblonga* was prominent in the summer and in April 1989; its maximum integrated density was 1.798 X 10^6 organisms m^{-2} in July 1989 (Fig. 37). In 1988, this species was concentrated between depths of 80 m and 100 m, while in 1989 and 1990 it was more uniformly distributed between depths of 40 m and 200 m.

Of the subdominant rotifers in the 1988 - 1990 samples (*Keratella quadrata*, *Kellicottia longispina*, *Filinia terminalis*, and *Collotheca pelagica*), *K. longispina* was the only species with similar maximum integrated densities for 1988, 1989, and 1990 (Fig. 38). In contrast, *K. quadrata* and *F. terminalis* were only abundant in 1989, with most organisms of

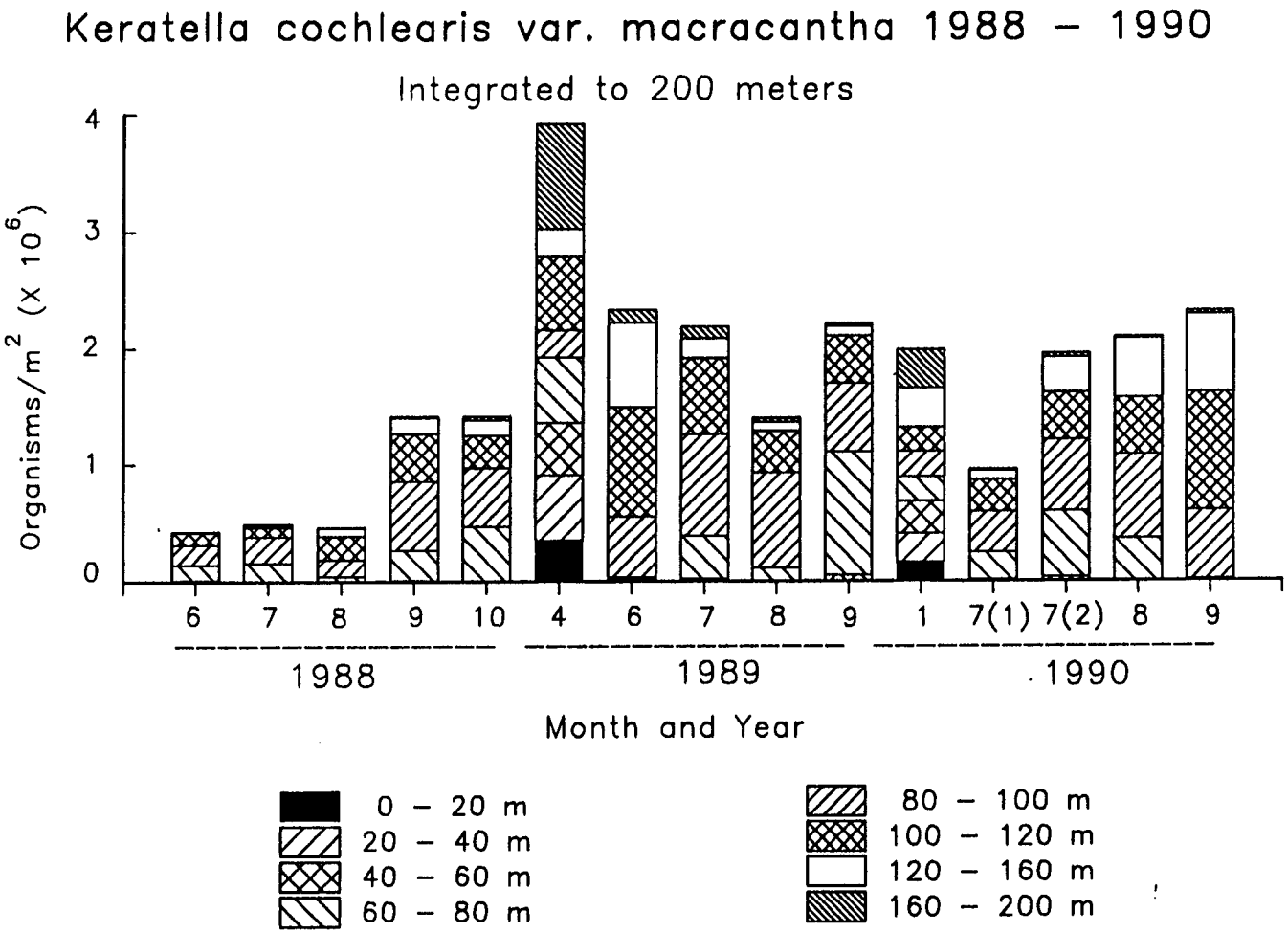


Figure 35. Density of Keratella cochlearis at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

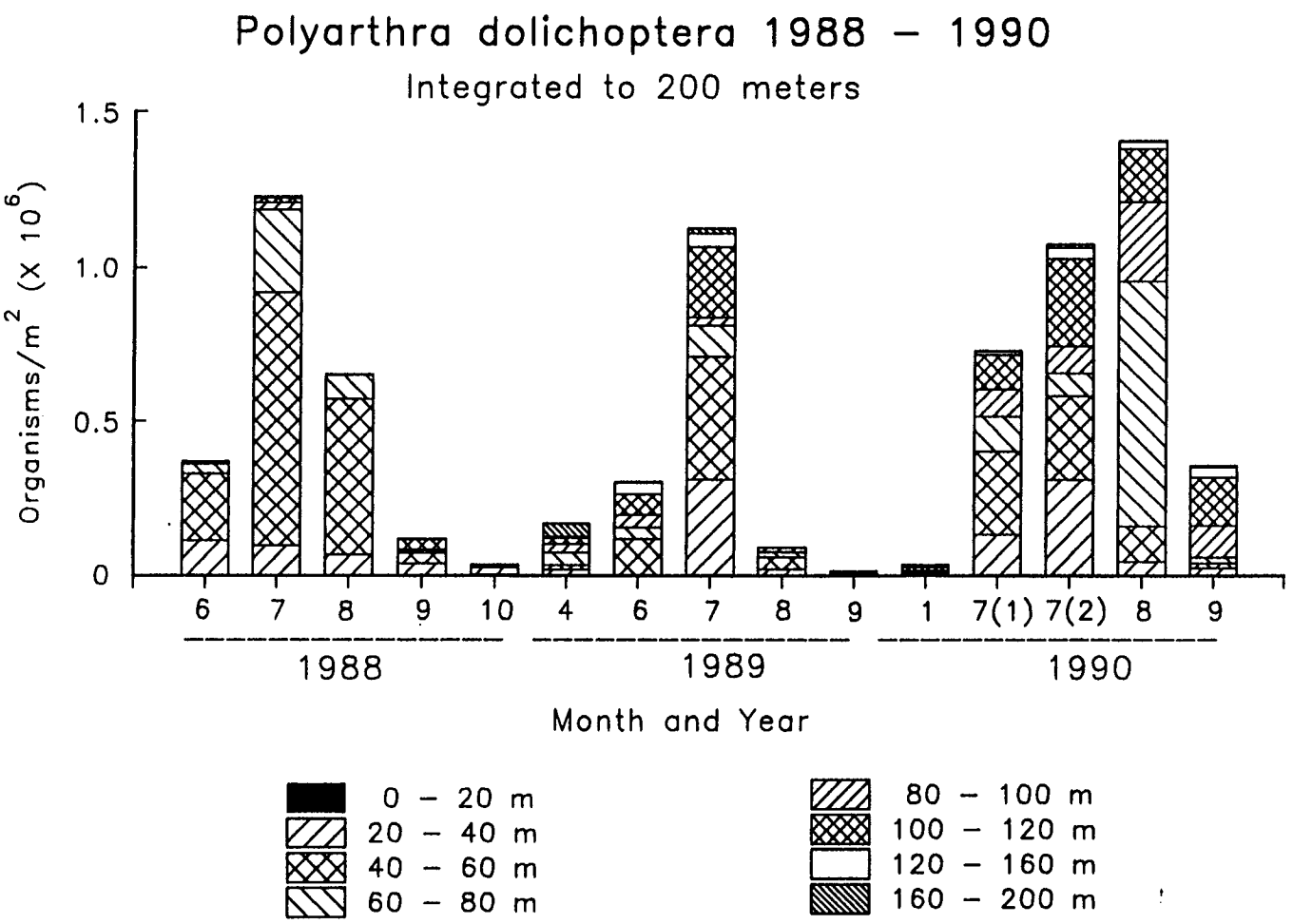


Figure 36. Density of Polyarthra dolichoptera at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

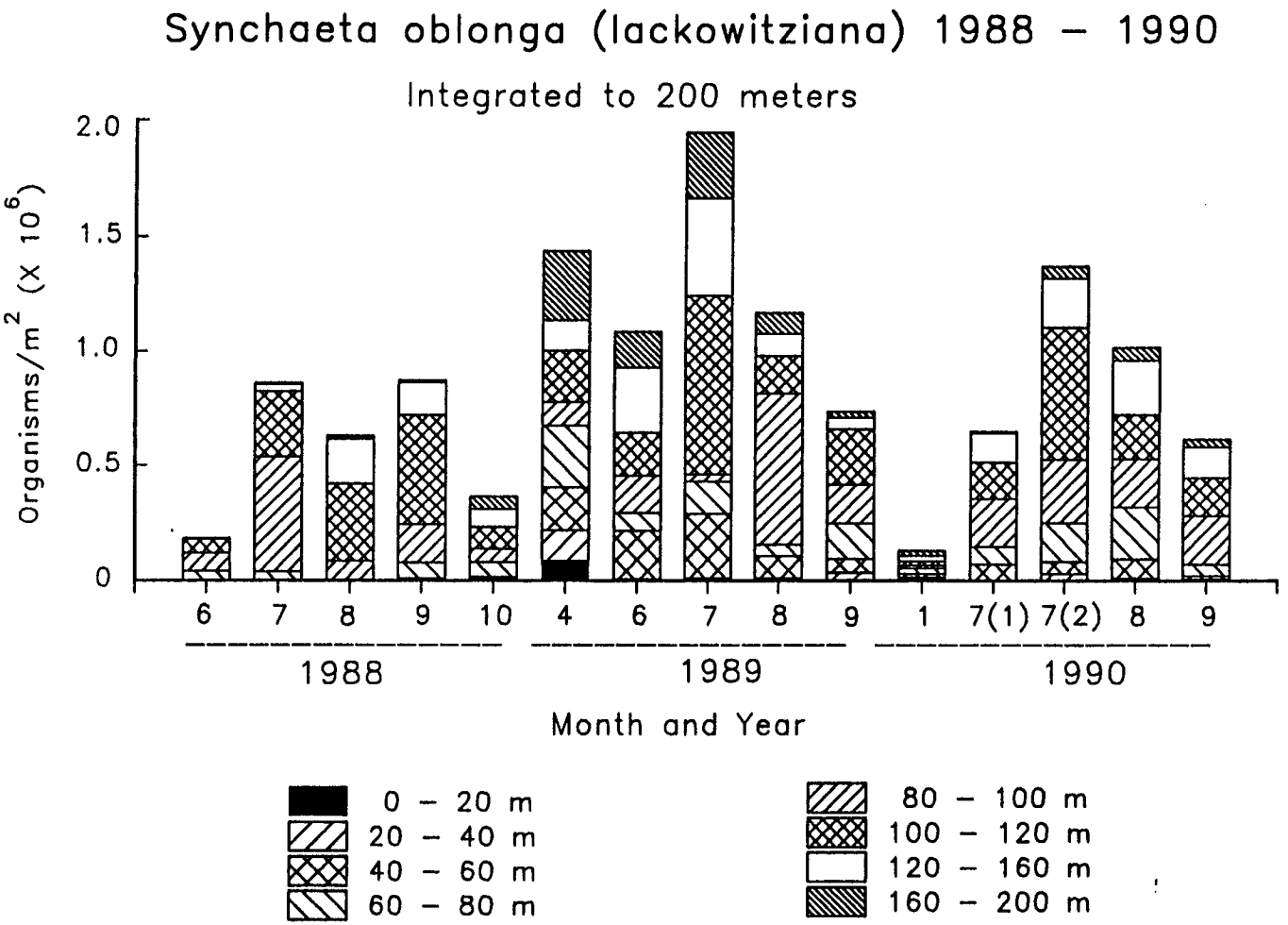


Figure 37. Density of Synchaeta oblonga at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

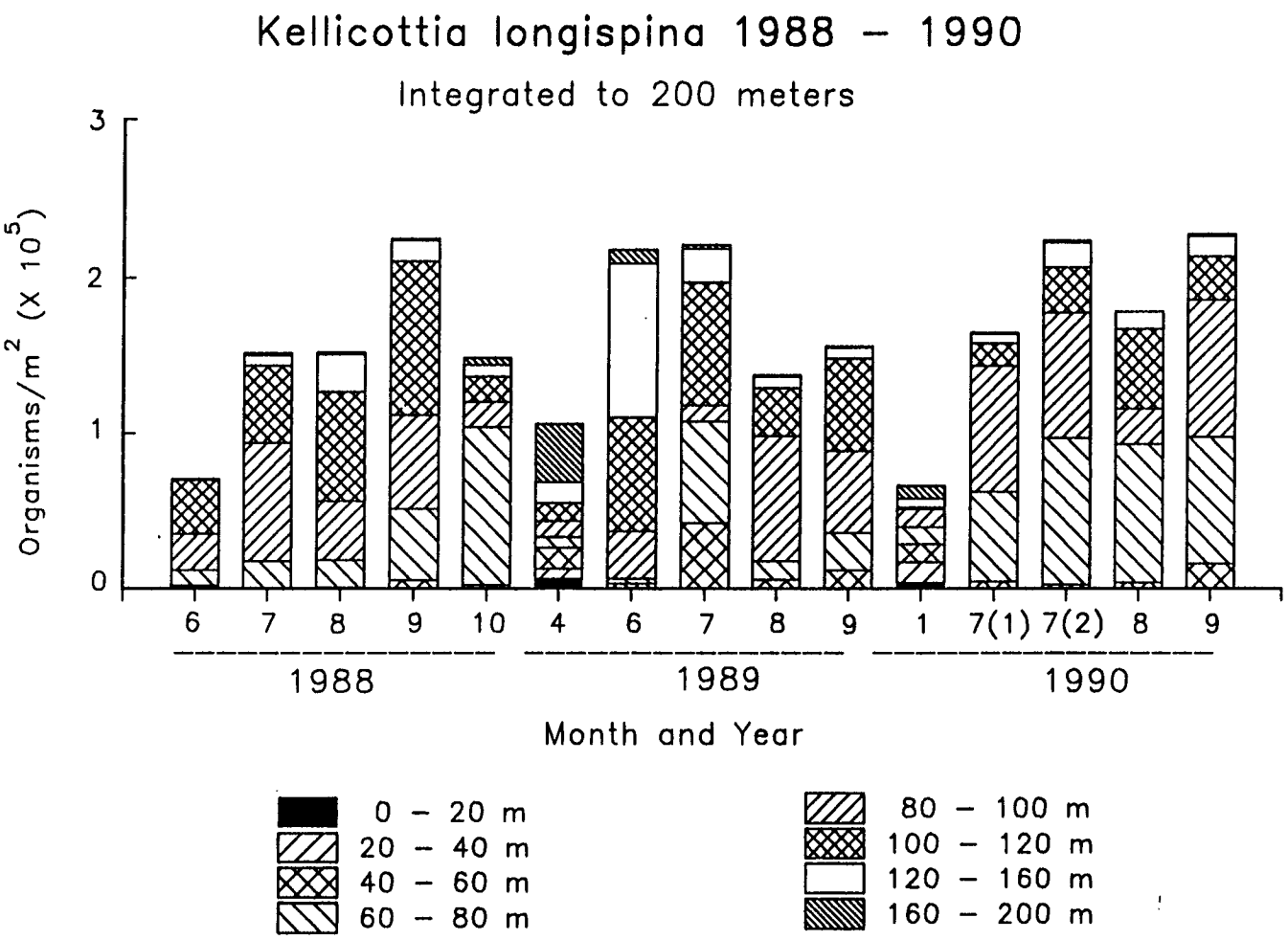


Figure 38. Density of Kellicottia longispina at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

these populations distributed between depths of 80 m and 160 m (Figs. 39 and 40). Maximum densities of *C. pelagica* occurred in 1990 at depths below 120 m (Fig. 41).

Vertical Migration. The most consistent pattern of vertical migration was found in 1990 for *Bosmina longirostris*, the dominant crustacean in Crater Lake (Fig. 42). From July 2 to September 6, the maximum density of this species was about 20 m higher in the water column during the day than at night. However, migration patterns in *Daphnia pulicaria*, the other dominant crustacean, were less predictable. Vertical movements by this species were most obvious from samples obtained in July and September 1989 and in August 1990 (Fig. 43). In all three of these sample sets, the vertical upward shift in maximum density was about 40 m. Diurnal patterns of vertical movement in the rotifers were inconsistent and unpredictable (Figs. 44 - 50). Diurnal movements were not evident for some taxa on particular sampling dates (e.g., *Keratella cochlearis* in September 1988, 1989, and 1990; *Keratella quadrata* in September 1988 and 1989, and in July, August, and September 1990), whereas other taxa exhibited both upward and downward diurnal shifts in maximum density (e.g., *Polyarthra dolichoptera* in July and August 1990).

Community Properties

Species Diversity. Patterns of species diversity and dominance in the zooplankton of Crater Lake were analyzed for the 1988-1990 sampling period. Species diversity, as expressed by the information measure (H'), was relatively low and dominance (R) was high near the water surface in the summers of 1988 and 1990 when thermal stratification was present (Figs. 51 and 52). However, this pattern was not evident in the summer of 1989. The mean number of zooplankton taxa in samples from the upper 20 m of the water column, when thermal stratification occurred (i.e., in July, August, and early September), also was lower in 1988 and 1990 than in 1989; the means for these years were 2.3 (1988), 5.0 (1989), and 3.8 (1990). Mechanisms that accounted for these patterns of diversity probably involved complex interactions between physical processes and corresponding effects on

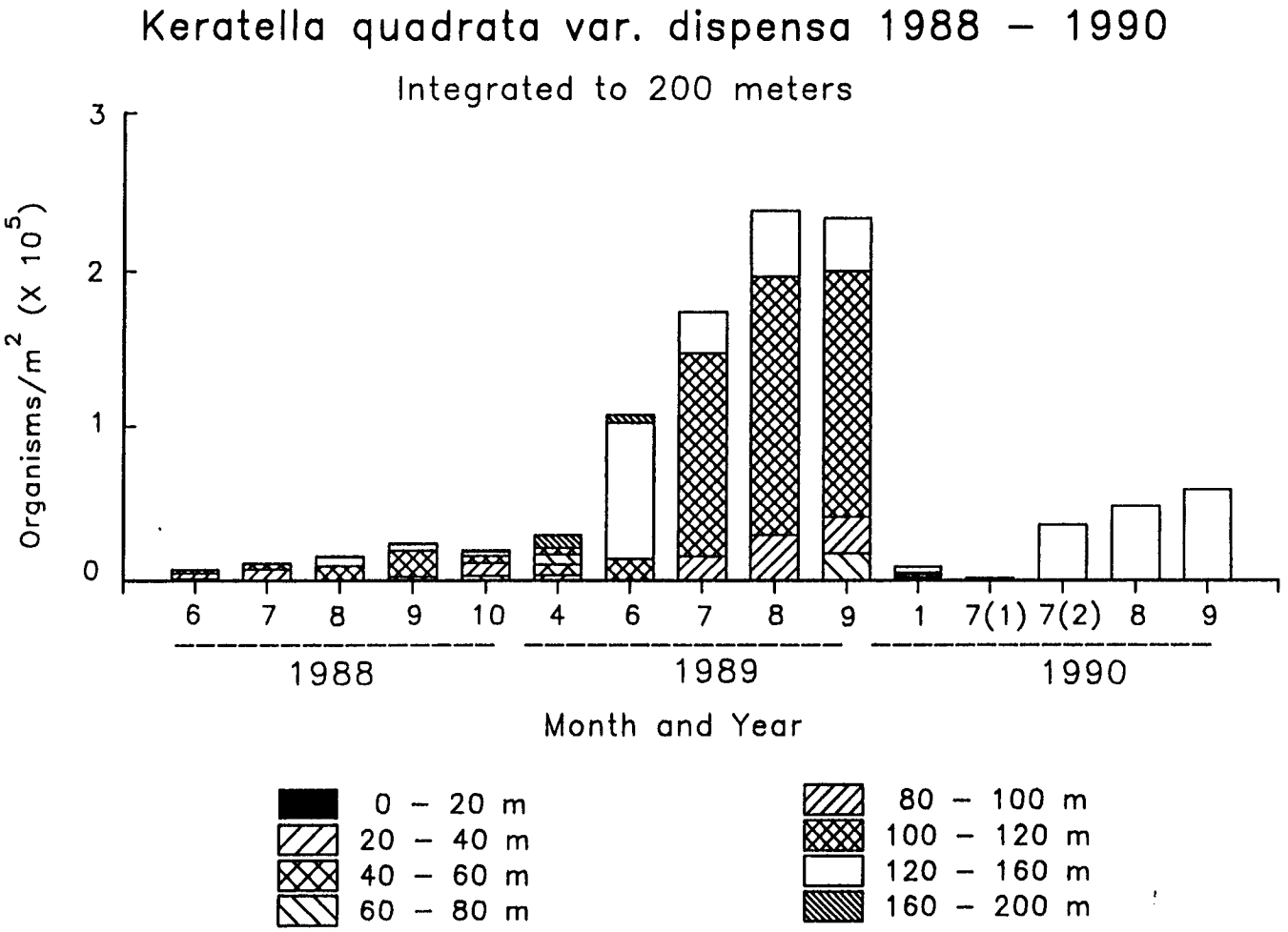


Figure 39. Density of Keratella quadrata at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

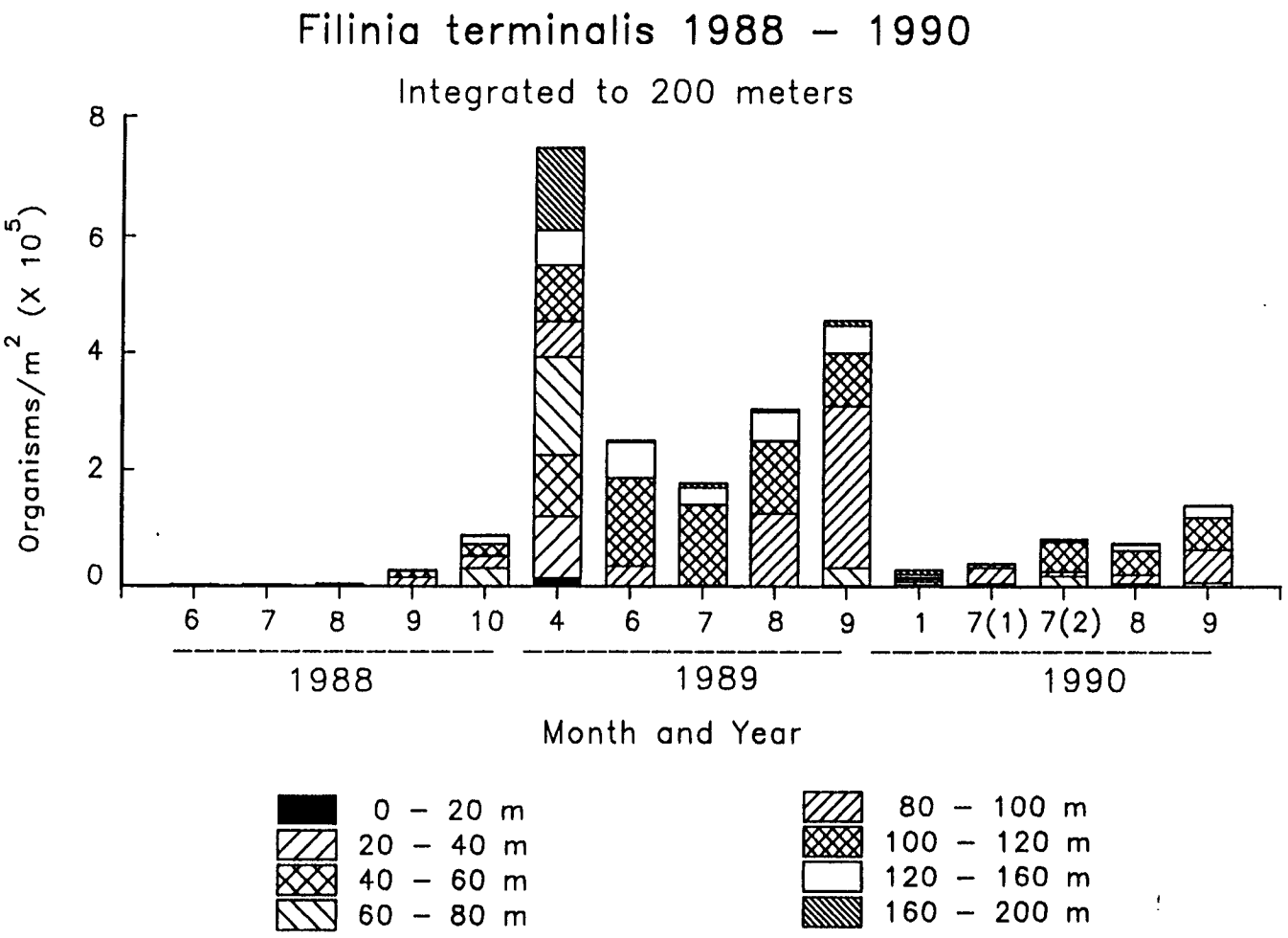


Figure 40. Density of Filinia terminalis at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

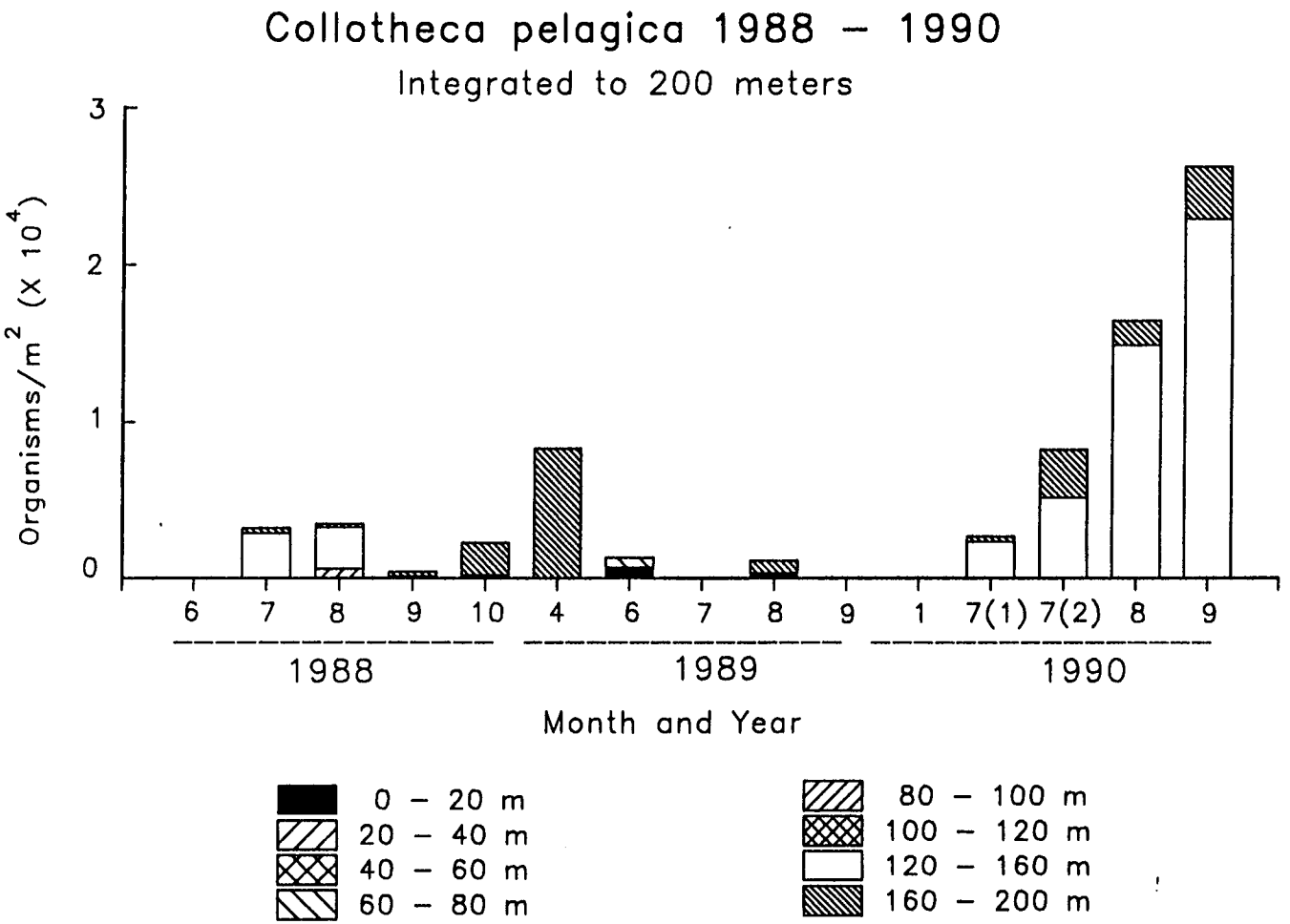


Figure 41. Density of Collotheca pelagica at Station 13 integrated to a depth of 200 m in the water column. Data represent samples obtained from vertical net tows between June 1988 and September 1990.

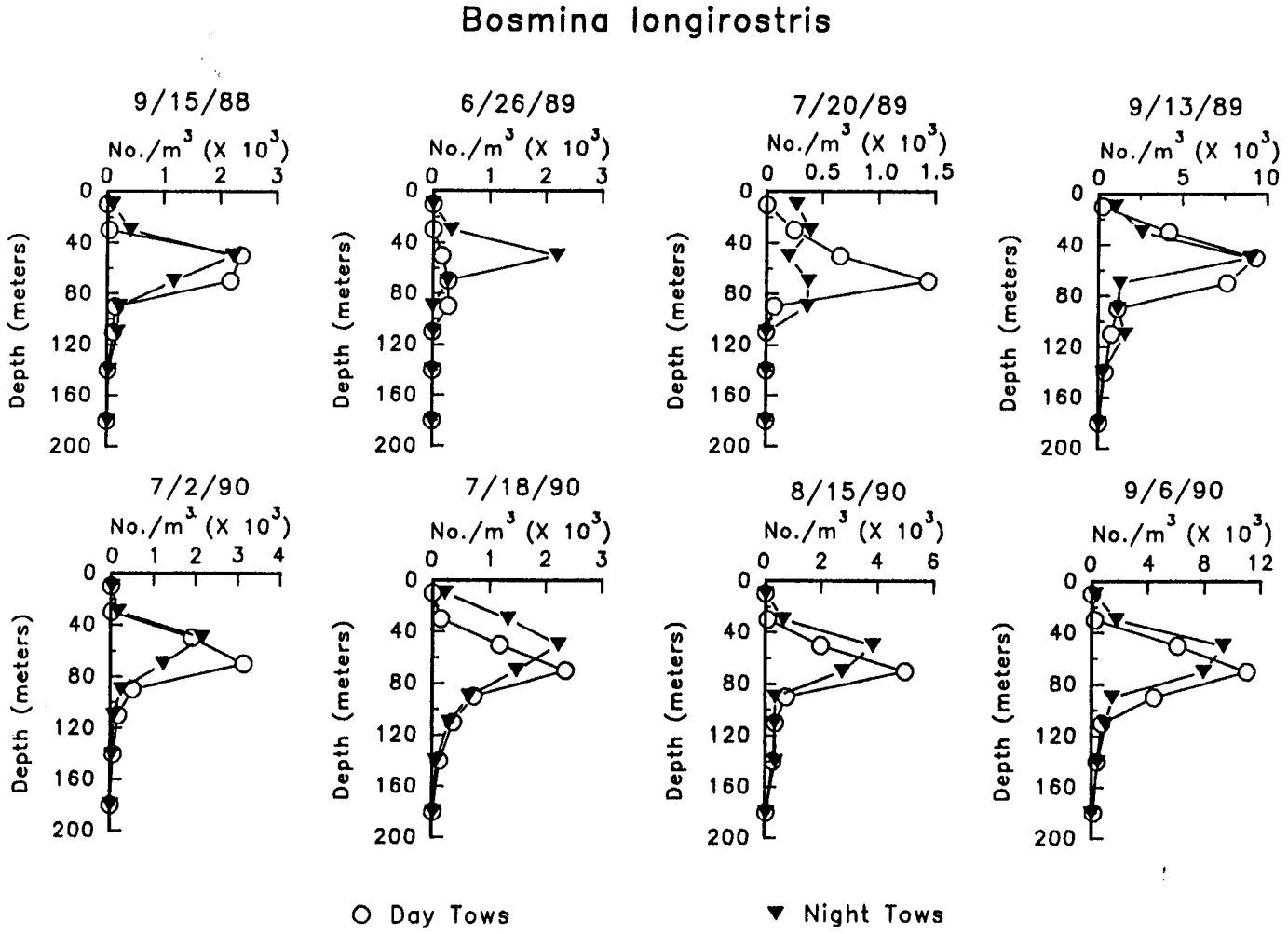


Figure 42. Vertical distribution of Bosmina longirostris at Station 13 during the day and night on selected dates between September 1988 and September 1990.

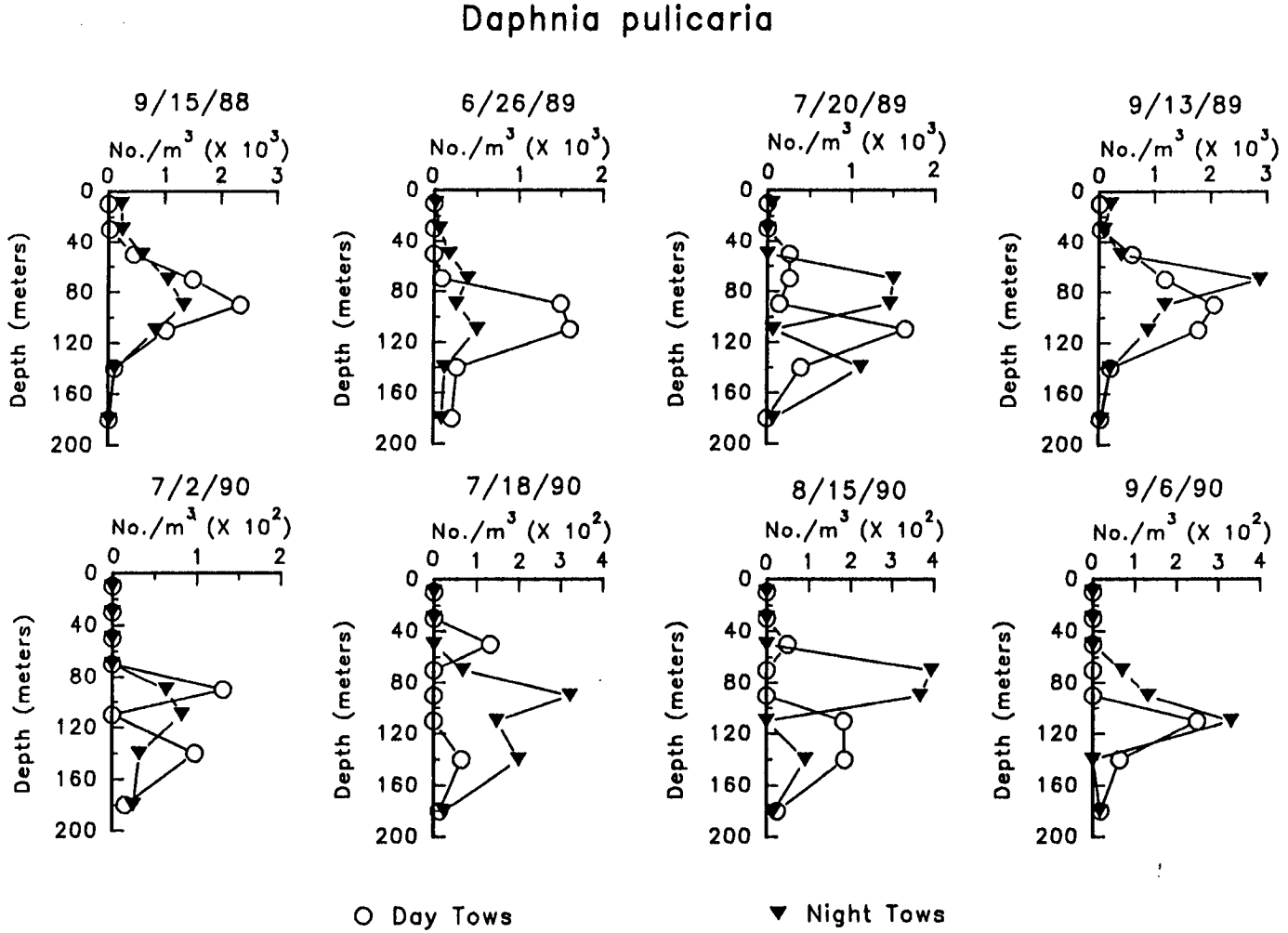


Figure 43. Vertical distribution of Daphnia pulicaria at Station 13 during the day and night on selected dates between September 1988 and September 1990.

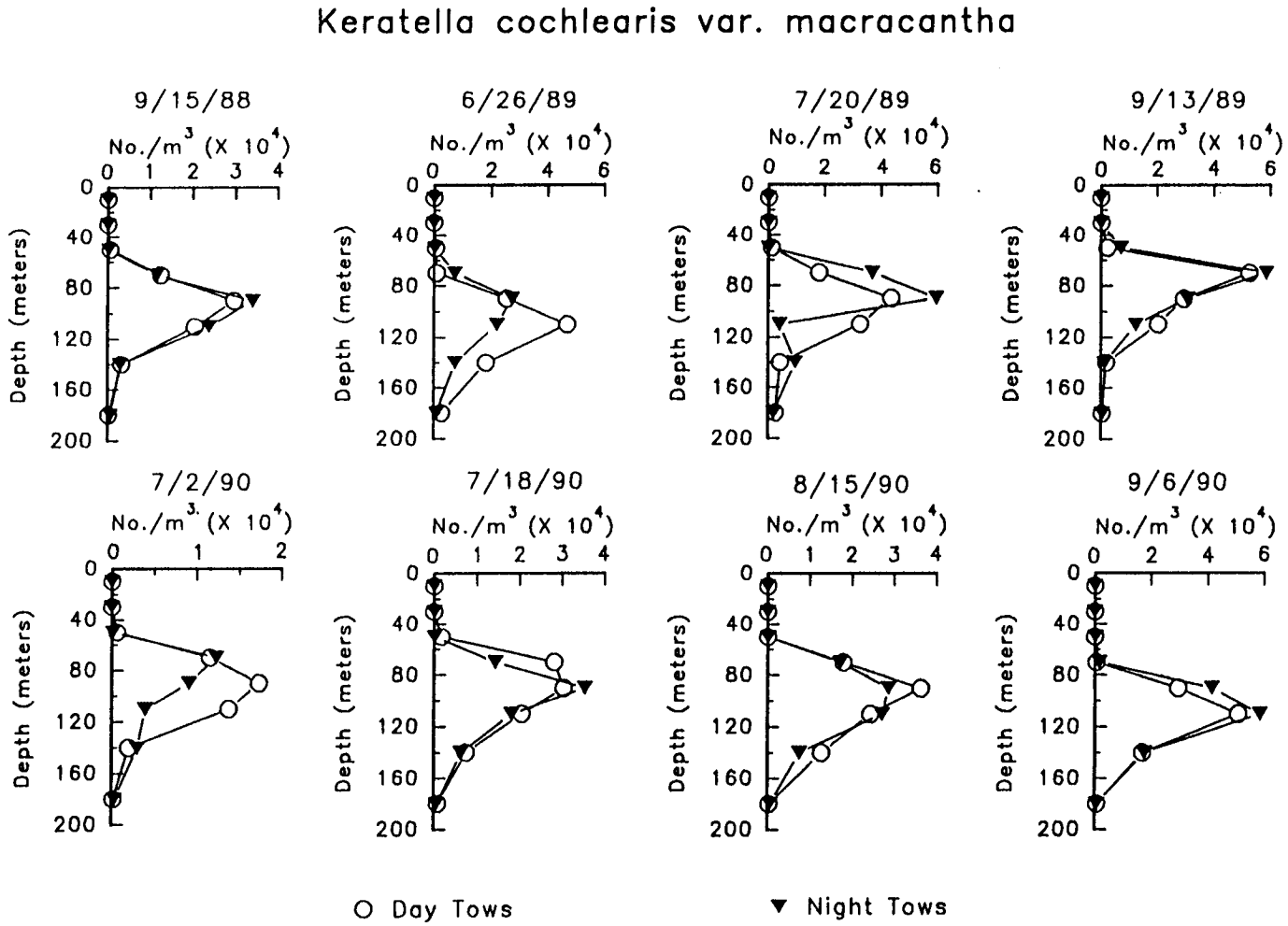


Figure 44. Vertical distribution of Keratella cochlearis at Station 13 during the day and night on selected dates between September 1988 and September 1990.

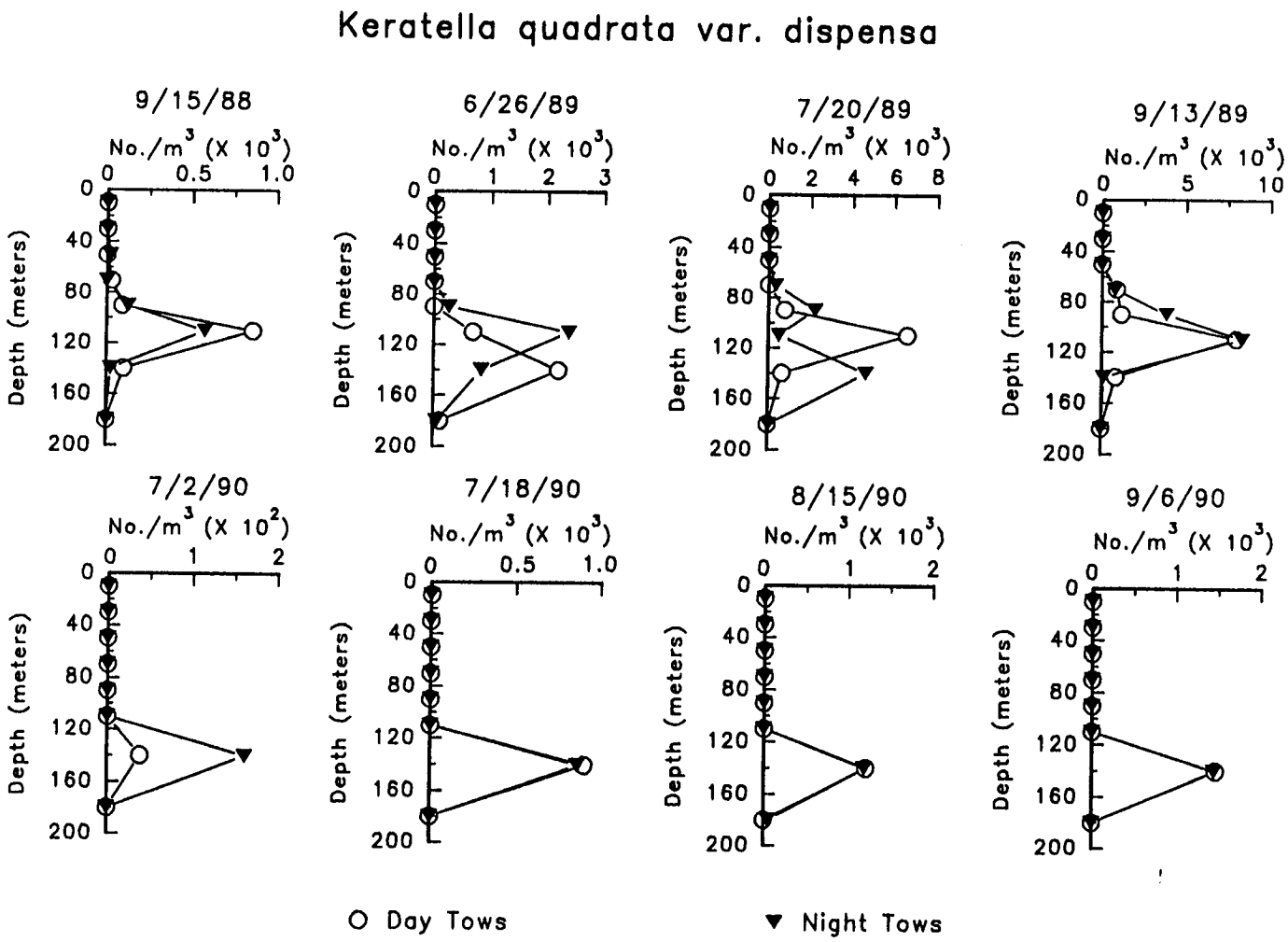


Figure 45. Vertical distribution of Keratella quadrata at Station 13 during the day and night on selected dates between September 1988 and September 1990.

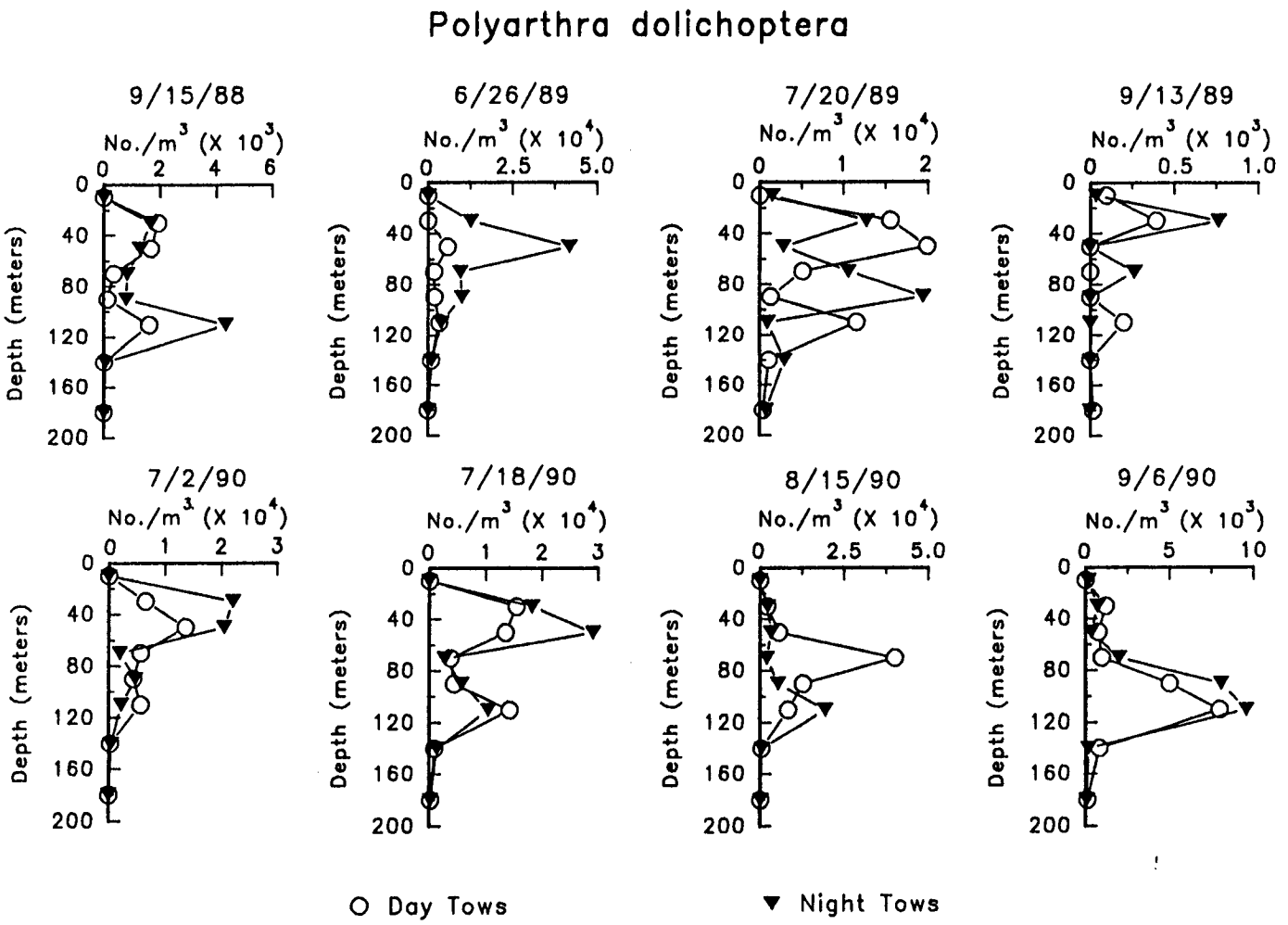


Figure 46. Vertical distribution of Polyarthra dolichoptera at Station 13 during the day and night on selected dates between September 1988 and September 1990.

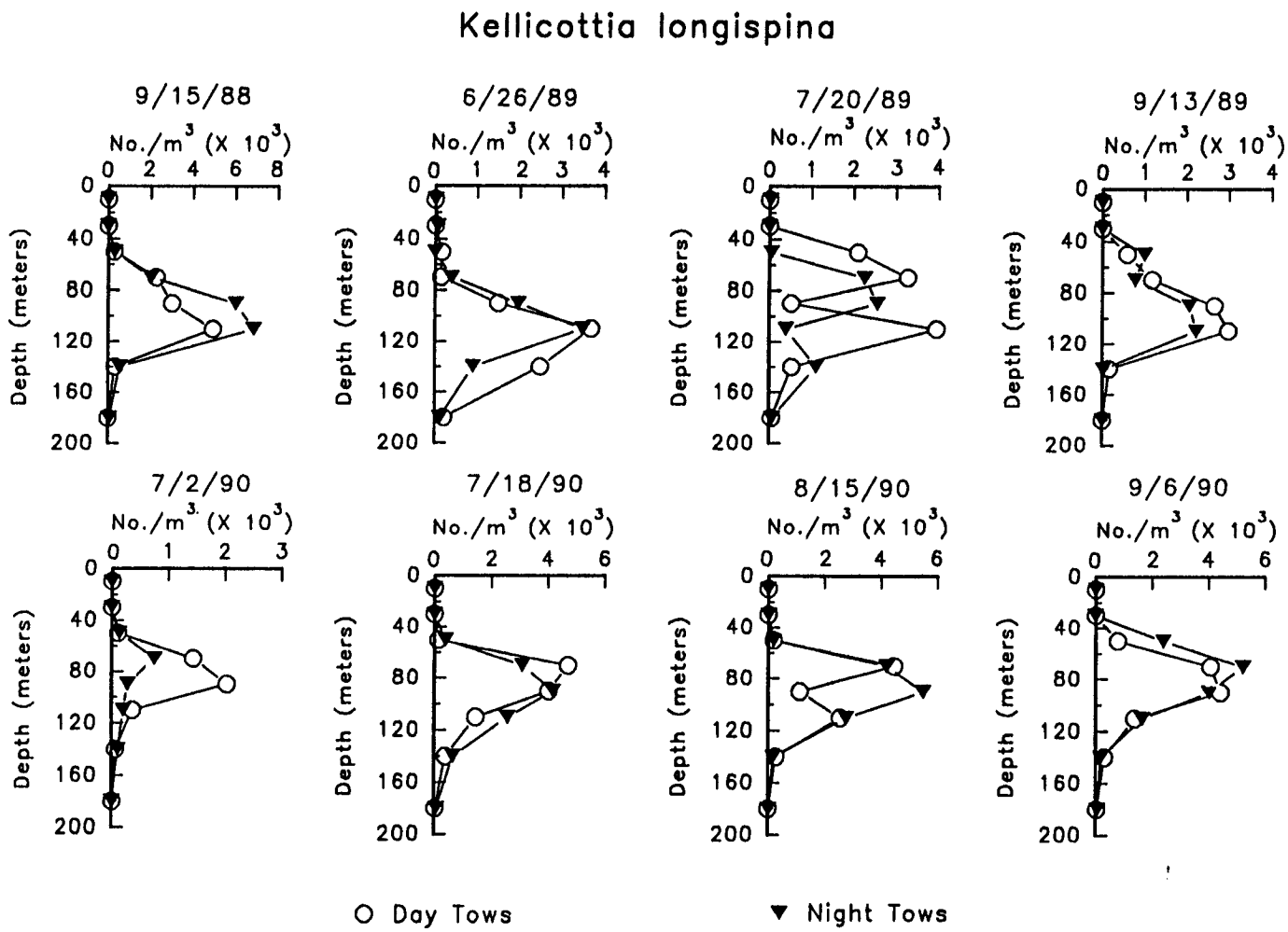


Figure 47. Vertical distribution of Kellicottia longispina at Station 13 during the day and night on selected dates between September 1988 and September 1990.

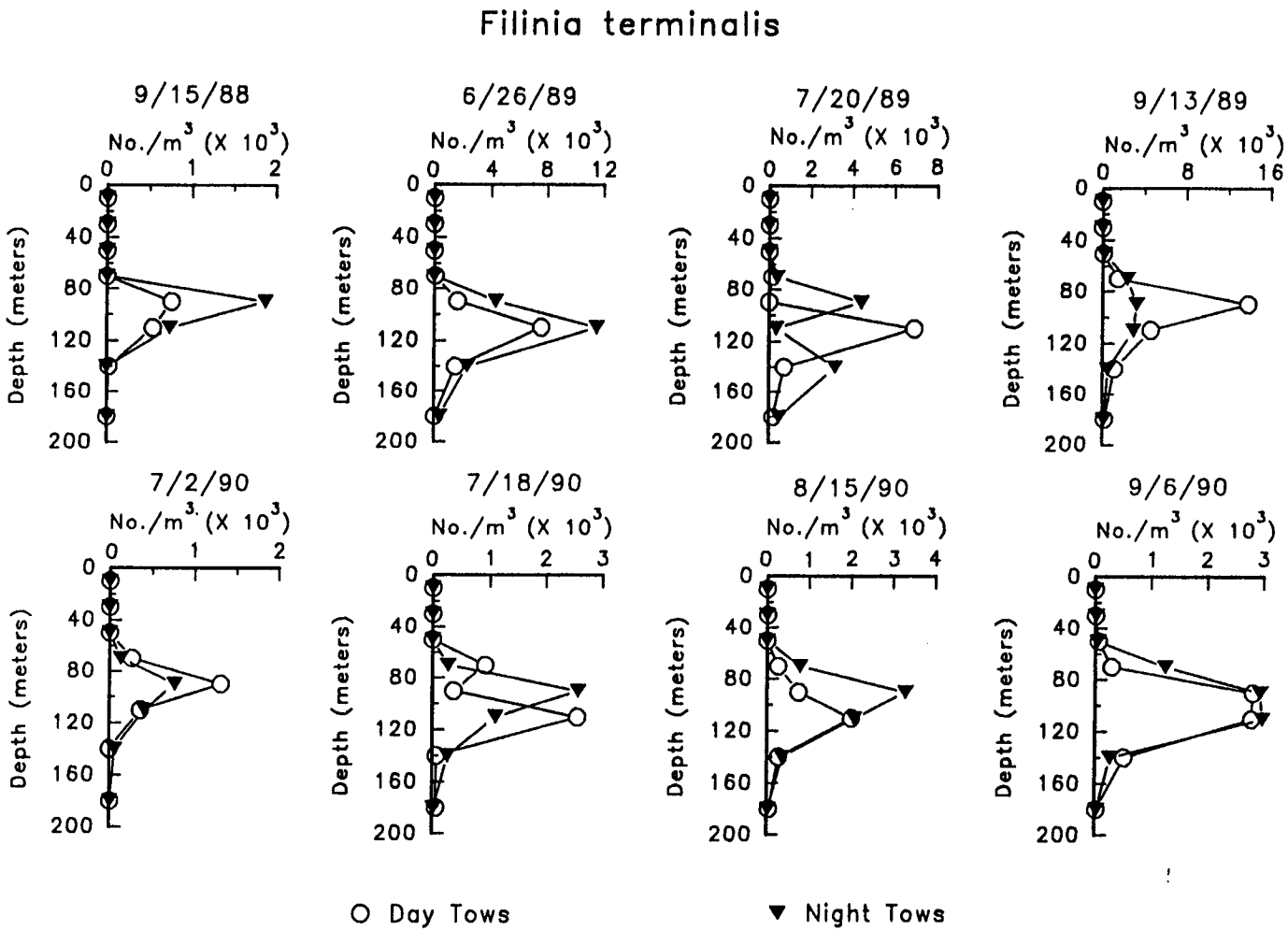


Figure 48. Vertical distribution of Filinia terminalis at Station 13 during the day and night on selected dates between September 1988 and September 1990.

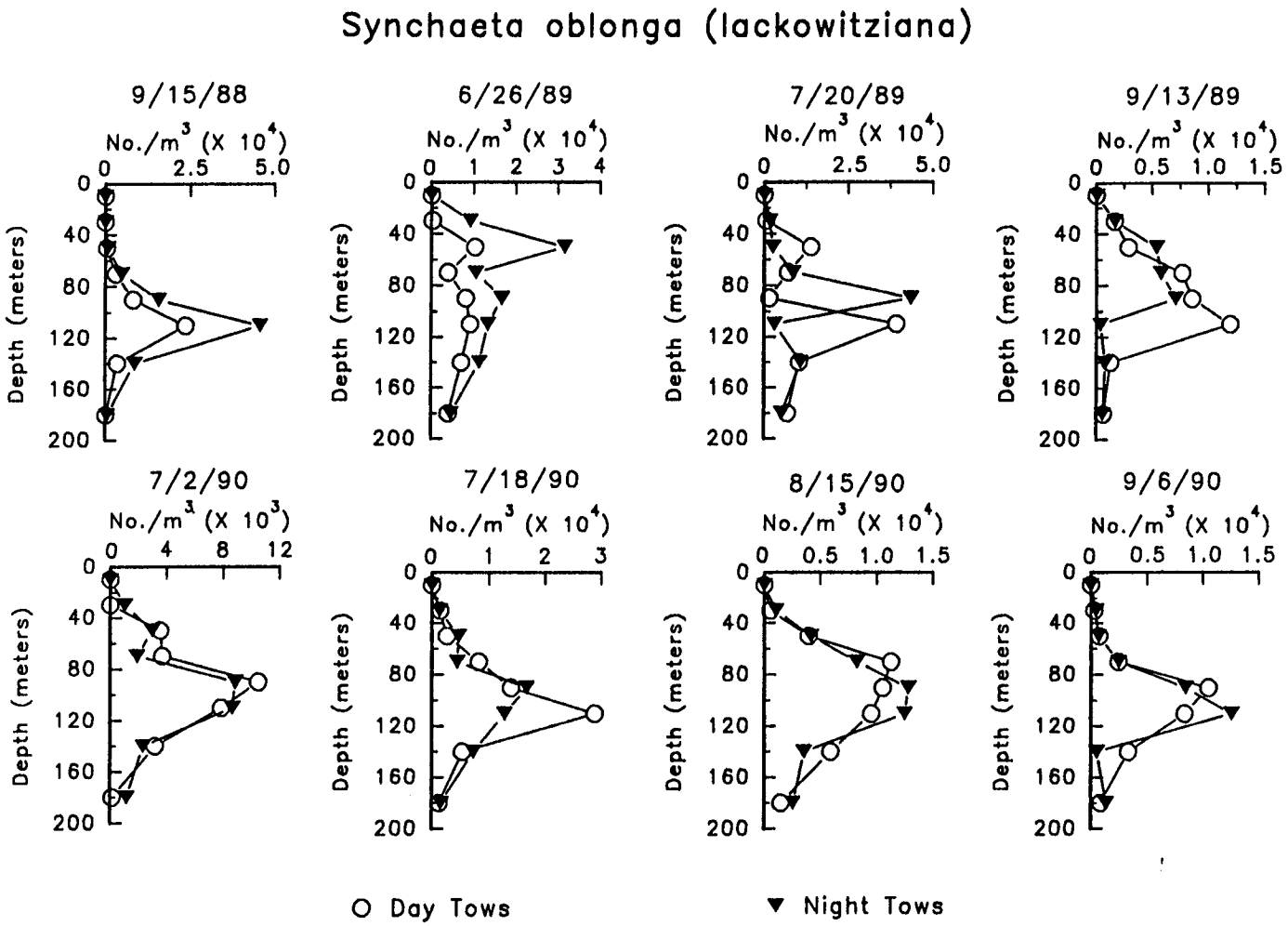


Figure 49. Vertical distribution of Synchaeta oblonga at Station 13 during the day and night on selected dates between September 1988 and September 1990.

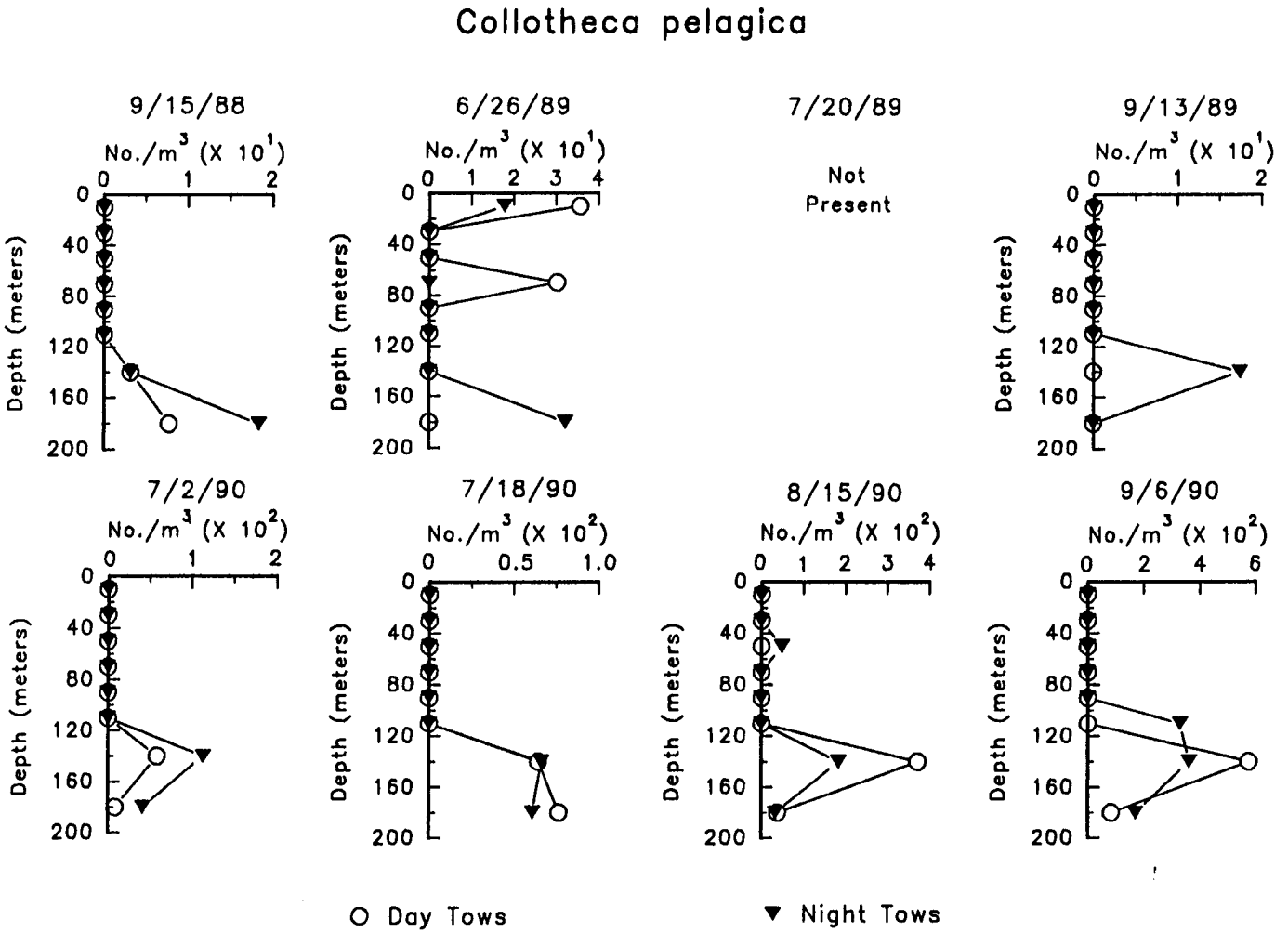


Figure 50. Vertical distribution of Collotheca pelagica at Station 13 during the day and night on selected dates between September 1988 and September 1990.

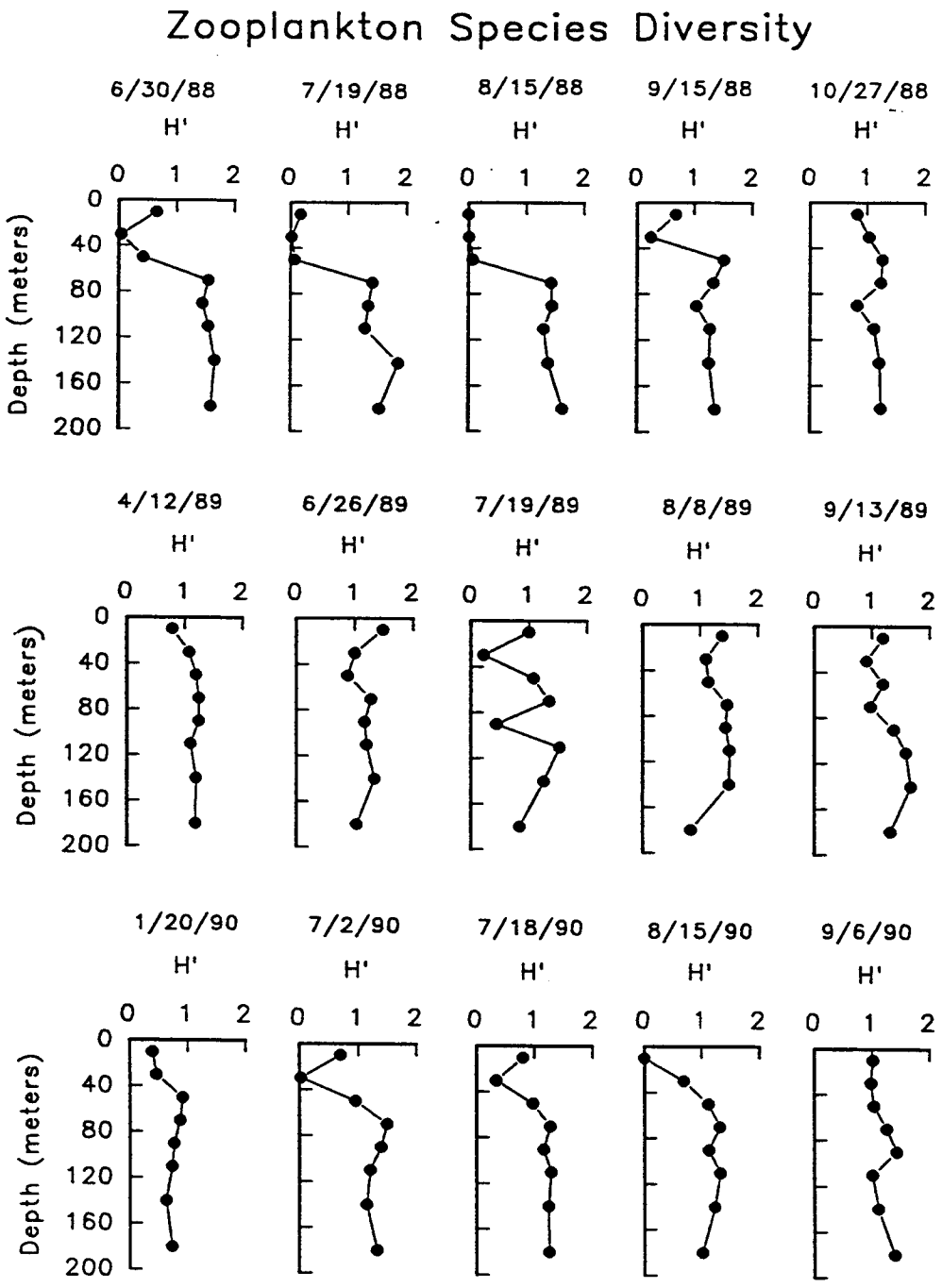


Figure 51. Vertical patterns of species diversity (H′) in zooplankton assemblages at Station 13 between June 1988 and September 1990.

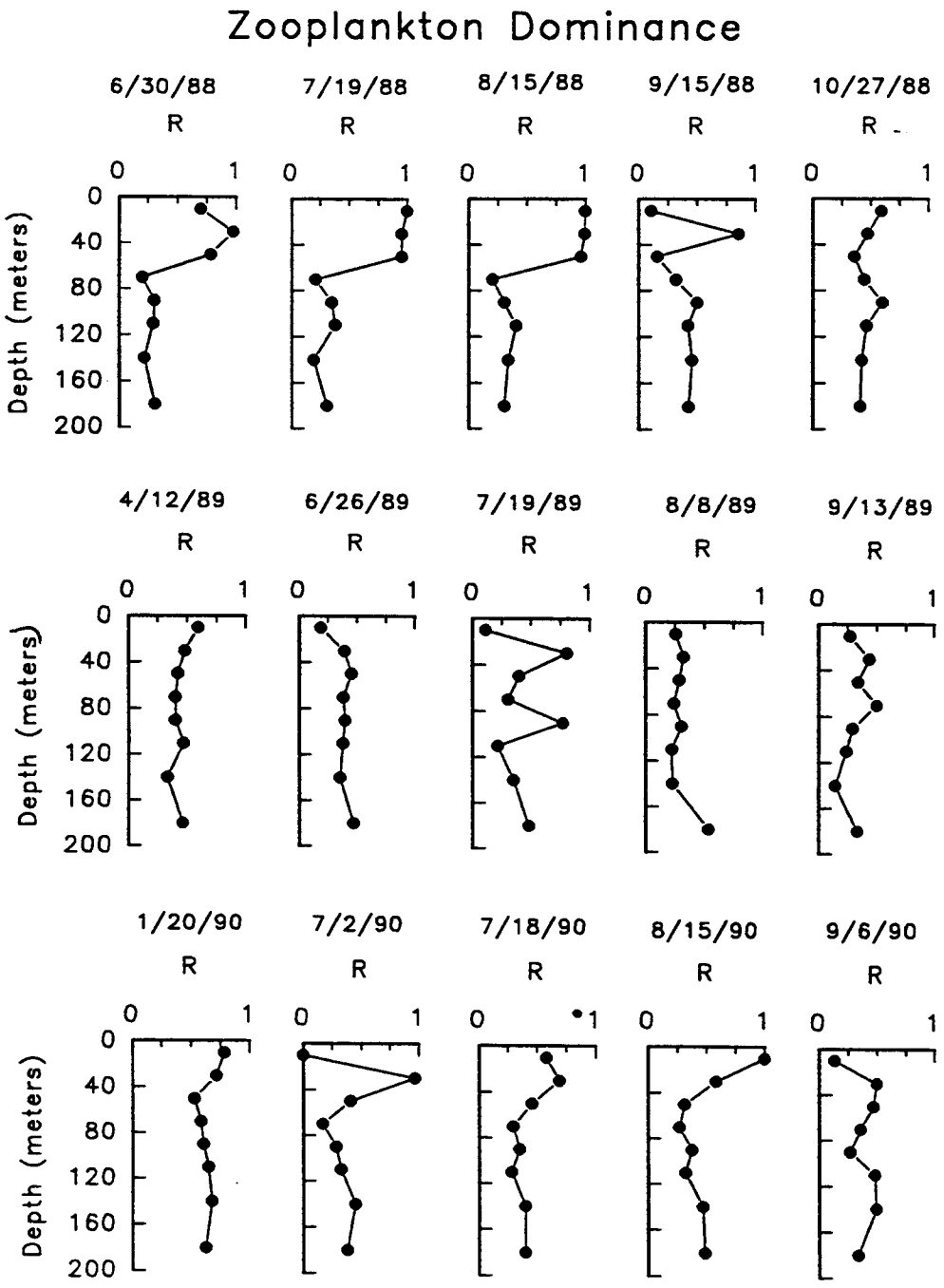


Figure 52. Vertical patterns of dominance (R) in zooplankton assemblages at Station 13 between June 1988 and September 1990.

food resources and migratory patterns. Certainly, patterns of species diversity in 1989 provided indirect evidence for short periods of mixing in the upper water column during the season when thermal stratification usually minimizes vertical transport. In any case, zooplankton species richness in Crater Lake was relatively low, as only 13 taxa were collected in the 298 samples obtained between July 1985 and September 1990.

Assemblages of Species. The cluster analysis of the 1986 zooplankton data partitioned the samples into four groups, clusters S, F, K, and P (Fig. 53). Sampling in the summer and early fall 1986 examined relatively large segments of the water column, namely depth intervals from 20 m to 80 m, 80 m to 120 m, 120 m to 200 m, and 200 m to 500 m. Cluster S consisted of samples found between 20 m and 80 m during the summer; dominant species in this assemblage were *Keratella cochlearis*, *Polyarthra dolichoptera*, and *Bosmina longirostris* with relative abundances of 52.7%, 39.1%, and 6.2%, respectively (Fig. 54). By September this assemblage had changed to 83.5% *K. cochlearis* and 7.7% *Filinia terminalis* and was different enough to be separated into its own cluster (cluster F). Cluster K included samples taken between depths of 80 m and 200 m in June and July, and between 80 m and 120 m in August and September. Dominant taxa in cluster K were *K. cochlearis* (73.4%) and *Philodina acuticornis* (12.7%). The deep-water zooplankton assemblage, located between depths of 200 m and 500 m in June and July, and between 120 m and 500 m in August and September (cluster P), consisted of 69.3% *P. acuticornis* and 19.4% *K. cochlearis*. Mean species richness, species diversity, and dominance were similar for the four clusters (Table 7). However, the density of organisms in the deep-water samples (cluster P) was only 3,849 m^{-3}, in comparison to means of 58,177, 83,300, and 96,064 organisms m^{-3} for clusters S, F, and K, respectively. Moreover, a matrix of similarity values comparing the centroids of the four clusters indicated that clusters S, F, and K were more similar to each other than any of these were to cluster P (Table 8).

In 1987 the water column was sampled from the water surface to a depth of 200 m, and at a finer spatial resolution than in 1986. The cluster analysis of the 1987 data divided

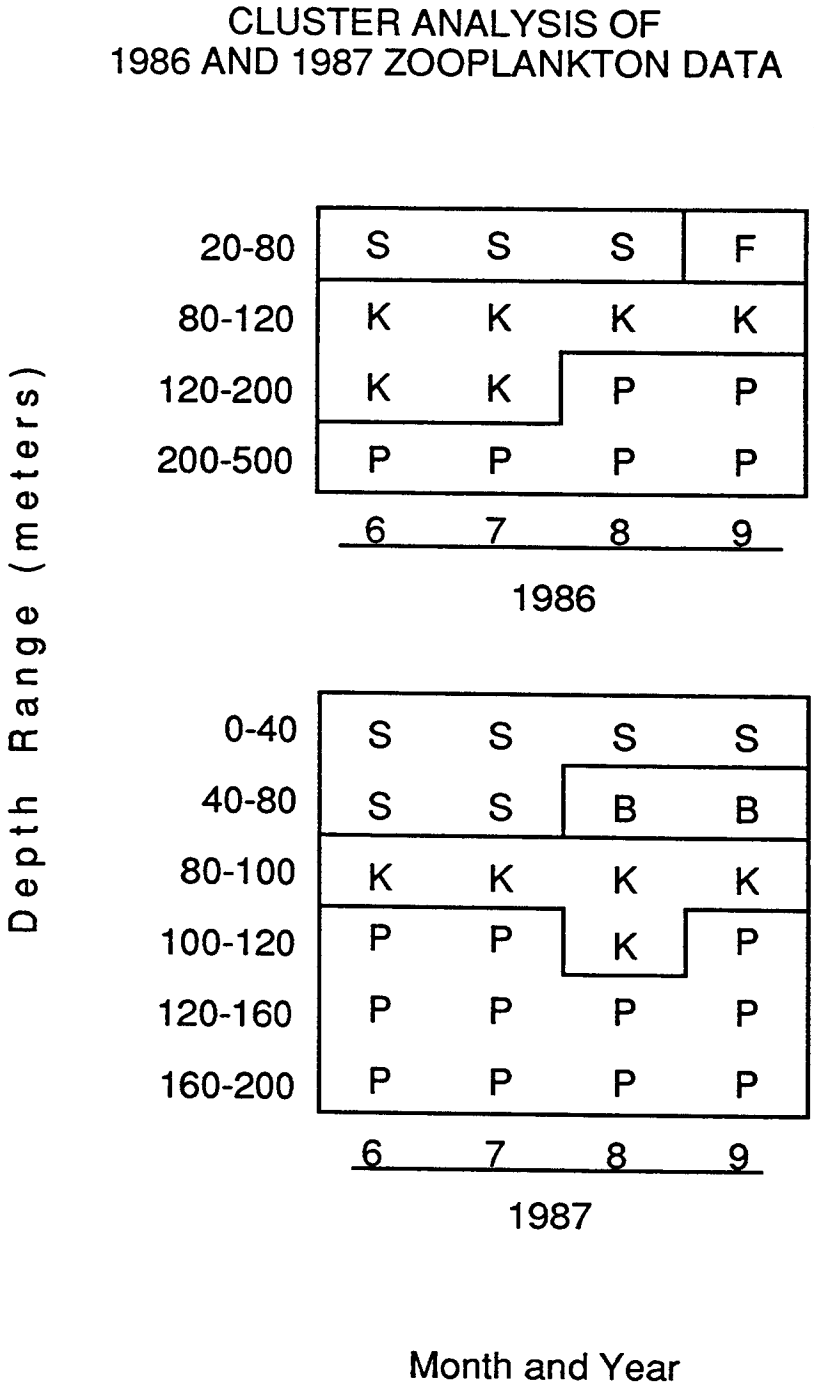


Figure 53. Four-cluster structure of 1986 and 1987 zooplankton data. Data represent samples obtained at Station 13 from various depth segments of the water column.

Table 7. Mean species richness, species diversity (H'), dominance (R), and density in samples grouped into four clusters by a CLUSB analysis of the 1986 zooplankton data.

Cluster	Cluster Size	Mean Species Richness	Mean Species Diversity (H')	Mean Dominance (R)	Mean Density (no./m³)
S	3	7.7	0.953	0.532	58,177
F	1	8.0	0.673	0.677	83.300
K	6	8.2	0.856	0.595	96,064
P	6	7.3	0.919	0.553	3,849

Table 8. A matrix of similarity values (SIMI) comparing the centroids of four clusters derived from the CLUSB analysis of the 1986 zooplankton data. Mean similarity between each centroid and the centroids of the other five clusters are listed at the bottom of the table.

Cluster	S	F	K	P
S	--			
F	0.829	--		
K	0.795	0.983	--	
P	0.228	0.275	0.432	--
Mean Similarity	0.617	0.696	0.737	0.312

the samples into four groups (Figs. 53 and 55), two in the upper 80 m of the water column (clusters S and B), one between depths of 80 m and 120 m (cluster K), and another between depths of 100 m and 200 m (cluster P). The assemblage represented by cluster S was dominated by *Polyarthra dolichoptera* (65.3%), *Bosmina longirostris* (16.8%), and *Synchaeta oblonga* (15.0%). Samples in cluster B had five dominant taxa: *B. longirostris* (38.7%), *Keratella cochlearis* (16.2%), *Kellicottia longispina* (13.8%), *P. dolichoptera* (15.4%), and *S. oblonga* (9.1%). *K. cochlearis*, *S. oblonga*, and *Philodina acuticornis* were dominant between depths of 80 m and 100 m (cluster K), with relative abundances of 57.1%, 15.0%, and 11.5%, respectively. Below a depth of 110 m (cluster P), dominance shifted to *P. acuticornis* (74.3%). Of the four assemblages identified by the cluster analysis, mean density of zooplankton (Table 9) was higher in samples that represented depths below 80 m (clusters K and P) than in samples from nearer the surface (clusters S and B). Mean species diversity was high and dominance low in samples represented by cluster B, possibly indicating physical conditions that were favorable for a more equitable distribution of taxa. A comparison of cluster centroids for the 1987 data (Table 10) also indicated low similarity between assemblages living below a depth of 100 m and those found in the upper 80 m of the water column.

The 1988 - 1990 zooplankton data provided the opportunity to do a more complete analysis of community structure, as the data set included samples obtained in January (1990), April (1989), and October (1988), as well as the series of day-night tows. Consequently, the cluster structure generated for this period was more complex, and perhaps more indicative of seasonal and temporal variations in the water column than structures found for 1986 and 1987.

A six-cluster structure was considered the most interpretable configuration for the 1988 - 1990 zooplankton data (Fig. 56). Three of the clusters were relatively large (clusters P, K, and F), while the other three (clusters S, D, and C) consisted of five or fewer samples that partitioned out on the basis of a unique combination of dominant taxa. In general,

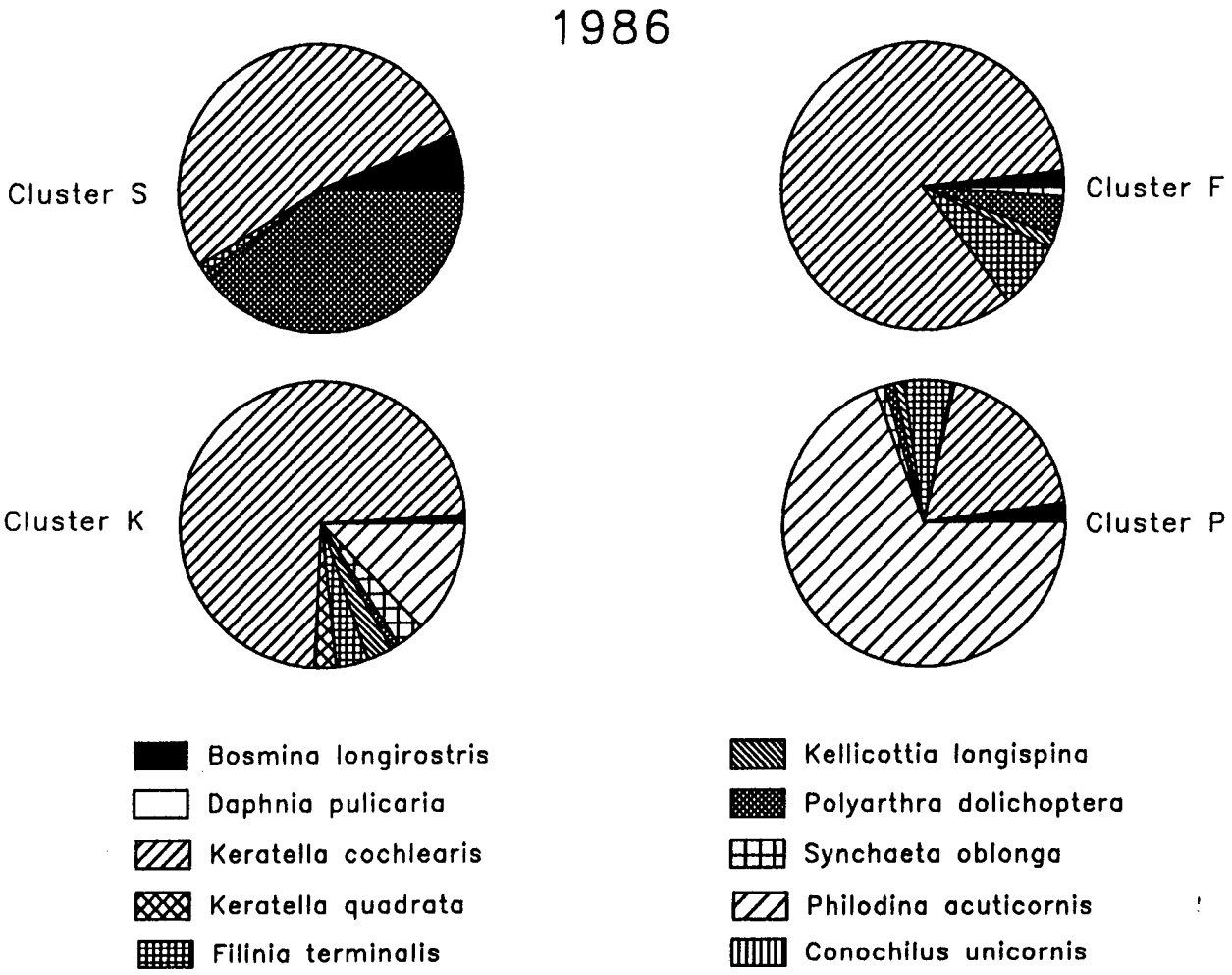


Figure 54. Mean relative abundance of zooplankton taxa in samples grouped into clusters S, F, K and P by the CLUSB analysis of the 1986 data set.

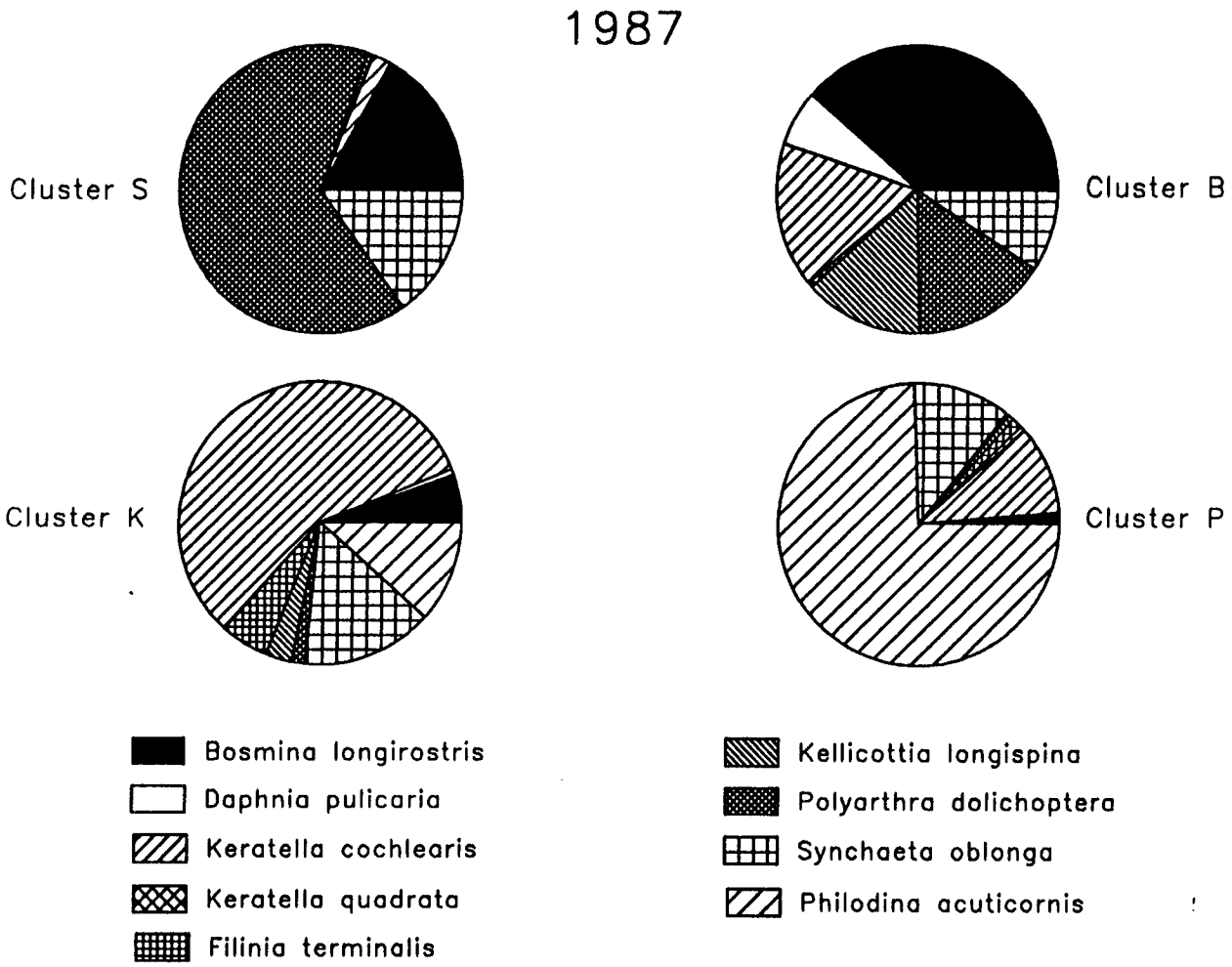


Figure 55. Mean relative abundance of zooplankton taxa in samples grouped into clusters S, F, K and P by the CLUSB analysis of the 1987 data set.

Table 9. Mean species richness, species diversity (H'), dominance (R), and density in samples grouped into four clusters by a CLUSB analysis of the 1987 zooplankton data.

Cluster	Cluster Size	Mean Species Richness	Mean Species Diversity (H')	Mean Dominance (R)	Mean Density (no./m³)
S	6	4.3	0.708	0.543	13,161
B	2	6.5	1.496	0.200	8,101
K	5	8.0	1.150	0.447	51,258
P	11	7.9	0.752	0.497	30,334

Table 10. A matrix of similiarity values (SIMI) comparing the centroids of four clusters derived from the CLUSB analysis of the 1987 zooplankton data. Mean similarity between each centroid and the centroids of the other three clusters are listed at the bottom of the table.

Cluster	S	B	K	P
S	--			
B	0.551	--		
K	0.127	0.464	--	
P	0.044	0.092	0.353	--
Mean Similarity	0.241	0.369	0.315	0.163

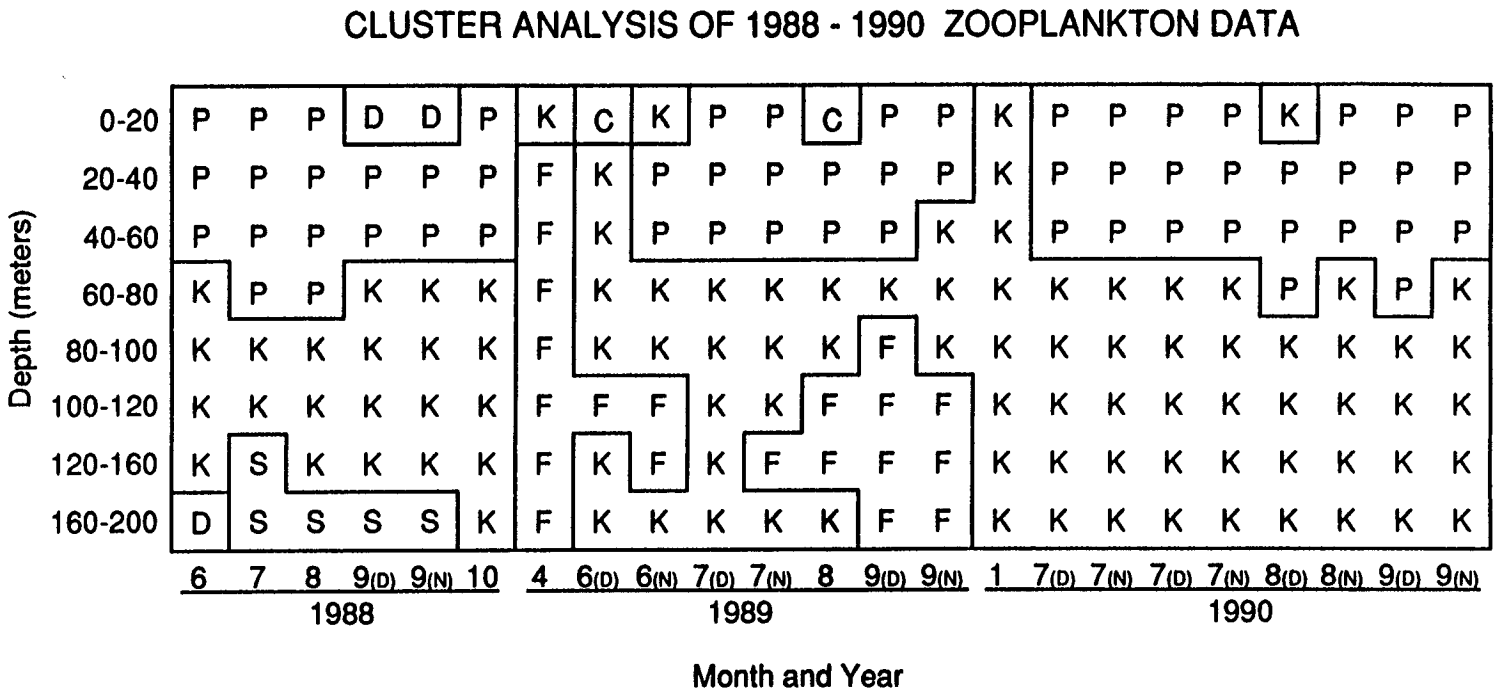


Figure 56. Six-cluster structure of the 1988-1990 zooplankton data. Data represent samples obtained at Station 13 from various segments of the water column.

cluster P consisted of samples from the upper 60 m of the water column during the summer and fall. These samples were dominated by *Polyarthra dolichoptera* (51.9%), *Bosmina longirostris* (26.0%), and *Synchaeta oblonga* (13.2%) and had relatively low mean species diversity and relatively high mean dominance (Fig. 57; Table 11). In addition, the mean density of animals in the samples of cluster P was 12,219 organisms m^{-3}, which was less than 45% of the mean densities in samples of clusters K and F, the other two large assemblages. Samples in clusters K and F had the highest mean densities, 29,590 and 32,339 organisms m^{-3}, respectively. Cluster K represented samples that were collected mostly below a depth of 60 m in the summer and fall, and throughout the water column in June 1989 and January 1990. These samples were dominated by *Keratella cochlearis* (47.4%) and *S. oblonga* (30.5%). Samples in cluster F were very similar in species composition to those in cluster K, but in addition to *K. cochlearis* and *S. oblonga*, *Filinia terminalis* also was dominant with 13.5% of the total density. Samples in cluster F were collected in 1989 below a depth of 80 m in summer and fall, and throughout the water column in April. Cluster D was made up of three samples that had high densities of *Daphnia pulicaria*; two of these were collected near the water surface in September 1988 and one at a depth of 160 to 200 m in June 1988. Mean relative abundance of *D. pulicaria* for samples in the other clusters was less than 7%. The two samples in cluster C were taken near the water surface in June and August 1989. These samples had a peculiar mixture of dominant taxa: *K. cochlearis* (13.1%), *B. longirostris* (12.5%), *P. dolichoptera* (12.5%), and *S. oblonga* (33.6%). *P. dolichoptera* and *B. longirostris* were usually distributed higher in the water column than *K. cochlearis*, whereas *S. oblonga* was more ubiquitous in distribution than the other taxa. Samples in cluster S were dominated by *K. cochlearis* (21.3%), *S. oblonga* (23.1%), and *Philodina acuticornis* (37.1%), and were collected from deep water (120 m and 200 m) in July, August, and September 1988. The dominance of *P. acuticornis* in cluster S was consistent with its deep-water distribution in 1986 and 1987. Highest similarities among cluster centroids (Table 12)

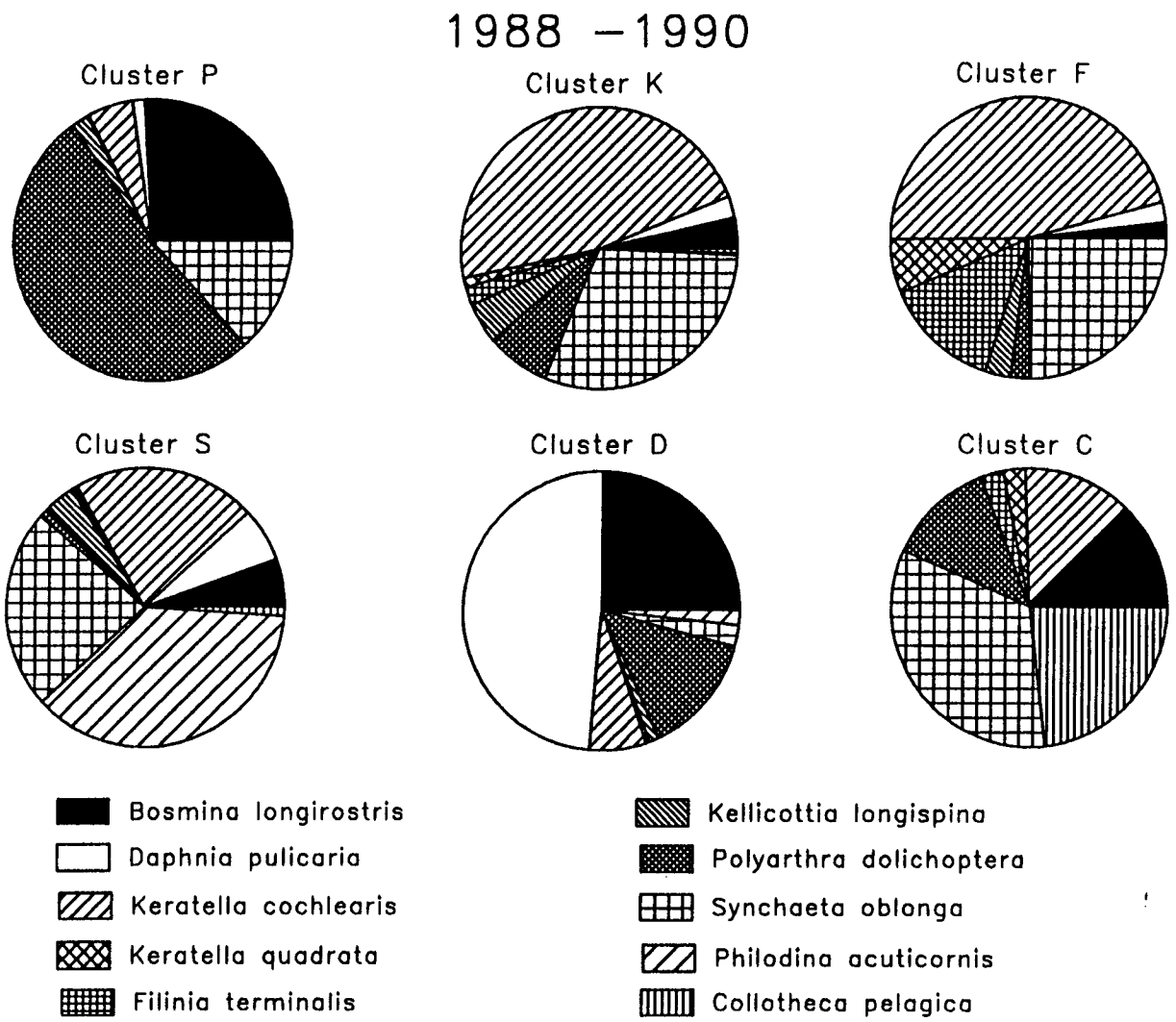


Figure 57. Mean relative abundance of zooplankton taxa in samples grouped into clusters P, K, F, S, D and C by the CLUSB analysis of the 1988-1990 data set.

Table 11. Mean species richness, species diversity (H'), dominance (R), and density in samples grouped into six clusters by a CLUSB analysis of the 1988-1990 zooplankton data.

Cluster	Cluster Size	Mean Species Richness	Mean Species Diversity (H')	Mean Dominance (R)	Mean Density (no./m³)
P	58	4.9	0.800	0.521	12,219
K	96	7.3	1.166	0.404	29,590
F	20	7.5	1.370	0.315	32,339
S	5	9.8	1.552	0.328	1,690
D	3	4.7	1.035	0.242	142
C	2	5.0	1.437	0.095	125

Table 12. A matrix of similarity values (SIMI) comparing the centroids of six clusters derived from the CLUSB analysis of the 1988-1990 zooplankton data. Mean similarity between each centroid and the centroids of the other five clusters are listed at the bottom of the table.

Cluster	P	K	F	S	D	C
P	--					
K	0.335	--				
F	0.230	0.965	--			
S	0.217	0.631	0.592	--		
D	0.262	0.196	0.179	0.262	--	
C	0.536	0.678	0.608	0.508	0.196	--
Mean Similarity	0.316	0.561	0.515	0.442	0.219	0.505

were between K and F (SIMI = 0.965), K and C (SIMI = 0.678), and K and S (SIMI = 0.631).

In summary, zooplankton communities in the upper 200 m of the water column of Crater Lake usually partitioned into two primary assemblages. One assemblage occurred in the upper 60 m and was present in the summer and fall. The other assemblage was prominent below a depth 60 m but also occurred near the water surface in winter and spring. Both assemblages exhibited local modifications in patterns of dominance as best indicated by clusters K and F.

Zooplankton Cycles

Total zooplankton densities and biomasses, integrated to a depth of 200 m, for all data obtained from July 1985 through September 1990 were examined for temporal patterns (Fig. 58). To facilitate interpretation, smooth curves were fit to the data (10th order polynominal), and high and low periods of density and biomass were identified for comparisons with other physical and biological variables. The mathematical model was arbitrarily chosen to illustrate seasonal and annual fluctuations and had no biological significance or predictive value in itself. The most obvious zooplankton maximum was in 1985 and 1986. In some years zooplankton biomass increased during the year (1985, 1987, 1989, and 1990); in other years it decreased (1986 and 1988). Furthermore, the pattern of zooplankton density did not always correspond to the pattern for biomass, indicating annual variations in species composition.

Integrated densities plotted for the two dominant crustaceans indicated that *Bosmina longirostris* followed a pattern similar to that found for total zooplankton biomass (Figs. 59). However, the density of *Daphnia pulicaria* did not begin to increase until summer of 1987, and it was only abundant in the water column in 1988 and 1989.

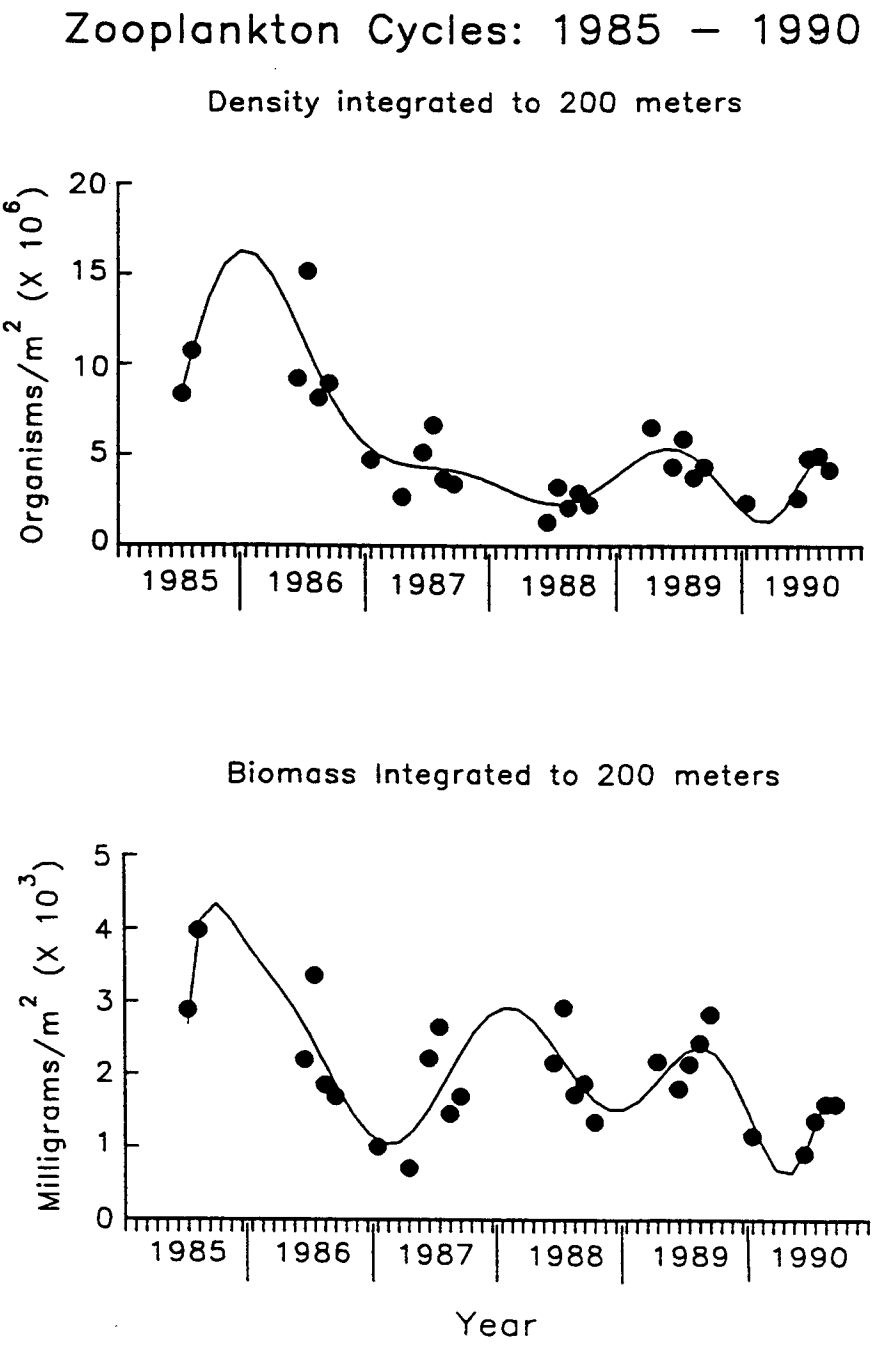


Figure 58. Temporal variation in total zooplankton density and biomass between July 1985 and September 1990. Values represent the integrated density and biomass between the water surface and a depth of 200 m at Station 13.

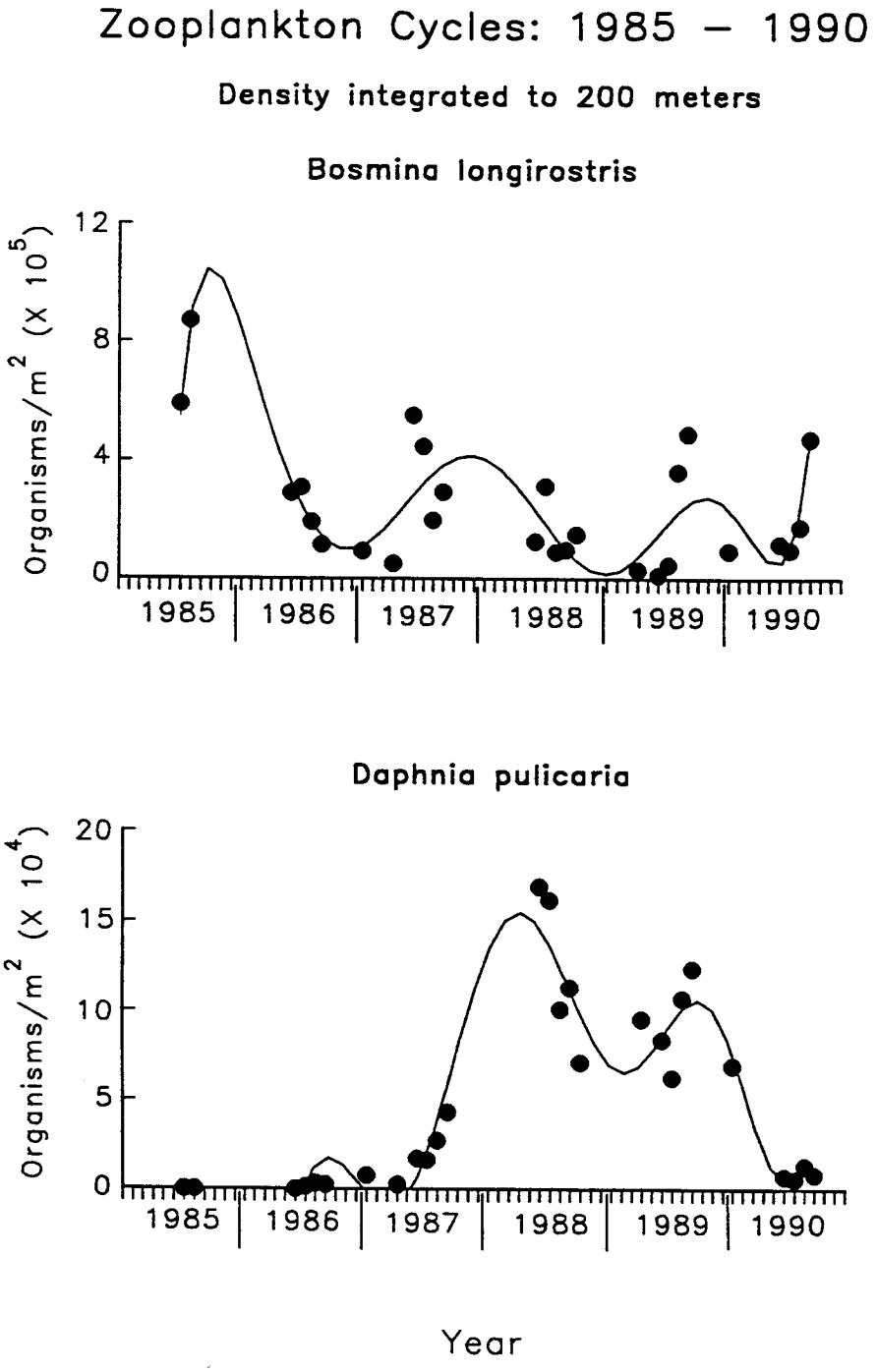


Figure 59. Temporal variation in the density of Bosmina longirostris and Daphnia pulicaria between July 1985 and September 1990. Values represent the integrated density between the water surface and a depth of 200 m at Station 13.

Patterns of integrated density for the rotifers were variable (Figs. 60 - 62). *Keratella quadrata* and *Kellicottia longispina* had density maxima in 1985 but were relatively rare between 1987 and 1990 (Fig. 60). *Keratella cochlearis* and *Polyarthra dolichoptera* had their maximum density in 1986; however, the latter taxon exhibited a more uniform density than the former throughout the study (Fig. 61). Density maxima for *Synchaeta oblonga* occurred in 1987, 1989, and 1990; *Filinia terminalis* reached maxima in 1985, 1986, and 1989 (Fig. 62).

Discussion

Early studies of the zooplankton of Crater Lake were limited in scope but suggested that the assemblage probably consisted of one species of *Daphnia*, one species of *Bosmina*, and several species of rotifers (Karnaugh 1988). Specimens of *Daphnia* collected by Evermann (1897), Kemmerer et al. (1924), Brode (1938), Hasler (1938), Hasler and Farner (1942) and Hoffman (1969) were identified as *D. pulex*. However, based on a taxonomic revision of the cladocerans (Brooks, 1957) and a recent examination of material by Dr. Korinek, it is likely that all specimens of *Daphnia* collected before and after 1970 were actually *D. pulicaria* (Karnaugh 1988). In addition, specimens of *Bosmina* collected in 1913 by Kemmerer et al. (1924), and identified as *B. longispina*, were probably *B. longirostris*, the same taxon collected during this study (Karnaugh 1988) and by Hoffman (1969).

Little information was available about rotifer populations in Crater Lake before 1982. Kemmerer et al. (1924) collected *Kellicottia longispina, Kerattella quadrata* and an unknown species of *Asplanchna* in 1913. These taxa and seven other species of rotifers (*Keratella cochlearis, Polyarthra dolichoptera, Philodina acuticornis, Filinia terminalis, Synchaeta oblonga, Conochilus unicornis* and *Collotheca pelagica*) were counted in samples obtained from 1985 through 1990, although *Asplanchna* was not found until August and September, 1990. It was impossible to determine whether or not the seven new taxa found in this study also were present in the lake in 1913 because the early set of samples were lost

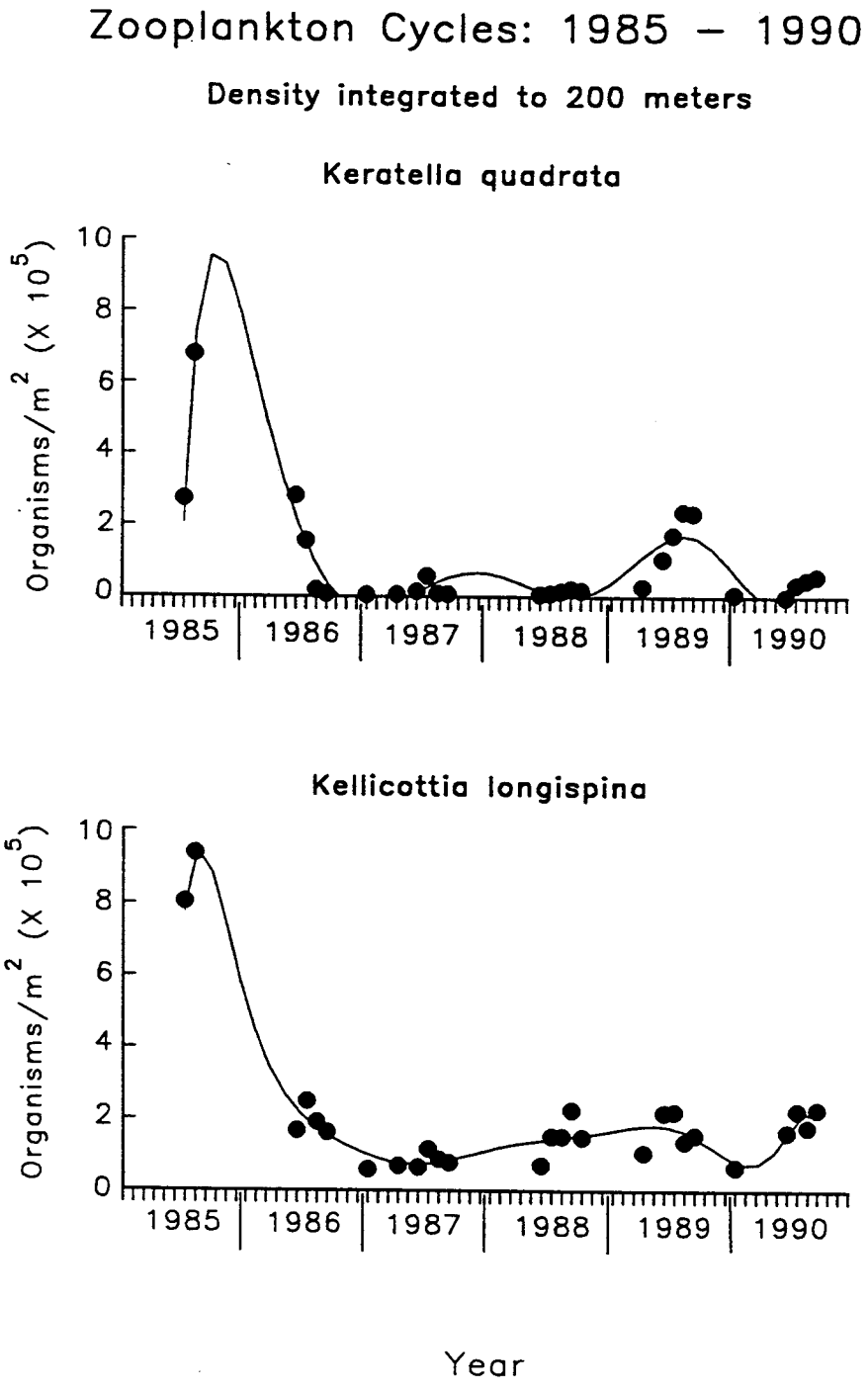


Figure 60. Temporal variation in the density of Keratella quadrata and Kellicottia longispina between July 1985 and September 1990. Values represent the integrated density between the water surface and a depth of 200 m at Station 13.

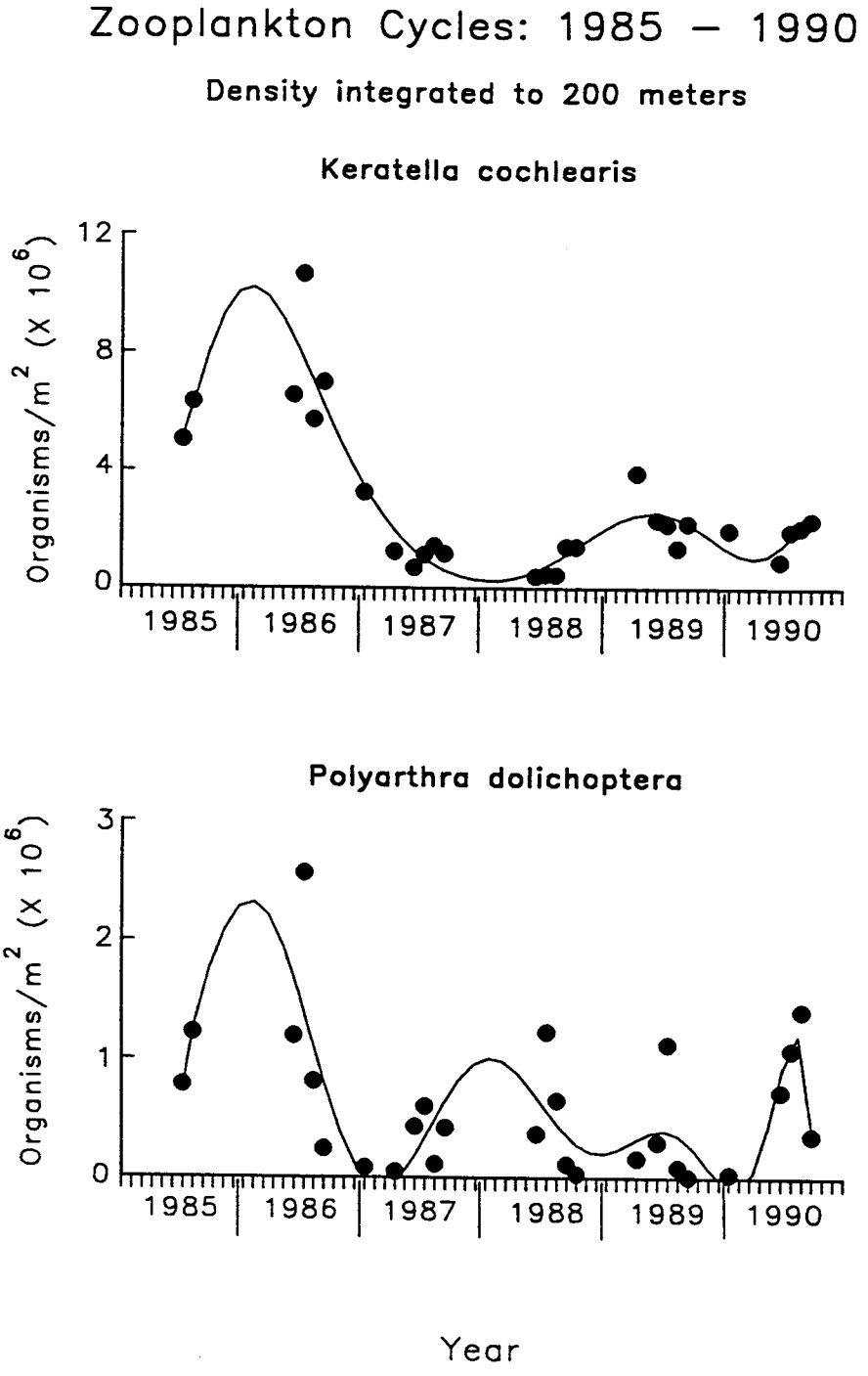


Figure 61. Temporal variation in the density of Keratella cochlearis and Polyarthra dolichoptera between July 1985 and September 1990. Values represent the integrated density between the water surface and a depth of 200 m at Station 13.

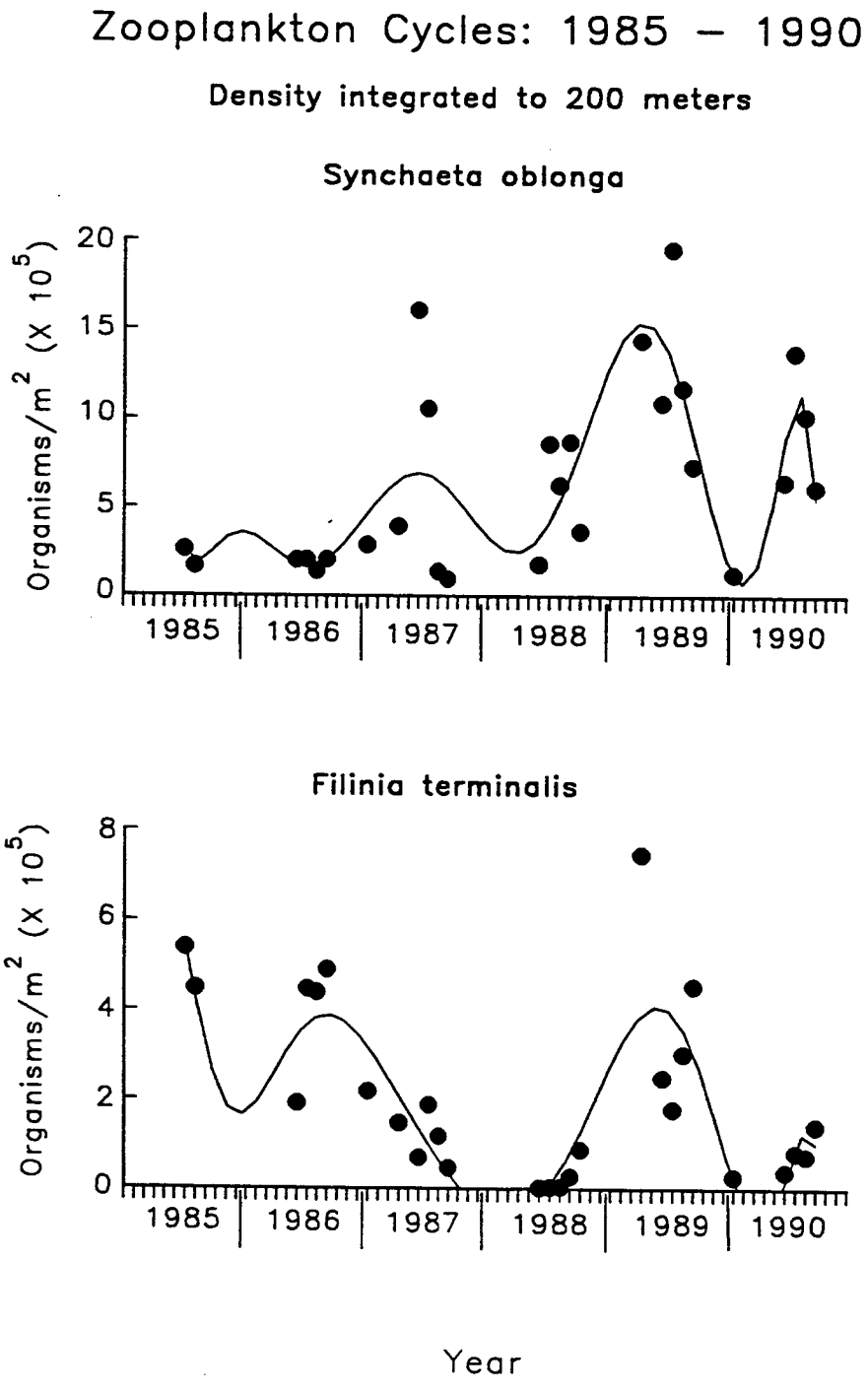


Figure 62. Temporal variation in the density of Synchaeta oblonga and Filinia terminalis between July 1985 and September 1990. Values represent the integrated density between the water surface and a depth of 200 m at Station 13.

The structure and function of zooplankton assemblages have been associated with many abiotic and biotic features of lake ecosystems, namely climatic conditions (Patalas 1990), lake morphology (Fryer 1985, Dodson 1992), water quality (Anderson 1974, Sprule 1975), elevation (Reed and Olive 1958, Anderson 1974), latitude (Patalas 1990), competitive interactions (Dumont 1977, Hebert 1982, Gilbert 1985), and fish predation (Brooks and Dodson 1965, Dini and Carpenter 1992). In oligotrophic lakes, zooplankton assemblages typically include copepods, cladocerans and rotifers, and the number of rotifer taxa usually is greater than the number of taxa in the other two taxonomic groups combined (Table 13). In Crater Lake the number of rotifer taxa (11) was much greater than the number of cladoceran taxa (2), whereas copepods were present in only one sample collected between 1985 and 1990. Mechanisms that account for the rarity of pelagic copepods in Crater Lake remain unclear, but absense may be related to the outcome of competitive interactions with cladocerans (DeMott 1989).

Seasonal changes in the taxonomic composition of zooplankton have been associated with competitive interactions among species, changing water quality, and temperature (Pejler 1962, Miracle 1977, Hebert 1982, Gliwicz and Pijanowska 1989, and DeMott 1989). Cold stenothermal taxa are usually abundant in winter and early spring, warm stenotherms occur during the summer months, and other eurythermal taxa often are present throughout the entire year. However, many rotifer taxa are known to exhibit a tolerance for a relatively wide range of temperature (Berzins and Pejler 1989). According to autecological information in the literature, the zooplankton assemblage in Crater Lake includes cold stenothermal, warm stenothermal, and eurythermal taxa (Table 3). Most zooplankton taxa are present in the lake throughout the year and reach maximum abundances in the metalimnion and hypolimnion during the summer. Therefore, patterns of temperature alone are of limited value for explaining the distribution and abundance of zooplankton in the lake. Seasonal replacement of congeneric taxa commonly observed in many lakes (Miracle 1977) was not observed in Crater Lake, although some replacement on an annual

Table 13. Number of copepoda, cladocera and rotifer taxa collected from the pelagic zones of selected oligotrophic lakes.

Lake (Country)	Copepoda	Cladocera	Rotifera	Reference
27 Colorado lakes (USA)*	1.30 (0-2)**	1.60 (0-5)	4.80 (0-20)	Pennak (1957)
340 lakes & ponds (Canada)*	2.35 (1-10)	2.66 (0-17)	--	Anderson (1974)
73 alpine lakes (Canada)*	1.70 (0-4)	0.88 (0-4)	--	Anderson (1971)
36 subalpine lakes (Canada)*	1.94 (1-4)	1.42 (1-8)	--	Anderson (1971)
7 arctic-boreal lakes (Canada)*	6.86 (3-11)	6.71 (5-8)	--	Reed (1964)
7 mountain lakes (Norway)*	1.31 (1-2)	2.52 (0-4)	5.72 (3-8)	Blakar et al. (1979)
Konigssee (Germany)	--	--	20	Laxhuber (1987)
Rara (West Nepal)	2	2	5	Okino et al. (1986)
Bhimtal (India)	2	1	4	Sharma et al. (1985)
Nainital (India)	2	1	5	Sharma et al. (1985)
Great Bear (Canada)	4	1	--	Patalas (1975)
Superior (Canada/USA)	12	6	--	Patalas (1975)
Odell (USA)	1	1	--	Malick (1971)
Mashu (Japan)***	1	1	8	Anonymous (1979)
Crater (USA)	0	2	10	present work

* Mean value
** ( ) = minimum and maximum number
*** Caldera lake similar to Crater Lake

time scale occurred between depths of 120 m and 200 m. In this depth segment, maximum abundances of *Conochilus*, *Philodina*, and *Collotheca* were observed in 1985, between 1986 and 1988, and in 1990, respectively.

Seasonal maxima of many zooplankton taxa in Crater Lake exhibited annual variation. For example, *Bosmina longirostris* and *Daphnia pulicaria* reached their maximum abundance in either June or July of 1988, but not until September in 1989 (Figs. 33 and 34). Moreover, seasonal succession of maximum abundances of closely related taxa observed in many lakes (Hutchinson 1967) was not evident in Crater Lake. The absence of such successional trajectories was probably related to adaptations that allowed vertical separation of similar taxa in the water column (DeMott 1989, King 1972, 1980).

The zooplankton assemblage in Crater Lake may undergo long-term changes in density and biomass. Most of the taxa found during the 10-year study had maximum abundances in 1985 or 1986 and subsequently exhibited variable densities at a lower level until the end of the study. The relatively high densities of *Daphnia pulicaria* in 1988 and 1989 may have been related to a decrease in fish predation, whereas mechanisms associated with an increase in the density of *Synchaeta oblonga* between 1988 and 1990 were unclear. Year-to-year changes in the density of *Daphnia* were not unusual, as such variations were reported in earlier studies of Crater Lake (Hasler and Farner 1942, Hoffman 1969). Cyclic changes in *Daphnia* populations also have been observed in other lakes (McCauley and Murdoch 1987). Data from the 10-year study support the hypothesis that the population dynamics of *Daphnia pulicaria* in Crater lake is coupled with changes in the age structure and density of associated zooplanktivorous fish populations, changes that are not completely understood at this time.

Between 1985 and 1990, wind mixed the water column of Crater Lake in winter and spring to a depth of about 200 m (McManis 1992). Consequently, most zooplankton taxa were uniformly distributed in the upper 200 m of the water column between January and June. Temperature increased near the lake surface in early summer, and mixing decreased

with the onset of thermal stratification, a process that was usually complete by August. With the formation of a shallow epilimnion (5 - 20 m), zooplankton taxa tended to segregate into different segments of the water column (Figs. 53 and 56). During stratification, all taxa were rare between the water surface and a depth of 20 m, i.e., in the epilimnion. Although some change in vertical distribution was observed during the summer and fall months, most zooplankton taxa exhibited maximum abundances in one of three different depth segments: 20 - 80 m, 80 - 120 m, and 120 - 200 m (Table 14). *Polyarthra dolichoptera* and *Bosmina longirostris* were usually dominant between depths of 20 m and 80 m. *Kellicottia longispina* also was present in this segment of the water column in some years, and *Asplanchna* was found in September 1990. The depth segment between 80 m and 120 m supported relatively high densities of *Synchaeta oblonga*, *Keratella cochlearis* and *Filinia longispina*, and in most years *D. pulicaria*, *Keratella quadrata* and *K. longispina*. *Philodina acuticornis*, *K. quadrata* and Conochilus unicornis reached maxima in the deepest depth segment (120 - 200 m) during some years; in other years this region was dominated either by *K. quatrata* and *Collotheca pelagica* or by *C. pelagica* and *P. acuticornis*.

Partitioning of the water column by the zooplankton resulted in a separation of taxa with similar feeding modes and mechanisms (Table 14). The upper-depth segment (20 - 80 m) was dominated by a grasping, filter-feeding polyphagous crustacean (*Bosmina*), a grasping, piercing-sucking phytophagous rotifer (*Polyarthra*), a phytophagous, filter-feeding rotifer (*Kellicottia*) and a predatory rotifer (*Asplanchna*). The middle-depth segment (80 - 120 m) was occupied by a polyphagous, filter-feeding crustacean (*Daphnia*), two polyphagous, filter-feeding rotifers (*Keratella cochlearis* and *K. quadrata*), a triptophagous, filter-feeding rotifer (*Filinia*), and two grasping, piercing-sucking, phytophagous rotifers (*Synchaeta* and *Polyarthra*). The most common zooplankton taxa in the deepest depth segment (120 - 200 m) were a phytophagous, filter-feeding rotifer (*Philodina*), a triptophagous, filter-feeding rotifer (*Conochilus*), a polyphagous, filter-feeding rotifer (*K. quadrata*), and a phytophagous, trapping rotifer (*Collotheca*). These patterns suggested

Table 14. General partitioning of the water column of Crater Lake from July through September by the zooplankton assemblage relative to feeding mode and method.

Depth Stratum	Feeding Mode	Feeding Method	Taxon
20-80 m	polyphagous (1985-90)	filtering/grasping	*Bosmina*
	phytophagous (1985-90)	grasping/piercing/sucking	*Polyarthra*
	phytophagous (1990)	filtering	*Kellicottia*
	ominivorous (1990)	predatory	*Asplanchna*
80 - 120 m	polyphagous (1988-89)	filtering	*Daphnia*
	polyphagous (1985-1990)	filtering	*Keratella cochlearis*
	polyphagous (1988-1990)	filtering	*Keratella quadrata*
	phytophagous (1985-90)	grasping/piercing/sucking	*Synchaeta*
	triptophagous (1985-90)	filtering	*Filinia*
	phytophagous (Sept. 1990)	grasping/piercing/sucking	*Polyarthra*
120-200 m	phytophagous (1985-88)	filtering	*Philodina*
	triptophagous (1985)	filtering	*Conochilus*
	polyphagous (1985-87)	filtering	*Keratella quadrata*
	or	or	or
	phytophagous (1988-90)	trapping	*Collotheca*
	polyphagous (1990)	filtering	*Keratella quadrata*

that vertical segregation of closely related taxa promoted co-existence, whereas different feeding modes and mechanisms facilitated the co-existence of more distantly related taxa within the same region of the water column (DeMot 1989). Therefore, stability of the water column during thermal stratification and the exceptionally transparent water of Crater Lake, which permitted phytoplankton populations to exist to a depth of 200 m (Debacon and McIntire 1991), were probably related to the maintenance of the temporal and spatial patterns in the zooplankton assemblage.

The population of *Polyarthra dolichoptera* was concentrated between depths of 20 m and 80 m throughout the study until September 1990, when its relative abundance was greatest between depths of 80 m and 120 m. This spatial shift in the density of *Polyarthra* corresponded to an increase in the density of *Asplanchna* in the 20 - 80 m depth segment. What caused the change in distribution of *Polyarthra* remains unclear because *Asphanchna* is not known to feed significantly on *Polyarthra* (Gilbert 1980). In any case, the downward movement of the *Polyarthra* population observed in September 1990 probably resulted in an increase in its competitive interactions with *Synchaeta*, as both taxa use the same food resources.

Vertical distribution of zooplankton in Crater Lake also may be related to the depth of effective light penetration. The depth at which the irradiance is 1% of the intensity at the surface is usually between 80 m and 100 m (see Photometer section). Therefore, most zooplankton taxa in the lake inhabit regions of the water column that receive light energy at relatively low levels. During most of the 10-year study, *Daphnia* was found at depths between 80 m and 120 m, a distribution that may have minimized its vulnerability to predation by zooplanktivorous fish (see Ecology of Kokanee Salmon and Rainbow section). In 1990 the density of the *Daphnia* population decreased significantly while the proportion of the population found between 120 m and 200 m increased, possibly in response to an increase in predation by kokanee salmon (Fig. 63). Stirling et al. (1990) found that an increase in planktivore density in Lake St. George was associated with an increase in the

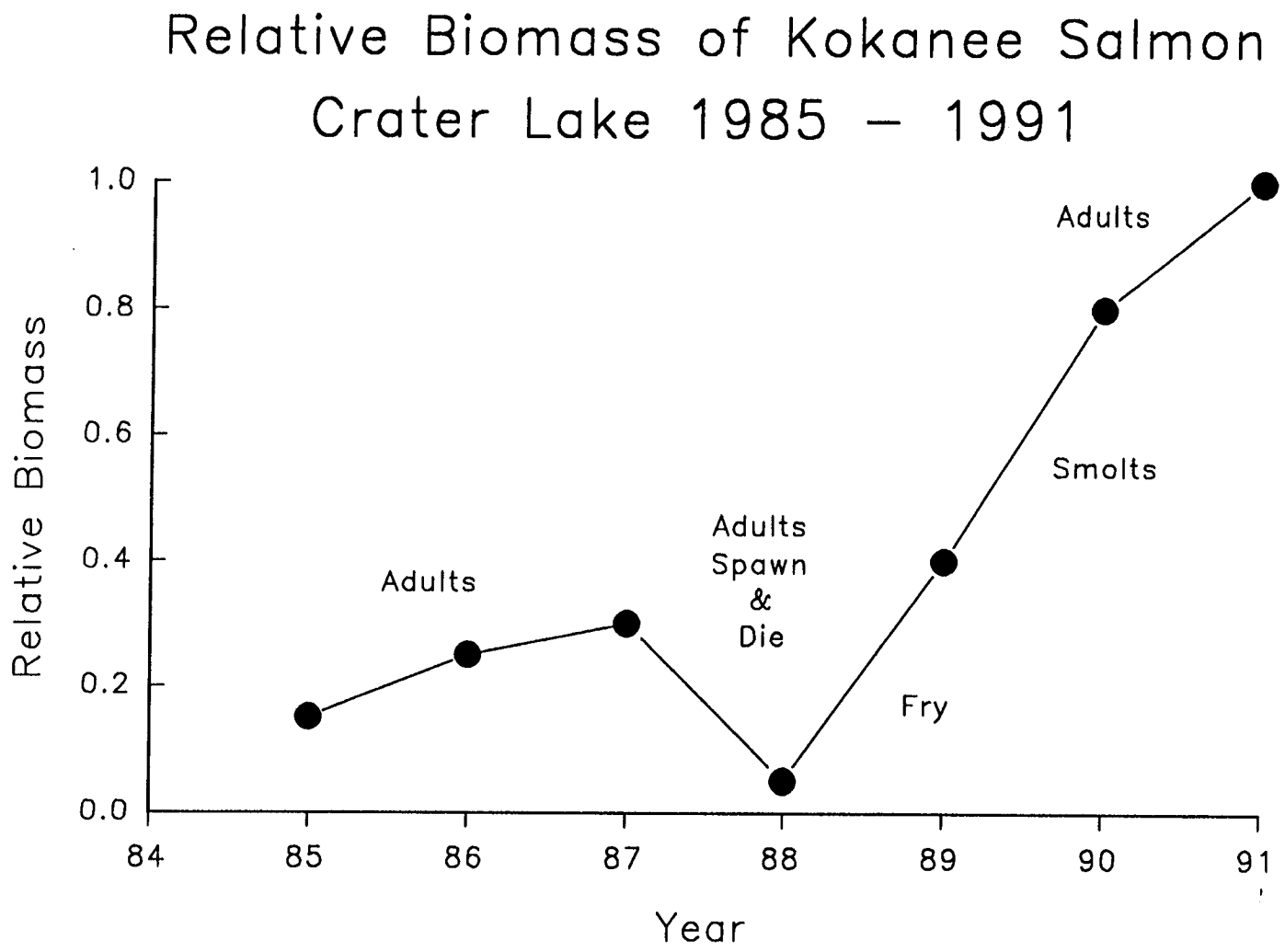


Figure 63. Relative biomass of kokanee salmon in Crater Lake and associated life history stages between 1985 and 1991.

hypolimnetic residence time of *Daphnia galeata mendotae*. In contrast, *Bosmina longirostris* was able to maintain high densities between the depths of 20 m and 80 m, possibly because its smaller size allowed it to escape predation more easily than *Daphnia* (DeMott 1989). The low densities of *Polyarthra* and *Bosmina* observed in the epilimnion of Crater Lake may have been related to light inhibition and a decrease in the diversity of food resources during thermal stratification (see Phytoplankton and Photometer section).

Irradiance also was associated with patterns of diel vertical migration, especially in the case of the cladocerans. *Bosmina* and *Daphnia* moved vertically as much 20 m and 40 m during a 24-hr period, respectively, although the patterns were not consistent over the sampling period (September 1988 to September 1990). Similar distances for *Bosmina* and *Daphnia* were reported in the literature (Wetzel 1983). Migratory patterns of the rotifers were either not apparent or unpredictable. The largest displacement of population biomasses observed during the sampling period was approximately 20 m, a distance that exceeds values reported in the literature (Wetzel 1983). However, the sampling strategy used in the 10-year study of Crater Lake prevented an exact measure of migratory distances because the water column was sampled in 20-m and 40-m segments. Therefore, overestimations of distances could have occurred when populations were concentrated near the boundary of one of the depth segments.

Relationships between the zooplankton and phytoplankton assemblages in Crater Lake are still poorly understood. During thermal stratification (July - September), the zone of maximum primary production occurs at depths between 40 m and 80 m, and a deep-water chlorophyll maximum is located at approximately 120 m below the water surface (see Phytoplankton section). Since nitrate levels are below detection limits in the upper 200 m of the lake (see Temperature and Water Quality section), nutrient recycling by the diverse assemblage of zooplankton below the metalimnion may have pronounced

effects on the location of the deep-water chlorophyll maximum (Abbott et al. 1984) and associated spatial and temporal patterns of primary production (Lehman 1980, Henry 1985). In other words, zooplankton may influence the productivity of Crater Lake by reducing the loss of nutrients from the euphotic zone.

Daphnia pulicaria is a major prey species of kokanee salmon in Crater Lake (see Ecology of Kokanee Salmon and Rainbow Trout). This salmon population usually is dominated numerically by a single age class, and because these animals die after spawning, the population is subject to large cyclic changes in biomass. Adult kokanee were abundant in Crater lake between 1985 and 1987, and they spawned successfully in the winter of 1987-88 (see Ecology of Kokanee Salmon and Rainbow Trout). Therefore, the biomass of the salmon population was low in 1988 and 1989 when the density of *D. pulicaria* was relatively high (Fig. 63). In 1990 smolt-size salmon were observed in large schools, often numbering several hundred-thousand individuals each (see Ecology of Kokanee Salmon and Rainbow Trout). This large increase in the number of smolts between 1989 and 1990 was concurrent with a sharp decline in the density of *D. pulicaria* (Figs. 34 and 59), the zooplankton taxon with the largest body size.

Research in relatively shallow lakes has indicated that the abundances of rotifers and small crustaceans tend to increase when the density of crustaceans with a large body size is reduced by fish predation (Brooks and Dodson 1965, Gliwicz and Pijanowska 1989). This pattern was not observed in Crater Lake because the presence or absence of *Daphnia* apparently did not have an appreciable effect on the distribution and abundance of the other zooplankton taxa. Presumably, the vertical partitioning of the upper 200 m of the water column by these taxa and the great depth of the lake accounted in part for a lack of clear density-dependent relationships between *D. pulicaria* and other smaller species of zooplankton.

Upwelling of nitrogen-rich water from the deep basins of Crater Lake (below a depth of 200 m) also may influence the distribution of zooplankton in the water column. The annual volume of upwelled water is determined by climatic conditions during the winter and spring months (McManis 1992). Nitrate-enriched water probably stimulates primary production (see Phytoplankton section), which in turn increases food resources for zooplankton. Data from the 10-year study indicated that high densities of zooplankton observed in 1985 and 1986 corresponded to a period of high chlorophyll concentration, a correspondence that perhaps was related to a pattern of upwelling that enhanced nutrient inputs into the euphotic zone during those years. If this hypothesis is correct, changes in zooplankton density during the study indicated that nutrient inputs from upwelling events were relatively low between 1987 and 1990.

In summary, dynamics of the zooplankton assemblage in Crater Lake are complex and probably influenced by fish predation and nutrient recycling from the deep lake. Therefore, biological processes in the lake may be regulated by both top-down (predation) and bottom-up (nutrient supply) control mechanisms (Carpenter et al. 1985), which probably do not occur at the same relative intensity each year. Knowledge of relationships between such mechanisms and the trophic dynamics of lake ecosystems merit further study (McQueen et al. 1986).

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Ecology of Kokanee Salmon and Rainbow Trout in Crater Lake, Oregon with Comments on Long-term Implications of Fish Introductions

Mark Buktenica and Gary L. Larson

Crater Lake was originally barren of fish. From 1888 through 1941, Crater Lake was stocked with approximately 1.8 million rainbow trout *(Oncorhynchus mykiss)*, brown trout *(Salmo trutta)*, cutthroat trout *(Oncorhynchus clarki)*, steelhead *(Oncorhynchus mykiss)*, and coho ("silverside") salmon *(Oncorhynchus kisutch)* (Buktenica 1989). Wallis and Bond (1950) identified six kokanee salmon *(Oncorhynchus nerka)* in samples collected in the lake in 1939 and 1947. These fish were previously presumed to be coho salmon. Because there are no records of stocking of kokanee salmon into Crater Lake, the kokanee were probably inadvertently mixed with other fish and stocked into the lake. Rainbow trout and kokanee salmon are the only two species of fish now known to inhabit the lake.

Fisheries investigations at Crater Lake date back to 1896 (Table 1). Many of the studies were of short duration (e.g., one day), and sample sizes were often small. The most comprehensive works included a study of food habits and growth of fish by Hassler and Farner (1942) and a general survey of flora and fauna of Crater lake by Brode (1938). Although these studies provided an invaluable historical data base, little was known about the ecology of the fishes in Crater Lake prior to the studies reported in this section.

Studies of the fish of Crater Lake were resumed in 1985 as part of the congressionally-mandated 10-year study. The goal of these new studies was to develop a better understanding of the ecological role of non-native fish in Crater Lake.

Table 1. Fisheries investigations at Crater Lake, Oregon.

Years of Study	Primary Topic	Sample Size				References
		Rainbow Trout	"Silversides"	Kokanee	Unspecified	
1896	Fitness of Crater Lake as Fish Habitat	--	--	--	--	Evermann (1897)
1933	Food Habits of Oregon Trout	1	0	0	0	Dimick and Mote (1934)
1933	Food Habits	0	0	0	70	Hubbard (1933) (Unpublished)
1934	Food Habits	4	46	0	0	Brode (1935)
1934-1936	Floral and Faunal Survey Food Habits	0	214	0	0	Brode (1938)
1937	Creel Census	--	--	--	--	Hasler (1938)
	Age and Growth	124	151	0	0	
1937-1940	Creel Census	--	--	--	--	Hasler and Farner (1942)
	Age and Growth	0	0	0	749	
	Food Habits (1940)	0	0	0	79	
1939,1947	Identification of Kokanee Salmon in Crater Lake, Oregon	0	6	0	0	Wallis and Bond (1950)
1952-1953	Food Habits	6	4	0	0	Baird (1956)
1953-1956	Food Habits	117	44	0	0	Patten and Thopmson (1957) (Unpublished)
1966	Age and Size	0	0	0	179	Kibby (1966) (Unpublished)
1982	Gill net capture Feasibility	34	5	0	0	Fortune and Toman (1982) (Unpublished)

Methods

From 1985 through 1991, fisheries investigations were divided into several phases or projects with related objectives. Some of these studies were published prior to this report. When this is the case, a citation accompanies reference to the earlier publication. In 1985 R. Thorne and D. Marino conducted a hydroacoustic survey of the lake (Thorne and Marino 1986, Marino 1987). The objective of their work was to estimate the abundance of different size classes of fish and to characterize fish distribution. In 1986 and 1987 a survey was initiated to document and compare the length, weight, growth, age, morphology, food habits, and distribution of adult rainbow trout and kokanee salmon in Crater Lake and to evaluate the ecology of each species relative to the limnological characteristics of the lake (Buktenica 1989). Fish sampling in 1988 and 1989 was substantially reduced because of commitments to other research programs at Crater Lake. Sampling in 1988 consisted of a single gill-net set in early January. Sampling in 1989 occurred from April through September, with the majority of the effort in June. An expanded sampling program was instituted in 1990-91 to evaluate fish length, weight, growth, condition, age, food habits, distribution, relative abundance and relative biomass.

Capture Techniques and Field Measurements

Horizontal gill nets were set overnight on the shelf-like areas around Crater Lake to a depth of 20 m (Fig. 1). Floating and sinking multifilament nets measuring 38 m x 3 m were used. Mesh sizes ranged from 19 mm to 51 mm square mesh, in five 7.6-m panels. Fish also were captured by angling with artificial lures along the lakeshore. In 1986 and 1987 a downrigger was modified to troll for fish in the

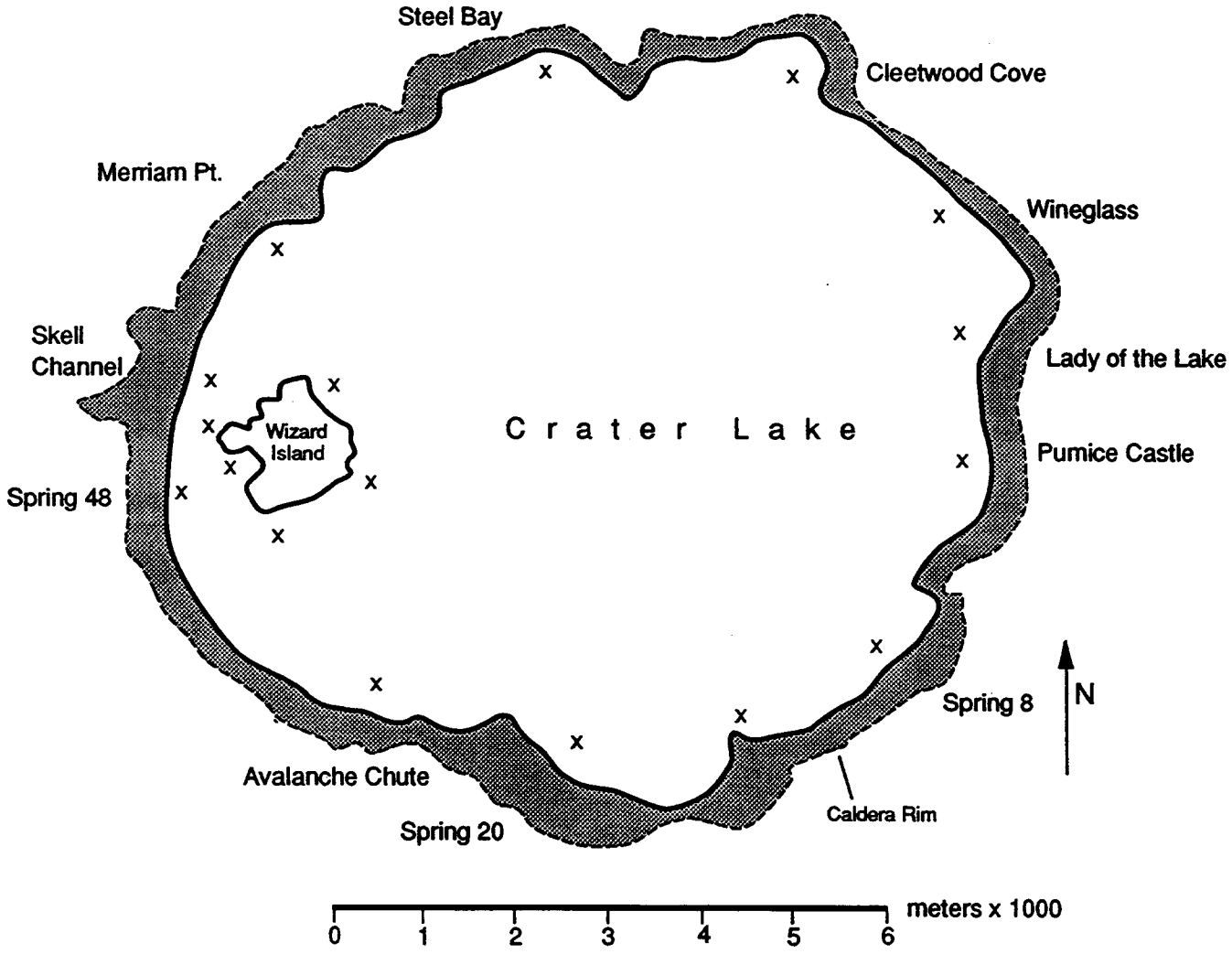


Figure 1. Location of horizontal gill-net Sets (X) on Crater Lake, Oregon.

offshore areas between the 100 m and 589 m contour. Artificial lures or lures with a flasher were attached to the cable at intervals of 5 m starting at 5 m and ending at 100 m. A similar lure was trolled behind the boat to fish near the surface of the lake.

Fork length and total length of fish captured were measured to the nearest millimeter on a 0.6-m measuring board. Whole-fish weights were determined on a Homs top-loading temperature-compensated spring dial scale (1,000 g in 2 g increments) to the nearest gram.

Age

Scales were taken to age fish by scraping with the blunt edge of a scalpel blade just below the posterior margin of the dorsal fin and above the lateral line (Jearld 1983). Six scales from each fish were cleaned and mounted between two microscope slides. Mounted scales were viewed through a microfiche projector to determine the age of each fish. Distance between the scale focus, annuli, and margin were taken on a subsample of scales collected in 1986 and 1987 using a BioSonics optical pattern recognition system (OPRS). The OPRS consisted of a microscope, video camera, monitor, real-time video-frame grabber, digitizing tablet, microcomputer, and software. Data describing distances between circuli and optical images were stored on computer disks and archived. Length-frequency analysis and modal-progression analysis were used as age-validation techniques (Jearld 1983).

The international convention for aging fish in the northern hemisphere is to designate January 1 as the birth date of fish, even if the annular ring or slow-growth zone is not complete by this date (Jearld 1983). Because very few fish were captured between October and April at Crater Lake due to the inaccessibility of the lake in the

winter, the terminal edge of the annular ring was used to designate age class of fish captured between June and September instead of scale development on January 1. Fish in their first year of life, before development of the first annular ring, were designated as age-0+ fish. Fish captured after the development of the first annular ring and prior to completion of the second annular ring were designated age-I+ fish, except when otherwise noted. The same convention was used to designate members of subsequent age groups (II+, III+, IV+, V+, and VII+).

Growth and Condition

Growth of Crater Lake fish was assessed using length at age and length at maturity. Fulton's Condition Factor was used to assess condition of fish (Ricker 1975, Anderson and Gutreuter 1983). This condition factor (K) is defined as $K=(W/L^3)X$, where W equals whole weight (including stomach contents) in g, L equals length in mm, and X is an arbitrary scaling constant so that the small decimal values can be more easily comprehended. Comparisons of conditions factors were limited to comparisons of fish of the same species at 50-mm size classes except when otherwise noted.

Food Habits

In 1986 and 1987 whole fish were fixed in 10% formalin, primarily to harden fragile stomach contents. These fish were later transferred to ethanol. In subsequent years, stomachs were removed from fish in the field and placed in 70% ethanol. Contents of each stomach were flushed (from the esophagus to the pyloric sphincter) and stored in 70% ethanol in individual containers. It was found that use of formalin

was not necessary if stomachs were flushed with ethanol within several months of collection.

Stomach samples were sorted with the aid of a binocular dissecting microscope with magnification of 6x to 50x. The contents were identified to the lowest possible taxonomic group when either an intact individual was present or when an intact and readily identifiable body part was present. The head capsule of midge larvae, the thorax or genitalia of pupae or adult caddis flies, and the thorax or head capsule of hymenopterans were sufficient for identification of these groups. When possible, prey were identified to genus or species to determine mean weights and to classify the taxa into functional groups (Appendix 1). The taxa were grouped into higher taxonomic categories (e.g. family and order) for determinations of percent occurrence and percent composition of the diet by weight and by number of food items. Zooplankton samples were diluted to an acceptable concentration and two 1-ml subsamples were counted. Zooplankton samples were enumerated when either whole specimens were intact or individual eye spots were intact. Samples were counted in a rectangular counting chamber with longitudinal divisions under a binocular dissecting microscope (40x). Counts of subsamples were multiplied by their corresponding dilution factors to obtain the total zooplankton count for each stomach sample.

Replicate sets of 1 to 100 of the least-digested individuals of each taxa were sorted for weight measurements. Estimated weights were applied to many taxa when intact specimens were not available based on equivalent-sized specimens preserved in ethanol in various collections available from R. Wisseman and N. Anderson (Oregon State University, Department of Entomology). Samples were dried to a constant weight at 60° Celsius and then placed in a desiccator to cool to room temperature.

Dry weights were measured on a Mettler H16 Balance (accuracy 0.05 mg) and a Cahn 4100 Electrobalance (accuracy 0.005 mg). All weights were uncorrected for partial digestion and for any effects of preservation in formalin and ethanol. All stomach samples collected in 1986 and 1987 were processed and a subsample of the stomachs collected in 1988, 1989, and 1991 were processed.

Food habits of kokanee salmon and rainbow trout were assessed by determining the frequency of occurrence of prey types in fish stomachs and percent composition of prey types in the diet by number and weight. Frequency of occurrence describes the uniformity with which a group of fish selects their diet (Bowen 1983). Percent composition by number and percent composition by weight provides some information on the relative importance of individual food types to the nutrition of fish (Hynes 1950, Bowen 1983). Also, the percent composition of the diet by vertical distribution in the water column (by weight), the percent composition by aquatic or terrestrial origin (by weight), and the mean weight of food items were analyzed. Chironomid larvae were assumed to have been taken from the benthos and their biomass derived in the lake, *Daphnia* were assumed to have been taken from the midwater column and their biomass derived in the lake, and Lepidoptera adults were assumed to have been taken at the surface and their biomass derived in the terrestrial environment. The biomasses of adult Trichoptera and Ephemeroptera were assumed to be derived either in the lake or in the caldera springs. Odonata adults, which feed extensively as adults and may migrate great distances, were classified as terrestrial (Appendix 1). All percent composition values were calculated for each stomach sample, and means were calculated for fish groups of interest (e.g., by species, year, and age).

Distribution

Evaluations of fish distribution were based on hydroacoustic surveys conducted in 1985 and 1987 and from captures and direct visual observations of fish made from 1985 through 1991. In 1985 Thorne and Marino (1986) used a BioSonics model 101 dual receiver 420 KHz transceiver, 6/15 degree dual-beam transducer, Ross 250C chart recorder, BioSonics 171 recording interface, Sony PCM-F1 digital signal processor, and Beta-format video cassette recorder. A portable dual-trace oscilloscope was used to monitor system performance. All components operated from 110 volt AC current and were powered by a 500 volt-amp static inverter which was driven from two 12-volt batteries wired in parallel. The lake was surveyed over several days in August, 1985 using a stratified random sampling design. The strata were nearshore (0 to 91.4 m contour) and offshore (91.4 to 589 m contour) zones of the lake, and day versus night (Marino 1987).

In 1987 a BioSonics model 101 420 KHz scientific sounder with a single 15° transducer was used. The output was recorded on an EPC model 1600S paper chart recorder with a model 165 BioSonics chart recorder interface, and monitored on a Hewlett Packard model 1703A storage oscilloscope. The system operated off 110-volt AC current supplied by an on-board model EX650 Honda generator. A nominal beam width of 17° was used. Use of hydroacoustic methods for assessment of fish distribution and abundance were described in detail by Thorne (1983), Johanesson and Mitson (1983), Burcynski (1979), and Forbes and Nakken (1972).

The 1987 acoustic survey was conducted during a seven-day period in early September. Because the 1985 survey indicated that fish distribution in Crater lake was strongly biased toward shore, a stratified random sampling design was used and

included nearshore (0 to 100 m contour) and offshore (100 to 589 m contour) zones of the lake and six four-hour periods of time (day and night) (Buktenica 1989) (Fig. 2).

Relative Abundance and Relative Biomass

Catch per unit effort (CPUE) was used to evaluate relative abundance and weight per unit effort (WPUE) was used to assess relative biomass. Catch per unit effort and WPUE represented the number of fish captured and the weight of fish captured (respectively) in a 33-m section of gill net, per gill net set.

Results

Capture

Gill netting was the most efficient method to capture rainbow trout and kokanee salmon (Buktenica 1989, Buktenica and Larson 1990). The downrigger and angling provided samples from the offshore zone and during the day when gill nets were not effective. No rainbow trout or kokanee salmon less than one year old were captured.

Age and Length

Scales of Kokanee salmon varied greatly in size and shape even when taken from a small area of the same fish. Most kokanee scales exhibited a weak but persistent annular check or node near the focus. The second, third, and fourth annuli, when they occurred, were well developed. Many scales exhibited signs of reabsorption or abrasion, particularly along the dorsal and ventral margins. Regenerated scales were common. Scales of sexually mature (ripe) kokanee in the fall of 1987 and in January, 1988 were absorbed. The annuli designating age I+ formed in the summer

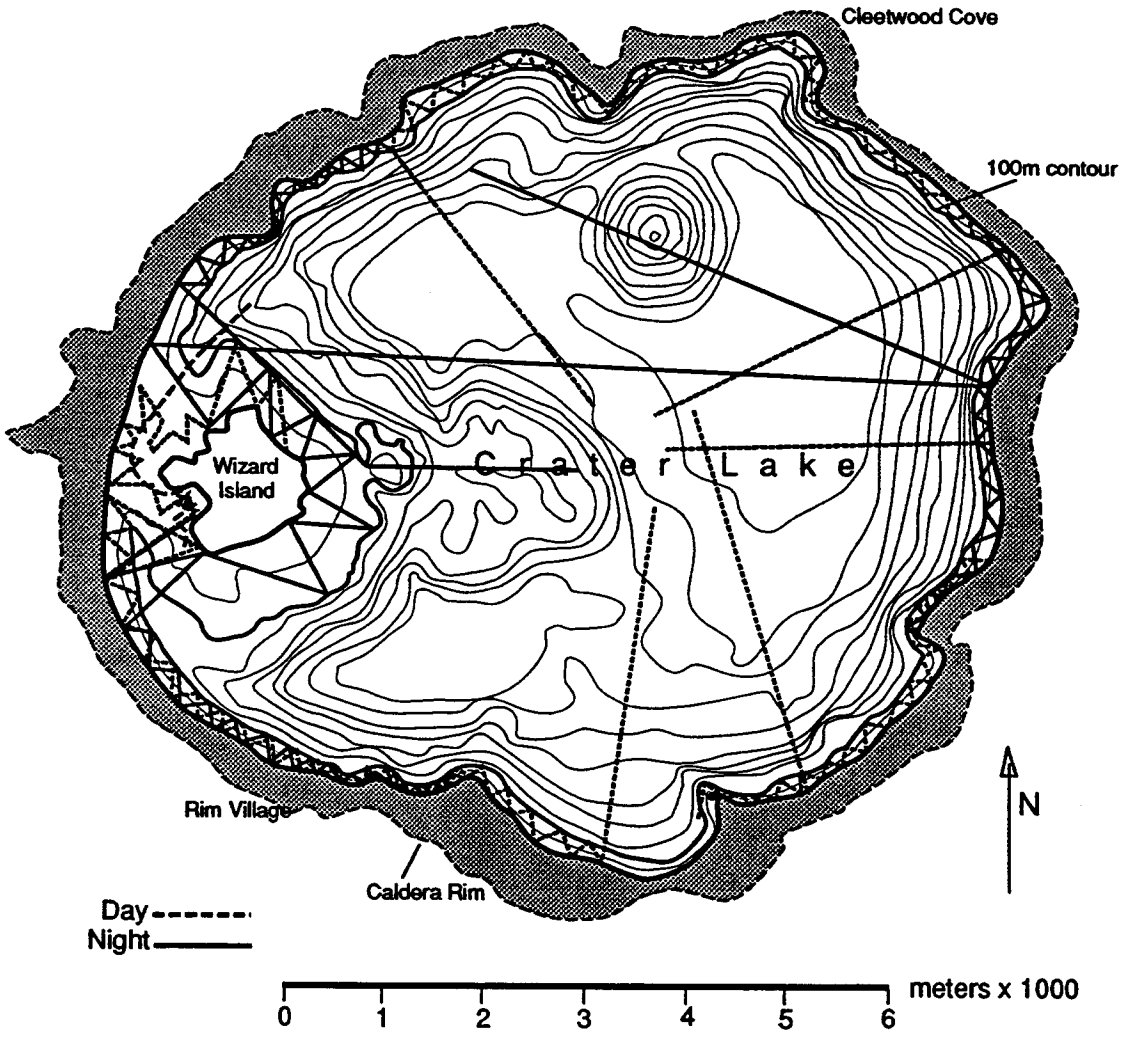


Figure 2. Map of Crater Lake, Oregon, with the approximate locations of hydroacoustic transects in 1987.

season for kokanee (Fig. 3). Scales from age I+ fish captured in May had wide spacing between circuli throughout the scale, whereas scales collected in June, July, and August had more-closely spaced circuli along the scale margin. Formation of annular rings by age II+ and III+ kokanee occurred during winter months.

Rainbow trout scales varied less in size and shape than did kokanee scales. The first annulus occurred very close to the focus and it was well-defined. Subsequent annuli also were well defined. Absorption and abrasion of scales generally occurred in IV+ or older fish. Scales of some older fish exhibited wide spacing between circuli prior to June and close spacing, resembling an annular ring, later in the summer. These last two features may have indicated spawning or post-spawning adults.

Analysis of age-frequency and length-frequency histograms suggested one dominant year class for kokanee salmon in 1986 and 1987 (Fig. 4). Gill-net sets on January 6 provided the only samples for 1988 (Fig. 5). These fish were either ripe with loose eggs or milt or partially to fully spawned-out. Scales were either non-existent or unreadable on spawning adults as mentioned above, although modal progression of both age- and length-frequency plots from 1986 through 1988 provided strong evidence that these kokanee were age III+ from the 1984 cohort. Age- and length-frequency histograms from 1989 to 1991 indicated a more complex population structure than that present from 1986 through 1988 (Figs. 5 and 6).

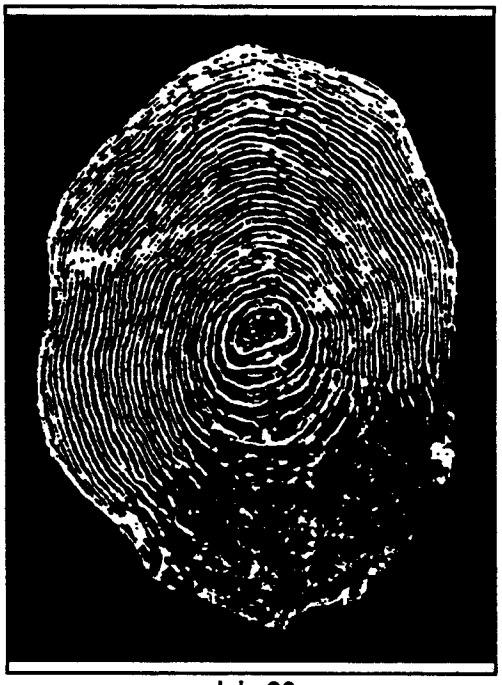
Rainbow trout had a more complex population structure than did kokanee salmon (Figs. 7, 8 and 9). The composition of the rainbow trout population seemed to shift toward larger size classes and older-aged fish between 1986 and 1991.



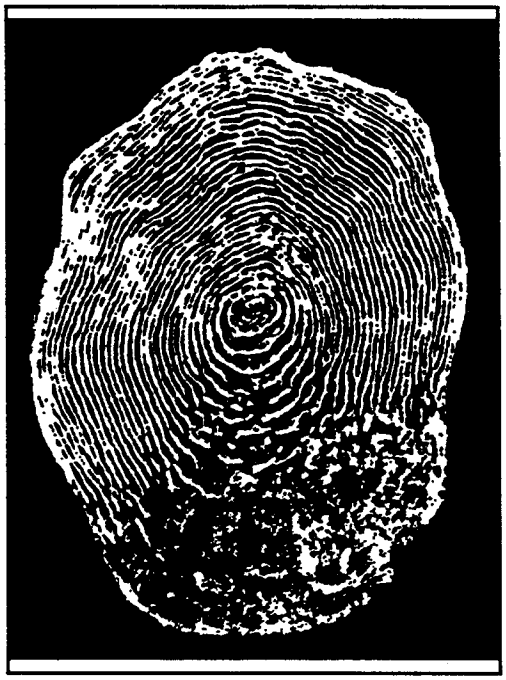
May 15



June 30



July 30



August 15

Figure 3. Age-I+ kokanee salmon scales from fish collected in May, June, July, and August. Image size is not proportional to actual size.

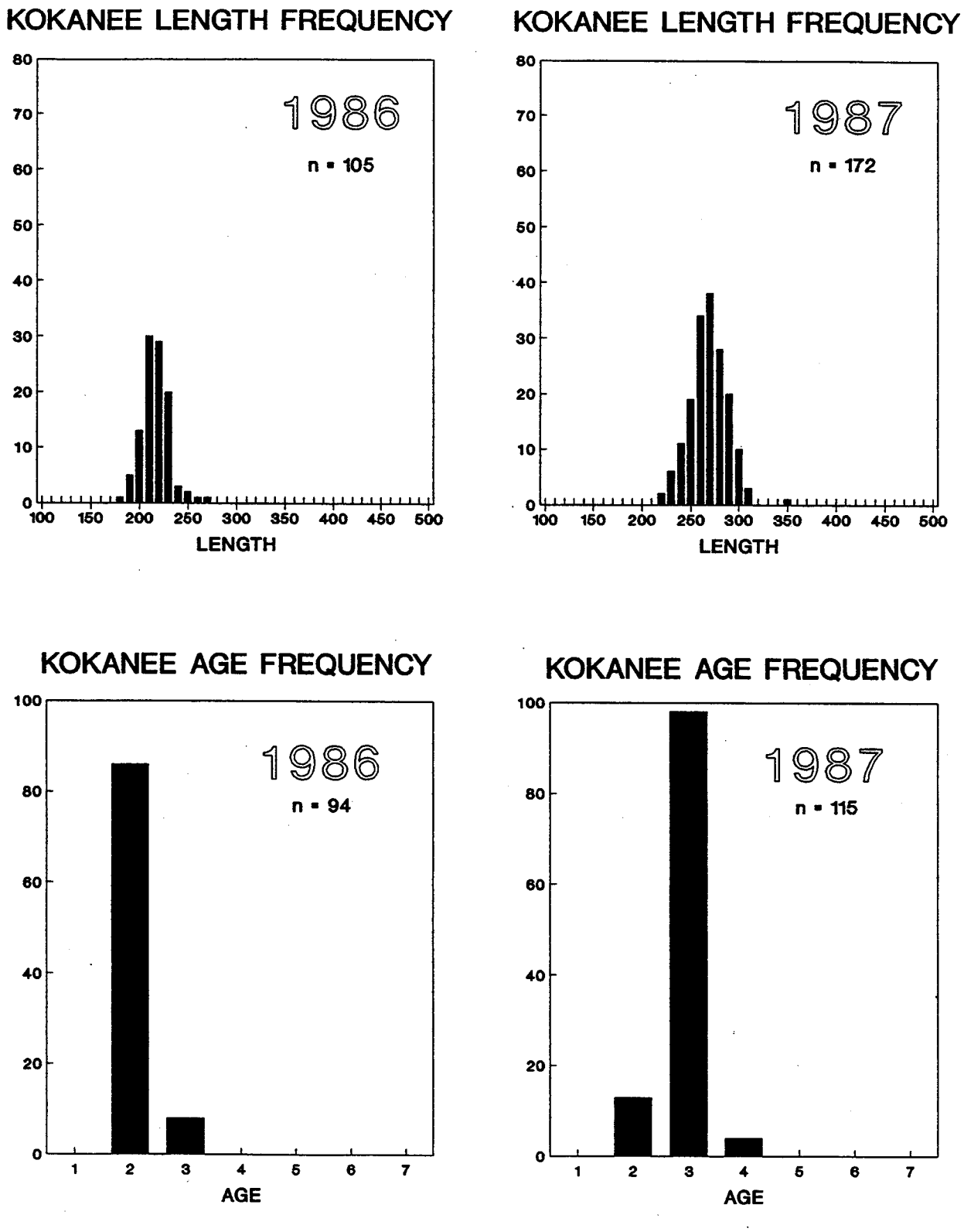


Figure 4. Length-frequency and age-frequency histograms for kokanee salmon captured in 1986 and 1987, Crater Lake, Oregon.

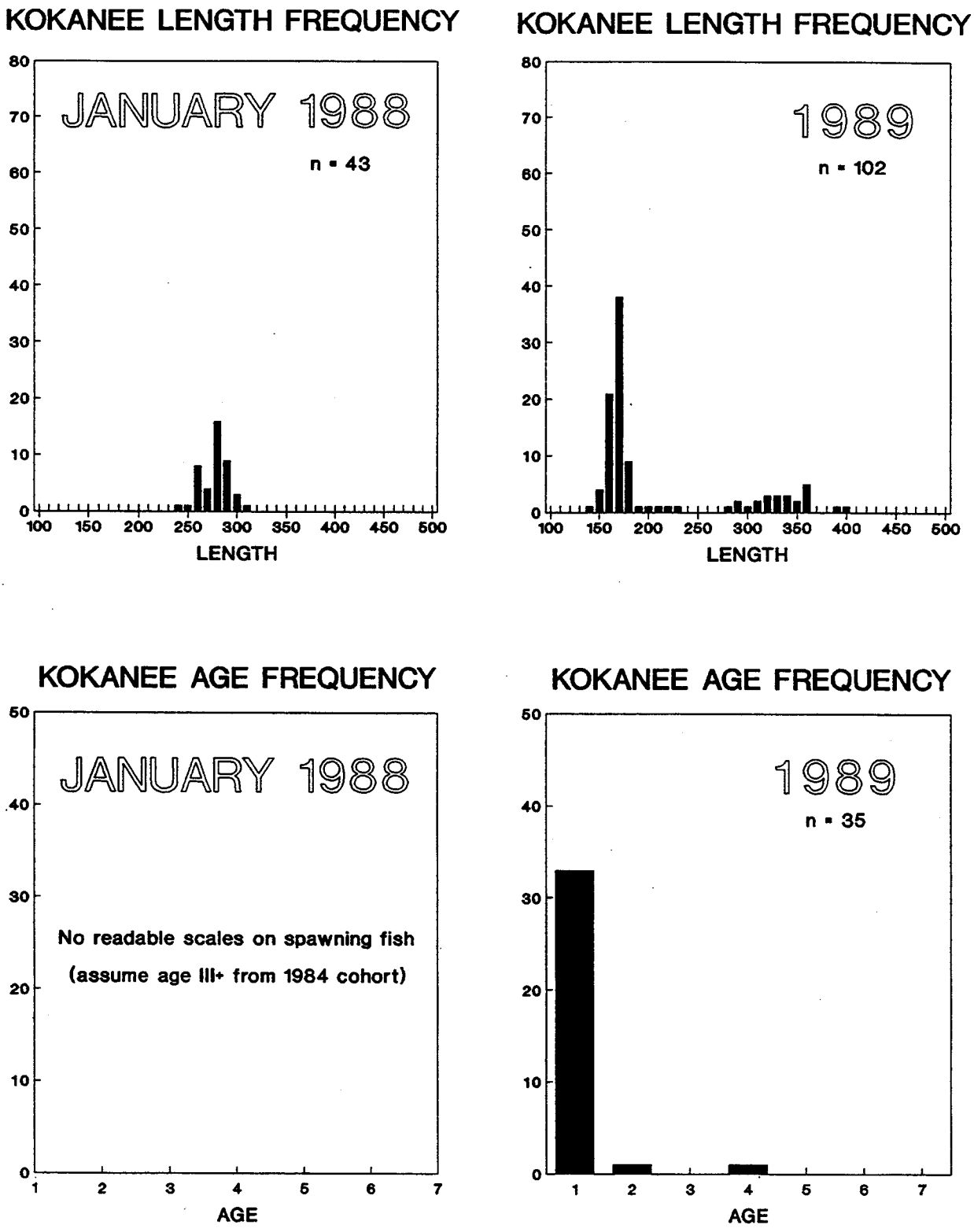


Figure 5. Length-frequency and age-frequency histograms for kokanee salmon captured in 1988 and 1989, Crater Lake, Oregon.

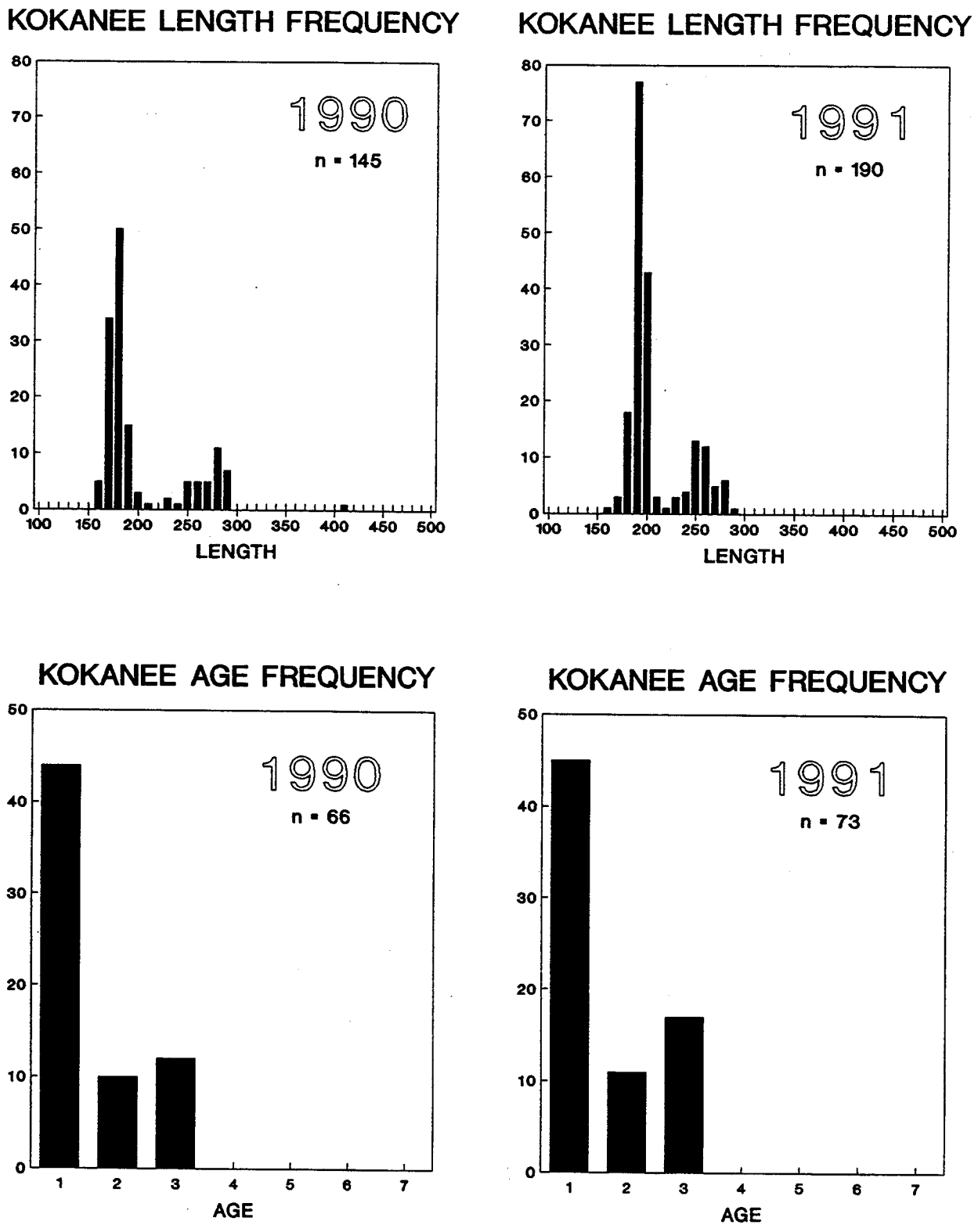


Figure 6. Length-frequency and age-frequency histograms for kokanee salmon captured in 1990 and 1991, Crater Lake, Oregon.

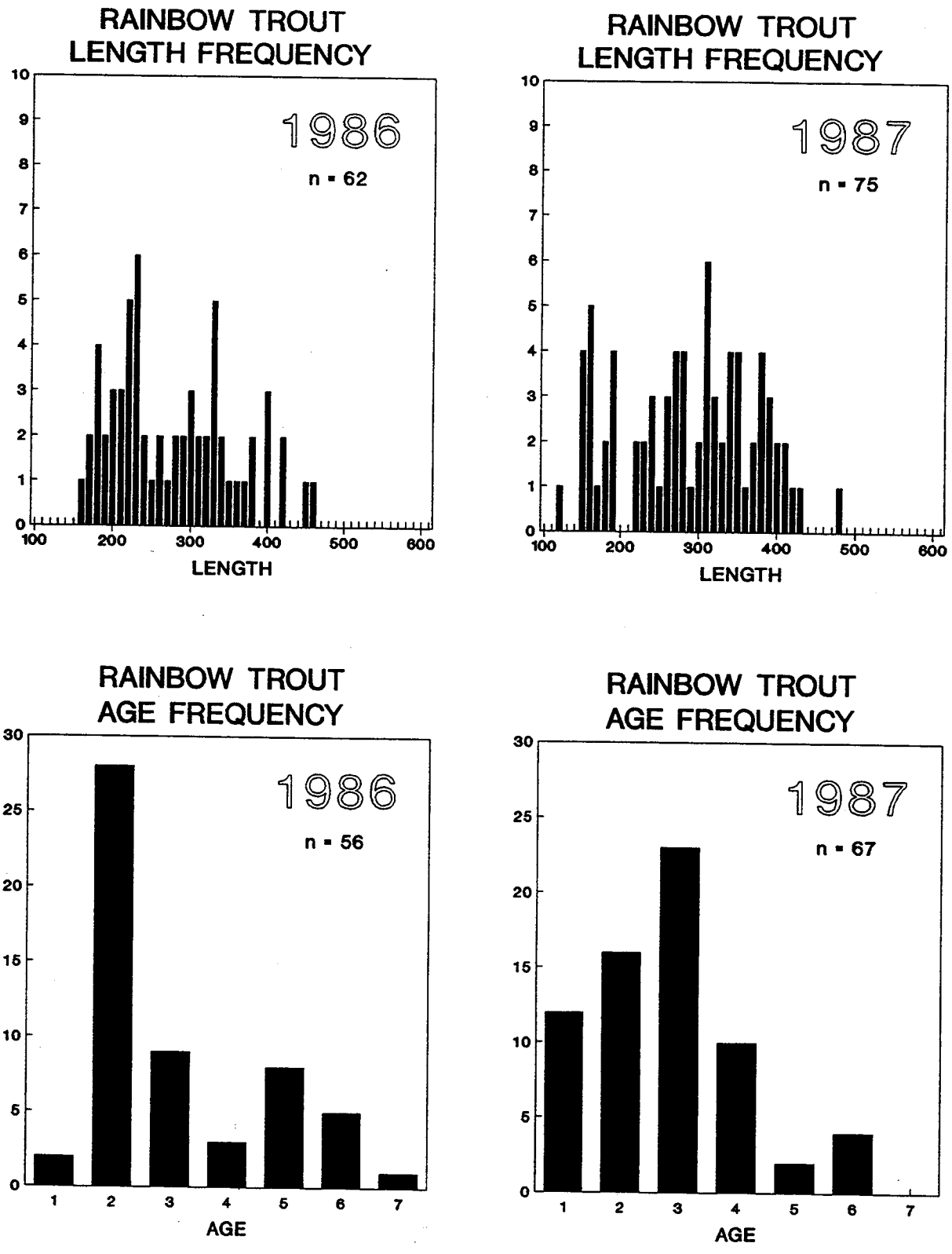


Figure 7. Length-frequency and age-frequency histograms for rainbow trout captured in 1986 and 1987, Crater Lake, Oregon.

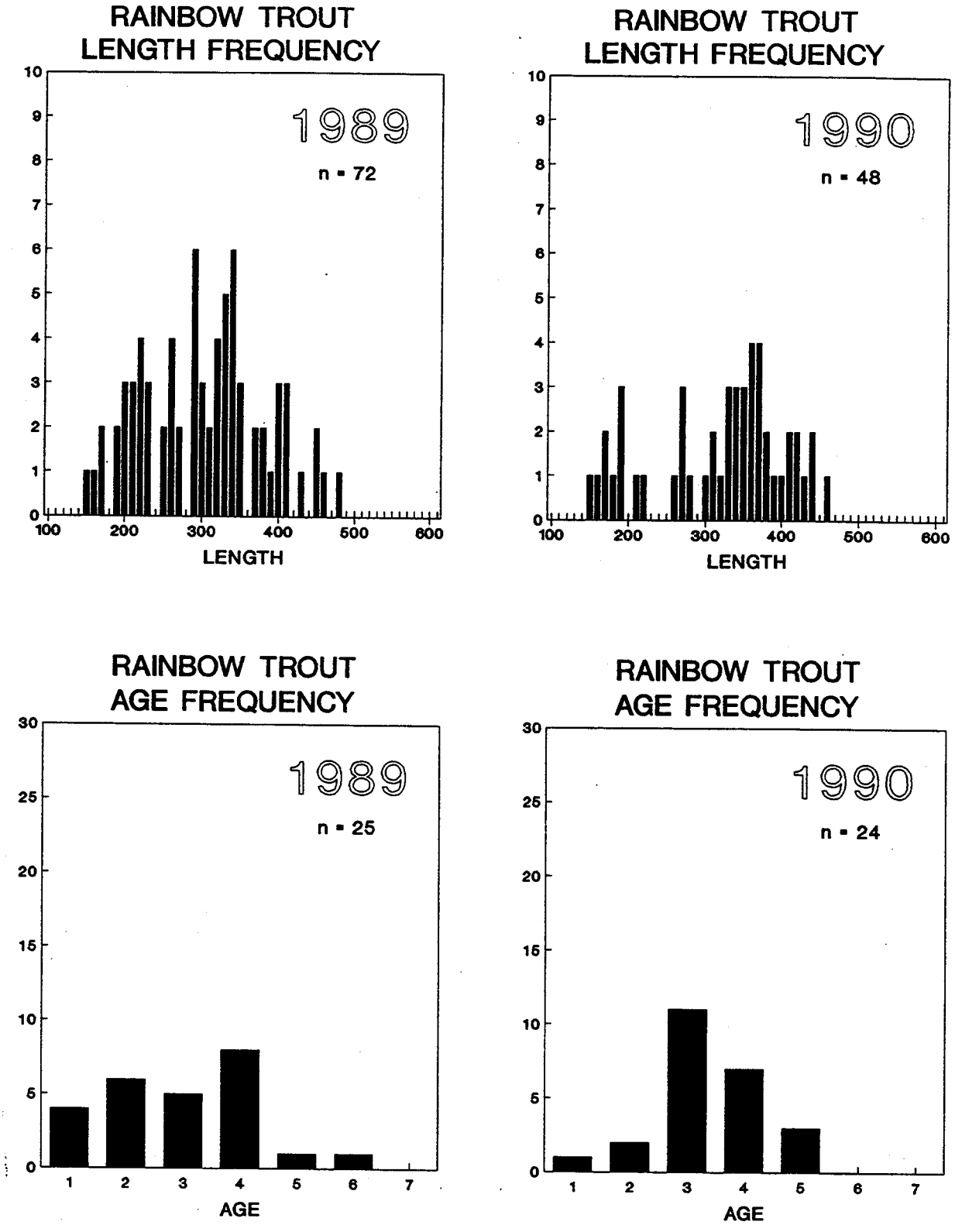
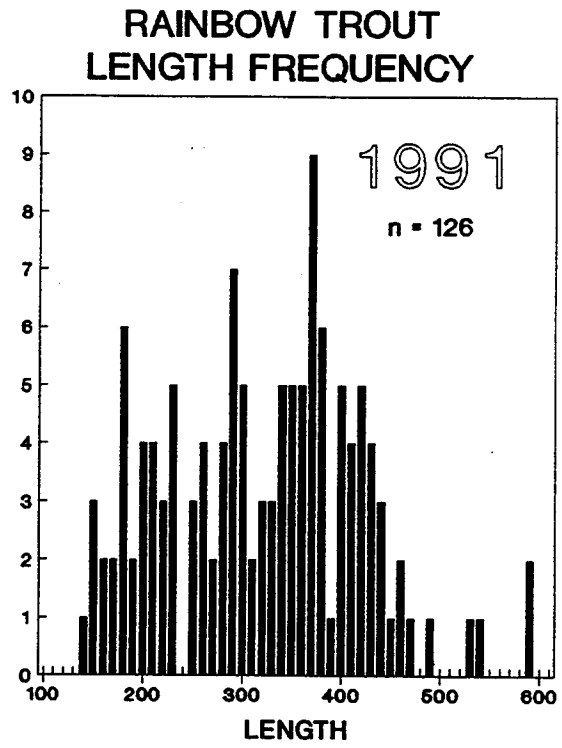


Figure 8. Length-frequency and age-frequency histograms for rainbow trout captured in 1989 and 1990, Crater Lake, Oregon.



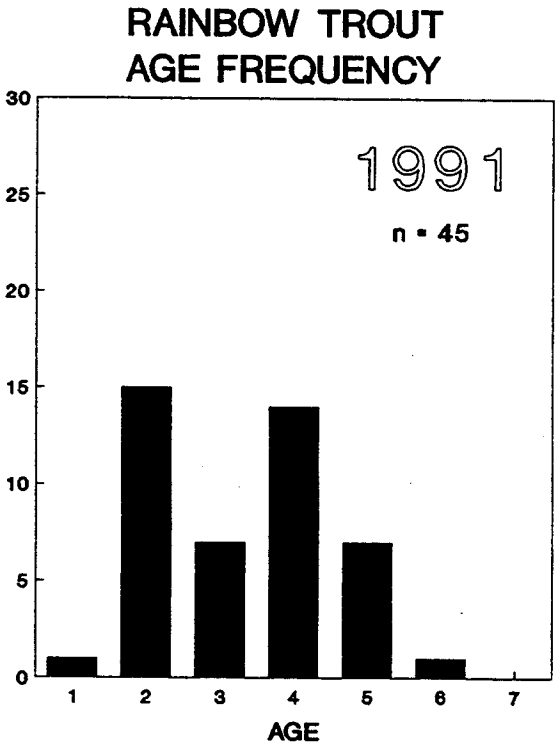


Figure 9. Length-frequency and age-frequency histograms for rainbow trout captured in 1991, Crater Lake, Oregon.

Growth

Fork length at age was calculated for kokanee salmon and rainbow trout in 1986 and 1987 (Fig. 10, Table 2). In 1986 and 1987 rainbow trout grew rapidly in a near linear fashion until age IV when there was the tendency for the annual increments to diminish (Fig. 10). For rainbow trout, data from 1986 and 1987 were combined for growth estimates by length at age to obtain larger sample sizes for each age class; this required the assumption that the lake environment was in a steady-state equilibrium. However, there was no reason to believe that Crater Lake was in a steady state. In fact, length data from 1986 through 1991 indicated that the average length of rainbow trout increased from 274 mm in 1986 to 315 mm in 1991, which suggested that the lake environment was not at steady state. For this reason, comparisons of length at age of rainbow trout from other lakes were not included. Average lengths of rainbow trout by year were 1986, 274 mm; 1987, 283 mm; 1988, not available; 1989, 298 mm; 1990, 315 mm; and 1991, 315 mm.

The kokanee in 1986 were nearly all age II, in 1987 they were nearly all age III. Therefore, data from the two years were necessarily combined for kokanee salmon lengths at age. Age data and length-frequency data strongly suggested that one dominant year class of kokanee existed in Crater Lake; therefore, the basic assumption of the model was not violated for kokanee salmon. Length at maturity was also used to evaluate growth of kokanee salmon (Table 3). The 1989 entry, in Table 3, for Crater Lake represents the length of maturing kokanee salmon averaged over the summer sample period and under estimates the length at maturity. Values from other lakes in Table 3 are from samples taken in late September through late

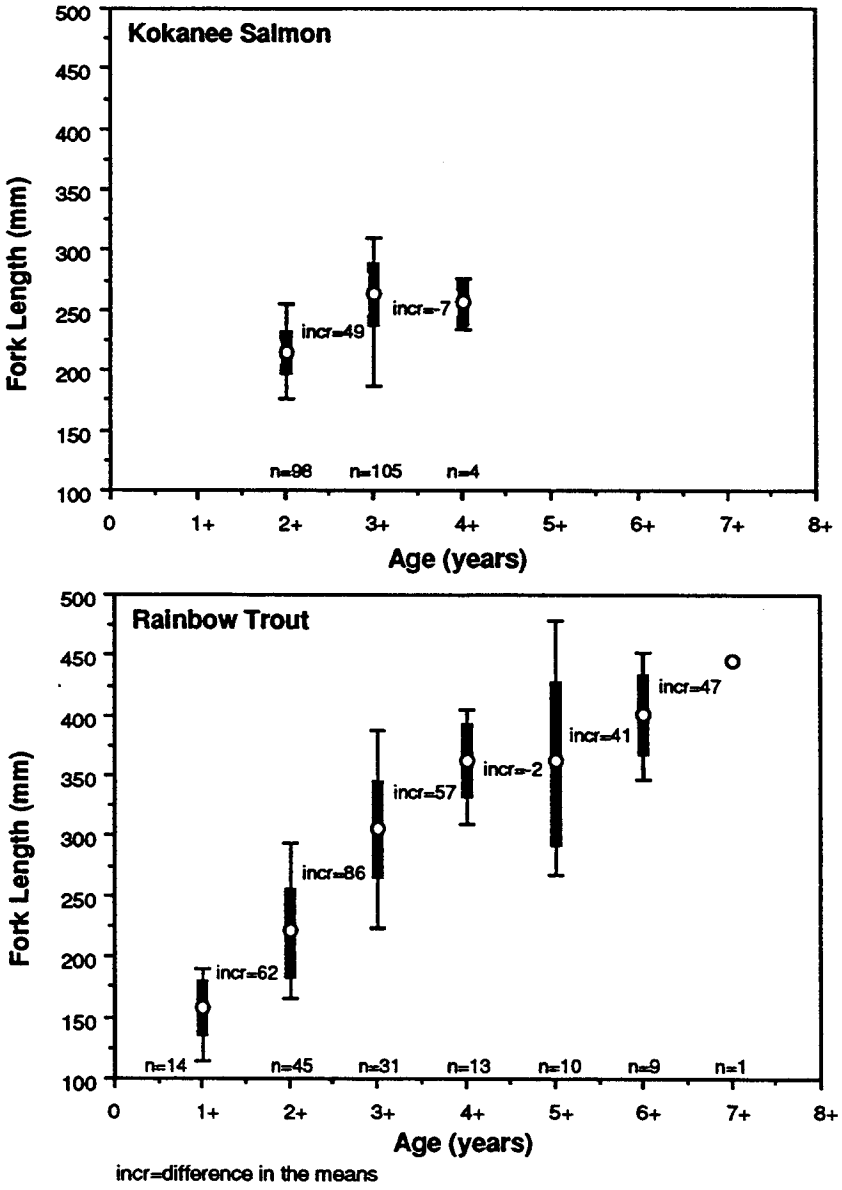


Figure 10. Mean fork length, mean length increments between age classes (incr), standard deviation (bar), range (T-bar), and sample size (n) by age for kokanee salmon and rainbow trout, Crater Lake, Oregon, 1986 and 1987.

Table 2. Total length (TL) and fork length (FL) at age (mean and/or range in mm) for Kokanee salmon from Lakes in Colorado, Idaho, Oregon, and British Columbia.

	Age I		Age II		Age III		Age IV	
Lake and Citation	TL	FL	TL	FL	TL	FL	TL	FL
Pend Oreille, Idaho[a]			175		221		231	
		51-76		178-203				
Nicola Lk., British Columbia, Moore Creek (Lorz and Northcote 1964)				155-185		205-270		215-275
Elk Lake, Oregon[a]	147		196		249			
Odell lake, Oregon[a]	178		259		356			
Horsetooth Lake, Colorado[a]	190		257		325			
Cultus Lake, British Columbia[a]	244		381		442			
Crater Lake, Oregon (Hasler 1938)[b]		135		371		414		441
Crater Lake, Oregon (Buktenica 1986-87)			233	212	290	267		
Crater Lake, Oregon (Buktenica 1989)	176	161						

[a] Carlander 1969
[b] Silversides

Table 3. Length at maturity (mm) of kokanee salmon in Pacific Northwest lakes. Data for lakes other than Crater Lake are courtesy of Oregeon Department of Fish and Wildlife.

Lake	Sex[c]	Length Range	Average Fork Length	Sample Number	Year(s)	Productivity
Crater Lake, OR	f	262-302	283	10	1988 (Jan)	oligotrophic
	f and m	238-300	273	43	1988 (Jan)	
	f	290-395	337	20	1989 (Jun-Sept)	
	f and m	274-395	331	24	1989 (Jun-Sept)	
Waldo, OR	f	302-358	330	5	1988	oligotrophic
	f and m	302-403	333	12	1988	
Fourmile, OR	f	NA	216	NA	1979-1988 (missing 1981)	oligotrophic
Miller, OR	f	NA	198	NA	1979-1988	oligotrophic
Odell, OR	f	NA	326	NA	1979-1988	oligotrophic
Cresent, OR[b]	f	NA	343	NA	1979-1988	oligotrophic
Lake of the Woods, OR[b]	f	NA	225	NA	1979-1988	oligotrophic
Paulina, OR[b]	f	NA	387	11453	1978-1988	mesotrophic
Suttle, OR	f and m	210-356	273	269	1984-1988	mesotrophic
Wickiup Resv., OR	f and m	210-389	263	148	1986-1988	mesotrophic

[a]NA = No data available.
[b]= stocked. All others are not currently stocked.
[c]F = female and M = male.

October (John Fortune, Oregon Department of Fish and Wildlife, pers. comm.). Since rainbow trout may spawn several times during their lifetime, length at maturity was not very useful to evaluate growth.

Condition Factors

Fulton's condition factors by length class for kokanee salmon from 1986 through 1991 indicated a strong trend of peak condition in 1987 and declining condition in subsequent years (Table 4). No clear trend was apparent in condition factors for rainbow trout from 1986 through 1991 (Table 5). Peak condition of different size classes of rainbow trout classes occurred in different years. Nearly all size classes exhibited a reduction in condition from 1990 to 1991.

Food Habits

Kokanee salmon tended to feed on four major food groups. The major groups and the percent occurrence of the groups were: Chironomidae larvae and pupae, 90%; Trichoptera, 39%; Amphipoda, 39%, and Cladocera, 33%. These food groups stood out in importance when percent composition of the diet by weight (89% combined) and by number (91%) were considered (Fig. 11). Cladocerans were under represented in percent composition by weight and number because many were partially digested and could not always be counted (Buktenica 1989). Rainbow trout fed on a greater number of food groups than did kokanee salmon. Major groups and their percent occurrence included Trichoptera, 65%; Chironomidae, 60%; Coleoptera, 60%; Hymenoptera, 48%; other Diptera 38%; Gastropoda, 35%; Hemiptera, 23%; Ephemeroptera, 21%, and Arachnida, 20%) (Fig. 11). The nine

Table 4. Fulton condition factors By length class for kokanee salmon in Crater Lake, Oregon for 1986 through 1991. Sample size is in parentheses.

Length Class(mm)	1986	1987	1989	1990	1991
-149	---	---	1.178 (4)	---	---
150-199	1.158 (17)	---	1.160 (71)	1.114 (106)	0.987 (139)
200-249	1.170 (76)	1.372 (36)	1.277 (3)	1.141 (8)	0.898 (22)
250-299	1.270 (2)	1.333 (130)	1.263 (4)	1.237 (31)	0.933 (27)
300-349	---	1.264 (6)	1.261 (13)	---	---
350-399	---	---	1.153 (7)	---	---
400-	---	---	---	1.106 (1)	---

Table 5. Fulton condition factors by length class for rainbow trout in Crater Lake, Oregon for 1986 through 1991. Sample size is in parentheses.

Length Class (mm)	1986	1987	1989	1990	1991
100-149	---	1.267 (3)	1.231 (1)	1.357 (1)	1.210 (4)
150-199	1.171 (12)	1.423 (14)	1.254 (8)	1.308 (7)	1.160 (16)
200-249	1.145 (17)	1.290 (8)	1.138 (11)	1.223 (2)	1.132 (13)
250-299	1.091 (10)	1.219 (13)	1.243 (16)	1.089 (6)	1.096 (23)
300-349	1.083 (12)	1.075 (19)	1.217 (19)	1.161 (12)	1.146 (18)
350-399	1.065 (6)	1.139 (13)	1.116 (9)	1.112 (12)	1.089 (27)
400-449	1.224 (4)	1.014 (4)	1.085 (5)	1.156 (7)	1.037 (17)
450-499	0.914 (1)	---	0.880 (3)	1.230 (1)	1.088 (4)
500-549	---	---	---	---	1.119 (2)

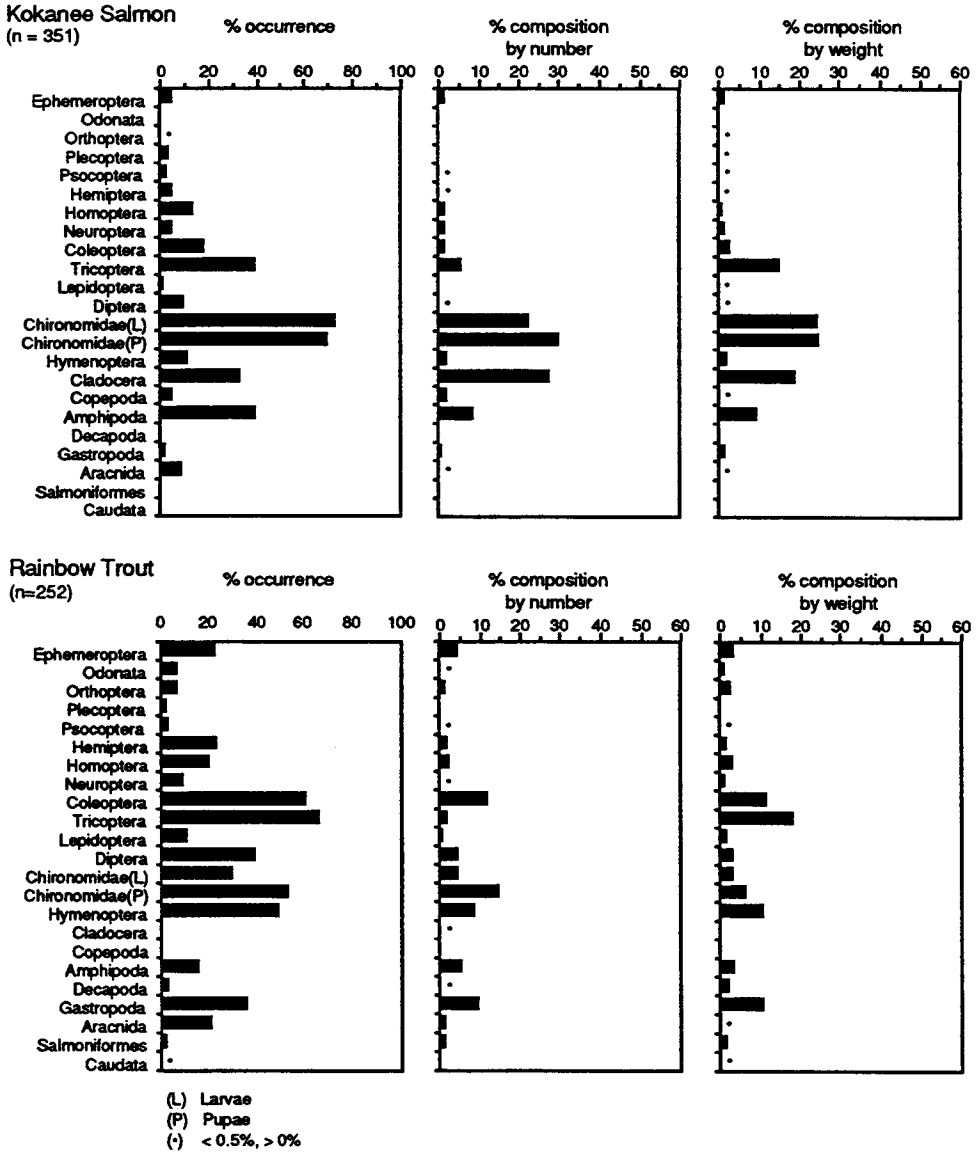


Figure 11. Percent occurrence, percent composition by number, and percent composition by weight of the dates of kokanee salmon and rainbow trout, Crater Lake, Oregon.

food groups listed above accounted for 66% of the diet by weight and 60% of the diet by number for rainbow trout. Food items found in stomachs of rainbow trout and kokanee salmon are listed by taxonomic groups in Appendix 1.

The occurrence of zooplankton in the diet of kokanee salmon varied by year (Table 6). The kokanee sampled in 1988 were in spawning condition and had fed exclusively on *Daphnia pulicaria* with the exception of one fish that had eaten 18 chironomids in addition to *Daphnia*. The stomach linings of the spawners had thinned to transparency. When *Daphnia* decreased in occurrence in the diet from 1989 through 1991, *Bosmina longirostris*, *Chydorus sp.*, and Copepoda (Cyclopoida and Harpacticoida) increased in occurrence. Cyclopoida was the dominant copepod in stomach samples.

Kokanee characteristically fed on a large number of small-bodied prey. The average number of prey per stomach sample was 1,611 (Table 7) and the mean weight of prey items was 1.38 mg. Fifty-six percent of the diet was assumed to be taken from the midwater column, 37% from the benthos, and 7% from the lake surface. Kokanee fed almost solely on aquatic food types.

Rainbow trout fed on large-bodied food types primarily from the lake bottom and the lake surface, with an average of 253 food items per stomach and a mean weight of 10.9 g (Table 7). The mean weight of food items per stomach increased from 4.22 mg for age-I+ trout to 18.22 mg for age-VI+trout (Buktenica 1989). The mean weight of food items was lower for kokanee salmon and rainbow trout captured by gill net than for those captured by angling. Predation by rainbow trout on kokanee salmon was documented for the first time during this study in 1989. Similar

Table 6. Percent occurence of zooplankton in the diet of kokanee salmon in Crater Lake, Oregon for 1986 through 1991.

	1986	1987	1988	1989	1990	1991
Cladocera	18.3	49.7	100.0	92.9	53.3	36.2
Daphnia	18.3	49.7	100.0	92.9	13.3	1.7
Bosmina	0.9	0.0	0.0	7.1	40.0	29.3
Chydorus	0.0	0.0	0.0	0.0	13.3	10.3
Copepoda	0.0	0.6	0.0	0.0	6.7	24.1
No. of stomachs examined	105	165	11	14	15	58

Table 7. Sample size, average number of food items per sample, mean weight of food items, by percent composition by vertical distribution in the water column (by weight), and percent composition by aquatic versus terrestrial origin (by weight) of food items for kokanee salmon and rainbow trout from Crater Lake, Oregon for 1986-1991.

Species	Sample Size	Average Number of Food Items per Sample	Mean Weight of Food Items	Percent Composition by Vertical Distribution			Percent Composition by Aquatic VS. Terrestrial Origin	
	(N)	Count	(Milligrams)	Surface	Column	Benthos	Aquatic	Terrestrial
Kokanee Salmon	351	1611	1.38	7	56	37	96	4
Rainbow Trout[a]	252	249	409.47	33	15	52	71	29
Rainbow Trout[b]	247	253	10.88	34	13	53	70	30

[a] All rainbow trout including trout with fish and salamanders.
[b] All rainbow trout excluding trout with fish and salamanders.

observations continued through 1991. In 1991, 4 of 51 (8%) of the rainbow trout caught in gill nets contained kokanee.

Distribution

The hydroacoustic techniques used during the 1985 acoustic survey allowed for the estimation of fish size based on target strength (Eherenberg, 1974). Scatter plots of unweighted target detections showed two aggregations of fish regardless of location on the lake or time of day (Figs. 12 and 13). These aggregations were best separated at a target strength of -58.3 Db (43 mm). Fish detections were then categorized as small (<43 mm) or large (≥43 mm). Although the scatter plot data are not corrected for sample volume, they are still representative of fish distribution as the sample volume was the same regardless of location or time of day. When detections were normalized by the volume of water sampled, the density of fish in all categories was greatest at the surface, except at night in the offshore zone when large fish were not observed near the surface.

Marino (1987) found that fish near the shore, regardless of size, inhabited shallower water during the day than at night (Table 8). Mean depth of fish offshore did not significantly differ between day and night. However, the scatter plots appeared to indicate an upward migration of large fish at night, or an increase in large fish density in a higher sample strata. Marino (1987) alternately suggested that a downward migration of fish in the offshore zone at night occurred because there were no large fish detected near the surface and the density of fish increased in a lower sample strata. The detection of 49% fewer large fish offshore at night compared to detections during the day, and the detection of 50% more large fish

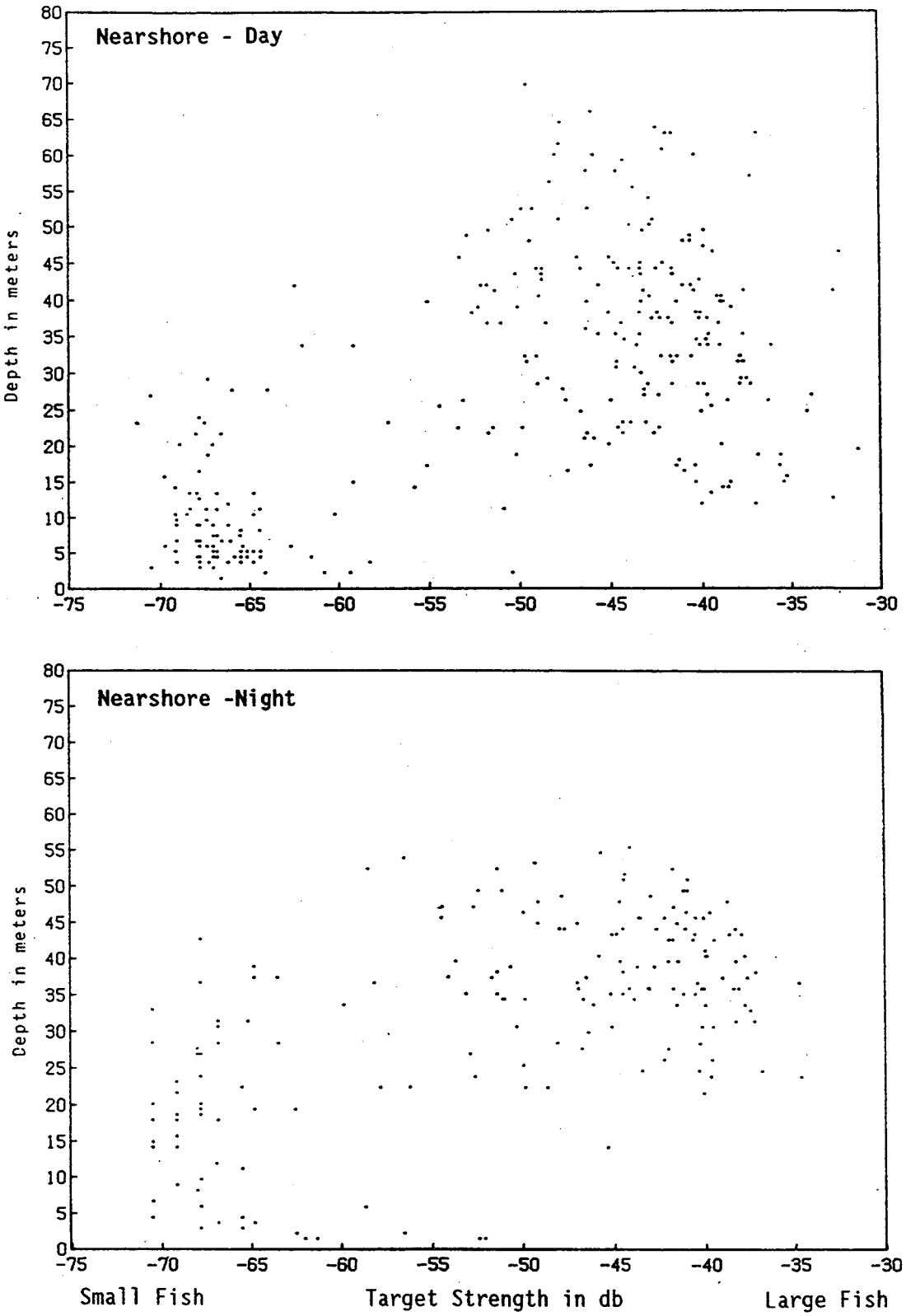


Figure 12. Unweighted hydroacoustic target detections in the nearshore zone of the lake, during the day and at night in August 1985, Crater Lake, Oregon (from Marino 1987).

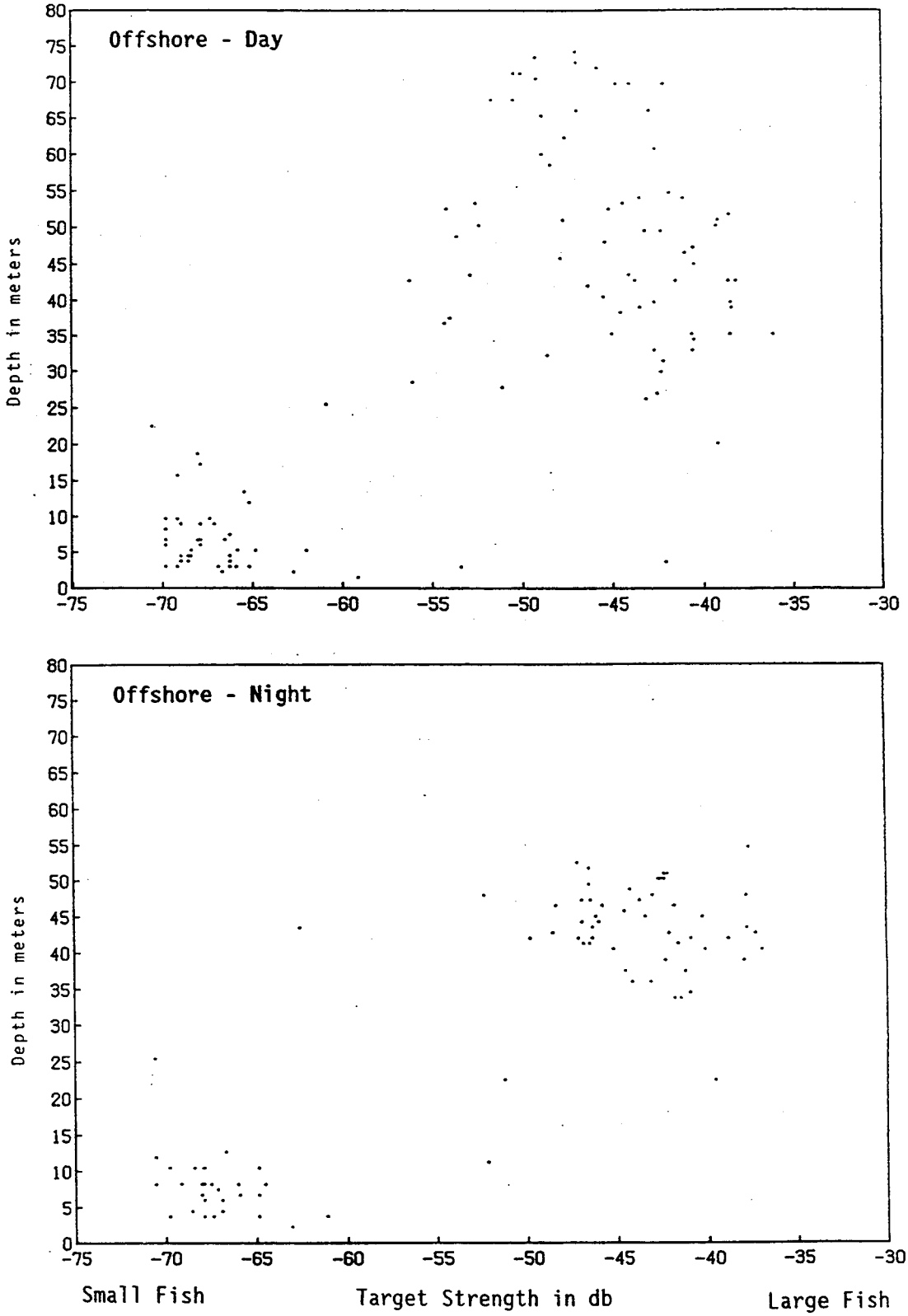


Figure 13. Unweighted hydroacoustic target detections in the offshore zone of the lake, during the day and at night in August 1985, Crater Lake, Oregon (from Marino 1987).

Table 8. Normalized mean depth of fish in the lake during the day and at night for 1985 (Marino 1987) and 1987 (Buktenica 1989) in Crater Lake, Oregon.

		Nearshore		Offshore		Mean
Year	Catagory	Day	Night	Day	Night	Day+Night
1985[a]	Small Fish (≤ 43mm)	10.0	19.7	7.5	9.0	11.6
	Large Fish (> 43mm)	34.9	37.7	44.7	42.5	38.1
	All Fish	22.5	28.7	26.1	25.8	25.8
1987[b]	All Fish	14.6	17.1	57.7	19.8	27.3

[a] No replicate nightime transects.
[b] Replicate nightime transects.

nearshore at night compared to during the day indicated that a migration of large fish occurred shoreward at night. Densities of small fish were higher nearshore than offshore, day and night. However, population estimates were higher offshore than nearshore for small and large fish (Table 9).

The hydroacoustic techniques used in the 1987 acoustic survey did not allow for estimates of fish size. The survey revealed a pattern of diel vertical migration for fish inhabiting the offshore zone (Fig. 14, Table 8). Median depth at which fish were found offshore ranged from 75 m during the day to 19 m at night, which indicated a 56-m daily vertical migration. The maximum depth of detection was 98.5 m. An opposite vertical migration was indicated by the nearshore data (Fig. 14, Table 8). Median depth of fish nearshore ranged from 2 m in the day to 17 m at night. Because near-constant boat speed was maintained during the surveys, fluctuations in the number of fish observed through time may have revealed horizontal migrations between nearshore and offshore areas (Fig. 15). The increase in fish per hour at night in the nearshore zone may have represented a horizontal shoreward migration, or it may have represented greater susceptibility of nearshore fish to the acoustic beam at night than during the day. If fish were strongly associated with the lake bottom for foraging or for cover during the day, their echoes may not have been distinguishable from the bottom echoes. At night, the fish may have left the substrate or drifted away from the caldera wall where they were detected (Thorne and Marino, 1986).

Fish-capture techniques were used in 1986 and 1987 in conjunction with hydroacoustic techniques to assess fish distribution. Downrigger captures verified that fish offshore occurred at deep depths during the day. The downrigger was fished

Table 9. Fish population estimates, for August 1985 in the nearshore and offshore zones of the lake, during the day and at night, in Crater Lake, Oregon (after Marino 1987).

Catagory	Nearshore	Offshore	Total
Small Fish	24,941	91,612	116,553
Large Fish	25,791	78,830	104,621
All Fish	50,732	170,442	221,174

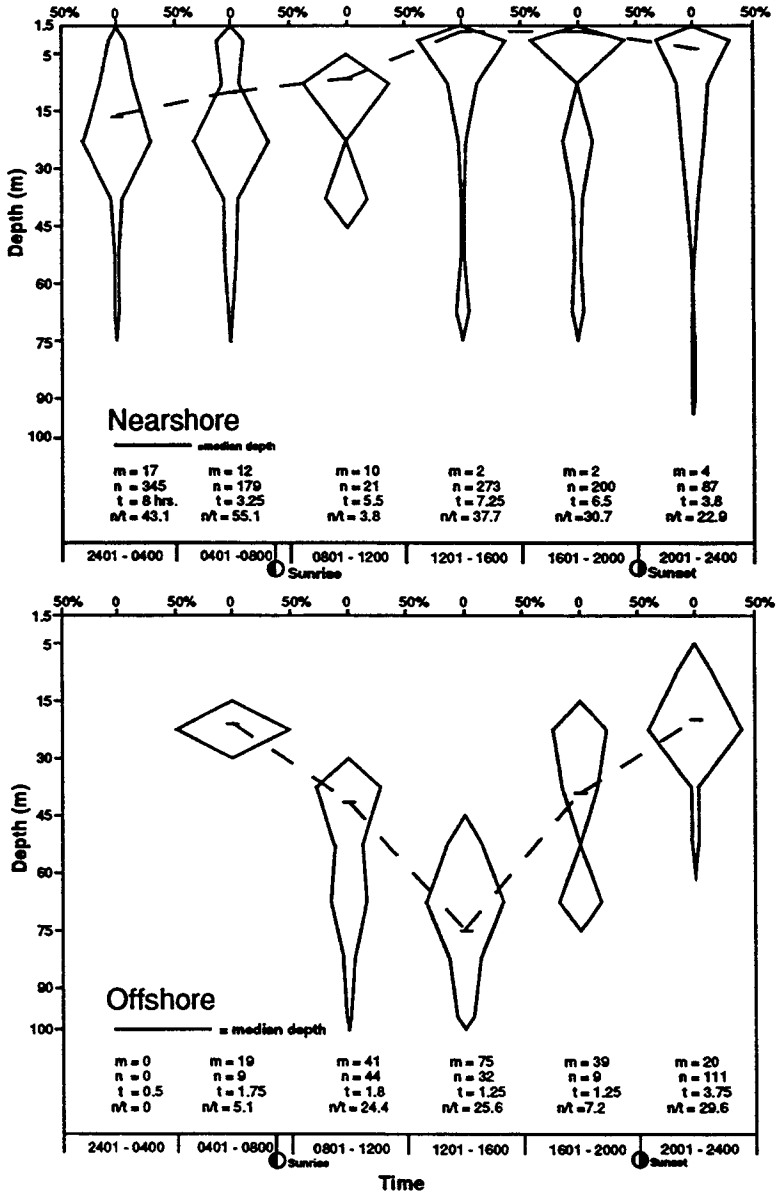


Figure 14. Diel vertical distribution patterns of nearshore and offshore fish in Crater Lake during September 1987, presented as percentage of total sonar contacts. m = median depth, n = number of fish detections, t = total time of transects in each time period, and n/t = fish detections per hour.

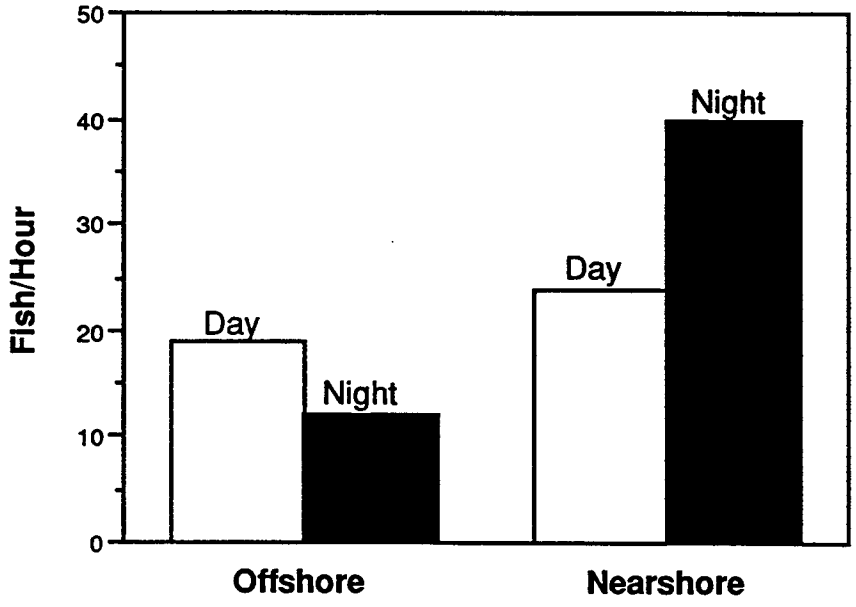


Figure 15. Total sonar contacts per hour (fish/hr), during September 1987 in the nearshore and offshore zones of Crater Lake during the day and night.

offshore between 1200 hours and 2000 hours. Thirty-one fish, all kokanee, were captured. The median depth of fish capture was 65 m and the maximum depth of capture was 86 m. Angling was conducted along the shoreline during the day and in the evening. Most fish caught by angling were rainbow trout. Twenty-one of the 25 kokanee captured by angling were captured after 1800 hours; 20 were captured after 1900 hours. Overnight gill net sets along the shore of the lake were successful in capturing kokanee salmon and rainbow trout.

Schooling behavior of kokanee had been reported in isolated years in the 1960's and 1970's by park personnel. Schools of kokanee were actually seen for the first time as part of the 10-year limnological study in 1989 when schools of several hundred kokanee were observed from mid-morning to mid-afternoon. The fish appeared to be 75-100 mm in length. They either closely followed the shoreline, swimming in 1 to 2 m of water, or they swam near the lake surface in the offshore zone of the lake.

In 1990, schools of kokanee of different size classes were observed in the nearshore and offshore areas of the lake. Numbers and sizes of the schools appeared to be greater than in 1989. Schools that were presumed to be young-of-the-year kokanee were observed by SCUBA divers in the area of Cleetwood Cove. These fish were estimated to be 25 to 60 mm in length. In June, 1990 a single school of fish, estimated to contain 200,000 individuals 100 to 150 mm in length, took 42 minutes to swim past a boat dock at Cleetwood Cove.

The number of kokanee schooling appeared to increase again in 1991. A nearly constant series of schools swam along the shoreline in the early summer, with the schools separated by about 30 to 100 m. In 1991, no schools were observed during

Table 10. Catch per Unit Effort for Kokanee Salmon and Rainbow Trout in Crater Lake, Oregon for June Only and June through July 20 for 1986 Through 1991.[a]

	Kokanee Salmon		Rainbow Trout	
Year	June	June/July	June	June/July
1986	4.4	4.7	1.0	1.0
1987	10.0	6.5	3.0	1.3
1988	NA	NA	NA	NA
1989	24.0	14.5	13.7	8.0
1990	NA	21.3	NA	2.0
1991	42.7	24.8	4.6	4.3

[a] NA signifies no data available.

The CPUE for kokanee salmon for June doubled from 1986 to 1987, doubled again from 1987 to 1989, and nearly doubled again from 1989 to 1991. There were no changes in sample procedure that could account for these dramatic increases. The rate of capture of rainbow trout was too low and variable to assess trends.

Kokanee salmon weight per unit effort (WPUE) increased dramatically from 1986 to 1989 (Table 11). Kokanee WPUE may have risen slightly from 1989 to 1990 (June through July 20 data) and then dropped in 1991 even though CPUE continued to rise (Fig. 16). Rainbow trout WPUE varied due to small sample sizes and large variability in size of fish captured.

Discussion

Kokanee salmon in Crater Lake appeared to exhibit a cyclic pattern in population age structure, condition, abundance, and biomass. One dominant year class of kokanee was present in 1986 and 1987. Most of this year class spawned in January 1988 at age III+, although some individuals spawned at age II+ and age IV+. Age-class dominance in kokanee salmon of Crater Lake was noted by Kibby (1966). Dominant year classes in kokanee populations were reported in Odell Lake, Oregon (Lewis 1971) and Flathead Lake, Montana (Hanzel 1984). Kokanee are a landlocked form of sockeye salmon and sockeye populations usually have a dominant and a sub-dominant spawning year. Some sockeye populations exhibit striking 4-to-5 year spawning cycles (Scott and Crossman 1973). Mechanisms for maintaining the dominant or cyclic patterns are variable. Dominant year classes of fry often deplete zooplankton forage in their nursery lakes as appears to be the case in Crater

Table 11. Weight per Unit Effort (mg) for Kokanee Salmon and Rainbow Trout in Crater Lake, Oregon for June Only and June through July 20 for 1986 Through 1991.[a]

	Kokanee Salmon		Rainbow Trout	
Year	June	June/July	June	June/July
1986	468.2	535.5	85.5	351.3
1987	1922.7	1352.6	828.0	377.6
1988	NA	NA	NA	NA
1989	3814.3	2213.8	4397.3	2562.7
1990	NA	2352.5	NA	845.8
1991	3543.0	2106.0	1887.7	2318.7

[a] NA signifies no data available.

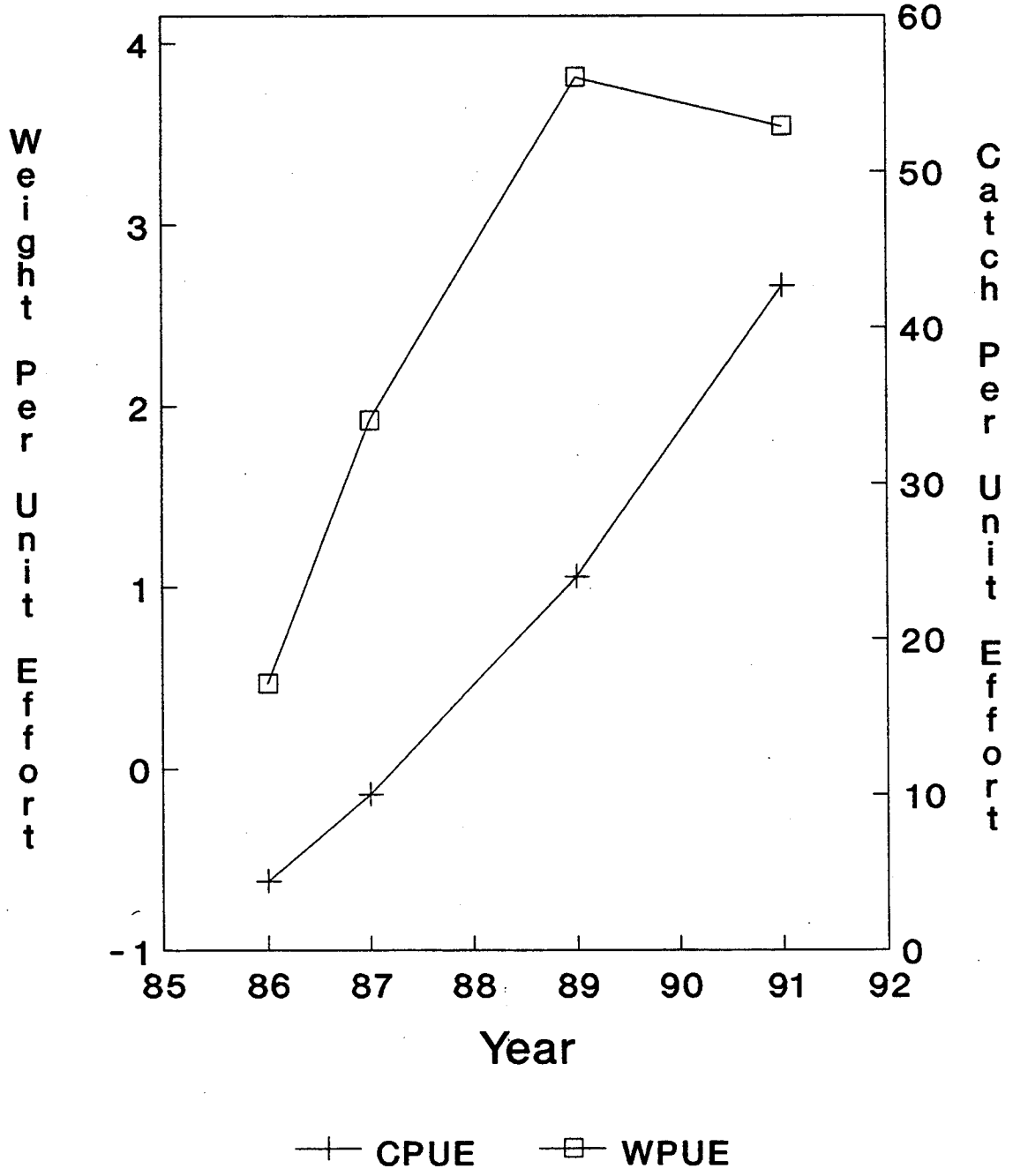


Figure 16. Relative abundance or catch per unit effort (CPUE) and relative biomass or weight per unit effort (WPUE) for kokanee salmon, Crater Lake, Oregon.

Lake in 1990-91 (see Zooplankton section). The recovery of the zooplankton biomass may take several years depending on limnological characteristics of the lake. The Crater Lake kokanee population structure diversified in terms of age structure and length- frequency distribution from 1989 through 1991.

Catch per unit effort of kokanee rose dramatically during the course of this study. It is unclear why catch per unit effort increased between 1986 and 1987 as most of the kokanee were of the same year-class. Weight per unit effort closely followed catch per unit effort until 1989 when relative biomass declined while the relative abundance continued to rise. The drop in biomass may be explained in part when looking at the condition of kokanee over this same time period. As relative abundance rose, the condition of the kokanee fell significantly (Fig. 17). Fecundity and recruitment probably declined with the dramatic drop in condition. The maturing kokanee captured during the fall of 1991 appeared thin and emaciated with poor gonad development. The kokanee population should collapse in the mid-1990's if the population is displaying cyclical patterns of age structure, condition, abundance, and biomass. The collapse may be followed by a single, dominant year class of low abundance and high condition.

Growth of kokanee salmon varied with condition and abundance. At low abundance, kokanee growth was comparable to growth of other kokanee populations in oligotrophic lakes in Oregon and elsewhere (Table 2, Table 3).

Age-frequency and length-frequency relationships for rainbow trout indicated that the population was composed of multiple age classes and multiple size classes. Age- and length-frequency histograms suggested a trend toward an increase in relative abundance of older age classes and larger fish from 1986 to 1991. The average fork

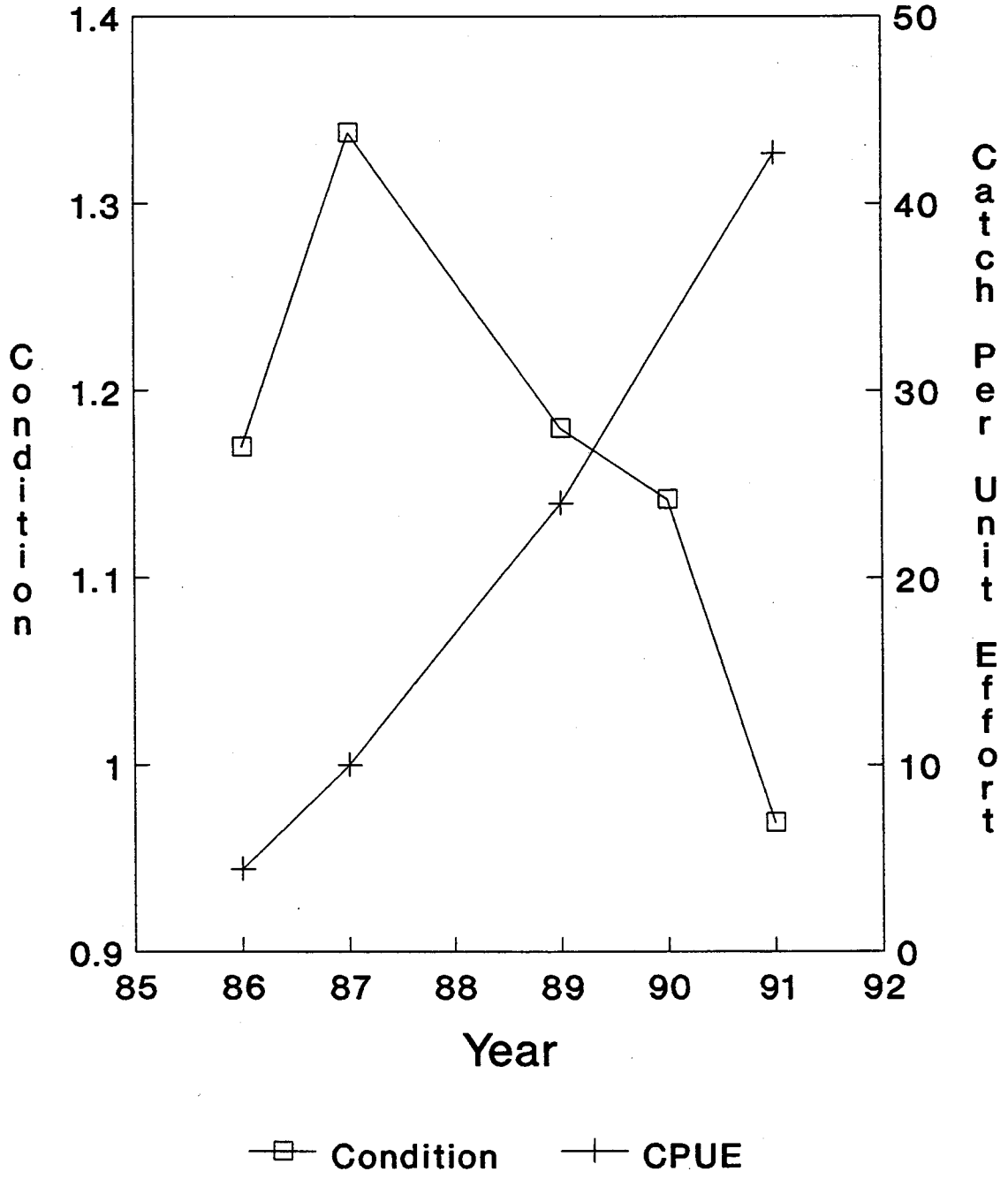


Figure 17. Fulton's condition factor and relative abundance or catch per unit effort (CPUE) for kokanee salmon, Crater Lake, Oregon.

length and the percentage of the trout population over 400 mm in length also increased during the study period. The increase in these population characters corresponded to an increase in the relative abundance of kokanee salmon (Figs. 18 and 19). These data suggest that the average length and perhaps the maximum length of trout in Crater Lake may be dependant on the availability of kokanee salmon as part of the prey base. If kokanee abundance is cyclic in nature, then length-frequency trends for rainbow trout may also be cyclic. Previous investigators at Crater Lake found the growth and average size of rainbow trout and "silversides" to be greater than found in this study for trout and kokanee salmon (Hasler 1938, Hasler and Farner 1942).

Kokanee feed primarily on zooplankton (Cordone et. al. 1971, Rieman and Bowler 1980, Scott and Crossman 1973). When zooplankton abundance is low, they often feed on chironomid pupae and larvae, and to a lesser degree, other benthic organisms (Northcote and Lorz 1966, Scott and Crossman 1973). During this study, *Daphnia pulicaria* was particularly important in the diet of kokanee. The percent occurrence of *Daphnia* in the diet of kokanee followed the same trend as the abundance of *Daphnia* in the lake. As *Daphnia* decreased in abundance in the lake between 1988 and 1991, other cladocerans and copepods increased in percent occurrence in the diet of kokanee.

Previous investigations of food habits of fish at Crater Lake demonstrated that *Daphnia* fluctuated greatly in importance in the diet of "silversides" and kokanee. Hubbard (1933) stated that *Daphnia* comprised 14% of the fish food. Brode (1935) found *Daphnia* in 74% of the stomachs of fish sampled (mostly "silversides") in 1934,

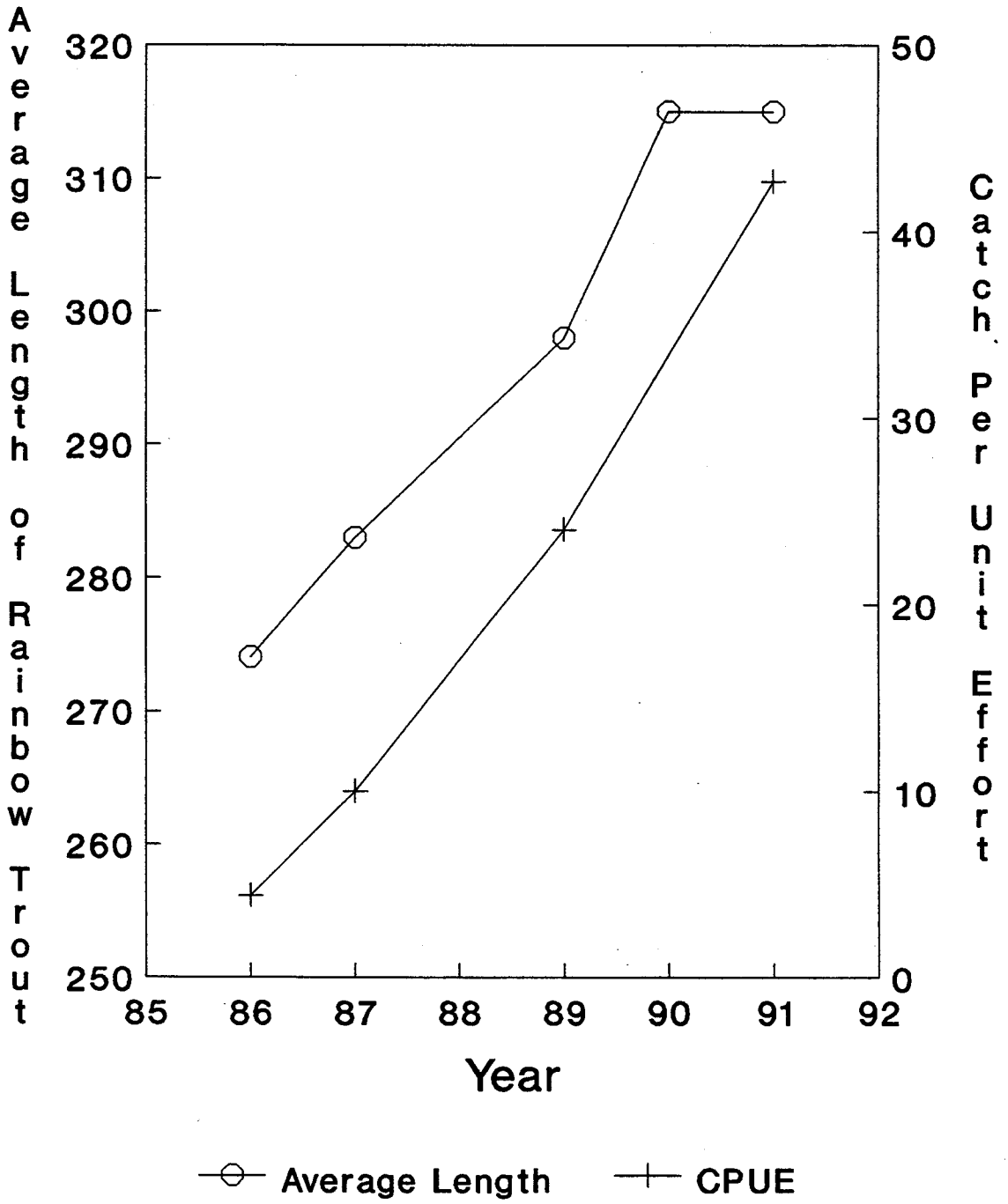


Figure 18. Average fork length for rainbow trout and relative abundance or catch per unit effort (CPUE) for kokanee salmon, Crater Lake, Oregon.

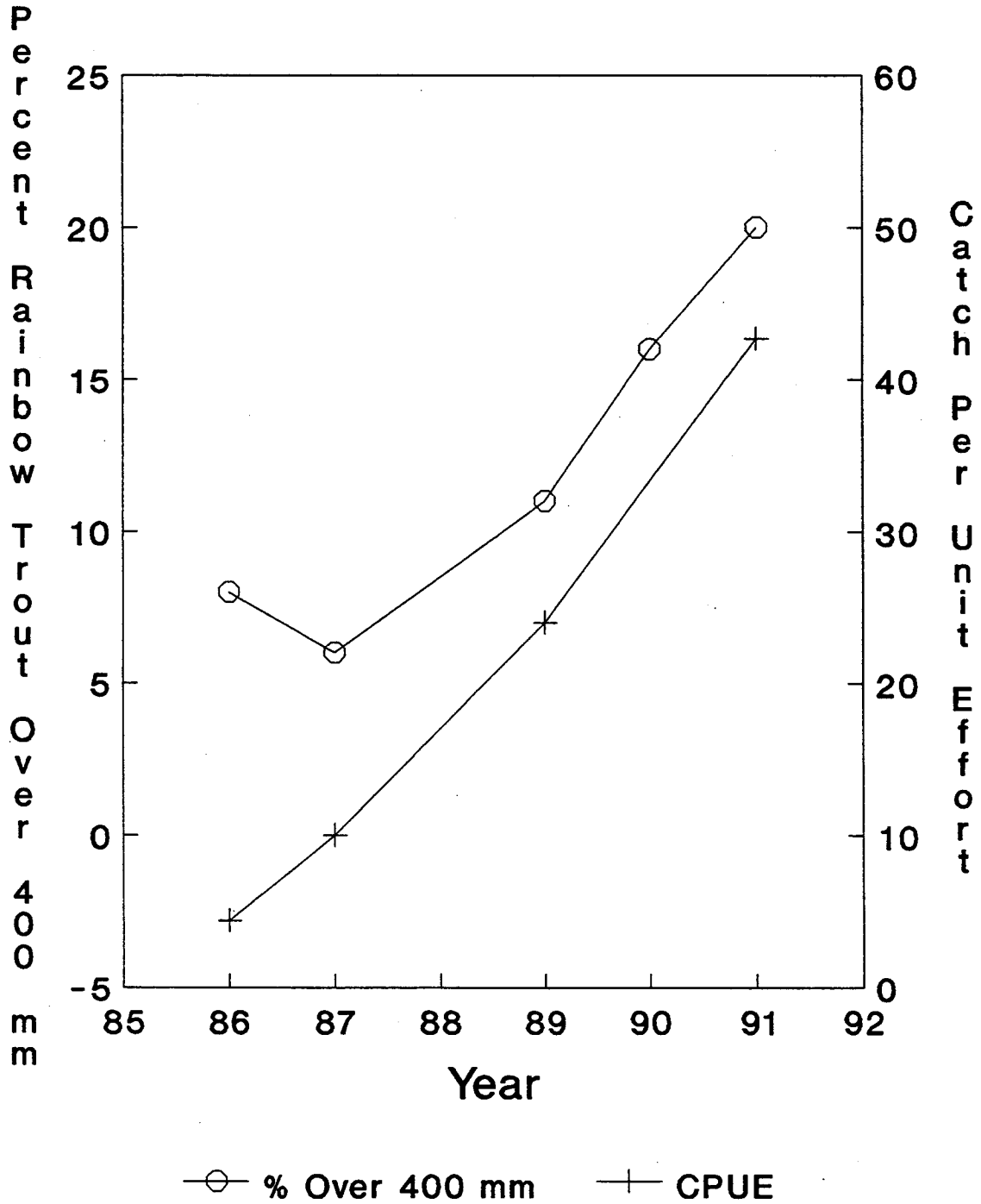


Figure 19. Percent composition of rainbow trout over 400 mm and relative abundance or catch per unit effort (CPUE) for kokanee salmon, Crater Lake, Oregon.

and in 51% of the stomachs of fish sampled from 1934 to 1936 (Brode 1937). *Daphnia* accounted for 62% of the total fish food by volume in 1934 and 34% of total fish food by volume from 1934 to 1936. In 1940 Hasler and Farner (1942) found *Daphnia* in only one silverside stomach. They noted that the absence of *Daphnia* in surface plankton tows, conducted from the surface to 100 m, contrasted to its abundance in similar tows in 1937 (Hasler 1938). Patten and Thompson (1957) did not record any *Daphnia* in stomach samples of kokanee, although this may have been a result of sample preparation. They concluded that the important food types (by frequency and by volume) for kokanee were Diptera (Chironomidae), Trichoptera, and Amphipoda. These same food types, plus Cladocera, were the primary food types of importance for kokanee during this study.

Rainbow trout typically feed on benthic and terrestrial invertebrates, although piscivory is common and planktivory may occur (Scott and Crossman 1973). Rainbow trout fed on a greater variety of food types then kokanee salmon did during this study. Although the relative importance of particular food types varied between past studies the general food habits of trout and salmon were similar with those found here. Kokanee fed heavily on taxa found in the midwater column and off the lake bottom. Rainbow trout fed off the lake bottom and on insects from the lake surface. Patten and Thompson (1957) stated that "the stomach contents indicate that rainbow feed as actively at the surface as below . . . while most of the kokanee foods were taken below the surface." Where their diets overlapped, kokanee tended to take smaller-bodied taxa. Patten and Thompson also noted "the kokanee usually preferred the smaller forms of the insect orders."

Crater Lake kokanee are morphologically better adapted to feed on smaller prey than the prey consumed by rainbow trout because kokanee have narrower mouths and a greater number of gill rakers that are longer and closer together than the trout's (Buktenica 1989, Buktenica and Larson 1990). Gill raker counts were within the expected ranges for each species (Mottley 1936, Vernon 1957, Bidgood and Berst 1967, Nelson 1968, Kurenkov 1977).

Chironomids were important in the diet of rainbow trout and kokanee salmon, however, over 95% of the chironomid larvae eaten by kokanee were of the genus *Heterotrissocladius* (previously misidentified as *Parametriocnemus* in Buktenica 1989). Only four rainbow trout stomachs were found to contain prey of this genus. This is the same genus collected by the authors in the deep basin of the lake with the one-man submersible Deep Rover (see Benthic Macroinvertebrate section). *Heterotrissocladius* larvae were also collected in pelagic zooplankton tows. *Heterotrissocladius* larvae found in the stomach samples and the zooplankton tows were all in the fifth larval instar suggesting that this chironomid begins it's migration to the lake surface before pupation in Crater Lake. Salamanders and small fish were found in the stomachs of trout in earlier studies, but not found in trout stomachs during this study until 1989.

Distributions of fish within lakes represent responses to dynamic interactions among physical, chemical, and biological components of lake ecosystems. Vertical and horizontal migrations of fish are common and are believed to be responses to the interaction among some combination of these components. The most pertinent components appear to be feeding habits closely linked to light intensity (Ricker 1938, Northcote et al. 1964, McDonald 1973), avoidance to predation (Eggers 1978,

Wurtsbaugh and Li 1985), competition (Collins 1971), behavioral thermoregulation (Finnel and Reed 1969), and spawning (Lorz and Northcote 1964). It is difficult to evaluate the relative importance of these variables to the distribution patterns of fish because the interactions are dynamic and complex. Northcote et al. (1964) observed vertical diel migration of kokanee to reverse in succeeding years. In Lake Tahoe, relative abundance of kokanee and rainbow trout that were captured in offshore and nearshore gill net catches fluctuated seasonally (Cordone et al. 1971).

Kokanee salmon distribution patterns varied during the 10-year lake studies program. Through 1987, kokanee were primarily found offshore in deeper water during the day, at night they migrated shoreward and to shallower water. Observations from 1989 to 1991 suggested that the predominant distribution pattern for kokanee reversed from that found earlier. Kokanee were observed schooling nearshore during the day, closely following the shoreline. The high occurrence of pelagic cladocerans in the kokanee stomach samples combined with several observations of kokanee feeding in the offshore zone of the lake at dusk suggested that kokanee dispersed offshore and, perhaps, migrated downward at night. This was supported by the low catch rates of kokanee in the gill nets at night in the latter part of the summer. Capture success indicated that some kokanee remained nearshore at night throughout the summer. During this study, pelagic *Daphnia* were typically found at highest densities between 80 m and 120 m in depth during the day and an average of 40 m shallower at night (see Zooplankton section).

Rainbow trout appeared to remain nearshore throughout the study, shallower during the day and deeper at night. However, several trout were observed near the surface of the lake in the offshore zone of the lake during the day.

One of the most interesting aspects of the distribution of Crater Lake fish is the unusually deep occurrence and the great magnitude of diel migrations. A maximum depth of 81 m was recorded for an acoustic target in 1985 in Crater Lake and 98.5 m in 1987. The maximum depth of capture of kokanee in Crater Lake was 86.25 m in 1987. The maximum depths of occurrences for kokanee reported in the literature include 28.5 m in Horsetooth Reservoir, Colorado (Horak and Tanner 1964); 36.5 m in Lake Tahoe, California (Cordone et al. 1971); 30.0 m in Odell Lake, Oregon (Lewis 1972); and 36.5 m in Flathead Lake, Montana (Hanzel 1984).

The deep-water occurrences of offshore fish may be related to the deep penetration of light in Crater Lake, and perhaps the deep-water occurrences of chlorophyll and zooplankton. There does not appear to be a direct relationship between fish distribution and temperature, dissolved oxygen, or pH because the thermoclines were shallow, and dissolved oxygen and pH were fairly uniform throughout the water column. Apparently distributions of Crater Lake fish were most closely associated with feeding habits. Kokanee salmon are believed to feed primarily on cladocerans and chironomids in the deep-water offshore zone of the lake. Rainbow trout appeared to feed primarily in the nearshore area of the lake, rising to shallower depths during the day and feeding heavily on insects from the lake surface. The schooling behavior of kokanee salmon, when relative abundances of younger age classes were high, is perhaps a remnant behavior from the anadramous form, sockeye salmon, which seeks surface outflows for ocean migration.

Long-term Implications of Fish Introductions

Kokanee salmon and rainbow trout play different ecological roles in Crater Lake. The salmon and trout differed in morphology (Buktenica and Larson 1990), food habits, and the cyclic nature of age structure, distribution, abundance, biomass, and condition. The differences in feeding habits and distributions are likely a response, in part, to morphological and behavioral differences between kokanee salmon and rainbow trout. Direct and indirect interactions between the two species may also account for some proportion of the observed differences.

There has been a considerable amount of work on the dynamics of trophic interactions of limnetic lake communities (Hrbacek et al. 1961, Henrikson et al. 1980, Benndorf et al. 1984, Shapiro and Wright 1984, Carpenter et al. 1985, McQueen et al. 1986). Much of this work emphasized how fish affect community structure and organization through direct and indirect interactions. Historically this discussion has focused on two seemingly contradictory views. The first view conceptualizes lake ecosystems as being driven from the "bottom up" (controlled by producers), where nutrient loading determines the productivity and biomass of phytoplankton, zooplankton, planktivorous fish, and piscivorous fish. The second view conceptualizes lakes as being driven from the "top down" (controlled by consumers), where the top consumer, often a piscivorous fish, influences the community structure and biomass of lower trophic levels. These interactions affect the availability of dissolved nutrients and nutrient recycling rates (Hrbacek et al. 1961, Henrikson et al. 1980, Shapiro and Wright 1984). Both the top-down and bottom-up pathways may affect water clarity, primarily as a function of changes in the phytoplankton community (Henrikson et al. 1980, Shapiro 1980, Benndorf et al. 1984, Shapiro and Wright 1984). An increase in a

pelagic zooplanktivorous fish, such as kokanee salmon, could be associated with a decrease in lake clarity, but the relationship between zooplankton community characteristics and lake clarity remains unresolved.

The structure and organization of lake communities is a dynamic response to controls and interactions from both the top down and the bottom up (Carpenter et al. 1985, Benndorf et al. 1984). McQueen et al. (1986) found the bottom-up controls to be strongest at the bottom of the food web (nutrients to phytoplankton to zooplankton) and to weaken as one moves up the food web. Conversely, top-down effects are strongest between top consumers and weaken as one moves down the food web. The predictability of responses of community subunits weakens as you move away from the controls.

Trophic interactions are also dynamic in the benthic sub-community. Fish introductions may alter benthic community structure and organization through a variety of poorly-understood pathways. These changes may be expressed as local extinctions (Reimers 1979), changes in relative abundance, changes in distribution (Macan 1966a, Macan 1966b), reduced mean weights of prey species, or reduced biomass of benthic prey populations (Post and Cucin 1984).

Fish have the potential of altering the nutrient and energy flows through trophic interactions within and between benthic and limnetic communities. In addition to feeding on prey in both communities, fish intercept many larvae and pupae before these prey types leave the lake as adults. Fish also intercept aquatic and terrestrial adult invertebrates at the lake's surface, before the invertebrates sink to the lake bottom. Excretions from the fish help to recycle nutrients within and between the two communities (Tatrai 1987).

The limnetic invertebrate community in Crater Lake is relatively simple and devoid of invertebrate predators. Recently, the limnetic zooplankton community has been dominated in number by rotifers. Previous zooplankton investigations between 1896 and 1969 found *Daphnia* abundance to range from very rare to very abundant and dominance to shift between rotifers, *Bosmina* and *Daphnia* (see Zooplankton section). The current community structure is consistent with that of a zooplankton community under predatory control; preferential feeding by zooplanktivorous fish has been shown to cause a shift in zooplankton community structure from large-bodied cladocerans to small-bodied cladocerans and rotifers (Brooks and Dodson 1965).

Changes in abundance of *Daphnia* appear to be related to changes in the relative biomass of kokanee salmon in Crater Lake (Fig. 20). In Fig. 20, the dashed lines represent estimates in kokanee biomass between sample points, based on life history results presented earlier. The 1985 to 1987 data represent the biomass of one dominant year class of fish. In January, 1988 most of this year class spawned and died. Biomass of kokanee rose through 1990 as fry from the 1987, 1988, and 1990 year classes grew in body size. In 1991 kokanee biomass fell, corresponding with a decrease in condition. Apparently, kokanee salmon were effective in cropping the *Daphnia* population and altering zooplankton community structure during the study period.

Little biomass or abundance data for benthic biota were available to evaluate possible impacts of introduced fish to this community in Crater Lake (see Benthic Macroinvertebrate section). Both rainbow trout and kokanee salmon interact with the benthic community. The salamanders *Ambystoma macrodactylum* and the Crater Lake

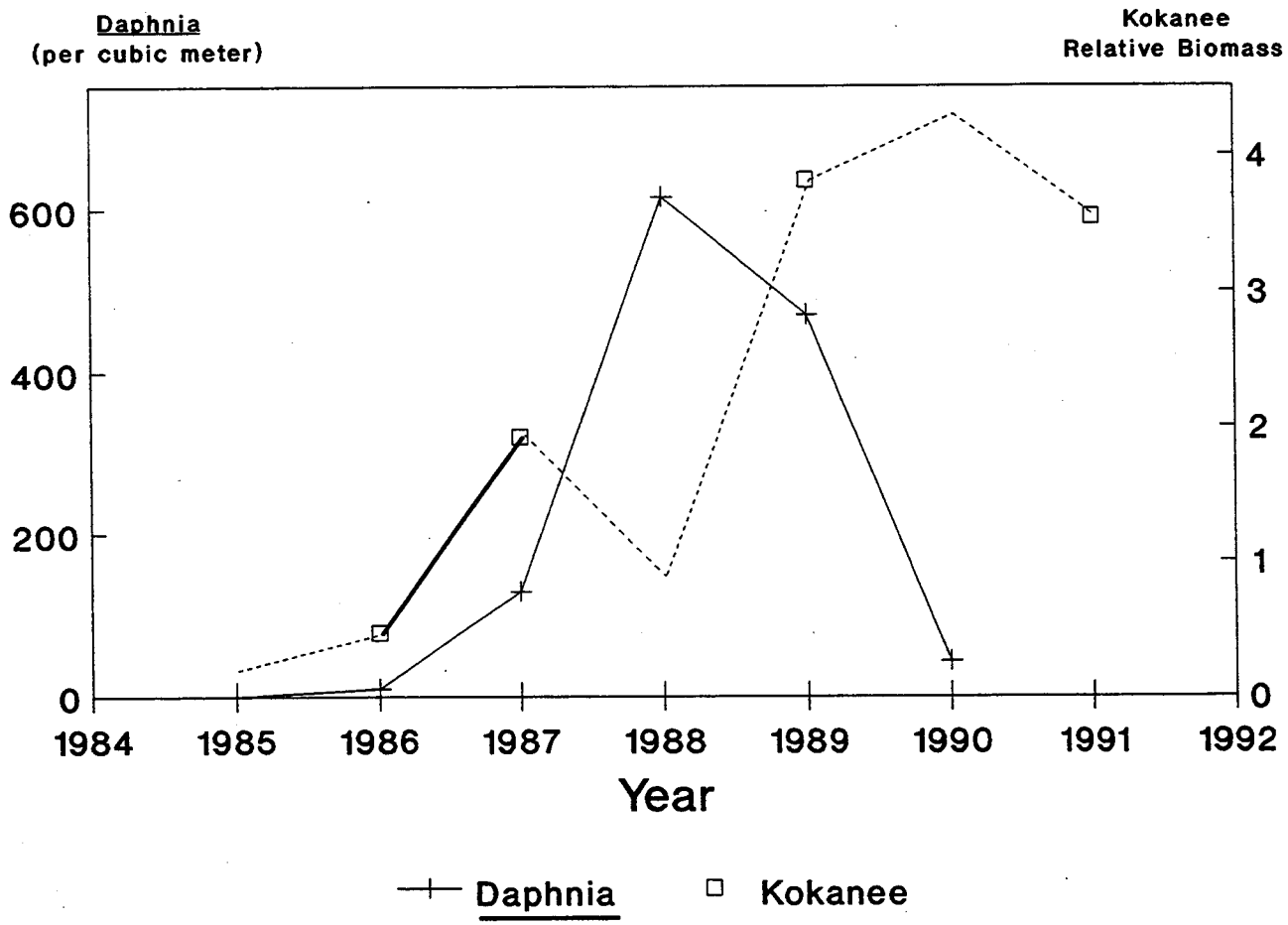


Figure 20. Relative biomass of kokanee salmon and density of Daphnia in Crater Lake, Oregon. The dashed lines represent estimates between sample points based on kokanee salmon life history stages. Densities of Daphnia were integrated from 0 to 200 m in depth from May through September.

Newt, *Taricha granulosa mazamae*, were once common in the lake (Brode, 1938). *Ambystoma macrodactylum* was extremely rare during the study period, the Crater Lake Newt was seldom observed. Both species of salamander were found, in small numbers, in trout stomach samples.

It is clear from the discussion above that introduced fish in Crater Lake have the potential to impact limnetic and benthic community structures and nutrient flux within and between the communities. With a better understanding of the ecology of the fish in Crater Lake, future work should address long-term implications and mitigation of historic fish introductions.

Acknowledgments

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Appendix 1. Life Stage, Mean Weight, and Percent Composition by Aquatic Versus Terrestrial Production (by Weight) and by Vertical Distribution in the Water Column (by Weight) for each Prey Taxa Found in Kokanee Salmon and Rainbow Trout Stomach Samples, Crater Lake, Oregon.

Taxa	Life Stage[a]	Mean wt. (mg)[b]	%Comp. by A vs T[c]	% Comp. by Vert. Dist.[d]	Comments
EPHEMEROPTERA					
Baetidae					
Callibaetis sp.	L	2.45	A	B	-mostly pre-emergent larvae
ODONATA					
Anisoptera	A	(70.0)	T	S	-all adults
Zygoptera	A	(12.0)	T	S	-all adults
ORTHOPTERA	A	100.0	T	S	
PLECOPTERA					
Chloroperlidae	L	(4.0)	A	B	
	A	(4.0)	A	S	
Sweltsa sp.	A	--	A	S	
Triznaka pintada	A	--	A	S	
PSOCOPTERA	A	0.18	T	S	-all adult bark lice
HEMIPTERA					
Aquatic					
Gerridae	A	9.0	A	S	
Corixidae	A	3.31	A	B	-all adults
Notonectidae					
Notonecta sp.	A	10.0	A	B	-all adults
Terrestrial					-no dominant taxa
Misc. large	A	37.97	T	S	
Misc. small	A	0.82	T	S	
Pentatomidae	A	16.11	T	S	
HOMOPTERA					
Cicadellidae	A	0.32	T	S	-common
Membracidae	A	5.82	T	S	-rare
Cicadidae	A	104.5	T	S	-rare
Aphidae	A	0.09	T	S	-common, all winged adults
NEUROPTERA					
Hemerobiidae	A	0.805	T	S	-all adults
Sialidae					
Sialis rotunda	L	6.31	A	B	
	A	(8.0)	A	S	
COLEOPTERA					
Aquatic					
Dytiscidae	L	(5.0)	A	B	
	A	9.06	A	B	
Hydrophilidae	A	0.75	A	B	-rare
Terrestrial					
Misc. large	A	15.04	T	S	-mostly arboreal
medium	A	2.99	T	S	taxa, fewer
small	A	0.24	T	S	-ground and shoreline taxa
Buprestidae	A	--	T	S	
Elateridae	A	--	T	S	
Scolytidae	A	--	T	S	
Staphylinidae	A	--	T	S	

Appendix 1 (continued)

Taxa	Life Stage[a]	Mean wt. (mg)[b]	% Comp. by A vs T[c]	% Comp. by Vert. Dist.[d]	Comments
TRICOPTERA					-case dwellers weighted without cases
Rhyacophilidae					
Rhyacophila sp.	L	(5.0)	A	B	-rare, stream dweller
Hydroptilidae					
Hydroptila sp.	L	(0.25)	A	B	
	P	(0.20)	A	C	
	A	(0.15)	A	S	
Polycentropidae					
Polycentropus variegatus	L	2.75	A	B	
	P	2.51	A	C	
	A	2.29	A	S	
Limnephilidae					
Clistoronia magnifica	L	(20.0)	A	B	-5th instars in organic cases
	P	(32.0)	A	C	
	A	(29.2)	A	S	
Dicosmoecus atripes	L	(75.0)	A	B	-5th instars in mineral cases
	P	(36.4)	A	C	
Ecclisomyia conspersa	L	6.26	A	B	-range of instars
	P	4.01	A	C	
	A	(3.0)	A	S	
Imania sp.	L	(2.0)	A	B	-rare, stream taxa
Neophylax sp.	L	(3.0)	A	B	-rare, stream taxa
Psychoglypha sp.	L	(10.0)	A	B	-rare, stream taxa
Limnephilus sp.	A	(4.0)	A	S	-adults only
L. acula	A	--	A	S	
L. fagus	A	--	A	S	
L. spinatus	A	--	A	S	
LEPIDOPTERA	A	44.48	T	S	-all adults
DIPTERA					
Brachycera large	A	4.04	T	S	-misc. terrestrial taxa
medium	A	1.35	T	S	
small	A	0.63	T	S	
Nematocera					
Misc.	A	0.298	T	S	
Tipulidae	L	2.0	A	B	
	A	4.90	A	S	
Chironomidae	L	0.26	A	B	
	P	0.25	A	C	
Tanypodinae					
Procladius sp.	L	--	A	B	
Zavrelimyia sp.	L	--	A	B	
Diamesinae					
Diamesa sp.	L	--	A	B	
Pseudodiamesa sp	L	--	A	B	
Orthocladiinae					
Cricotopus sp.	L	--	A	B	
Heterotrissocladius sp.	L	--	A	C	
Orthocladius sp.	L	--	A	B	

Appendix 1 (continued)

Taxa		Life Stage[a]	Mean wt. (mg)[b]	% Comp. by A vs T[c]	% Comp. by Vert. Dist.[d]	Comments
DIPTERA (continued)						
Chronominae						
Phaenopsectra sp.		L	--	A	B	
HYMENOPTERA						
Ichneumonoidea						
Misc.						
parasitroids	large	A	12.55	T	S	
	medium	A	1.50	T	S	
	small	A	0.238	T	S	
Formicidae	large	A	37.0	T	S	
	medium	A	9.59	T	S	
	small	A	0.76	T	S	
CLADOCERA						
Daphia pulicaria		--	0.011	A	C	
Bosmina longirostris		--	0.0015	A	C	
Chydorus sp.		--	--	A	C	
COPEPODA						
Harpacticoida		--	0.011	A	C	
Cyclopoida		--	0.011	A	C	
AMPHIPODA						
Talitridae						
Hyalella azteca		--	0.57	A	B	
DECAPODA						
Astacidae						
Pacifasticus leniusculus		--	596.0	A	B	
GASTROPODA		--	4.72	A	B	-weights include shell
Planorbidae						
Vorticifex effusa		--	--	A	B	-common
Lymnaeidae						
OSTRACODA		--	0.011	A	B	
PELECYPODA		--	0.6	A	B	
ARACHNIDA						
Misc.	large	--	7.25	T	S	
	medium	--	2.08	T	S	
	small	--	0.29	T	S	
Acari		--	(0.01)	A	B	

[a]Life Stage: L = larvae, P = pupae, A = adult

[b]Mean weights of food items from replicate sets of one to one hundred individuals of the least digested individuals of each taxa. ( ) denotes estimated weights based on equivalent sized specimens)ethanol preserved) in data sets available through R.W. Wisseman and N.H. Anderson, Oregon State University, Department of Entomology.

[c]Percent Composition of the Diet by Aquatic vs Terrestrial production: A = aquatic, T = terrestrial.

[d]Percent Composition of the Diet by Vertical Distribution in the Water Column: S = water surface, C = mid-water column, B = benthos.

-- denotes data not available.
Species identifications by R.W. Wisseman, Oregon State University, Department of Entomology.

Benthic Macroinvertebrates of Crater Lake and Caldera Springs[1]

R.W. Wisseman, N.H. Anderson, M. Buktenica, and G. Larson

A brief, qualitative survey of the benthic macroinvertebrate fauna of Crater Lake was conducted during the summers of 1988 and 1989. Emphasis was placed on determining the taxa present and describing habitats occupied by the taxa. Relative abundance of common taxa in various habitats is described in this report.

Methods

Sampling and collecting benthic macroinvertebrates from habitats in Crater Lake was challenging. It was impossible to sample the littoral zone, which consisted primarily of large rock and bedrock substrates, to obtain samples for quantitative analysis. Below 100 m, the deep-water moss, *Drepanocladus*, covered most of the bottom and prevented complete closure of dredges. Although the mud of the abyssal plains could be sampled using a dredge, the great depths involved made this a time-consuming chore. In the summer of 1988, submerged funnel traps were deployed in the littoral zone in an attempt to obtain semi-quantitative estimates of adult insect production from several habitat types. Severe wave action prevented successful operation of these traps. Thereafter, greater emphasis was placed on obtaining qualitative collections of benthic macroinvertebrates from the littoral zone.

Scuba divers obtained sweep-net samples from substrates at a number of locations in the lake (Table 1). The effective sampling depth of the divers was limited to above 15 m. At each location, divers used a hand-held sweep net with a collection bag

[1]In this section, the term springs refers to inlet streams, not hydrothermal springs within the lake, unless noted otherwise.

Table 1. Locations of transects sampled for benthic macroinvertebrates by divers.

Boat dock (Wizard Island) at 0, 20 and 25 ft depths; Fumarole Bay (Wizard Island) at 0, 6, 10 and 30 ft depths; Black Sand Beach (Wizard Island) at 0, 10, 20, 25, 30, 40, and 50 ft depths; Macrophyte beds and gravel substrates near springs 21 and 48; Buoy bay (boat moorage area) at 10, 15, 20, 25, 30, 35, 40, 45, and 50 ft depths; Lady of the Lake at 0, 10, 20, 30, 40 and 50 ft depths; Steele Bay at 0, 12, 20 and 40 ft depths; Phantom Ship at 0, 15, 20, 25 and 40 ft depths.

(250 μm mesh) and scrub brushes to collect samples from several substrates at several depths. Samples from all microhabitat types present along a transect were collected. Microhabitat types included: bedrock faces, boulder surfaces, cobble bars, gravel bars, bars of sand and fine gravel, submerged macrophytes, beds of filamentous green algae, accumulations of fine particulate organic matter (FPOM) or ooze between boulders, accumulations of wood and bark fragments, branch and bole-wood, and moss (not *Drepanocladus*) on the lake margin. Opportunistic collections were made in portions of the shore zone by hand-picking from rocky substrates and using dip nets (250 μm mesh).

A metered cable and boat winch were used to acquire a limited number of samples with a ponar dredge from several areas of the lake. Some of the core, box, and slurpy samples acquired during dives by the Deep Rover submarine were examined also. Chironomid midges found in deep-water sediment traps and in zooplankton tows were examined.

Window traps (Jonsson et al. 1986) were installed at several points around the lake shore to capture adult aquatic insects to augment taxonomic information. The traps could not be emptied often enough to provide anything but general information on flight

period. UV light traps were run on an intermittent basis at the boat house on Wizard Island to obtain adult insects. Chironomid pupal exuviae were collected from floating debris. Stomach content samples from several hundred rainbow trout (*Oncorhynchus mykiss*) and kokanee salmon (*O. nerka*) also were examined (see Ecology of Kokanee Salmon and Rainbow Trout section).

Qualitative collections were made in caldera inlet streams by hand-picking invertebrates and using a kick-net. Twelve, 0.25-m^2 emergence traps were also placed over selected habitats in springs 9, 20 and 42. These traps collected emerging adult insects from June 29 to September 18, 1989.

Genus- or species-level identification of many groups that required the assistance of specialists was prohibited by lack of funds. Samples have been archived for future study in the event that funding becomes available or specialists volunteer their time to identify samples. A number of North American experts volunteered their time to identify some of the material.

Benthic macroinvertebrates from all types of samples were sorted from sample matrices, counted, and recorded according to major taxonomic groups. Except for Diptera, most insects were identified to the species level. Only a small portion of the chironomid midge material was identified.

Because the lake has a relatively simple gastropod, crayfish, and amphipod fauna, these taxa were routinely identified to the species level. Only selected oligochaete samples were identified. The mite *Algophagopsis* was noted when encountered in samples because of special interest (see Biological Notes on New Species of Aquatic Mite from Crater Lake). Most of the non-insect invertebrate specimens were archived.

Results and Discussion

Macroinvertebrate taxa identified from Crater Lake and caldera springs associated with the lake are listed in Table 2 along with information about the habitats with which the taxa were associated. Tables 3-10 list the relative abundance of taxa collected by scuba divers along transects at several points around the lake shore. Table 11 records the species and numbers of mayflies, stoneflies and caddisflies collected in emergence traps over caldera springs. Table 12 lists some of the more common aquatic insect adults collected in window traps placed around the lake shore.

Benthic Zones and Habitats

Crater Lake benthic habitat zones were easily described with standard limnological and oceanographic terms. Benthic habitat zones and subzones in Crater Lake were tentatively classified as follows: supralittoral; eulittoral; sublittoral, euphotic, and caldera slope zone (with ooze and moss subzones); profundal (with dysphotic caldera slope and abyssal plain subzones).

Supralittoral Zone. The supralittoral was the area of the shore wetted by wave action. Boulder and bedrock substrates predominated in this zone around much of the lake shore, but there also were several gravel beaches on shelves in bays and coves (e.g., Black Sand Beach and Steele Bay). Semiaquatic Collembola and saldids were locally abundant in the supralittoral. Collembola were extremely abundant on rocks above the waterline at Emerald Pool. Rocks in the supralittoral zone supplied molting, resting, and mating sites for adult aquatic insects.

Table 2. Presence of macroinvertebrates in various habitat types in Crater Lake, Oregon and caldera springs. P = present, gen = present but not associated with a habitat, rock = rock surfaces, ooze = pockets of fine particulate organic matter, macr = submerged macrophytes, algae = benthic algae, moss = Drepanocladus, mud = mud on abyssal plains, str = caldera inlet steams, fish = found in rainbow trout and kokanee guts. A question mark next to a taxon indicates unconfirmed identification.

	Lake Littoral Zone				Lake Profundal			
TAXON	gen.	rock	ooze	macr	algae	moss	mud	str.	fish
Hydra		P		P					
Porifera (?Ephydatia robusta)		P							
Turbellaria		P	P			P	P	P	
Nematoda		P	P			P	P		
ANNELIDA		P	P	P	P	P	P	P	
Enchytraeidae		P	P			P		P	
Lumbriculidae			P			P			
?Rhynchelmis			P			P			
Nais		P	P						
?Specaria fraseri			P						
Stylaria lacustris			P						
?Bothrioneurum vejdovskyanum			P						
Limnodrilus hoffmeisteri			P						
Rhyacodrilus montana			P						
Hirudinea		P	P	R					
CRUSTACEA									
Cladocera		P	P	P	P	P			
Copepoda		P	P	P	P	P	P		
Ostracoda		P	P	P	P	P	P		
Hyalella azteca		P	P	P	P				
Pacifasticus (P.) l. klamathensis		P							
MOLLUSCA									
Menetus (M.) opercularis		P	P	P					
Vorticifex effusa effusa		P	P	P	P				
Stagnicola (S.) apicina		P	P	P	P				
Sphaeriidae		P	P	P		P			
Algophagopsis		P	R			P			
Acari		P	P	P	P	P		P	
Collembola	shore, especially Emerald Pool								
ODONATA									
Coenagrionidae	adults collected along shore; no larvae from lake								
Anax	same								
EPHEMEROPTERA									
Baetis bicaudatus								P	
Callibaetis ferrugineus		P	P	P	P				
Paraleptophlebia cf. debilis		P			P				

Table 2 continued.

TAXON	Lake Littoral Zone gen.	rock	ooze	macr algae		Lake Profundal moss	mud	str.	fish
PLECOPTERA									
Sweltsa borealis-larvae		P						P	
Sweltsa exquisita								P	
Paraleuctra occidentalis								P	
Zapada columbiana								P	
Megarcys subtrunctata								P	
HEMIPTERA									
Notonecta undulata									P
Gerris nyctalis		present at Emerald pool							
Cenocorixa wileyae									P
Corisella decolor									P
Saldidae		shore							
MEGALOPTERA									
Sialis rotunda		P	P	P	P				P
TRICHOPTERA									
Rhyacophila chilsia								P	
Rhyacophila oreta								P	
Rhyacophila norcuta								P	
Rhyacophila tralala								P	
Rhyacophila vaccua								P	
Rhyacophila vaefes								P	
Rhyacophila verrula								P	
Rhyacophila vocala								P	
Hydroptila rono		P	P	P	P			P	P
Polycentropus variegatus		P		P				P	P
Dolophilodes pallidipes								P	
Parapsyche elsis								P	
Clistoronia magnifica		P	P	P				P	P
?Desmona								P	
Dicosmoecus atripes		P							P
Ecclisomyia conspersa		P		P				P	P
Homophylax ? insulas								P	
Imania cidoipes								P	
Limephilus acula									P
Limnephilus fagus									P
Limnephilus insularis								P	P
Limnephilus spinatus									P
Limnephilus-unknown female								P	P
Psychoglypha								P	
Neothremma didactyla								P	

Table 2 continued.

TAXON	Lake Littoral Zone					Profundal			
	gen.	rock	ooze	macr	algae	moss	mud	str.	fish
COLEOPTERA									
Dytiscidae		P	P	P	P				P
Agabus tristus		P	P	P	P				
Potamonectes striatellus		P	P	P	P				
Sanfilippodytes		P	P	P	P				
Hydrophilidae		R							P
OTHER DIPTERA									
Dixidae								P	
Psychodidae								P	
Simulium hunteri								P	
Prosimulium travisi								P	
Simulidae								P	
Syrphidae			P						
Thaumaleidae								P	
Tipulidae		P						P	
CHIRONOMIDAE	P	P	P	P	P	P	P	P	P
Brillia retifinis								P	
Chironomus			P						
Corynoneura								P	
Cricotopus	P							P	P
Diamesa	P								P
Eukiefferiella	P								
Eukiefferiella brehmi group								P	
Eukiefferiella devonica	P								
Eukiefferiella gracei group								P	
Eukiefferiella minor	P							P	
Heterotrissocladius oliveri/subpilosis			P				P		P
Limnophyes	P								
Micropsectra	P				P			P	
Microtendipes	P								
Orthocladius-Cricotopus	P							P	P
Orthocladius (Eudactylocladius)	P							P	
Orthocladius (Euorthocladius)									P
Parametriocnemus								P	
Phaenopsectra	P							P	P
Procladius (Holotanypus)									P
Psectrocladius octomaculatus group	P				P				
Pseudodiamesa	P							P	
Rheotanytarsus								P	
Sympotthastia								P	
Synorthocladius	P								
Zavrelimyia	P								P

Table 3. Benthic macroinvertebrates collected by divers in sweep-net samples, and miscellaneous collections at the Wizard Island boat dock and Emerald Pool in 1988-89. R= rare, C= common, and A= abundant. FPOM is fine particulate organic matter.

	Boat Dock Area			Emerald
Habitat type	Boulder	FPOM	Gravel	Pool
Depth in feet	0-2	25	20	& Misc.
NON-INSECT				
Porifera	C			
Oligochaeta	A	C		
Stagnicola apicina	C	C	C	
Menetus opercularis	A	C		
Vorticifex effusa effusa	A	C	C	
Sphaeriidae				C
Cladocera		A	C	
Copepoda		A	C	C
Ostracoda				C
Hyalella azteca	C	A	A	C
Pacifasticus klamathensis				C
Algophagopsis	A			
Collembola				A
EPHEMEROPTERA				
Callibaetis ferrugineus		R	C	A
HEMIPTERA				
Gerris nyctalis				C
Saldidae				R
MEGALOPTERA				
Sialis rotunda		C		C
TRICHOPTERA				
Hydroptila rono	C		R	C
Clistoronia magnifica		A	R	
Polycentropus variegatus	C		C	
COLEOPTERA				
Dytiscidae	C			C
Hydrophilidae				R
DIPTERA				
Chironomidae-larvae	A	C	A	A

Table 4. Benthic macroinvertebrates collected by divers in sweep-net samples at Fumarole Bay on Wizard Island in September 1988. R = rare, C = common, and A = abundant. Relative abundance is reported for sweep-net samples. FPOM is fine particulate organic matter.

Habitat type	Margin Detritus	Gravel	Filament. algae	Macrophyte vegetation	FPOM
Depth in feet	0	6	10	10	30
NON-INSECT					
Hydra				12	
Oligochaeta	C	25	20	32	20
Hirudinea	C				
Sphaeriidae		40			200
Menetus opercularis	C	10		180	
Vorticifex effusa effusa		75		18	6
Cladocera			32	2	>100
Copepoda		4	22	2	>1000
Ostracoda				2	>10000
Hyalella azteca	C	190	10	50	3
Acari			2	12	
EPHEMEROPTERA					
Callibaetis ferrugineus	C	7	40	150	
MEGALOPTERA					
Sialis rotunda		6		12	20
TRICHOPTERA					
Hydroptila rono		1		2	
Clistoronia magnifica				6	
Polycentropus variegatus		19		46	
DIPTERA					
Chironomidae-larvae		2	146	54	160
Chironomidae-pupae			10		
Syrphidae	R				

Table 5. Benthic macroinvertebrates collected by divers in sweep-net samples along a transect in the littoral zone at Black Sand Beach on Wizard Island in July 1989. Relative abundance in sweep-net samples is reported.

Habitat type	FPOM					BOULDER				
Depth in feet	20	25	30	40	50	10	25	30	40	50
NON-INSECT										
Turbellaria										4
Nematoda				4						
Oligochaeta	16	60	80	28	440	4	4	24	40	12
Sphaeriidae	100	660	800	60	48			16	8	16
Gastropoda	4	52	100	60	48	10	8	56	60	300
Cladocera		12	12	130	40					
Copepoda	8	600	200	300	560	24	4	8	60	20
Ostracoda		4	4	4	16				8	8
Hyalella azteca	12	100	16	20	56	68	60	108	120	180
Algophagopsis					24	>100	2400	>500	720	480
Acari				4						
MEGALOPTERA										
Sialis rotunda	12	52		8	20			24		
TRICHOPTERA										
Polycentropus variegatus						20		8	16	8
Clistoronia magnifica	Old larval cases and egg masses common to abundant.									
COLEOPTERA										
Dytiscidae						36	12	16	4	4
DIPTERA										
Chironomidae-larvae	40	272	40	184	600	304	256	116	512	284
Chironomidae-pupae		4	8	4		12	16	16	60	8

Table 6. Benthic macroinvertebrates collected by divers in sweep-net samples in the littoral zone near springs 21 & 48 in September 1988. R = rare, C = common, and A = abundant. Relative abundance in some sweep-net samples is reported.

	Near Spring 21		Near Spring 48	
Habitat type	Macrophyte	Gravel	Macrophyte	Gravel
Depth in feet	6	6	7	5
NON-INSECT				
Turbellaria		R		
Nematoda				12
Oligochaeta	28	A		75
Hirudinea	4	R		
Sphaeriidae	8	C	20	A
Stagnicola apicina			4	12
Menetus opercularis		R	160	7
Vorticifex effusa effusa	190	C		1
Cladocera	12	C	100	C
Copepoda	12	C	>1000	C
Ostracoda	2	R	>10000	C
Hyalella azteca	46	C	600	C
Algophagopsis		R		
EPHEMEROPTERA				
Callibaetis ferrugineus	6		1100	3
Paraleptophlebia		R		2
PLECOPTERA				
Sweltsa borealis				1
MEGALOPTERA				
Sialis rotunda			4	34
TRICHOPTERA				
Hydroptila rono	36	C	100	9
Clistoronia magnifica	22	C	124	16
Dicosmoecus atripes			8	
Ecclisomyia conspersa	4		8	1
Polycentropus variegatus	28	R	4	6
COLEOPTERA				
Dytiscidae	4	R	20	
DIPTERA				
Chironomidae-larvae	620	A	440	75
Chironomidae-pupae	130		68	

Table 7. Benthic macroinvertebrates collected by divers in sweep-net samples in the littoral zone at Buoy Bay in July 1989. Relative abundance in sweep-net samples is reported. FPOM is fine particulate organic matter.

Habitat type	Sand & fine gravel						Wood frags.	Wood branch	FPOM			
	ca. 0.25 meters-square								ca. 0.1 meters-square			
Depth in feet	10	15	20	25	30	35	25	26	35	40	45	50
NON-INSECT												
Turbellaria	4	4		50				40	12		4	
Nematoda		40	8								16	
Oligochaeta	140	320	160	160	80	8	50	10	200	100	80	80
Hirudinea	100	40	40	40	16	24	130	22	24	48	20	20
Sphaeriidae		160	120	30	20			2	68	60	12	
Gastropoda			16		8			30	16			4
Cladocera					8					12		8
Copepoda							10			16		52
Ostracoda			8		20	4	10		48	60	64	60
Hyalella azteca	4	60	64	50	8	20	70	24	104	88	4	64
Algophagopsis			16									
TRICHOPTERA												
Ecclisomyia conspersa	4											
Polycentropus variegatus						4		4				
COLEOPTERA												
Dytiscidae	4	4	8				20	4				
DIPTERA												
Chironomidae-larvae			8			4	10			8	8	

Table 8. Benthic macroinvertebrates collected by divers in sweep-net samples in the littoral zone at Lady of the Lake in July 1989. Relative abundance in sweep-net samples is reported.

Habitat type	Moss	Rock face	Rock face	Rock face	Rock face	Rock face	Rock face
Depth in feet	0-5	0-5	10	20	30	40	50
NON-INSECT							
Turbellaria	1	1	1	2	12	8	
Oligochaeta	400	1		22	72	60	280
Hirudinea	40		1	2	24	20	
Sphaeriidae		1		2	40	4	12
Gastropoda	>100	75	78	82	488	500	120
Cladocera						20	
Copepoda	1	1	37	50	16	100	30
Ostracoda					4		
Hyalella azteca	160	12	24	11	60	64	4
Algophagopsis	8	4		4	12	52	30
TRICHOPTERA							
Hydroptila rono	100	8	4	7	8	4	
Clistoronia magnifica	egg masses common						
Ecclisomyia conspersa			1	4	176	300	32
Polycentropus variegatus	4	1	3	1	12		2
COLEOPTERA							
Dytiscidae	3	1	3	4			
DIPTERA							
Chironomidae-larvae	1400	57	18	32	56	40	8
Chironomidae-pupae	120	3	1	1		4	

Table 9. Benthic macroinvertebrates collected by divers in sweep-net samples in the littoral zone at Steele Bay in July 1989. R = rare, C = common, and A = abundant. FPOM is fine particulate organic matter. Relative abundance is reported for sweep-net samples.

Habitat type	Coarse gravel	Sand fine gravel		FPOM	Boulder		
Depth in feet	1	12	40	20	12	20	40
NON-INSECT							
Turbellaria							2
Nematoda				128			
Oligochaeta		1280	100	160	6		2
Hirudinea	C	4	24	40	8		
Sphaeriidae		60	16	16			
Gastropoda	R				60	42	16
Cladocera			8			10	10
Copepoda				8	4	4	4
Ostracoda					8	2	
Hyalella azteca	24	40	112	840	8	16	16
Algophagopsis		60		16	400	40	50
TRICHOPTERA							
Clistoronia magnifica	R						
Ecclisomyia conspersa	4						
COLEOPTERA							
Dytiscidae	3			160	90	46	
DIPTERA							
Chironomidae-larvae		8	8	40	16	14	16
Chironomidae-pupae		8			10		
Hesperoconopa		4					

Table 10. Benthic macroinvertebrates collected by divers in sweep-net samples in the littoral zone at Phantom Ship in September 1988. R = rare, C = common, and A = abundant. Relative abundance is reported for sweep-net samples.

Habitat type	Cobble Rubble	Filament. Algae	FPOM	Boulder		
Depth in feet	0-1	0-1	15	15	25	20-40
NON-INSECT						
Hydra						8
Turbellaria			1		1	
Oligochaeta	A	1	A	160	113	80
Hirudinea			20			12
Sphaeriidae				4	8	12
Gastropoda	A	6	20	64	78	148
Cladocera			R	4	39	24
Copepoda			120		30	60
Ostracoda			40		4	8
Hyalella azteca			C	104	55	80
Algophagopsis	A	1	A	A	A	A
EPHEMEROPTERA						
Paraleptophlebia		1				
PLECOPTERA						
Sweltsa borealis	R					
TRICHOPTERA						
Hydroptila rono	R	15	80	32	6	
Clistoronia magnifica			80	16	63	32
Ecclisomyia conspersa	C	R		4	6	
Polycentropus variegatus				12		4
COLEOPTERA						
Dytiscidae	C	10	4			
DIPTERA						
Chironomidae-larvae	C	10	20	124	7	28
Chironomidae-pupae					2	8

Table 11. Collections of adult Ephemeroptera, Plecoptera, and Trichoptera in emergence traps set over caldera inlet streams in summer 1989. Values are converted to number per square meter. Samples from Spring 9 for the period July 23 to August 21 were lost. A question mark next to a taxon indicates unconfirmed identification.

Spring	9	9	20	20	20	42	42	42
No. of traps	5	5	3	3	2	4	4	4
Date range	Jun 29 Jul 23	Aug. 21 Sep 19	Jun 29 Jul 23	Jul 23 Aug 2	Aug 21 Sep 18	Jun 29 Jul 23	Jul 23 Aug 2	Aug 2 Sep 18
Baetis bicaudatus	0	1	0	3	0	0	1	1
TOTAL EPHEMEROPTERA	0	1	0	3	0	0	1	1
Sweltsa borealis	18	0	0	3	0	54	26	18
Sweltsa exquisita	0	0	0	0	0	0	0	2
Paraleuctra occidentalis	13	0	0	0	0	2	0	0
Zapada columbiana	1	0	0	0	0	1	1	0
Megarcys subtrunctata	1	0	0	0	0	0	0	0
TOTAL PLECOPTERA	32	0	0	3	0	57	27	20
Rhyacophila chilsia	0	6	0	0	0	0	45	53
Rhyacophila oreta	2	0	0	0	0	0	0	1
Rhyacophila norcuta	1	0	15	1	0	0	0	0
Rhyacophila tralala	0	0	0	0	0	1	0	0
Rhyacophila vaccua	0	6	0	0	0	0	0	0
Rhyacophila vaefes	0	0	0	0	0	36	5	0
Rhyacophila vocala	8	0	4	7	0	0	0	0
Hydroptila rono	0	0	1	120	24	0	2	
Polycentropus variegatus	0	0	0	7	2	0	2	1
Dolophilodes pallidipes	0	6	0	0	0	0	0	0
Parapsyche elsis	7	0	0	0	0	0	0	0
Clistoronia magnifica	0	0	0	0	2	1	9	1
?Desmona	0	0	0	0	0	0	0	1
Ecclisomyia conspersa	525	0	56	1	0	580	31	0
Homophylax ? insulas	0	1	0	0	2	0	0	0
Imania cidoipes	0	0	7	0	0	0	0	0
Limnephilus-unknown female	0	0	0	0	2	0	0	0
Limnephilus insularis	0	0	0	0	0	0	0	1
Neothremma didactyla	70	107	0	3	14	0	0	0
TOTAL TRICHOPTERA	612	126	82	138	46	618	94	58
GRAND TOTAL	644	127	82	144	46	675	122	79

Table 12. Aquatic insects other than Diptera captured in window traps along the shore of Crater Lake in the summer of 1989. Em = Emerald Pool, Fum = Fumarole Bay, Dock = boat dock.

June 28-July 23, 1989		Shore near springs				Wizard Island			
	Total	9	20	21	42	Em	Fum	Dock	Steele Bay
Callibaetis ferrugineus	4					2	2		
Sweltsa borealis	21	9			6	6			58
Sialis rotunda	584					12	72	500	
Hydroptila rono	1			1					
Clistoronia magnifica	1							1	
Ecclisomyia conspersa	157	133	16	1	7				2
Imania cidoipes	1			1					

July 23-August 21, 1989		Shore near springs				Wizard Island			
	Total	9	20	21	42	Em	Fum	Dock	Steele Bay
Callibaetis ferrugineus	18					3	12	3	
Sweltsa borealis	3				2	1			
Sialis rotunda	20					16	4		
Hydroptila rono	119	4	56		6	34	14	5	
Polycentropus variegatus	1						1		
Neothremma didactyla	1	1							

August 21-Sept. 18, 1989		Shore near springs				Wizard Island			
	Total	9	20	21	42	Em	Fum	Dock	Steele Bay
Callibaetis ferrugineus	1							1	
Paraleptophlebia	2					2			
Sweltsa borealis	5								5
Sialis rotunda	1						1		
Hydroptila rono	41			28	1	1	6	1	4
Polycentropus variegatus	6			2				2	2
Dicosmoecus atripes	45							45	
Neothremma didactyla	1	1							
Rhyacophila Vaccua Complex	1	1							

Wind and wave action sometimes formed wrack lines of decaying organic matter, composed mostly of senescent filamentous algae and tree pollen, on some rocky beaches at the waterline. On Wizard Island, these wrack lines in the supralittoral harbored syrphid flies, hydrophilid beetles, and midge larvae. Semiaquatic moss occurred in isolated patches on rocks and logs at several points along the lake shore. These patches offered excellent concealment and harbored a variety of aquatic invertebrates in relatively high densities.

Eulittoral Zone. Shallow waters near shore that were disturbed by wave action comprised the eulittoral zone. This zone extended 5 to 10 m below the water surface around much of the lake, except on protected shores where it was only 1 or 2 m deep. Wave action kept substrates clear of accumulations of FPOM, silt, and sand. Epibenthic habitats in this zone were: steep-sloping bedrock faces (common); boulder/rubble talus-slope deposits (abundant); sand bars on low sloping shelves (rare); gravel bars on low or moderate sloping shelves (occasional); sand/gravel pockets between boulders (abundant); coarse particulate organic matter accumulations such as branches, wood chips, and bark chips (rare); submerged macrophyte beds on sheltered shores with low sloping sand-gravel shelves (rare); filamentous green algae patches(rare). The submerged macrophyte beds were rare enough that their classification as a separate infralittoral zone was not warranted.

Nostoc algae and aquatic lichens were abundant on stable rocks in the eulittoral zone. Density of their growth on surfaces appeared to be inversely related to the severity of wave action. On windward shores such as at Steele Bay, *Nostoc* and lichens were scattered and restricted to stable boulder tops. Gravel and cobble, which were periodically rolled by waves, were free of growth.

Bedrock faces and boulder/rubble substrates were by far the dominant habitat type in the eulittoral zone, and most of the common littoral invertebrates were found there. Total densities of invertebrates were in the 1,000's per m^2 on lee shores, whereas richness and density on rocky shores with severe wave action were considerably less. Snails and caddisflies were the large and conspicuous members of rock communities.

Invertebrate distribution and abundance on rocky substrates in the eulittoral appeared to be influenced by several physical factors. The first was the severity of wave action. A number of taxa (see Appendix I) were common to abundant on lee shores, (i.e., from Wizard Island around the south shore to about Phantom Ship) but were rare or absent on windward shores of the lake, (i.e., from about Phantom Ship around the north shore to Llao Point). Surface roughness of particular rock types appears to limit the distribution and abundance of some invertebrates. The pumice deposits around Wizard Island were extremely rough in contrast to the relatively smooth basaltic rocks along the main lake shore. Flatworms and the caddisfly *Ecclisomyia* were conspicuously absent on pumice but common to abundant in other parts of the eulittoral zone.

Temperature may have affected the distribution and abundance of some invertebrate taxa on rock and other substrate types. Surface water in shallow, sheltered bays on the leeward shore heated up during the summer months. This water undoubtedly accumulated many more degree days than more exposed shores, where exchange rates with the colder open lake water was greater.

Sand, sand/gravel, or gravel bars in the eulittoral zone were generally of rare to occasional occurrence. These habitats were found wherever shelves or benches were on the caldera wall or in the channel area between Wizard Island and the main shore. However, sand and gravel pockets between boulders were abundant. Invertebrate

richness and density in these pockets and in bars was typically lower than on rock surfaces.

Wave action concentrates coarse particulate organic matter (CPOM) in the eulittoral zone, although these accumulations were rare. CPOM was composed of tree branches, wood chips, bark chips, conifer needles, and conifer cones. Relatively large accumulations were found about 6 m deep in Buoy Bay. Faunal richness was poor in this habitat. Oligochaetes, midges, and leeches were the sedentary invertebrates present. Swimmers such as amphipods, copepods, ostracods, and dytiscid beetles were also present.

Submerged macrophyte beds were present at limited areas near springs 21 and 48 where protected, shallow benches of sand-gravel substrate extended out from shore. Invertebrate richness was high, and densities were very high in these beds (Table 5).

Patches and beds of filamentous green algae occurred locally in protected waters of the eulittoral zone. Patches sometimes covered 100's of square meters and could be thick and dense-enough to completely blanket rocks beneath. Oligochaetes, microcrustaceans, amphipods, mites, *Callibaetis*, *Hydroptila*, dytiscids, and midge larvae were associated with large patches sampled at Phantom Ship and Fumarole Bay.

Endobenthic habitat, which may support invertebrate communities, occurs where deep, loose deposits of cobble/rubble on talus-slopes of the caldera wall extend into the lake, and where loose pumice deposits occur near Wizard Island. Some invertebrates, such as the stonefly *Sweltsa borealis*, may be more abundant in the endobenthos than on surface substrates.

Sublittoral, Euphotic, Caldera-slope, Ooze Zone. This zone was found on steep slopes of the caldera wall below the region of wave action. Brode (1938) remarked on

the "diatomaceous ooze" that was abundant in pockets between boulders in the lake. This "ooze," which had a bleached appearance, was a conspicuous substrate below about 10 m on the caldera slopes. It was composed of fine detritus derived from diatoms, filamentous algae, pollen from terrestrial vegetation, insect exuviae and fragments (derived from aquatic and terrestrial taxa), and particles derived from flocculation.

The ooze layer was up to a meter thick in some rock pockets, although typically it was a few centimeters to a few decimeters thick. Tolerant, lentic taxa that inhabit this ooze layer or the mineral substrates beneath it, were the mayfly, *Callibaetis ferrugineus*, and the alderfly, *Sialis rotunda*. Collector-gatherers (e.g. microcrustaceans, amphipods, oligochaetes, and midge larvae) were often found in great abundance in the ooze. Less-tolerant taxa and scraper taxa were absent or rare. This ooze was probably a food source of moderate nutritional value.

Although pockets between boulders were filled with ooze, boulder tops protruded through this layer. Also, ooze did not accumulate on sheer rock faces. Ooze-free rock islands appeared to harbor substantially the same invertebrate fauna as found on rocks in the eulittoral zone. The snails *Stagnicola* and *Vorticifex* were observed by divers to occur on rocks as far down as sight allowed (50+ m). Snails were observed on rocks "several" hundred feet deep by operators of the submersible.

Many insect taxa found in the eulittoral may not be adapted to colonize substrates below 30-50 m. For example, for all of the caddisfly taxa present, the female must swim or crawl into the water to attach eggs. The depth to which these caddis females can swim is limited. Other insect taxa may be limited in how deep they can penetrate by requirements of the pupal stage. For example, alderfly (*Sialis rotunda*) larvae crawl out of the water and burrow into moist areas of the lake margin to pupate.

Sublittoral, Euphotic, Caldera-Slope, Moss Zone. One of the more unique benthic habitats of Crater Lake was the extensive beds of the moss *Drepanocladus*, which covered much of the caldera slopes from about 30 to 120 m. Macroinvertebrates found from these mossy substrates are listed in Table 1. Most of the invertebrates in the moss were worms, sphaeriid clams, microcrustaceans, and mites. The only insects were chironomid midges.

Profundal-Dysphotic Caldera Slope Zone. This zone occurred below the moss zone on caldera slopes. It was below the level where enough light penetrated for primary production to occur. Large rock substrates were the dominant habitat. Little else was known about habitat and substrates. Biological samples were not obtained from this zone.

Profundal-Abyssal Plain Zone. Substrates in the abyssal plain were mud. Based on a limited number of cores and dredge samples taken in this zone, the macroinvertebrate fauna was not rich. Taxa occurring were: Turbellaria, Nematoda, Oligochaeta, Copepoda, Ostracoda, and the midge *Heterotrissocladius oliveri/subpilosis*. Densities were relatively low, but this is not unusual for the muddy bottom of a deep lake.

Faunal Elements

In general, macroinvertebrate richness was moderate in Crater Lake and probably comparable to other large, cold oligotrophic lakes in the northern hemisphere. If all taxonomic groups were identified to the genus/species level (particularly benthic microcrustaceans, sphaeriid clams, oligochaets and chironomid midges), a more direct comparison could be made. Brode (1938) predicted that benthic faunal productivity in

this ultra-oligotrophic lake would be low because of harsh physical constraints and nutrient- poor water. However, productivity of the total invertebrate community, at least in the eulittoral zone, appeared to be relatively high. Standing crops of invertebrates on some protected rocky shores probably exceeded 10,000 invertebrates per m^2.

One of the striking features of the Crater Lake fauna was that few obligate lake-dwelling taxa were found. Most of the taxa identified to the genus or species level were facultatively associated with lakes and can be found in lotic waters in the Pacific Northwest (Appendix I). The midge *Heterotrissocladius oliveri/subpilosis*, the caddisfly *Clistoronia magnifica*, and probably the mite *Algophagopsis*, were among the few identified taxa that were strictly associated with lentic waters.

Many conspicuous taxa in the eulittoral and sublittoral zone of Crater Lake also are common residents of montane streams and rivers in the Pacific Northwest. Their presence in a lake habitat was unusual, although understandable because habitat conditions in the eulittoral were similar to those of streams and rivers. Most of the taxa that were identified to the species level are widely distributed and common in streams, lakes, and rivers in at least western North America. Some of the more abundant taxa present are Holarctic in their distribution (e.g., *Hyalella azteca* and *Heterotrissocladius oliveri/subpilosis*). Thus, the bulk of the taxa present were common and had excellent dispersal capabilities.

An oligochaete worm and a mite *Algophogopsis* were forms new to science. Their ranges are unknown because the macroinvertebrate fauna of so few Cascade Range lakes has been examined. Endemic taxa may eventually be found in Crater Lake, although the likelihood is low because this caldera lake is relatively young. Crater Lake can be

likened to a recently-created volcanic island. This large, relatively isolated body of water is probably still being colonized at a moderate rate by new taxa. Few probably survive to establish reproducing populations. It would be informative to examine cores from the abyssal plain to get an indication of the colonization rate of chironomid midge taxa during the lake's 7,000-year-long history.

Some of the taxa recorded can be classified as transient or of accidental occurrence in the lake (e.g., the Odonata and most of the Hemiptera). Most of the Hemiptera records were from fish stomachs, leaving one to wonder about the richness of the invertebrate fauna prior to introduction of fish. Analysis of core samples could provide information on this subject.

Although only a few of the midge taxa have been identified, those taxa known to be present inhabit the full spectrum of trophic conditions of the lake: ultra-oligotrophic, mesotrophic, eutrophic, and even dystrophic (Saether 1975, 1979). This is not surprising, considering the array of microhabitats present in the littoral zone of the lake. Wave-swept rocky substrates will harbor more intolerant taxa. Ooze deposits, prevalent everywhere below the wave action zone, mimic mesotrophic or eutrophic conditions. Organic matter (CPOM and FPOM) is packed by wind and waves into rock crevices in the lake margin, producing dystrophic conditions. The midge genera and species groups identified thus far, with a few exceptions, are commonly found in streams and rivers of the Cascade Mountains.

Among the denizens of the Crater Lake benthos, *Algophagopsis* and *Heterotrissocladius oliveri/subpilosis* have unique, or at least poorly documented, life histories. *Algophogopsis*, a new species, is a herbivorous mite that is common or abundant on rock surfaces and moss in the eulittoral and sublittoral zones of Crater

Lake. *Heterotrissocladius oliveri/subpilosis* is a chironomid midge that is common in oligotrophic lakes. In Crater Lake, it displays some behavioral/life history peculiarities that have not been reported in the literature. Mature fourth-instar larvae of *Heterotrissocladius*,which are the final instar, are found in pelagic waters throughout the lake. They were collected on a regular basis in zooplankton tows in the middle of the lake; stomachs of kokanee salmon that had fed off-shore often contained large numbers of fourth-instar larvae and pupae of this species; and deep-water sediment traps that were suspended well above the bottom trapped fourth-instar larvae on several occasions. The presence of final-instar midge larvae swimming in the pelagic zone of deep water lakes has not been reported before in the literature. Possibly pupae of this midge cannot ascend successfully through the water column from great depths. Therefore, final-instar larvae may swim towards the surface, and metamorphosis to the pupal stage may occur pelagically in surface waters.

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Appendix I. Supplementary information on the taxa of benthic macroinvertebrates identified from Crater Lake and its caldera springs. *A question mark next to a taxon indicates unconfirmed identification.

Hydra (Cnidaria: Hydrozoa): Uncommon in the lake littoral. Collected from submerged macrophytes in Fumarole Bay and from protected boulder surfaces at Phantom Ship. Apparently restricted to shallow, warmer water in protected coves.

?Ephydatia robusta (Porifera): Occurrence in the lake littoral noted by Brode (1938). Immature sponges were found to be locally common during the summers of 1988-89 on rock faces and the underside of rough pumice boulders in protected shores of the lake. Small colonies were common on the underside of boulders in shallow waters around Wizard Island. Large colonies were observed in rock crevices of cliffs at Lady of the Lake.

Turbellaria: Flatworms are ubiquitous in the lake littoral. They occur in low to moderate densities on littoral rock substrates. Greatest numbers were found on smooth rock surfaces on more exposed shores, though they were occasionally found on sand/fine gravel, wood, moss, and FPOM in the littoral. They appear to be absent or very rare on the rough, pumice rocks around Wizard Island. Flatworms were also found rarely in the sublittoral *Drepanocladus* moss beds and in some of the profundal mud samples, though not at the greatest depths. Flatworms were common in the caldera springs.

Nematoda: Roundworms were occasional to common in some of the near shore samples taken. They seem to prefer finer mineral substrates (sand and gravel) and FPOM. Nematodes were taken in low numbers in samples of *Drepanocladus* and from mud bottoms in the profundal zone.

Annelida: Oligochaeta were common to abundant in nearly all littoral, sublittoral and profundal habitats. They were found on all substrate types. Only a fraction of the available material has been identified to date.

Annelida: Hirudinea (probably *Helobdella*) are common on smooth rock surfaces of wave-swept shores and in FPOM accumulations. Like the flatworms, they are not evident on the rough pumice rocks found around Wizard Island. They have been collected to depths of 50 feet in the littoral zone.

Cladocera, Copepoda, Ostracoda: Benthic related micro-crustaceans were present in all lake habitats, but not in the caldera springs. They have not been identified by specialists as of yet.

Hyalella azteca (Amphipoda): This widely distributed and common amphipod is ubiquitous in the littoral zone of Crater Lake. This species appears to be restricted to shallow water habitats. It was not found in deep-water dredge or sub samples. One specimen was found in a dredge sample of moss, sand and FPOM

at 26 meters, which represents the maximum recorded depth to date for Crater Lake. Brode (1938) mentions that *Gammarus* was introduced to the lake in the early 1900's as supplemental fish-food. Brode did not collect them in the 1930's, nor have they been found in our collections.

Pacifasticus (Pacifasticus) leniusculus klamathensis (Crustacea; Decapoda): This crayfish was probably introduced to Crater Lake earlier in the century in an attempt to augment fish-food sources. Predation by fish appears to limit its distribution to pockets around Wizard Island, where boulders restrict fish access. It is common in Emerald Pool on Wizard Island. Brode (1938) states that *Pacifasticus (Hobbsastacus) nigrescens* was the species stocked around Wizard Island. Horton Hobbs (pers. comm.) believes this was a mistaken identification and that the species stocked was *P. (P.) l. klamathensis*. If *P. (H.) nigrescens* (described from the San Francisco Bay area) was indeed stocked and persists in the lake, it would be of interest, since this species is now believed to be extinct.

Menetus (Menetus) opercularis (Gastropoda: Planorbidae): Is common to abundant in shallow water of protected shores. It is less common on more wave-swept shores. It can be found on rock surfaces, macrophytes and in FPOM accumulations. Occurrence has not been recorded below about 50 feet. This taxa appears to be restricted to shallow, more protected waters which warm considerably during the summer months. This taxa is the common Pacific Coast *Menetus*, although there is some confusion of names (Frest, pers. comm.). It is found in a variety of habitats, including lakes, rivers and streams.

Vorticifex effusa (Gastropoda: Planorbidae): This is the most abundant gastropod in the littoral zone of Crater Lake. It can be found on rock surfaces and in FPOM around the entire lake perimeter, to depths of 100+ meters. It is rarer where wave action is severe, but appears to be more tolerant to waves than the other two gastropods present. *V. effusa* is common in the Pacific Coastal region, and occurs in perennial well-oxygenated water, mostly in larger lakes and rivers, spring sources and spring-fed streams. Crater Lake is the type locality for *Paraphylox effusa diagonalis* (Henderson), now regarded as a synonym of *V. effusa* (Frest, pers. comm.).

Stagnicola (Stagnicola) apicina (Gastropoda: Lymnaeidae): Is the largest (high-spired) gastropod to be found in the lake, and has the same distribution as *Vorticifex* in the littoral zone. However, it is found in much lower numbers. Brode (1938) lists this taxa as *Lymnaea mazamae*. The origin of this name is uncertain. *S. apicina* is the common WA-OR large lymnaeid snail. It favors larger lakes and rivers and can tolerate slow-moving and relatively oxygen-poor perennial habitats. It has not previously been reported from Crater Lake (Frest, pers. comm.).

Sphaeriidae (Mollusca: Pelecypoda): Fingernail clams are common in FPOM accumulations and sand/gravel substrates in the littoral zone of the lake. They are present, but in lower numbers, on rock surfaces in more protected areas of the

lake. They have been found in *Drepanocladus* samples down to about 70 meters in depth, but not in mud samples from the profundal zone.

Algophogopsis n. sp. (Acari: Acariformes: Astigmata: Algophagidae): This new species of mite was found in great abundance on rock surfaces in the lake littoral zone and in *Drepanocladus* beds in the sublittoral zone. It appears to be associated with moss, aquatic lichen and *Nostoc* algae, and is probably herbivorous. It represents a unique life-history type for aquatic mites.

Acari: Aquatic mites other than *Algophogopsis* were found occasionally in many littoral habitats and in beds of *Drepanocladus*. They are also present in the caldera springs.

Odonata: Dragonfly adults (Anisoptera) are commonly seen along the lake margin, with damselfly (Zygoptera) adults being less commonly spotted. Brode (1938) and this study did not find larvae in lake littoral habitats or in fish stomachs.

Baetis bicaudatus (Ephemeroptera: Baetidae): This baetid mayfly which is common in colder, higher elevation streams of western North America, was common to abundant in caldera springs. Adults were collected from late July to September. Larvae are collector-gatherers.

Callibaetis ferrugineus (Ephemeroptera: Baetidae): This species is associated with FPOM, macrophytes and filamentous green algae beds in shallow depths of protected shores. It is found in abundance around Wizard Island and on the south and southwest shores of the lake, and is particularly abundant on submerged macrophytes. It was not found on the more wave-swept eastern and northern shores of the lake. Larvae are collector-gatherers. *Callibaetis ferrugineus* adults have been collected from June 28 to September along the shore of Crater Lake. Peak emergence appears to occur in late July. *Callibaetis ferrugineus* is a widely distributed and common Nearctic species, found in a great variety of lentic habitats and in slow-moving streams and rivers. It is a highly tolerant organism, and can be found in waters which are quite stagnant.

Paraleptophlebia cf. debilis (Ephemeroptera: Leptophlebiidae): Larvae of this mayfly taxon were rare in the lake littoral zone. They were found associated with gravel substrates beneath beds of submerged macrophytes off springs 21 and 48, and in filamentous green algae at Phantom Ship. Preference for protected shores and shallow depths is apparent. Larvae are collector gatherers. Adults have not been collected from the lake area. *Paraleptophlebia debilis* is a widespread and common in the Nearctic. It is typically found in streams and small rivers in areas of slower current. It has not been recorded as occurring in lakes.

Sweltsa borealis (Plecoptera; Chloroperlidae): Adults of this species are abundant along most of the lake shore during their peak emergence in June and July. However, only about a dozen larvae have been taken in all types of benthic

samples put together. It is suspected that larvae dwell in shallow water, hyporheic habitats where crevice and pore space is abundant in loose boulder and talus deposits. *Sweltsa borealis* is widespread and common in montane areas of western North America. This is a stream associated taxa, which has not been recorded from lakes as of yet. Wave action along the shore of Crater Lake probably provides a steady flow of water through hyporheic habitats, simulating stream current. Larvae are predaceous.

Paraleuctra occidentalis (Plecoptera: Leuctridae): Adults were occasional in emergence traps set over Spring 9 and 42. Collections were made in late June and early July, however this is an early season species throughout most of its range and peak emergence may have occurred prior to trap installation. This is one of the most common leuctrid stoneflies in montane areas of western North America. Larvae were not found in lake habitats. Larvae are shredders, and typically associated with small, cold streams.

Zapada columbiana (Plecoptera: Nemouridae): Larvae were common in most of the perennial caldera springs. Only 3 adults were collected in emergence traps, however. Larvae are shredders and associated with cold, montane streams. This is a common and widespread montane western North American stream species.

Megarcys subtrunctata (Plecoptera: Perlodidae): A single adult female was collected in an emergence trap at spring 9 on the caldera wall. This taxa is widespread in montane western North America. In the Cascade Mountains it is found in colder streams at higher elevations. Larvae are predaceous. The single female collected was brachypterous.

Notonecta undulata (Hemiptera: Notonectidae): One adult specimen was found in a fish stomach, and probably represents transient visitation to the lake. No nymphs or adults have been taken in benthic collections from the lake.

Gerris nyctalis (Hemiptera: Gerridae): This species was common in Emerald Pool on Wizard Island; which is a small, land-locked pool with no fish present. It is also well protected from wind. This is probably the only habitat where gerrids can persist.

Cenocorixa wileyae and *Corisella decolor* (Hemiptera: Corixidae): About 15 adult specimens were found in fish guts, and probably represent transient visitation to the lake by these corixid taxa. Corixids may have had breeding populations in warmer, shallow, protected areas of the lake littoral zone prior to the introduction of fish.

Saldidae (Hemiptera): Saldids were occasionally seen on rocks along the lake shore. Saldids are semi-aquatic.

Sialis rotunda (Megaloptera: Sialidae): Larvae are common in shallow water of the lake littoral zone along more protected shores of the lake. They are most often

associated with FPOM accumulations and macrophytes, but were also collected from rock surfaces. Adults were abundant around the shores of Wizard Island in July. This species is widespread in North America, and can be found in a variety of lentic and lotic habitats. Larvae are predaceous and ?collector-gatherers.

Rhyacophila chilsia (Trichoptera: Rhyacophilidae): This taxa was collected in emergence traps set over spring 9 (occasional) and 42 (abundant), and in benthic collections at springs 7 and 48. This is an uncommon rhyacophilid that is known from AK, ALTA, BC, WA and OR. It is associated with smaller cold, spring streams at mid to higher elevations. Larvae are predaceous. Positive adult-larval association was made for the first time with collections made in the caldera springs of Crater Lake. Larvae had many characteristics of the Betteni Group to which it has been assigned, but were distinctive from other species in this group where larval-adult associations have been made.

Rhyacophila norcuta: Larvae and adults have been collected from caldera springs 9, 20, and 21. Adults were common in emergence traps at spring 20. This taxa is common and widespread in maritime areas of the Pacific Coastal Mountains from BC to CA. It is usually associated with seeps, springs and very small streams. Larvae are predaceous.

Rhyacophila oreta: Three adult female specimens were taken in emergence traps at caldera springs 9 and 42. This taxa is commonly associated with seeps and small springs, and is widespread and common in montane western North America. Larvae are predaceous.

Rhyacophila tralala: One adult male was taken in emergence traps over caldera spring 42. This species is known from the Cascades and Coast Ranges of WA and OR. It is associated with seeps, springs and very small, cold streams. Larvae are predaceous.

Rhyacophila vaccua: Adults were collected from emergence traps at caldera spring 9. This is a widespread and common montane western North America rhyacophilid. It is associated with small to large streams. Larvae are predaceous.

Rhyacophila vaefes: Adults were common in emergence trap collections from caldera spring 42. This is a widespread and common montane western North America rhyacophilid, which is usually associated with mid to large size streams, and not springs. Larvae are predaceous.

Rhyacophila verrula: Two larvae were found in benthic samples taken at caldera spring 48. This is a widespread and common montane western North America rhyacophilid, that is associated with aquatic moss in cold streams of all sizes. Larvae are herbivorous on moss.

Rhyacophila vocala: Adults were collected occasionally in emergence traps at caldera springs 9 and 20. This is a widespread and common montane western North

America rhyacophilid, which is typically associated with mid to large size streams. Larvae are predaceous.

Hydroptila rono (Trichoptera: Hydroptilidae): This microcaddisfly was common to abundant in shallow waters of the lake littoral zone in all areas of the lake except the most severely wave swept shores (i.e from Phantom Ship around the north shore to Llao Point). It is common on rocks, macrophytes, and margin moss; and less common in heavy growths of filamentous algae and in FPOM accumulations. Their maximum depth of occurrence is about 40 feet. Adults were also common in emergence traps set at the base of spring 20. Larvae were not observed in the springs, except at their mouth, so adults may have worked their way under or through emergence trap nets. They were common in window trap collections. Larvae are piercer-herbivores, obtaining food by piercing algal cells and sucking out cell contents. This species is widespread and common in western North America. It is typically associated with streams and rivers, and has not been recorded from lake habitats to date.

Polycentropus variegatus (Trichoptera: Polycentropodidae): Adults were commonly observed along the lake shore from July through September, and were particularly abundant around Wizard Island. Adults were also collected occasionally in emergence traps at caldera springs 20 and 42. Larvae were most abundant in shallow water areas of protected shores, although they appear to occur around the entire lake. Larvae are associated with rock substrates and submerged macrophytes down to 50 feet in depth (maximum range of divers). They are most often found on the underside of rocks. Adult females were common in rainbow trout stomachs, having been eaten while returning to the water to deposit eggs. This taxa is widespread and common in western North America, and is found in a variety of habitats, including lentic and lotic ones. Larvae are predaceous and may spin nets to capture metazoans during part of their life cycle.

Dolophilodes pallidipes (Trichoptera: Philopotamidae): Six adults were taken in emergence trap collections at caldera spring 9. The presumed larvae was taken in benthic collections at spring 48. This taxa is widespread and common in western North America, and is usually associated with mid to larger size streams and not with small, cold springs. Larvae spin fine nets and filter FPOM and metazoans from running water.

Parapsyche elsis (Trichoptera: Arctopsychidae): Seven adults were taken in emergence trap collections at caldera spring 9. Larvae were common in benthic collections made at spring 48. This taxa is widespread and common in montane western North America. It is found in springs, and small to large colder size streams. Larvae are predaceous and spin coarse nets to capture drifting invertebrates.

Clistoronia magnifica (Trichoptera: Limnephilidae): This limnephilid caddisfly is one of the larger and more conspicuous invertebrates which inhabit shallow water areas of the littoral zone. Larvae are common to abundant along more protected shores, and rare or absent along more exposed shores (i.e. from ca. Phantom Ship

around the north shore to Llao Point). Larvae can be found on rocks, cliff faces, in FPOM accumulations between boulders and on macrophytes. Adults were found occasionally in emergence traps set over caldera springs, but these are believed to have crawled under trap nets. Larvae were not seen in benthic collections from the springs. Adults were rarely collected in window traps. Adults were commonly seen throughout late summer around the shore of the lake. Egg masses were found in abundance during dives at Black Sand Beach and Lady of the Lake. Masses were taken from rock faces as deep as 50 feet. This is probably a depth record for caddisfly egg masses. This taxa is common in permanent subalpine lakes and ponds in the Cascades. Larvae appear to be omnivorous. This is undoubtedly the *Limnephilus* taxa referred to by Brode (1938).

?Desmona (Trichoptera: Limnephilidae): A single adult female of this taxa was found in emergence trap collections at caldera spring 42. It is possibly an undescribed *Desmona* species (Wiggins. pers. comm.).

Dicosmoecus atripes (Trichoptera: Limnephilidae): Adults were commonly observed around the lake shore in the late summer. They were particularly noticeable around Wizard Island. A prepupae was found attached to a rock in shallow water near spring 7. Both larvae and pupae were occasionally present in fish stomachs. This taxa is widespread and common in montane western North America. It has a Holarctic distribution. Larvae are omnivorous.

Ecclisomyia conspersa (Trichoptera: Limnephilidae): Larvae of this limnephilid caddis are abundant in the lake littoral zone on smooth rock surfaces. They are conspicuously absent around Wizard Island, where the rock is primarily pumice with rough surfaces. Larvae have been found down to 50 feet in depth (maximum depth reached by divers). Larvae were common to abundant in the lower reaches of caldera springs. Adults were very abundant in spring emergence traps in the earliest time interval they were set out (June 29-July 23). Peak emergence is early in the summer. Larvae, pupae and adults were common in fish guts. This taxa is widespread and common in montane western North America. It is typically associated with small to large size streams at mid to higher elevations. It has not been recorded from lake habitats to date. Larvae are omnivorous, but appear to be primarily scraping algae in the littoral zone of Crater Lake.

Homophylax ?insulas (Trichoptera: Limnephilidae): Several adults were found in emergence trap collections at caldera springs 9 and 20. This genus is in need of revision. The taxa present in the caldera springs appears to be *H. insulas*. *Homophylax* is a relatively uncommon limnephilid genus associated with small streams, springs and seeps in montane areas of western North America. Larvae are probably shredders.

Imania cidoipes (Trichoptera: Limnephilidae): Adults of this taxa were found occasionally in emergence trap collections at caldera spring 20. One adult was also taken in a window trap at spring 21. This is an uncommon limnephilid

associated with seeps and springs at higher elevations in the Cascades. Larvae are scrapers. There are some significant differences evident in the morphology of the male genitalia, between the Crater Lake population and those found further north in the Cascades. Until further material is collected from throughout the range of this specie(s), we will note this as a variant of *I. cidoipes*.

Limnephilus spp. (acula, fagus, insularis, spinatus)(Trichoptera: Limnephilidae): No *Limnephilus* larvae have been collected from the benthos of the lake or caldera springs. Adults of these four species have been found in fish stomachs, and one specimen was found in an emergence trap at spring 42 (?crawled under the net). These probably represent transient adults. It is unlikely that larvae are anything but rare in the lake littoral.

Psychoglypha (Trichoptera: Limnephilidae): One larvae was taken in benthic collections made at spring 21.

Neothremma didactyla (Trichoptera: Uenoidae): Adults of this taxa were abundant in emergence trap collections at caldera spring 9, and less so at spring 20. Larvae were abundant in benthic collections made at spring 9, and also were present at spring 20 (occasional) and 48 (rare). This taxa is common at mid to higher elevations in the Cascades. It is associated with springs, and small to mid-size, cold montane streams. Larvae are scrapers.

Agabus tristus, Potamonectes striatellus, Sanfilippodytes (Coleoptera: Dytiscidae): Adults and larvae of dytiscid beetles are common in shallow, littoral waters of the lake. *Agabus tristus* (a larger taxa) and *Sanfilippodytes* (a small taxa) larvae and adults are uncommon. Agabus adults were found most often in fish stomachs. *Potamonectes striatellus* is a small dytiscid that is common in the shallow littoral around the entire lake. Larvae have been associated with rock substrates, FPOM, CPOM, and macrophytes. Adults are swimmers, though they will use any stable substrate for resting. Adults must return to the lake surface at periodic intervals to renew air supplies. Larvae and adult dytiscids were common prey items for fish. All of the dytiscids identified are widely distributed and common in North America. Both adults and larvae are aquatic predators.

Hydrophilidae (Coleoptera): Larvae and adult hydrophilid beetles are uncommon in the lake. Larvae were collected in organic matter accumulations on the lake margin on Wizard Island. Two adults have been found in fish stomachs.

Dixidae (Diptera): Larvae are occasional in caldera springs.

Psychodidae (Diptera): Adults were taken occasionally in emergence traps at caldera springs 9 and 42.

Prosimulium travisi and Simulium hunteri (Diptera): Blackfly larvae, pupae and adults have been collected from caldera springs 8 and 48.

Syrphidae (Diptera): Larvae of the rat-tail maggot were found occasionally in organic accumulations on the lake margin in Fumarole Bay on Wizard Island.

Thaumaleidae (Diptera): Larvae are of occasional to common occurrence in caldera springs, where they can be found on rock surfaces wetted by splashing water.

Tipulidae (Diptera): Tipulid larvae (genus unknown) have been taken in benthic collections at caldera springs 7 and 16.

Chironomidae (Diptera): Midge larvae are ubiquitous in the lake and caldera springs, and are common to abundant in most habitat types. Only a small fraction of the midge material has been identified to date. Ultimately, this family will account for much of the species diversity present in Crater Lake benthic communities. The number os species in the lake benthos probably exceeds 100.

Biological Notes on a New Species of Aquatic Mite from Crater Lake

N. H. Anderson and G. W. Krantz

In 1988, a collection of benthic invertebrates from the Phantom Ship area of Crater Lake (see Study Area and Facilities section) was found to contain an unusual aquatic mite (Fig. 1). Several thousand individuals were taken in a sample collected by a scuba diver at 5 m, using a brush to scrape a rock face. The mite was determined to be an undescribed species in the genus *Algophagopsis*. Subsequent collections showed that it was one of the most abundant benthic invertebrates in some habitats of Crater Lake, presently the only known location for the species.

The purpose of this report is to document the distribution of *Algophagopsis* sp. in Crater Lake and to provide notes on the morphology, life history, and behavior of the species.

Classification and Background

Mites belonging to five unrelated groups occur in freshwater habitats (Smith and Cook 1991). Those usually referred to as "water mites" belong to the Hydrachnida (suborder Prostigmata or Actinedida). Over 100 genera are included in the treatment of North American water mites by Smith and Cook (1991). The larval stage of water mites is typically parasitic on adult aquatic insects, whereas adults and nymphs are predators.

Algophagopsis is not a prostigmatic water mite but rather is placed in the suborder Astigmata (also known as Acaridida), superfamily Hemisarcoptoidea, Family Algophagidae. According to OConnor (1982), the family is composed of five named and two unnamed genera. Algophagid mites are not parasitic as larvae nor predaceous as

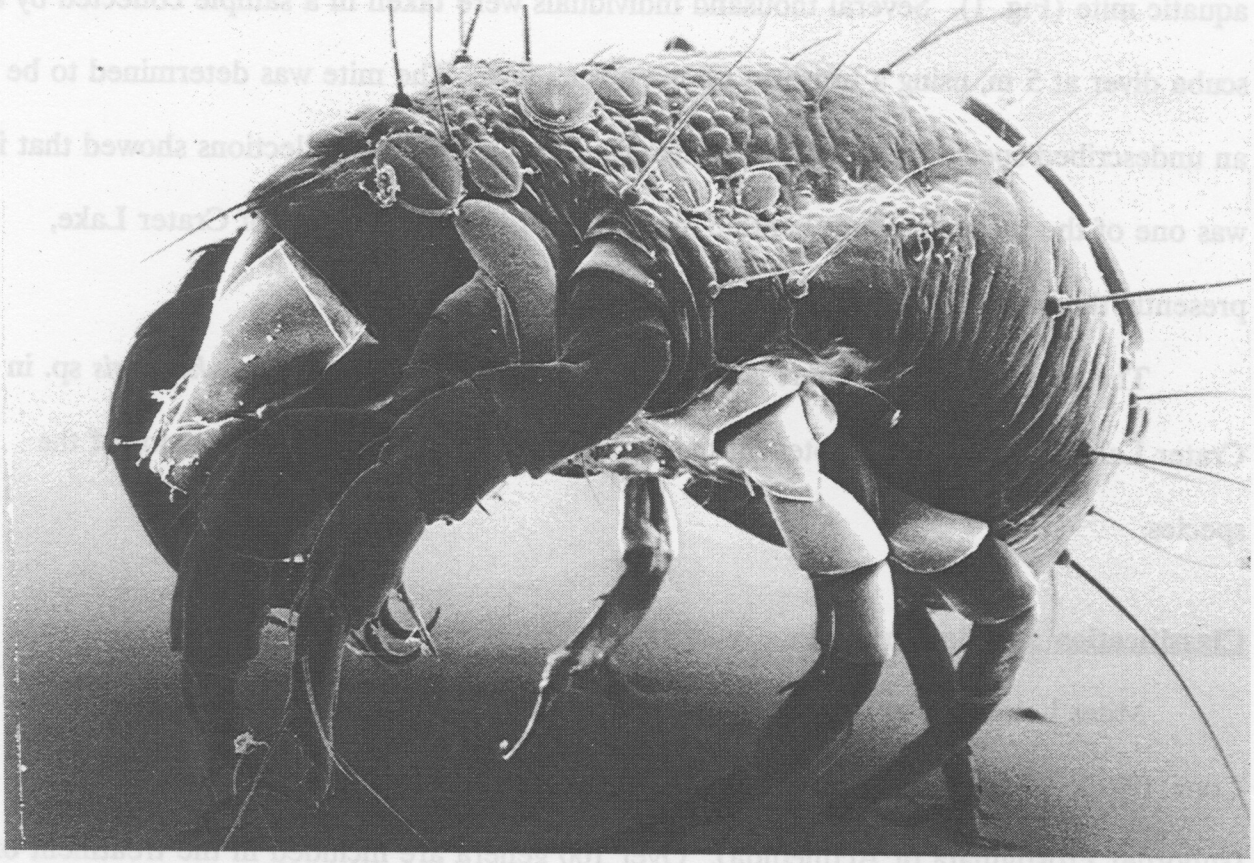


Figure 1. Scanning electron micrograph of the aquatic mite *Algophagopsis* n. sp. (x230). The specimen has been sonicated to remove a coating of *Cocconeis* diatoms; some diatoms are evident on the dorsum and posteriorly. The curved, elongate structure between legs I and II functions in osmoregulation.

nymphs and adults; they appear to be microorganismal feeders or algivorous. They inhabit sap fluxes and wet subcortical habitats (two genera), water-filled tree holes (one genus), algal mats in rivers (one genus), and brackish or intertidal waters (two genera). The only described species of *Algophagopsis*, *A. pneumatica*, was collected in Kings River, Fresno, California. It was observed to occur at densities as high as 1500/ft^2 in algal mats on submerged rocks in riffles (Fain and Johnson 1975).

Classification of the Family Algophagidae is currently being revised by Barry OConnor, University of Michigan, and Norman Fashing, College of William and Mary. Material from Crater Lake was sent to these specialists for description of the new species.

Algophagopsis n. sp. is a small (~ 1/2 mm), broadly ovoid opaque white or brownish mite with relatively long legs, each of which bears a large claw (Fig. 1). A pair of lens-like eyes are located on an elevated turret on the posterior margin of a small sclerotized prodorsal shield. The dorsum and venter of *Algophagopsis* n. sp. often carry a coat of diatoms, giving the integument a heavily ornamented appearance. Of special interest are the paired sclerotized axillary organs situated laterally between legs I and II, band-like structures which are thought to serve as osmoregulatory organs.

Distribution and Abundance in Crater Lake

The initial collection of *Algophagopsis* was from the Phantom Ship area in September 1988. It was abundant in the littoral zone in samples taken by a diver scraping rock surfaces down to about 15 meters. The dominant substrate in the samples was a crustose growth initially identified as the Cyanobacterium, *Nostoc*. However, further examination by Dr's. Harry Phinney and William Denison (Botany Dept., Oregon

State University) indicated that much of the crust was an aquatic lichen. Dr. Denison identified it as belonging either to the genus *Endocarpon* or to an undescribed genus. Brode (1938) reported aquatic lichen was of primary importance as a cover on rock surfaces in some areas of the lake.

Dr. Phinney observed that the fungal and algal elements occurred independently as well as in the symbiotic relationship of the lichen mat. He found that *Nostoc* was common as spherical growths, and that fungal mycelia were abundant. The mycelia were often interwoven with epiphytic diatoms, such as *Epithemia*. In summary, with the epilithic growth being composed of lichen, fungi, cyanobacteria (*Nostoc*), and diatoms, there was a wide selection of food that the mites could be using.

Benthic sampling in 1989 documented the widespread distribution of *Algophagopsis* at all depths sampled by scuba diving in Crater Lake (Table 1). The mite was abundant on firm substrates and absent or rare in areas of fine particulate matter. In Buoy Bay, where substrates were sand, small gravel, or wood fragments, 11 of 12 samples had no mites. Rock faces or boulder tops with a layer of lichen/*Nostoc* were the favored habitat for *Algophagopsis*. At Black Sand Beach, the diver collected paired samples down to 15 m. He scraped material from tops of boulders and collected from the pockets of organic fines trapped between boulders. The mites were abundant on the rocks at all depths but, except for the 15 m sample, they were absent in the fines (Table 1).

Mites were common in dredge collections of the moss *Drepanocladus aduncus* at depths between 46 and 65 m. The record depth for the mite was in moss collected by

Table 1. Relative abudance of *Algophagopsis* mites in benthos samples from Crater Lake in 1989 (collected by scuba divers unless otherwise noted).

Location	Substrate	Mite abundance at given depths					
Black Sand Beach		3m	8m	10m	12m	15m	
(Wizard Island)	Boulder tops	>100	2400	>500	720	480	
	Fine particulates	0	0	0	0	24	
Phantom Ship		6-12m					
	Rock face	>1000					
Steele Bay		>1m	4m	6m	12m		
	Boulder tops	--	400	40	50		
	Cobble/Gravel	0	--	--	--		
	Sand/Fine gravel	--	60	--	0		
	Fine particulates	--	--	16	--		
Lady of the Lake		1m	3m	6m	9m	12m	15m
(Skell Head)	Rock face	4	0	4	12	52	30
	Moss	8	--	--	--	--	--
Buoy Bay		3+5m	6m	8+9m	11m	12m	14+15m
	Sand/Fine gravel	0	16	0	0	0	0
	Fine particulates/Wood	--	--	0	0	--	--
Off Wizard I. Dock		26m	46m	48m	65m		75m
Ponar Dredge	*Drepanocladis* (No./10cc)	0	22	60	16,33,(4)[a]		(2)[a]

[a]The number in parenthesis is the mite abundance in senescent moss.
Deep Rover dives - mites recorded in *Drepanocladis* samples by Dr. Harry Phinney:
Dive 214, Sentinel Rock - 118 m.
Dive 219, S. of Wizard I. - 29 m, 46 m, 62m.

the Deep Rover submarine at 118 m (Table 1). This was also the deepest collection where the moss was reported to be in good condition (see Deep-water Benthic Communities section).

Algophagopsis also was abundant in mats of filamentous green algae in Emerald Pool near Wizard Island. A collection by Bob Truitt on August 23, 1991, from shallow

water (< 2 m) contained all stages of the mite in a mat of *Cladophora* whose strands were coated with the epiphyte *Epithemia*. Some spheres of *Nostoc* also occurred at the base of clumps of *Cladophora*. (Algae were all determined by Chris Lundberg, Botany Dept., Oregon State University). At the time of collection, water temperature in Emerald Pool was near 20°C. As this mite also occurs below 100 m where temperatures were less than 4°C, it tolerated a broad temperature range.

Life-History Observations in the Laboratory

Some mites survived in a laboratory at Oregon State University for over a year, but attempts to culture *Algophagopsis* were not successful. Appropriate conditions of food, substrate, and other requirements to maintain a reproducing colony in the laboratory have not been identified. The following notes may be useful in determining the life cycle of this enigmatic animal.

Several live *Algophagopsis* were found on stones from the Phantom Rock area that had been stored in a cold room from September 1989 to May 1990. They had survived for eight months in total darkness in an ice chest at 4°C. In October 1990, four rocks from the cold room were washed thoroughly and 457 mites were recovered, of which 30% were living. Density was estimated to be 16.1 mites/100 cm^2 (4.9/100 cm^2 living).

Adult mites were transferred to petrie dishes with small pieces of the volcanic rock and detritus from the storage container. Mite larvae were found after three days. This supported the hypothesis that *Algophagopsis* is viviparous because eggs had not been found in field collections. Young mites (0-2 weeks old) were transferred to another culture dish with small stones and the epilithic growth as a substrate and maintained at 13-17°C. At eight weeks, a sample was slide-mounted, and the life stages present were

one adult and five deutonymphs. Thus, under lab conditions, the first adult was obtained in 8 to 10 weeks. At 14 weeks, when all of the adults from the F_0 generation had died, the rearing was discontinued and the progeny were slide-mounted. The age-structure of the F_1 generation was: larvae - 0; protonymphs - 9; deutonymphs - 9; females - 6; and males - 4.

In August 1991, a vigorous population of mites was obtained in a mat of green algae from Emerald Pool. This population was maintained as a stock culture in aerated Crater Lake water at 15°C. The algae was primarily *Cladophora* with a heavy coating of *Epithemia* and other epiphytes. Adults in petrie dishes with the *Cladophora* substrate initially reproduced well, but the numbers of mites declined after 3 to 4 weeks. The decline was attributed to a decrease in food quality because the algae did not grow under lab conditions. Immature mites that were provided only with the flocculent detritus that built up in the stock culture of *Cladophora* lived for less than two weeks. Adult *Algophagopsis* (unknown age) on filter paper that had been conditioned for several days in the *Cladophora* mat lived for up to a month but did not reproduce. The inference from these observations was that the mite could withstand a long period of starvation or subsist on microbes that exploit cellulose. After 3 months the stock culture of mites declined to only a few individuals. The decline seemed to be associated with senescence of the algal mat and the epiphytes.

In summary, while it is apparent that *Algophagopsis* can tolerate a range of field and laboratory conditions, we have not been able to maintain a culture. We need to be able to rear it in order to make any progress on understanding the role of this abundant

species in Crater Lake. The limiting factor at present seems to be knowing what to feed it.

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Survey of Deep-water Benthic Communities

C. David McIntire, Harry K. Phinney, Gary L. Larson, and Mark Buktenica

In August 1989 a series of deep-water dives were made at selected locations in Crater Lake using Deep Rover, a one-person submersible (Dymond et al. 1989). The major goal of these dives was to identify the magnitude and characteristics of hydrothermal inputs to the deep lake. In addition, the National Geographic Society provided supplementary funds to support an initial survey of the deep-water benthic communities in the lake. This section reports the results of this preliminary survey and makes recommendations for future research.

A list of dives that provided samples of biological material from Crater Lake in August 1989 is presented in Table 1. Dives 219, 221, 225, and 227 were supported by the National Geographic Society and were designed to locate and collect biological specimens from deep-water benthic communities. In particular, biologists were interested in the distribution and abundance of a deep-water aquatic moss (*Drepanocladus*) and its associated epiphytic algae. Biological samples also were obtained from rocks collected during three dives for the U. S. Geologic Survey (dives 210, 212, and 214) and one dive designed for hydrothermal exploration (dive 228). All biological materials obtained from dives 210, 212, 214, 219, 221, 225, 227, and 228 were examined under the supervision of Dr. Harry K. Phinney (now deceased), Department of Botany & Plant Pathology, Oregon State University. Preserved specimens of *Drepanocladus* are deposited in the Oregon State University Herbarium and in the Natural History Collection at Crater Lake National Park. In addition, permanent slides of epiphytic and epilithic diatoms are now available for examination from C. David McIntire (Department of Botany & Plant Pathology, Oregon State University).

The untimely death of Dr. Phinney in November 1990 made it necessary to restructure this section of our final report to the National Park Service and National Geographic

Society. Here, we describe the results of Dr. Phinney's careful analysis of each sample obtained during the eight dives listed in Table 1. Also, we include observations recorded during his examination of a dredge sample taken at 48 m between Wizard Island and a point on the southwest shore directly below Crater Lake Lodge. In order to provide an accurate transcription of Dr. Phinney's observations, the description of each sample is written in a form similar to a taxonomic description, a format that corresponds closely to the original set of notes. Samples from each dive are listed in an order progressing from the most shallow to the deepest location. This descriptive section of the report is followed by an interpretive section that attempts to summarize the biological patterns revealed by the deep water exploration of Crater Lake in August 1989.

Table 1. A list of deep-water dives that provided samples of biological material from Crater Lake. All dives were made with the one-person submersible Deep Rover during August 1989.

Date	Dive #	Pilot	Location	Purpose
8/9/89	210	M. Buktenica	Llao Rock	Geology
8/11/89	212	M. Buktenica	Palisades Point	Geology
8/13/89	214	M. Buktenica	Sentinel Rock	Geology
8/20/89	219	M. Buktenica	South of Wizard Island	Biology
8/23/89	221	B. Robinson	South of Wizard Island	Biology
8/26/89	225	S. Earle	South of Wizard Island	Biology
8/28/89	227	M. Buktenica	Palisades Point	Biology
8/29/89	228	J. Dymond	Northeast Basin	Hydrothermal

Description of Samples

DIVE #210

Date: August 9, 1989
Location: Llao Rock
Pilot: Mark Buktenica
Field Director: Charles Bacon
Primary Purpose: Collection of geological specimens

Sample No. 1
Depth: 59 m
Substrate: Rock
Description: Suspension quite green, associated with fine flocculent material. Diatoms stalked, small amount of medium-size Oedogonium present along with some Gongrosira and Gomontia.

Sample No. 2
Depth: 59 m
Substrate: Rock
Description: Moss plants (Drepanocladus) appear very old, only leaf bases left, with lateral attaching rhizoids along the axis. Mosswas growing attached but very sparse in biomass. Strange acellular membranous-like material present, associated with very finely coiled and branched filaments (=bacteria ??). Epiphytic algae on the moss included Melosira undulata, Rhizoclonium, and large species of Oedogonium.

Sample No. 3
Depth: 90 m
Substrate: Sediment
Description: Moss consists of both Drepanocladus and Chiloscyphus. Epiphytes sparse, consisting of mostly Melosira undulata, Vaucheria, and Rhizoclonium heiroglyphicum. More algae on the Chiloscyphus than on the Drepanocladus.

Sample No. 4
Depth: 91 m
Substrate: Rock
Description: Two sprigs of living moss present. The only recognizable diatom remains were specimens of Melosira undulata, some cells with plastids. One clump of M. undulata filaments in good condition.

Sample No. 5
Depth: 102 m
Substrate: Rock
Description: Melosira undulata abundant and in good condition. Cymbella also present.

Sample No. 6
Depth: 149 m
Substrate: Rock
Description: No moss found. Melosira undulata present in both a living condition and with some dead cells. Diatom cells of a few other species also present.

Sample No. 7
Depth: 152 m
Substrate: Rock
Description: Sparse growth of Melosira undulata, about 50% of the cells in a living condition and the other 50% detrital.

Sample No. 8
Depth: 166 m
Substrate: Rock
Description: Melosira undulata abundant. No other taxa evident.

Sample No. 9
Depth: 173 m
Substrate: Rock
Description: All mineral detritus. No living cells observed.

Sample No. 10
Depth: 195 m
Substrate: Rock
Description: Silty brown material, with much fine suspended mineral particles and detrital diatoms. Diatoms include Melosira undulata in short filaments, and species of Amphora, Epithemia, and Campylodiscus. No cells with plastids.

Sample No. 11
Depth: 272 m
Substrate: Rock
Description: No detrital or live material; all mineral particles.

Sample No. 12
Depth: 324 m
Substrate: Rock
Description: Dark flocculent material often clinging in chunks that look like fecal pellets. No diatoms seen.

DIVE #212

Date: August 11, 1989
Location: Palisades Point
Pilot: Mark Buktenica
Field Director: Charles Bacon
Primary Purpose: Collection of geological specimens

Sample No. 1
Depth: 83 m
Substrate: Sediment
Description: Moss pristine, cell walls of leaves light reddish brown, walls of cells making up the axes much darker brown. Not many diatoms attached to moss, but with some Melosira undulata and stalked Cymbella and Gomphonema. Some epiphytic chlorophytes abundant, including a robust Vaucheria, large and small species of Oedogonium, Bulbochaete, Rhizoclonium hieroglyphicum v. macromeres, and Spirogyra. Tribonema bombycinum with mostly empty cells also present. Rhizoclonium with many cells of epiphytic Epithemia.

Sample No. 2
Depth: 94 m
Substrate: Rock
Description: Live moss with much living epiphytic algae. Moss leaves with serrate margins (maybe it is not Drepanocladus). Most abundant epiphytes include Melosira undulata, Rhizoclonium hieroglyphicum v. macromeres, and Vaucheria. Fairly abundant Melosira with gelatinous rod attachments; associated sediment also have much Melosira.

Sample No. 3
Depth: 116 m
Substrate: Rock
Description: Moss with serrated leaves and abundant lateral rhizoids. Epiphytes include Melosira undulata (abundant), Cladophora crispata, Tribonema bombycinum, and stalked and sessile diatoms, particularly species of Epithemia and Gomphonema. Associated suspended matter had mostly Melosira undulata in good condition.

Sample No. 4
Depth: 155 m
Substrate: Rock
Description: Mostly solitary detrital diatoms. Melosira undulata 50% living cells and 50% dead cells. Much fine mineral debris.

Sample No. 5
Depth: 199 m
Substrate: Rock
Description: Large amount of dark, finely divided, mineral (?) material. A small amount of Melosira undulata, mostly detrital; some cells with plastids but cells appear disrupted.

Sample No. 6
Depth: 227 m
Substrate: Rock
Description: Dark mineral ooze with no organisms.

Sample No. 7
Depth: 310 m
Substrate: Rock
Description: Much fine flocculent material with a few detrital diatoms, mostly Melosira undulata. Nothing appeared to be living.

Sample No. 8
Depth: 454 m
Substrate: Sediment
Description: Fragments of dead moss with no epiphytes.

Sample No. 9
Depth: 456 m
Substrate: Rock
Description: Material all detrital.

DIVE #214

Date: August 13, 1989
Location: Sentinel Rock
Pilot: Mark Buktenica
Field Director: Charles Bacon
Primary Purpose: Collection of geological specimens

Sample No. 1
Depth: 19 m
Substrate: Rock
Description: Mostly diatoms, small amount of Melosira undulata. Nostoc and Microthamnion also present. Much fragmented detrital material (diatomite).

Sample No. 2
Depth: 84 m
Substrate: Rock
Description: A few green, healthy plants of Drepanocladus. Melosira undulata robust and abundant. Moss is heavily grazed.

Sample No. 3
Depth: 92 m
Substrate: Sediment
Description: Moss sample with epiphytic Vaucheria (robust), Cladophora crispata (?), Tribonema bombycinum, Melosira undulata (robust) with gelrods, and Epithemia (abundant). Very few stalked diatoms. A few sprigs of very dark bristly Drepanocladus with many lateral rhizoids and "leaf" cells with plastids.

Sample No. 4
Depth: 118 m
Substrate: Rock
Description: Moss very green and lush with abundant epiphytes. Epiphytes include large and small species of Oedogonium, Bulbochaete, Melosira undulata, and many stalked diatoms (Cymbella and Gomphonema in particular). Less abundant epiphytes were Vaucheria, Rhizoclonium, Tribonema bombycinum, and Cladophora crispata. The protozoans Vorticella and Stentor also were present along with and large annelid worm.

Sample No. 5
Depth: 118 m
Substrate: Rock
Description: The moss (Drepanocladus) in good conditions. A diversity of epiphytic taxa observed including Oedogonium (large species), Bulbochaete, Rhizoclonium (?), many stalked diatoms (Cymbella and Gomphonema in particular), Epithemia, Nostoc, a little Melosira undulata, Cladophora crispata, and Vaucheria. Diatom stalks very numerous, long, and robust. Nostoc colonies soft and loose. Also, a new species of mite was found in this sample (Genus Algophagopsis, Family Algophagidae). This species is apparently new to science and has not yet been described in the literature.

Sample No. 6
Depth: 161 m
Substrate: Rock
Description: Melosira undulata observed in good condition and not much else.

Sample No. 7
Depth: 223 m
Substrate: Sediment
Description: Some of the moss (Drepanocladus) was in good condition, while some specimens look almost dead but with a few cells in the leaves with plastids. Epiphytes included large and small species of Oedogonium, Melosira undulata, Vaucheria, and Epithemia (in good condition).

Sample No. 8
Depth: 229 m
Substrate: Sediment
Description: Most moss plants appear to be dead, although a few cells in some of the leaves appear to have plastids.

DIVE #219

Date: August 20, 1989
Location: South of Wizard Island
Pilot: Mark Buktenica
Field Directors: David McIntire and Gary Larson
Primary Purpose: Collection of biological specimens

Sample No. 1
Depth: 26 m
Substrate: Sediment
Description: Drepanocladus with a diversity of epiphytic taxa which included Zygnema, stalked diatoms (Cymbella and Gomphonema), Tribonema bombycinum, Epithemia, Nostoc patches on leaves, large and small species of Oedogonium, and Bulbochaete with its own epiphytes. No Vaucharia, Cladophora, or Rhizoclonium observed. Some of the older, darker, eroded moss plants completely encased in Nostoc and many sessile epiphytic diatoms on older moss plants. Many of the moss specimens were dead-looking with very dark "stems" with eroded or grazed-off leaves; only occasional stems with leaves in good shape. Also, several ostracods were observed.

Sample No. 2

Depth: 29 m

Substrate: Sediment

Description: Drepanocladus in pristine condition. Epiphytic algae not abundant but diverse. Epiphytic taxa included large and small species of Oedogonium, Bulbochaete, stalked Cymbella, Gomphonema, Mougeotia, small dense reddish colonies of Nostoc, Spirogyra , Sirogonium, Tribonema bombycinum, Pediastrum boryanum, Melosira undulata with gelrod attachments, Phacus orbicularis, and Cosmarium. Oedogonium and Bulbochaete with normal cell contents including holdfast; small Oedogonium with oogonium, but too young to tell opening or decorations. Spirogyra represented by two species, one with 1 plastid and other with 4 plastids. The microfauna included an ostracod, Carchesium, and a mite (Algophagopsis).

Sample No. 3

Depth: 30 m

Substrate: Sediment

Description: Sample from dense moss bed. Common epiphytes include single plastid Spirogyra with conduplicate end walls, Zygnema, large and small species of Oegogonium, Bulbochaete, Vorticella, and large Nostoc colonies; Melosira undulata was present but not numerous. Older brown axes of moss with Tribonema bombycinum, Staurastrum, and Pleurotaenium. Bulbochaete shows signs of zoospore formation. Large Oedogonium with much epiphytic Epithemia. Diatom stalks associated with some of the green leaves. The brown moss plants (rather than green) from the bottom of the bed with very few epiphytes and with many of the plants lacking any plastids, although the cell wall structure seemed to show no breakdown. Leaves on darker brown axes often had plastids restricted to the center of the leaf. Leaf axes collect detritus. Most dark colored leaves have extensive areas of cells with plastids.

Sample No. 4

Depth: 38 m

Substrate: Sediment

Description: Dense field of pristine moss. Common epiphytes include Zygnema, Bulbochaete, Chaetosphaeridium globosum, large Oedogonium, Spirogyra with 1 plastid, stalked Cymbella, Nostoc in loose aggregations, Melosira undulata (each cell with a large lipid globule), and Mougeotia. Some dead Vaucheria on older parts of moss. Arcella thecas (?) observed. Dark, dead bottom layer of moss with large Oedogonium, Tribonema bombycinum, Melosira ambigua, and Fragilaria (?). In moss plants from the bottom of the mat, the cell walls have a reddish brown tinge, and while the overall appearance may be green, the plastids are often not easy to distinguish. Some plants are obviously detrital with leaves torn or missing, and without plastids, the cell walls becoming indistinct. These latter plants have fewer epiphytes.

Sample No. 5

Depth: 46 m

Substrate: Sediment

Description: Moss (Drepanocladus) pristine. Common epiphytes included stalked diatoms (Gomphonema and Cymbella), species of Spirogyra (with 1 and 4 plastids), large and small species of Oedogonium, Tribonema bombycinum, Nostoc, Melosira undulata (uncommon), Bulbochaete (abundant), Mougeotia, Vaucheria (not abundant), and Zygnema. A mite and the rotifer Philodina.

Sample No. 6

Depth: 53 m

Substrate: Sediment

Description: Moss sample from thick bed. Green moss leaves have patches of empty cells with no plastids. Epiphytes include large and small Oedogonium (holdfasts dark green!), Bulbochaete (abundant), Melosira undulata (dark brown with gelrods and large yellow lipid globules), filaments of Fragilaria, stalked Cymbella and Gomphonema, Tribonema bombycinum, Spirogyra (1 and 4 plastids), Melosira ambigua, large loose colonies of Nostoc, empty Vaucheria walls, Zygnema, Ophiocytium, Rhizoclonium, and Cladophora. The dark brown appearance of Melosira undulata is caused by dark brown cell walls.

Sample No. 7

Depth: 62 m

Substrate: Sediment

Description: Sample from dense moss bed; moss pristine. Moss leaf tips with stalked Gomphonema and some Cymbella. Other epiphytes include Tribonema bombycinum (abundant), loose colonies of Nostoc, large Oedogonium (probably 2 species), Vaucheria (some cells green, others empty), Zygnema, Oedogonium with dark green holdfasts, Bulbochaete, and Spirogyra with one plastid. In general, filamentous algae restricted in number and variety. Mites also observed in this sample.

Sample No. 8

Depth: 80 m
Substrate: Sediment
Description: Moss dark brown, apparently dead; leaves mostly missing; no plastids. Essentially no epiphytes on moss. Axes of moss dark red; leaf cell walls light brown, showing some evidence of breakdown. Most moss axes have no whole leaves, usually only leaf bases. Green Vaucheria and empty Vaucheria walls abundant, with sparse Epithemia. Oedogonium and Nostoc not observed. Only one strand of Melosira undulata observed, 3 living cells and 3 dead cells. Other algal taxa found include Bulbochaete, Spirogyra, Mougeotia, Zygnema, Tribonema (dead), Rhizoclonium, Cladophora, and detrital Campylodiscus.

Sample No. 9

Depth: 101 m
Substrate: Sediment
Description: Moss and algae both looked detrital. When washed free of sediment some moss leaves appear to have plastids in 70 - 85% of the cells but walls are dark. However, many leaves were removed from the axes by washing, and these leaves had no plastids. A few Melosira cells contain plastids in good condition. Live Vaucheria and Melosira found attached to moss and to each other.

Sample No. 10

Depth: 121 m
Substrate: Rock
Description: Moss with axis and leaves in good condition but there was no evidence of functional cell contents. The plant exhibited a pale yellow color. No epiphytes or associated algae seen on the moss. Nostoc and Melosira undulata present and attached to mineral particles.

Sample No. 11

Depth: 155 m
Substrate: Sediment
Description: "Old" moss bed covered with sediments, probably detrital. Also found a slurry of detrital diatoms with many specimens of Campylodiscus in various sizes.

DIVE #221

Date: August 23, 1989
Location: South of Wizard Island
Pilot: Bruce Robinson
Field Director: Mark Buktenica
Primary Purpose: Collection of biological samples

Sample No. 1

Depth: Continuous sample taken between 138 m and 229 m
Substrate: Fine sediment
Description: Much of the sample was detrital, but some living diatom material was observed along with gymnosperm pollen. Melosira undulata filaments numerous and long, with the majority of the cells empty or containing only disorganized and usually unpigmented material; a few cells contain plastids, often with little sign of other cytoplasmic components. Some living cells of Campylodiscus observed with cells of various sizes; perhaps more than one species. A number of motile gliding pennate diatoms observed along with a filament of Melosira pyxis, 21 cells long, every cell in optimal living condition.

DIVE #225

Date: August 26, 1989
Location: South of Wizard Island
Pilot: Sylvia Earle
Field Director: Gary Larson
Primary Purpose: Collection of biological specimens

Sample No. 1

Depth: 70 m
Substrate: Sediment
Description: Moss pristine, bright green, plastids flat against lateral walls, lipids abundant. Epiphytes include Oedogonium capitellatum, an Oedogonium with extremely long cells, a medium size Oedogonium with a long terminal seta, a very small Oedogonium with zig zag filaments, Vaucheria epiphytized by Epithemia, Melosira undulata, stalked Cymbella and Gomphonema (on tips of moss leaves), loose reddish Nostoc, Spirogyra, Palmodictyon viride, Microspora stagnorum, Microsterias, Zygnema, and Bulbochaete (not abundant). A few nematodes also were observed.

Sample No. 2
Depth: 78 m
Substrate: Sediment
Description: Moss is 95% living and 5% dark in color, probably dead. Moss with abundant epiphytic Vaucheria with long streamers in good condition. Older filaments of the Vaucheria epiphytized by Epithemia. Other epiphytes on moss include Spirogyra (1 and 2 plastid species), Melosira undulata, Tribonema bombycinum, a medium and large size Oedogonium, Microspora stagnorum, and Zygnema. The Melosira and other pennate diatoms often have large lipid globules.

Sample No. 3
Depth: 90 m
Substrate: Sediment
Description: One dead specimen of Drepanocladus with an abundant growth of Melosira undulata (alive) and a few stalks of Cymbella. Much glassy mineral fragments and detrital diatoms, especially Campylodiscus.

DIVE #227

Date: August 28, 1989
Location: Palisades Point
Pilot: Mark Buktenica
Field Director: David McIntire
Primary Purpose: Collection of biological specimens

Sample No. 1
Depth: 70 m
Substrate: Sediment
Description: This was a two-bag sample. Bag #1 had green moss in good condition, with epiphytic Zygnema, medium size Oedogonium, and Melosira ambigua. Bag #2 had dead Drepanocladus with only detrital diatoms and some light green patches of living filamentous algae. These patches included large and small species of Oedogonium, Spirogyra (1 and 2-plastid species with replicate cell walls), Melosira undulata, stalked Cymbella and Gomphonema, Palmodictyon, Bulbochaete, Vaucheria (empty cells), and Tribonema tenerrina.

Sample No. 2
Depth: 91 m
Substrate: Sediment
Description: Moss in good condition, some material with living dark, reddish cell walls. There could be another species of moss mixed in with this sample, as some specimens are with slightly serrate margins and no or very inconspicuous costa; this moss has many lateral rhizoids not seen in Drepanocladus. Algae associated with the moss sample include Melosira undulata with lipid drops, Tribonema bombycinum, Vaucheria, Cladophora crispata, a large Oedogonium, stalked Cymbella, and Gomphonema (abundant), Spirogyra (with 1 plastid), Tribonema tenerrima, and Bulbochaete (sparse).

Sample No. 3
Depth: 124 m
Substrate: Sediment
Description: Drepanocladus appears detrital. Much Melosira undulata, some in good shape, but some with empty frustules in the chains. Melosira undulata attached and in rafts tied together with gel rods.

Sample No. 4
Depth: 529 m
Substrate: Sediment
Description: Both Drepanocladus and Melosira appear to be detrital, without living cells. Moss without epiphytes or associated algae. Sediments mostly detrital material with dead Melosira cells.

Sample No. 5
Depth: 536 m
Substrate: Sediment
Description: All moss material dead, detrital plants. All associated diatoms dead as well. Several filaments of dead Oedogonium observed. Sediments were mostly detrital diatoms.

Sample No. 6
Depth: 545 m
Substrate: Sediment
Description: All moss and diatoms detrital, although some Melosira appeared alive. Detrital diatoms included long strands of Melosira undulata, isolated Epithemia, Cymbella, and Campylodiscus. A nematode, microcrustacean carapace fragments, and gymnosperm pollen were also observed in this sample.

DIVE #228

Date: August 29, 1989
Location: Northeast Basin - Box Core from Blue Pool
Pilot: Jack Dymond
Field Director: Robert Collier
Primary Purpose: Hydrothermal exploration

Sample No. 1
Depth: 559 m
Substrate: Sediment
Description: Detrital moss. Living Vaucheria with abundant traces of cytoplasm and plastids found. Detrital Epithemia and Campylodiscus observed; no filamentous algae other than Vaucheria and Tribonema.

DREDGE SAMPLES

Date: July 25-27, 1989
Location: On a line between Wizard Island boat dock and Crater Lake Lodge
Field Director:
Primary Purpose: Collection of biological specimens

Sample No. 1
Depth: 46 m
Substrate: Sediment
Description: Moss pristine, with stalked Gomphonema and Cymbella attached to tips of leaves. Other algae in the sample include a large Oedogonium with a dwarf male (no oogonium present), small Oedogonium, Bulbochaete (with long setae and holdfast retaining cell contents), Vaucheria, a little Melosira undulata, Spirogyra (1 and 4 plastid species), Amphora, Tribonema bombycinum, and Zygnema. Protozoans in the sample include Stentor cerulea and a Centropyxis theca.

Sample No. 2
Depth: 48 m
Substrate: Sediment
Description: Epiphytic Epithemia on moss leaves. Other algae in the sample included large and small Oedogonium (large form abundant), Melosira undulata, stalked Cymbella and Gomphonema, some Bulbochaete, Tribonema bombycinum, a little Nostoc, and Zygnema. Vaucheria rare.

Sample No. 3
Depth: 75 m
Substrate: Sediment
Description: Stalked Cymbella abundant with some stalked Gomphonema. Other algae in the sample included at least three species of Oedogonium, many epiphytic diatoms, Vaucheria (abundant), Bulbochaete, Tribonema bombycinum with very pale plastids (abundant), small species of Tribonema, Melosira undulata with many cells of epiphytic Cocconeis, and Melosira granulata (?). Small animals included the mite Algophagopsis and a rotifer in the axil of moss leaf (with a very distinct cogged corona).

Sample No. 4
Depth: 100 m
Substrate: Sediment
Description: The algae form long streamers on the tips of Drepanocladus plants. Algae 80 - 90% Vaucheria. Other algae included Rhizoclonium hieroglyphicum var. macromeres, Cladophora crispata (?), large Amphora, stalked Cymbella (large species) and Gomphonema, Tribonema bombycinum, Melosira undulata, and Spirogyra with 1 plastid (rare).

Interpretation and Discussion

The history of the discovery and identification of the moss growing deep in Crater Lake has been reviewed recently by Phinney (1989). This organism is of considerable scientific interest, as it generates relatively large biomasses at depths of 30 m or more below the water surface. Moreover, relationships between deep-water benthic moss, with its assemblage of epiphytic algae, and the nutrient dynamics and bioenergetics of the Crater Lake ecosystem are entirely unknown. Moss samples from deep-water locations in Crater Lake have been identified by ecologists and taxonomists as *Fontinalis* and *Drepanocladus* (Hasler 1938), *Fontinalis howellii* Ren. & Card. (Winona Welch, unpublished), *Fontinalis* (Brode 1938), *Drepanocladus fluitans* (Hedw.) Warnst. (Francis Drouet, unpublished), *D. fluitans* (John Rowley, unpublished), and *D. aduncus* (Hedw.) Warnst. (Elva Lawton, unpublished). More recently, moss samples collected south of Wizard Island during dive 219 were examined by W. B. Schofield, Department of Botany, University of British Columbia, and D. Norris, Department of Botany & Plant Pathology, Oregon State University. Dr. Schofield interpreted the samples as specimens of *D. exannulatus* (B.S.G.) Warnst., but suggested that the material had some characteristics in common with *D. aduncus* var. *polycarpus* (Bland. ex Voit) Roth. Dr. Norris, in agreement with Lawton, identified the moss as *D. aduncus*. In this report, we refer to the deep-water specimens from Crater Lake as *D. aduncus*.

Hasler (1938) reported finding the green mosses *Fontinalis* and *Drepanocladus* in dredge samples collected at a depth of 394 ft (120 m), while Brode (1938) suggested that the moss in Crater Lake (identified as *Fontinalis*) may be found at depths down to 200 m or more. The vertical distribution of *Drepanocladus aduncus*, as revealed by samples obtained in August 1989, is summarized in Table 2. From these observations, it was apparent that in Crater Lake *D. aduncus* occurred at depths below about 25 m, as no specimens were collected between this depth and the water surface. Dense beds of the moss were

Table 2. Summary of the distribution of *Drepanocladus aduncus* in Crater Lake, August 1989. Dives are the same as those listed in Table 1 and in the Description of Samples section. Comments were extracted from the notes of Harry K. Phinney.

Dive	Depth	Substrate	Comments
219	26 m	sediment	living, with a diversity of epiphytes
219	29 m	sediment	pristine
219	30 m	sediment	from dense bed
219	38 m	sediment	from dense bed
219	46 m	sediment	pristine
**	46 m	sediment	pristine
**	48 m	sediment	epiphytes abundant
219	53 m	sediment	from dense bed
210	59 m	rock	old plants, sparse
219	62 m	sediment	from dense bed
225	70 m	sediment	pristine with epiphytes
227	70 m	sediment	some living and some dead plants
225	78 m	sediment	95% living and 5% dead
219	80 m	sediment	brownish, detrital material
212	83 m	rock	pristine
214	84 m	rock	plants in good condition
210	90 m	sediment	no comment
225	90 m	sediment	detrital
227	91 m	sediment	plants in good condition
214	92 m	sediment	plant in living condition
212	94 m	rock	plants with many epiphytes
**	100 m	sediment	with many epiphytes on tips of plants
219	101 m	sediment	detrital
212	116 m	rock	plants with abundant lateral rhizoids
214	118 m	rock	plants in good condition with epiphytes
219	121 m	rock	cells with no living contents
227	124 m	sediment	detrital
219	155 m	sediment	detrital
214	223 m	sediment	with some living and some dead cells
214	229 m	sediment	detrital
227	529 m	sediment	detrital
227	536 m	sediment	detrital
227	545 m	sediment	detrital

**Record from dredge samples obtained July 25-27, 1989.

observed at depths between 30 m and 70 m, a region corresponding roughly to the zone of maximum primary production in the water column (see Phytoplankton section). However, the lower boundary of active growth was harder to establish because of uncertainties about the physiological state of samples obtained at depths below 100 m. The deepest collection of moss in which the plants were reported to be in good condition was taken from a rock at a depth of 118 m. All specimens collected below this depth were obtained from sediment and consisted of dead tissue, or in one case (dive 214 from 223 m), material with both living and dead cells. Therefore, best estimates of the upper and lower limits of distribution for *D. aduncus* are 25 m and 120 m, repectively. All specimens found below 120 m, including those with a few living cells, were probably part of detrital inputs which apparently can cascade down from the zone of maximum population growth. It is not surprising that living cells are found in specimens taken from depths below 200 m, as decomposition rates are undoubtedly low at such depths where the water temperature remains below 4° C throughout the year.

The lower distributional limit of *Drepanocladus aduncus* in Crater Lake presumably is determined by the depth of effective light penetration. The depth at which irradiance is approximately 1% of the intensity at the surface is usually between 80 m and 100 m, a range that corresponds closely to the lower limit of maximum population growth. Possible hypotheses accounting for the upper distributional limit include: (1) distribution is limited to the lower metalimnion and upper hypolimnion because of warm summer temperatures in the epilimnion; (2) population growth is inhibited in the upper 25 m of the water column by high irradiance; (3) the moss is excluded from the upper 25 m of the water column by grazing activities of aquatic animals; and (4) upper distribution is determined by nutrient limitation, particularly during thermal stratification in the summer. *D. aduncus* has been found submerged in shallow water and boggy habitats from Greenland to Alaska and in the western United States as far south as California (Crum and Anderson 1981). Consequently, distributional records are inconsistent with the temperature and light inhibition

hypotheses, unless the population in Crater Lake represents a distinct ecotype with different physiological requirements than other varieties of this species. Coffey and Clayton (1988) found that the lower distribution of bryophytes in Lake Wanaka (New Zealand) was determined by the grazing activities of a crayfish (*Paranephrops*). However, in Crater Lake there is no evidence to indicate that grazing is more intense in the upper 25 m of the water column than at greater depths. Moreover, relatively large mats of green filamentous algae (*Zygnema* and *Mougeotia*) often are observed in the upper 5 m of the littoral zone around Wizard Island, possibly indicating that benthic grazing has relatively little impact on autotrophic assemblages in shallow water regions of the lake. Therefore, based on limited distributional records for August 1989 and measurements of water column primary production between 1986 and 1990 (see Phytoplankton section), the nutrient limitation hypothesis seems to be the most reasonable explanation for the observed upper distributional limit of *D. aduncus* in Crater Lake.

The assemblages of algae attached to *Drepanocladus aduncus* and other deep-water benthic surfaces in Crater Lake were diverse and often consisted of representatives of the Chlorophyta, Bacillariophyceae, Xanthophyceae, and Cyanophyta (cyanobacteria). A summary of the algal taxa found in the samples listed in Table 1 is presented in Table 3. Some of these taxa were identified by Dr. Phinney to the species level, but in most cases his notes indicated the presence of a particular taxon by genus name only. Most of the living algae reported in Table 3 were observed growing epiphytically on moss at depths below 30 m, although a few taxa associated with some of the rocks collected during the geological dives were included in the list.

The green algae (Division Chlorophyta) were a prominent group of epiphytes associated with *Drepanocladus*. Moreover, some of the larger filamentous taxa (e.g., *Oedogonium*, *Cladophora*, and *Rhizoclonium*) often exhibited epiphytic assemblages of diatoms, particularly *Melosira undulata* and species of *Epithemia*, *Gomphonema*, and *Cymbella*. Chlorophytes were abundant epiphytes between depths of 20 m and 80 m and

Table 3. Summary of the distribution of benthic algae collected during the deep-water dives listed in Table 1. Letters in the table are used as follows: E = found growing epiphytically on moss or other algae; R = found growing on rock or sediment particles; L = observed in the living condition; and D = detrital cells abundant in at least one sample.

Taxon	Substrate	Depth Range (Meters)				
		20-40	40-80	80-120	120-200	200-560
Chlorophyta:						
Bulbochaete	E	L	L	L		
Chaetosphaeridium globosum	E	L				
Cladophora crispata	E			L		
Cosmarium	E	L				
Gomontia	R		L			
Gongrosira	R		L			
Microspora stagnorum	E		L			
Microsterias	E		L			
Microthamnion	R	L				
Mougeotia	E	L	L	L		
Oedogonium	E, R	L	L	L		L
Palmodictyon viride	E		L			
Pediastrum boryanum	E	L				
Pleurotaenium	E	L				
Rhizoclonium heiroglyphicum	E		L	L		
Sirogonium	E	L				
Spirogyra	E	L	L	L		
Staurastrum	E	L				
Zygnema	E	L	L	L		
Cyanobacteria:						
Nostoc	E, R	L	L	L	L	
Bacillariophyceae:						
Amphora	R				D	
Campylodiscus	R		D	D	D	L, D
Cocconeis	E		L			
Cymbella	E, R	L	L	L	L	D
Epithemia	E, R		L	L	D	L, D
Fragilaria	E	L				
Gomphonema	E	L	L	L		
Melosira ambigua	E	L	L			
Melosira pyxis	E					L
Melosira undulata	E, R	L, D	L, D	L, D	L, D	L,D
Xanthophyceae:						
Ophiocytium	E		L			
Tribonema bombycinum	E, R	L	L, D	L, D		L(?)
Tribonema tenerrina	E		L	L		
Vaucheria	E, R		L, D	L, D		L, D
Euglenophyta:						
Phacus orbicularis	E	L				

were present in some samples collected between 120 m and 180 m. *Oedogonium* was found on one moss sample from a depth of 223 m, the location of the deepest sample with living chlorophytes.

Filamentous xanthophytes also were abundant epiphytes in moss samples collected between depths of 40 m and 120 m. *Tribonema bombycinum* and species of *Vaucheria* were the most prominent of these taxa, the latter taxon often supporting an abundant assemblage of stalked and filamentous epiphytic diatoms. Of all the observed filamentous chlorophytes and xanthophytes, *Vaucheria* apparently had the greatest tolerance for low light levels, as living cells were observed growing on a detrital moss sample collected at a depth of 559 m.

The most abundant representative of the cyanobacteria in Crater Lake is *Nostoc*. This organism is particularly conspicuous in the shallow water regions around Wizard Island where small colonies grow attached to rocks along the shoreline. Its capacity to fix nitrogen undoubtedly contributes to the success of this taxon in the epilimnion during the summer months when the nitrate concentration is below the level of detection. However, the quantitative contribution of *Nostoc* and other cyanobacteria to the nitrogen supply in Crater Lake is unknown at the present. *Nostoc* also was found attached to rock surfaces at a depth of 121 m, and associated with *Drepanocladus* and epiphytic algae down to a depth of 118 m.

Sovereign (1958) published a comprehensive list of diatoms for Crater Lake, almost all of which are typical benthic taxa. Samples obtained for the 1958 study were collected from the littoral zone around Wizard Island. The most common diatom genera found in the August 1989 samples were *Melosira*, *Epithemia*, *Cymbella*, *Gomphonema*, *Rhoicosphenia*, *Navicula*, *Fragilaria*, and *Cocconeis*. These genera were frequent epiphytes on *Drepanocladus* and were often abundant at depths down to 120 m. With the notable exception of *Melosira undulata* (Ehr.) Kutz., the diatom taxa listed in Dr. Phinney's description of each sample (see Description of Samples section) were identified to genus. A more

Table 4. List of 41 common diatom taxa associated with a sample of *Drepanocladus aduncus* collected during dive 219 from a depth of 29 m.

Achnanthes calcar Cl.	*Eunotia pectinalis* var. *minor*
Achnanthes clevei Grun.	*Fragilaria brevistriata* Grun.
Achnanthes lanceolata (Breb.) Grun.,	*Fragilaria construens* (Ehr.) Grun.
Achnanthes minutissima Kutz.	*Fragilaria construens* var. *ventor* (Ehr.) Grun.
Achnanthes peragalli Brun. & Herib.	*Fragilaria pinnata* Ehr.
Amphora ovalis Kutz.	*Fragilaria pinnata* var. *trigona* (Brun & Herib.) Hust.
Amphora ovalis var. *pediculus* Kutz.	*Fragilaria virescens* Ralfs
Caloneis hyalina Hust.	*Gomphonema eriense* Grun.
Cocconeis klamathensis Sov.	*Gomphonema parvulum* (Kutz.) Rabh.
Cocconeis pediculus Ehr.	*Gomphonema* cf. *manubrium* Fricke
Cocconeis placentula var *euglypta* (Ehr.) Cl.	*Melosira undulata* (Ehr.)Kutz.
Cocconeis rugosa Sov.	*Navicula cryptocephala* var. *veneta* (Kutz.) Rabh.
Cymbella cistula (Hempr.) Grun.	*Navicula pupula* Kutz.
Cymbella mexicana (Ehr.) Cl.	*Navicula radiosa* Kutz.
Cymbella minuta Hilse *ex.* Rabh.	*Navicula viridula* Kutz.
Cymbella muelleri Hust.	*Nitzschia oregona* Sov.
Diatomella balfouriana Grev.	*Rhoicosphenia curvata* (Kutz.)Grun.
Diploneis elliptical (Kutz.) Cl.	*Rhoicosphenia curvata* var. *major* Cl.
Epithemia adnata (Kutz.) Breb.	*Synedra mazamaensis* Sov.
Epithemia sorex Kutz.	*Synedra parasitica* (W. Sm.) Hust.
Epithemia turgida (Ehr.) Kutz.	

detailed analysis of the epiphytic diatom flora indicated a diverse assemblages of species consisting of many of the same taxa found by Sovereign in 1958. For example, one moss sample collected during dive 219 from a depth of 29 m contained 41 abundant diatom species and varieties of species (Table 4) and many more rarer taxa. Of particular interest was *Melosira undulata*, a filamentous centric diatom that can attach to moss tissue and other surfaces by a series of gelatinous strands which are extruded through rows of pores in the cell wall. This relatively large species was a prominent epiphyte on both living and detrital moss throughout the water column. It has a relatively broad geographical distribution and is known to occur in the benthos of other deep-water lakes, e. g. , Lake Michigan (Stoermer and Yang 1969) and Lake Tahoe (Mahood et al. 1984).

The shallow-water littoral areas around Crater Lake and Wizard Island provide a possible source of algal cells for the deep-water epiphytic and epilithic assemblages. A survey of the shallow-water algal flora in July and August 1989 indicated that algae were

most abundant at locations where small springs entered the lake (see Phytoplankton section for location and descriptions). The most prominent genera at these locations were *Ulothrix, Cladophora, Nostoc, Calothrix, Oscillatoria, Gomphonema, Gomphoneis, Cymbella, Hannaea, Diatoma, Nitzschia, Synedra*, and *Navicula*. Species of *Gomphonema, Gomphoneis*, and *Cymbella* generated large biomasses of stalked, gelatinous colonies in late spring and early summer, after which time small mats of this material sloughed off the rocks and could be seen floating near the water surface in the lake. In addition, *Hydrurus faetidus* (Vill.) Trev., a gelatinous colonial chrysophyte, formed large green mats at the mouth of Spring 48 in July 1989. This organism is a cold-water species usually found in mountain streams in both the Eastern and Western United States (Smith 1950). In the small shallow pools around Wizard Island, representatives of the filamentous Zygnematales (Division Chlorophyta) formed conspicuous mats during the summer months throughout the entire 10-year study. The most common genera in this group were *Mougeotia, Spirogyra*, and *Zygnema*.

The epiphytic fauna associated with the deep-water moss was sparse, both in terms of numbers of individuals and species richness. A tardigrade (waterbear), 2 unidentified nematodes (roundworms), and 2 species of rotifers (probably *Collotheca* and *Philodina*) were observed. Several ciliates also were found, but the more motile forms were nearly impossible to identify under the conditions of observation. One of the motile forms appeared to be a species of *Stichotricha*, while a species of *Vorticella* and a species of stentorid were observed attached to the moss plants, usually in the axils of the leaves. One of the most interesting animals found in the moss samples, one from as deep as 118 m below the water surface, was an undescribed species of *Algophagopsis* (Family Algophagidae, suborder Astigmata, order Acariformes), a freshwater mite that is apparently new to science. This animal was very abundant in a sample taken from a rock face near Phantom Ship at a depth of 4.6 m.

Recommendations

Video tapes of the extensive moss beds at the bottom of Crater Lake (i.e., at depths between 30 m and 70 m) made during the August 1989 dives emphasized the need for additional research with benthic communities. The distribution and abundance of *Drepanocladus aduncus* is not only of interest from a taxonomic and autecological point of view, but also from a synecological perspective, because of the potential impact of this organism on nutrient supply and recycling. In addition, the moss provides a suitable surface for diverse assemblages of epiphytic algae and heterotrophic microorganisms which undoubtedly have significant effects on benthic primary productivity and nutrient availability in certain areas of the lake. Some research questions that need to be addressed in the future are:

1. What is the relative contribution of the deep-water moss population and its associated epiphytic assemblage to the total primary productivity of the lake?
2. How do rates of benthic primary production and turnover time in the benthic biomass compare with corresponding variables for the phytoplankton assemblage?
3. How does nutrient uptake by benthic autotrophs affect rates of primary production in the water column?
4. How do detrital inputs from the moss bed to the deep-water region of the lake (to depths > 200 m) affect nutrient dynamics and recycling in the lake?

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An Integrated View of the Crater Lake Ecosystem

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Lake Level Fluctuations

A unique combination of relatively simple hydrology and a long history of measurements of lake level fluctuations made it possible to study the relation between water budget and climate at Crater Lake. The lake basin serves as a large rain gage and evaporation pan, although a considerable amount of water is lost from seepage. Preliminary indications show that seepage is constant at observed lake levels and that more evaporation may occur on cool summer days than on warm summer days. Evaporation in winter may be much greater than commonly assumed because the lake surface is seldom capped by ice and snow. Precipitation is the major variable causing changes in the level of the lake (see section - Climate Variability at Crater Lake and its Effects on Lake Level). The simple graphic models shown in Figure 1 illustrate relations between precipitation and steady-state evaporation and seepage rates when the annual lake level is constant, when it declines 0.5 m, and when it increases by 0.5 m. Although actual changes in lake level will vary with the amount of evaporation regardless of amounts of precipitation, the latter is more important to lake-level changes because it varies more annually than the amount of water lost through evaporation.

Lake Clarity

Secchi disk clarity averaged 31.2 m in July and 25.2 m in August between 1978 and 1991 (Fig. 2). The depth of 1% of the incident surface light (clear photometer filter) averaged 85.7 m in July and 88.4 m in August between 1980 and 1989 (Fig. 2). Two zones of relatively high turbidity (expressed as percent light transmission) were

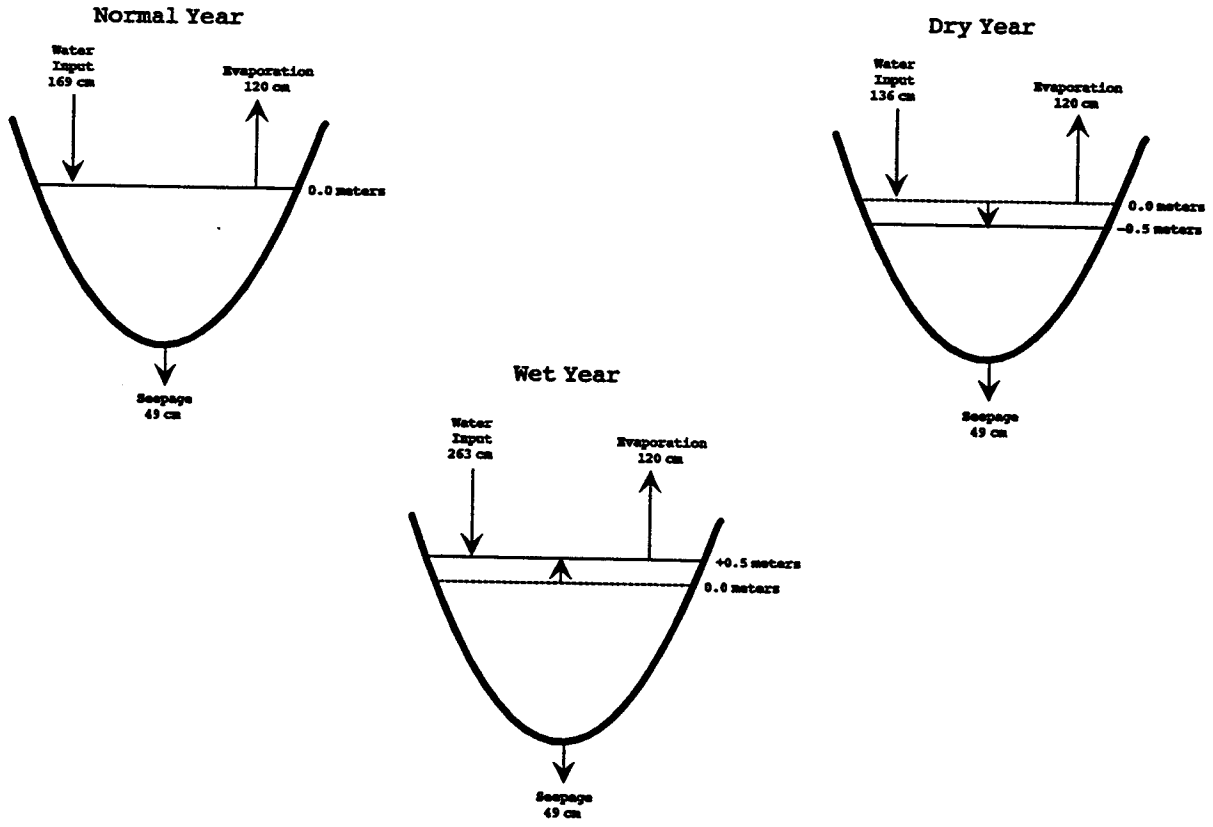


Figure 1. Relationships between precipitation, steady-state evaporation and seepage rates, and lake-level changes during a year of average precipitation, one with above average precipitation, and one with below average precipitation.

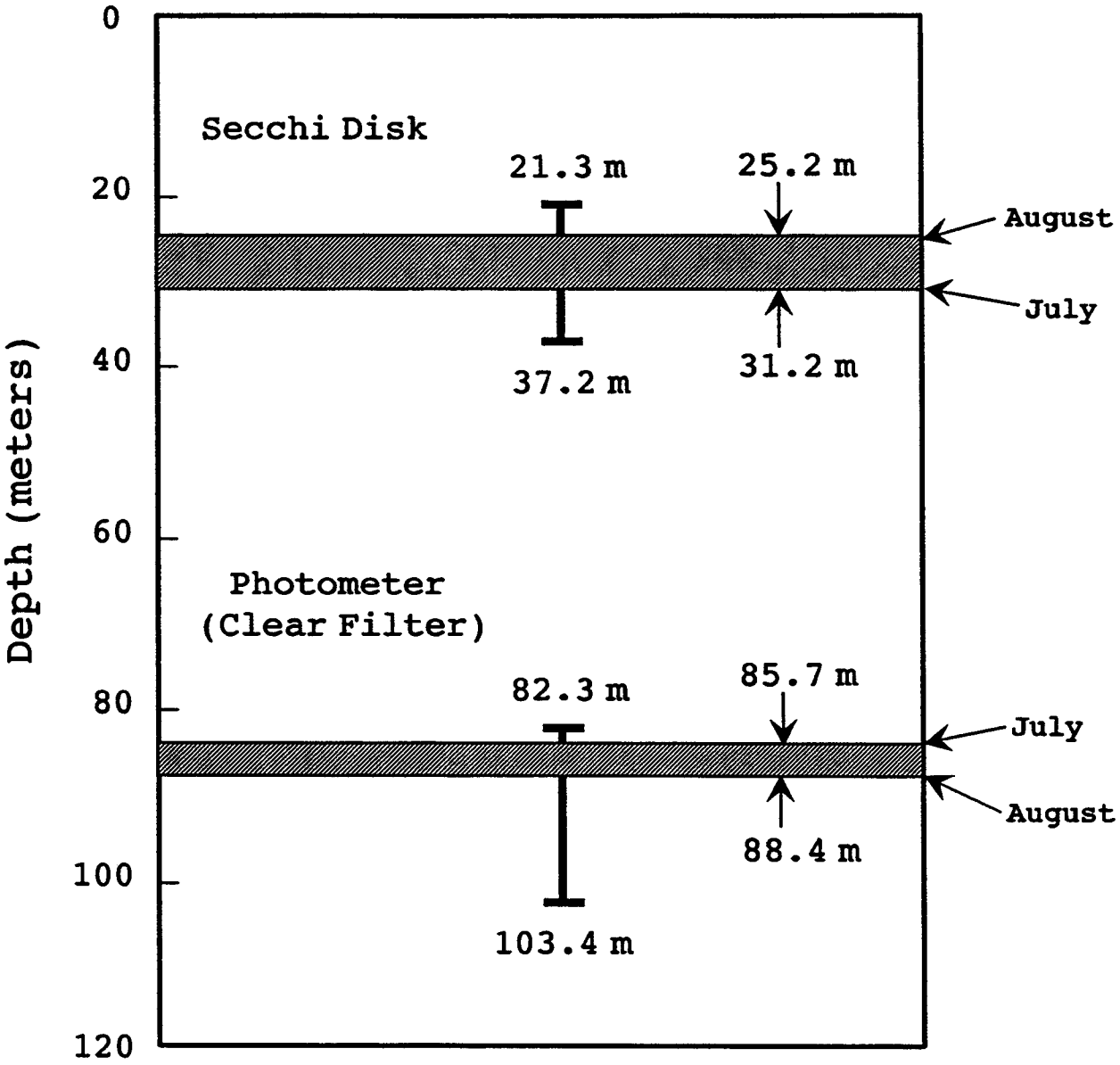


Figure 2. Simple model of the mean Secchi disk clarity readings for July and August and the maximum and minimum readings recorded in either July or August between 1978 and 1991; and the mean depths of 1% of the incident surface light for July and August and the maximum and minimum depths recorded in either July or August between 1980 and 1989.

observed in summer and fall; one was located between the 15 and 30 m depth interval and the other between the 60 and 120 m depth interval (Fig. 3). Changes in Secchi disk clarity corresponded to changes in the turbidity of near-surface waters. The depth of 1% of incident surface light was influenced by both of these layers of turbidity and by zones of lower turbidity between the lake surface and 60 m.

Seasonal changes in Secchi disk clarity and the depth of 1% incident light were observed. Although limited data were available for some seasons, the clarity of Crater Lake was relatively high in winter, decreased in spring, increased in late spring/early summer, decreased in summer, and increased in fall (Fig. 4). This general pattern of lake clarity is influenced by mixing characteristics of the water column and the densities of particles that absorb and scatter light (Fig. 5). In winter and spring the water column circulates to a depth of about 200 m, a process that dilutes the density of the suspended particles. Sometimes the lake exhibits reverse thermal stratification (i.e., a layer of cold water over a layer of warmer water) in winter and spring, in which case, particle densities in the reversed epilimnion can increase and reduce the near-surface clarity of the lake (see Transmissometer section). When the reverse thermal stratification begins to disintegrate, the thickness of the reverse epilimnion increases and near-surface clarity increases if the particle density is reduced by dilution. Potential sources of particles in winter and spring that can effect lake clarity include snow avalanches, wind storms that mix shore and near-shore sediments into the lake, dry-fall from the atmosphere, algae, and detritus. In spring, particles also enter the lake from mud slides and snow-melt runoff. During the summer/fall thermal stratification, some particles remain in the water column from winter and spring events and additional particles may be introduced by wind storms, rain events that increase the densities of

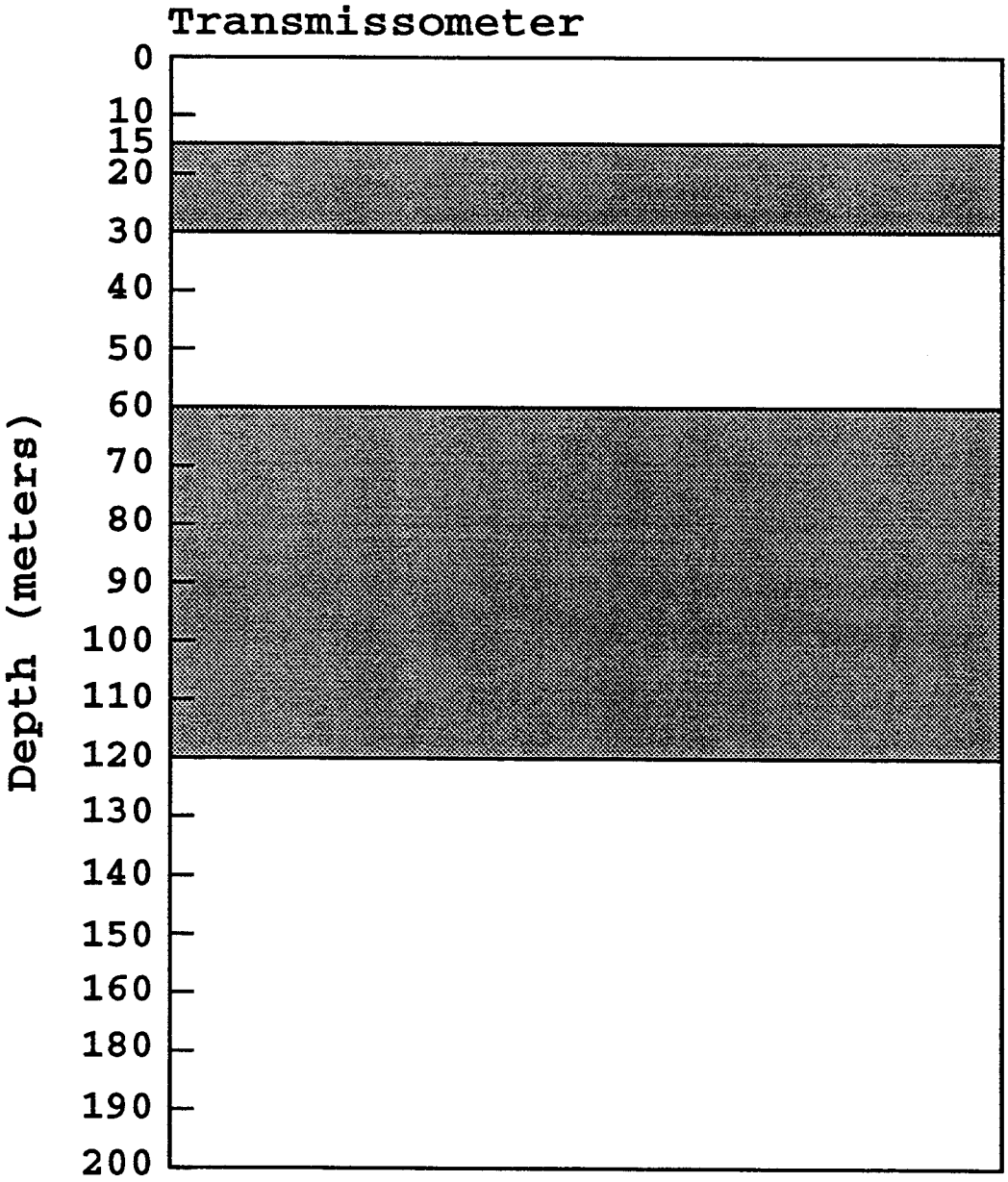


Figure 3. Simple model of the two zones of turbidity in the upper 200 m of Crater Lake during summer and fall.

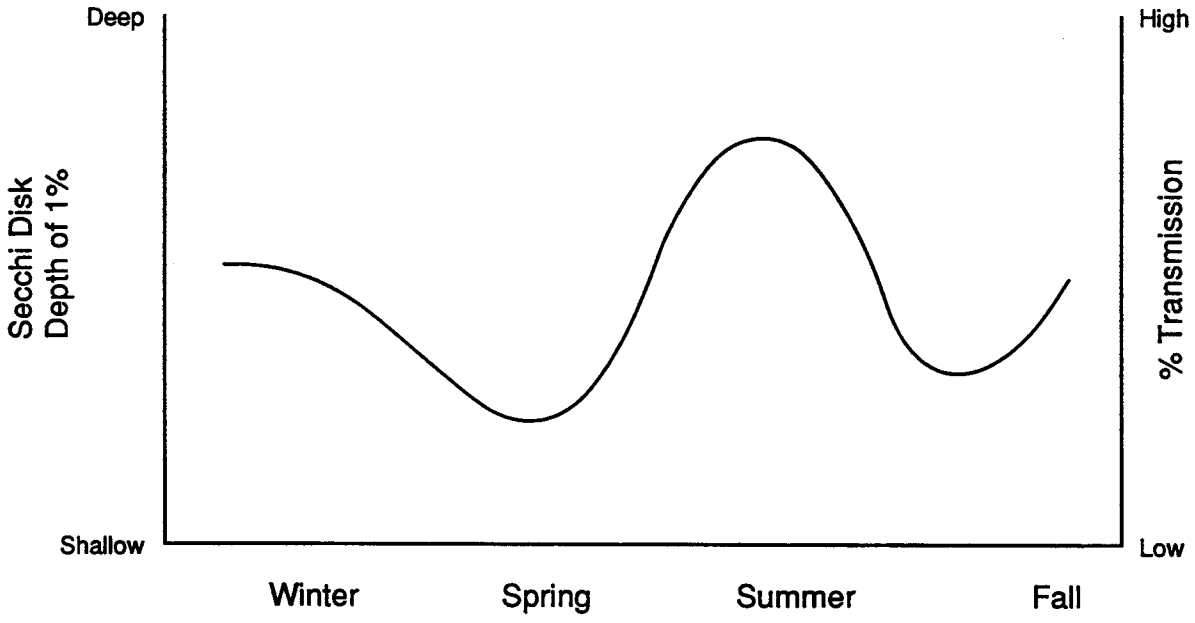


Figure 4. Simple model of the seasonal changes in lake clarity as measured with the Secchi disk, photometer (depth of 1% light) and transmissometer (percent transmission).

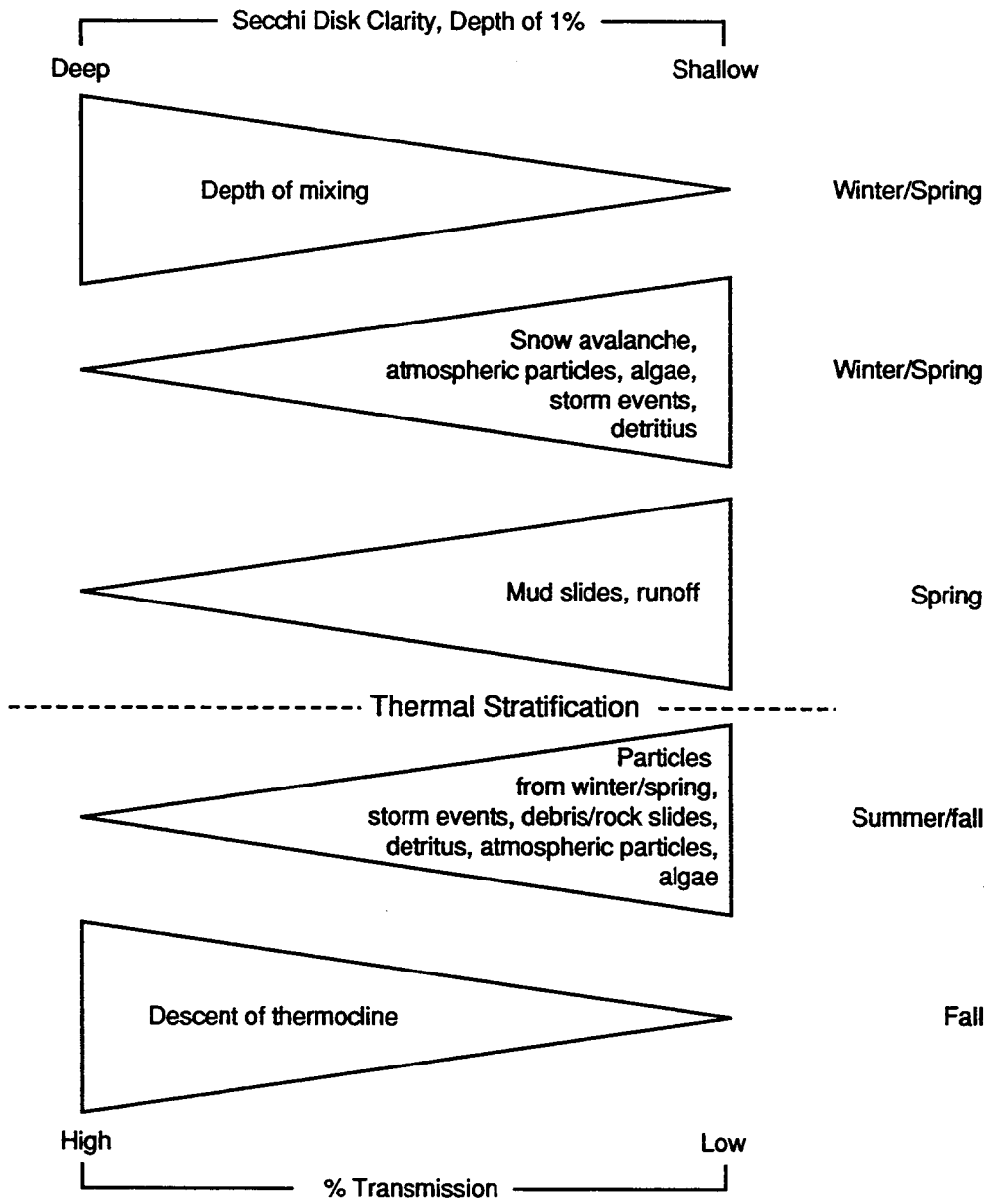


Figure 5. Simple model of the relationships between lake clarity (Secchi disk, depth of 1% incident surface light, and percent transmission), depth of mixing, and potential sources of particles that effect the turbidity of the lake. Variations in the density of particles and depths of mixing relative to lake clarity are shown in the triangles. The base of each triangle represents the maximum values of each variable, and the top (point) represents the minimum values. In each triangle indicating potential sources of particles, the actual particle density can be contributed by one or more of the variables.

turbidities in caldera streams, rock and debris slides, dry-fall from the atmosphere, algae and detritus. In fall the thermocline descends in depth. This process dilutes the particle densities and increases the near-surface clarity of the lake. However, severe fall storms that mix the shore and near-shore sediments into the lake, plus any increases in the turbidity of caldera streams, can decrease near-surface clarity.

Densities of suspended particles in the lake and the contribution from each potential source of particles undoubtedly varies from year to year. In some years mud slides may be the largest source of particles, whereas, snow avalanches or algae may be large sources in other years. Presently, it is not possible to assess the relative importance of any particular source of particles to lake clarity, with the exception of algae.

The dynamics of lake clarity results from a combination of the amount of primary production and the interactions of the lake with the weather and particles originating from the atmosphere and the terrestrial components of the watershed. Although algal densities were correlated with changes in Secchi disk clarity and transmissometer light transmissions (see sections - Clarity of Crater Lake Measured with a Secchi Disk, and Transmissometer), little is known about the effects of non-algal particles on lake clarity. A conceptual view of the interactions of algae and non-algal particles and Secchi disk clarity is shown in Fig. 6. Secchi disk clarity decreases with increasing phytoplankton cell density, but disk clarity decreases with increased densities of non-algal particles with a given density of algae. At low phytoplankton cell densities (extreme left of the graph), small changes in the density of non-algal particles can result in large changes in Secchi disk clarity. Similar relationships would be expected for the depth of 1% incident surface light and transmissometer measurements. Owing to the extreme clarity of Crater Lake, the dynamic changes in lake clarity observed during the present study were

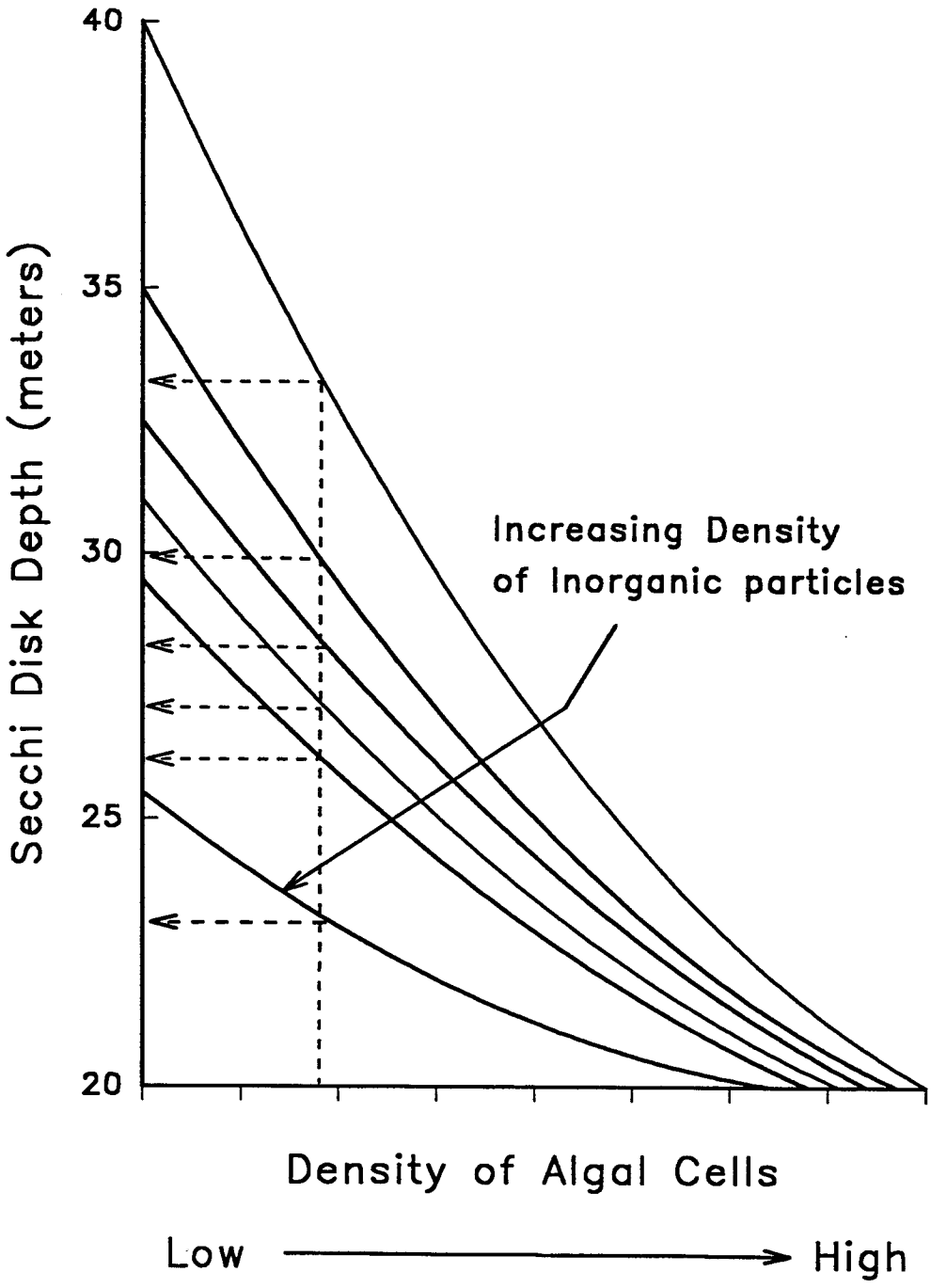


Figure 6. Simple model of the relationship between the density of algal cells and Secchi disk depth as a function of the density of inorganic particles.

probably due to small changes in the density of inorganic particles and algal cells. Such a conclusion is consistent with the interpretation given to the relationships of phytoplankton cell density and Secchi disk clarity shown in Figure 5 of the section, Clarity of Crater Lake Measured with a Secchi disk.

The August Secchi disk readings of 40 m in 1937 and 39 m in 1969 represent extreme clarity measurements for Crater Lake. Based on the conceptual view of the interactions among algae and non-algal particle densities and Secchi disk clarity, primary production and the density of non-algal particles probably were extremely low. Given the many potential sources of non-algal particles, the conditions required to obtain such deep Secchi disk readings would be very unusual. Such conditions were not present during the 10-year study and, consequently, comparable Secchi disk readings were not observed.

Physical, Chemical, and Biological Components

Biological components and processes of the Crater Lake ecosystem are strongly influenced by the physical processes of thermal stratification and upwelling from the deep lake. The physical environment interacts with the biological system through the control and regulation of energy and nutrient supplies within and outside the lake boundaries. For the purpose of summarization, it is convenient to divide the calendar year into two seasons, winter and spring when the lake circulates to a depth of about 200 m, and summer and early fall when the lake exhibits thermal stratification. Physical and biological processes have not been investigated in the lake during the months of November, December, and February.

In summer and early fall, the water column of Crater Lake is thermally stratified

and is characterized by primary production maxima between depths of 40 m and 80 m (Fig. 7). The chlorophyll maximum usually varies between the depths of 100 m and 140 m during this period. The depth of the epilimnion increases from about 5 m in early July to 20 m in September, whereas the hypolimnion includes the zone between 40 m below the lake surface and the lake bottom (ca. 589 m at its deepest location). At the time of thermal stratification, organisms distributed in the hypolimnion are isolated from any nutrient inputs from the atmosphere and catchment area. The lower hypolimnion, defined here as the zone between the depth of 200 m and the lake bottom, is the region of maximum detrital decomposition and nutrient regeneration. The lower hypolimnion also accumulates inputs from hydrothermal processes, inputs that, along with products of decomposition, are confined to this region until the occurrence of upwelling events in the winter and spring.

At the time of thermal stratification, autotrophic components of the biological system in the water column of Crater Lake partition themselves into a characteristic vertical pattern (Fig. 7). Annual and seasonal variations in this pattern are due primarily to fluctuations in the densities of a few dominant taxa. In the epilimnion and metalimnion the nannoplankton is dominated by *Nitzschia gracilis*, an organism that apparently is tolerant of extreme nitrogen limitation. Presumably, this species exerts some influence on lake transparency during the summer months, although its effect may be insignificant in comparison to the influence of inorganic suspended materials. In the zone of maximum primary production, between depths of 40 m and 80 m, the nannoplankton is dominated by species of *Ankistrodesmus, Dinobryon, Tribonema, Rhodomonas,* and dinoflagellates (*(Gymnodinium* and *Peridinium)*. The relative abundances of these taxa vary considerably from year to year, possibly because they

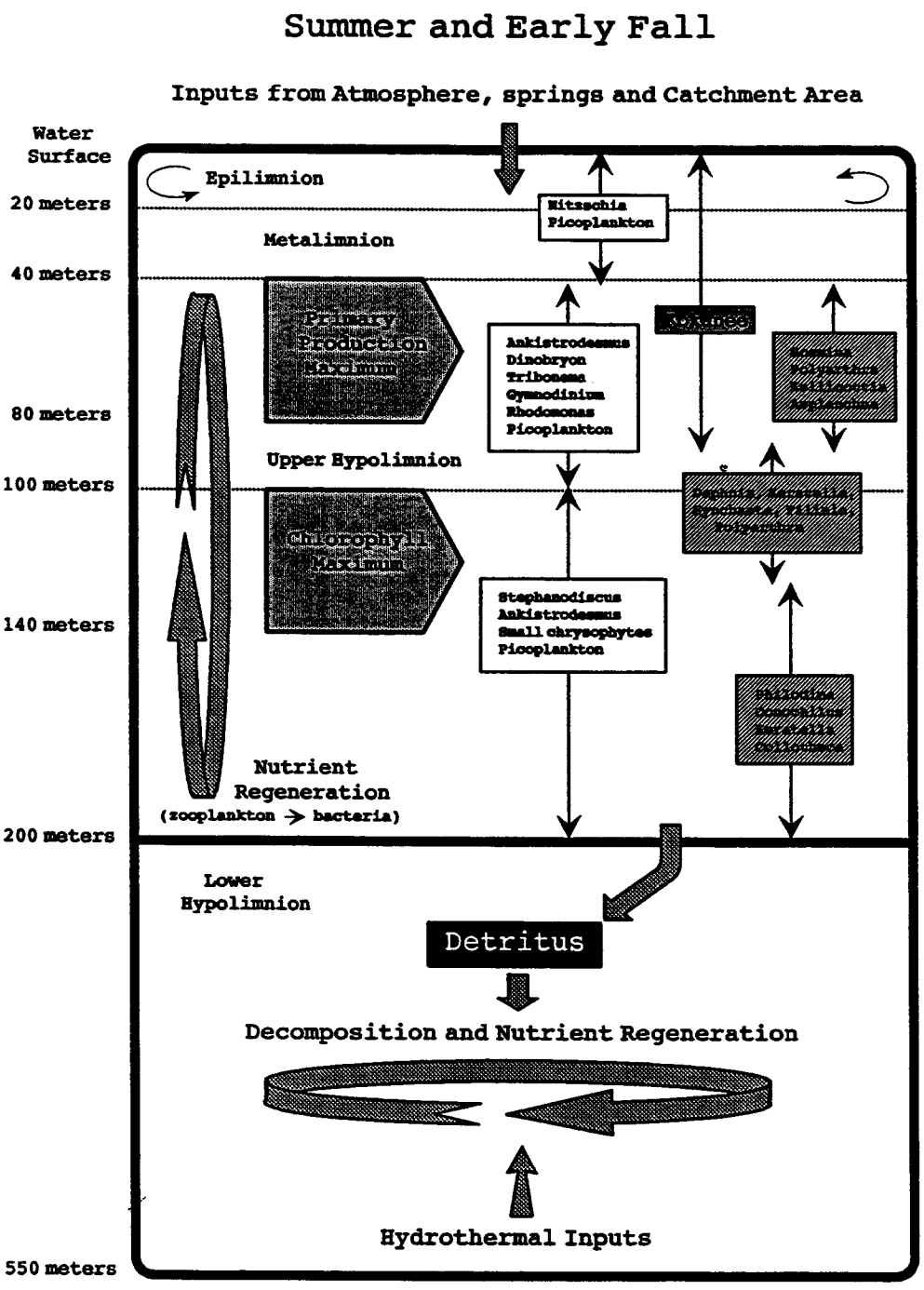


Figure 7. Simple model of the vertical distribution of physical, chemical, and biological components of the pelagic zone of Crater Lake in summer and early fall. Arrows in the epilimnion indicate a zone of circulation and mixing.

occur in the region of maximum photosynthesis and population growth. Below a depth of 100 m, the flora larger than 2 μm usually consists of *Stephanodiscus, Ankistrodesmus,* and some small chrysophytes. Recent data from the 10-year study indicate that small cyanobacteria (picoplankton less than 2μm in diameter) are distributed throughout the water column to a depth of at least 200 m. Although some preliminary data are available, the relative contribution of this group of organisms to the productivity of Crater Lake remains uncertain.

The zooplankton in Crater Lake also exhibit vertical stratification in the summer and early fall (Fig. 7). Although there is some overlap in distribution, species of *Bosmina, Polyarthra, Kellicottia,* and *Asplanchna* are dominant between depths of 40 m and 80 m, whereas *Daphnia, Keratella, Synchaeta, Filnia,* and *Polyarthra* are more abundant between 80 m and 120 m. Zooplankton assemblages found in water deeper than 120 m are often dominated by *Philodina, Conochilus, Keratella,* and *Collotheca.* Distributional data obtained from 1985 through 1990 suggest that coexistence of these taxa in their respective layers of the water column is facilitated by spatial and temporal separation and by differences in utilization of food resources. In the upper stratum, between depths of 40 m and 80 m, *Kellicottia, Polyarthra,* and *Bosmina* feed primarily on living phytoplankton. Moreover, between 1985 and 1990, *Polyarthra* reached maximum biomasses in years when *Kellicottia* was relatively rare (i.e., in 1986, 1988, 1989, and 1990). At depths between 80 m and 120 m, *Daphnia, Keratella cochlearis,* and *Keratella quadrata* are polyphagous, whereas *Synchaeta* and *Filinia* feed on living phytoplankton and detrital particles, respectively. In this zone the polyphagous taxa reached their maximum abundances in different years, *K. quadrata* in 1985, *K. cochlearis* in 1986, and

Daphnia in 1988 and 1989. The coexistence of *Synchaeta* and *Filinia* with these taxa may be related to their more specialized diets of living phytoplankton (*Synchaeta*) and detrital particles (*Filinia*). The diversity of zooplankton taxa below the depth of 120 m is relatively low, consisting of either an association of *Philodina, Conochilus,* and *K. quadrata* or just *Collotheca* and *K. quadrata*. The former group, which was abundant between 1989 and 1988 represented three different feeding modes (phytophagous, triptophagous, and polyphagous), whereas *Collotheca* and *K. quadrata*, which co-occurred in 1990, where classified as phytophagous and polyphagous, respectively. However, it is emphasized that information on the food habits of zooplankton was obtained from the literature, not from experiments with the Crater Lake taxa. Also, the extent to which food particle size contributes to niche differentiation of these taxa is unknown.

During the winter and spring months, physical processes in the water column of Crater Lake generate different patterns of circulation than the patterns observed when thermal stratification is present (Fig. 8). From January through May, the water column mixes to a depth of about 200 m, as mentioned above, during which time the concentration of chlorophyll and the densities of phytoplankton and zooplankton taxa remain relatively uniform throughout the water column to that depth. The primary production maximum is usually located between depths of 20 m and 60 m, a range that is approximately 20 m higher in the column than that observed during thermal stratification (Fig. 8). Although the lake does not mix completely to the bottom every year, some products of detrital decomposition and hydrothermal precesses are transferred to the upper 200 m of the water column from the deep lake by upwelling events. These events, which are variable from year to year, can occur between January and April. Data from

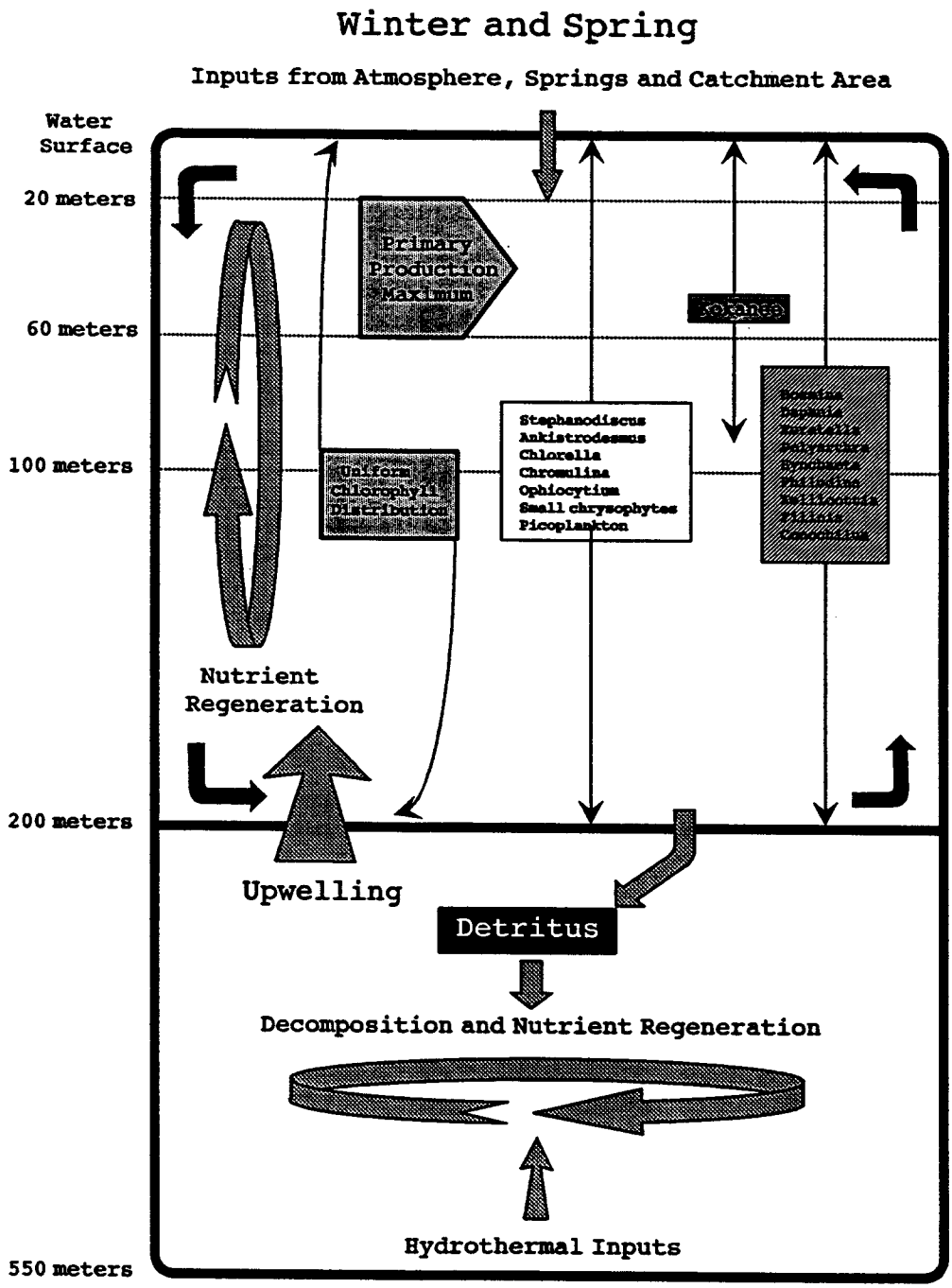


Figure 8. Simple model of the vertical distribution of physical, chemical, and biological components of the pelagic zone of Crater Lake in winter and spring. Black arrows indicate the region of complete circulation and mixing in the upper 200 m of the water column.

sediment traps indicate that upwelled nitrogen fluxes to the upper 200 m of the water column account for more than 70% of the total nitrogen input to the euphotic zone. Also, these data suggest that inputs of new nitrogen from the springs and caldera walls are relatively low and that nitrogen is recycled in the euphotic zone many times before it is transferred to the deep lake (Figs. 7 and 8).

In winter and spring, dominant phytoplankton in the euphotic zone of Crater Lake include species of *Stephandiscus, Ankistrodesmus, Chlorella, Chromulina, Ophiocytium,* and other small chrysophytes and picoplankton (Fig. 8). The taxonomic composition of this flora resembles the phytoplankton assemblage that is distributed between the depths of 100 m and 200 m in the summer and early fall (Fig. 7). In particular, *Stephanodiscus hantzshcii* is prominent in the water column throughout the entire euphotic zone in the winter and spring, but is restricted to depths below 100 m when thermal stratification is present.

Distributional patterns of zooplankton and fish populations in the winter and early spring are not completely understood. Limited data indicate that species of zooplankton are uniformly distributed throughout the water column to a depth of at least 200 m, and that a stratified pattern is not apparent in the part of the water column where mixing occurs. Kokanee salmon have been detected at depths down to 98 m in the summer (Fig. 7), but is not known whether or not this distribution changes seasonally or to what degree distribution is affected by the age structure of the population. Data obtained in the summer also indicate that rainbow trout are concentrated in the shallow, near-shore waters and are not pelagic.

Pelagic Food Web

A diagrammatic summary of the Crater Lake food web is illustrated in Fig. 9. This structure is based on the known composition of the flora and fauna in the lake and on information from the literature concerned with the food habits of individual taxa. Relationships in Fig. 9 relate to the trophic dynamics of the water column only, and the role of benthic invertebrates is treated as an input into the pelagic community. Arrows in the diagram represent flows of energy and nutrients.

Phytoplankton in Crater Lake serves as a food resource for crustacean zooplankton and rotifers. Some rotifers also utilize detrital particles, picoplankton, and other bacteria (not illustrated) as food resources. Kokanee salmon feed primarily on crustacean zooplankton, but can also benefit from inputs of terrestrial insects and benthic macroinvertebrates. The presence of large rainbow trout when kokanee are abundant indicate that at least some of the larger trout feed on juvenile kokanee. However, the principal diet of the rainbow trout is benthic macroinvertebrates and terrestrial insects. All functional groups of organisms contribute to the accumulation of detritus, much of which is decomposed in the euphotic zone of the lake, while the rest sinks into the deep lake and contributes nutrients that are regenerated by upwelling events. The relative importance of the energy flow between functional groups varies with season and with annual variations in climatic conditions and physical processes within and outside the lake boundaries.

Temporal Patterns of the Pelagic Food Web

During the period from 1985 to 1990, several components of the pelagic food web in Crater Lake exhibited important changes in structure and biomass. These changes are

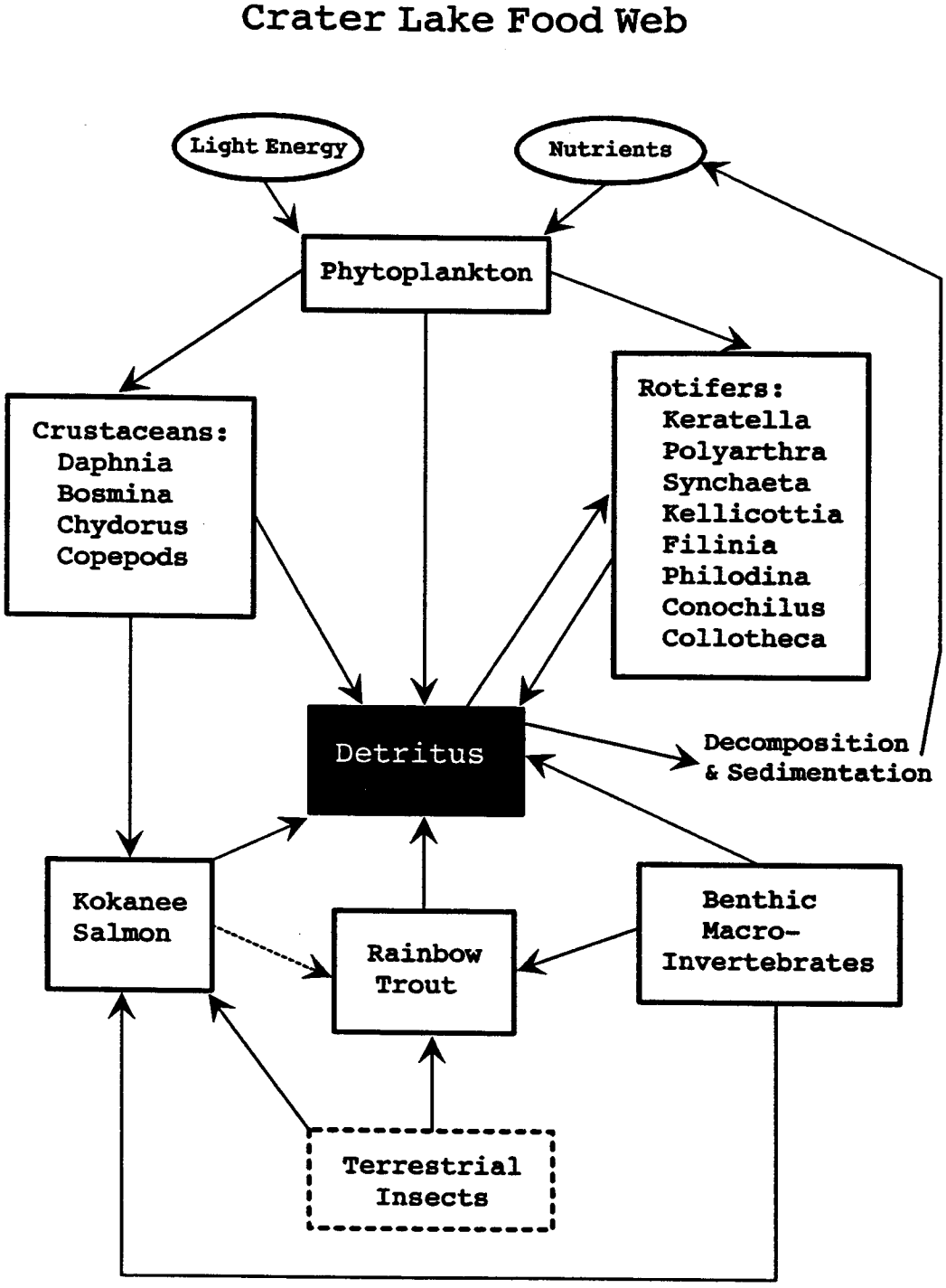


Figure 9. Simple model of the pelagic food web in Crater Lake.

represented in Figure 10 as circles with areas proportional to the relative biomass of each variable. The amount of primary production was low in 1985, increased to a maximum in 1987, and then decreased to intermediate levels between 1988 and 1990. Rotifer biomass was at the maximum level in 1985, decreased to the minimum biomass by 1988, and increased to intermediate levels in 1989 and 1990. *Bosmina* biomass was highest in 1985 and then remained at low levels between 1986 and 1990. *Daphnia* was absent in 1985, increased to a low level in 1986, increased to the maximum level by 1988, declined to an intermediate level in 1990, and was greatly reduced in 1990. Total zooplankton biomass was highest in 1985 and then declined to intermediate levels between 1986 and 1990, with the exception of a slight increase in 1989. Kokanee salmon biomass was low in 1985, increased to an intermediate level by 1987, decreased to a low level in 1988 and then increased to the maximum level by 1990.

These changes in structure and biomass of several important components of the pelagic food web are difficult to explain based on empirical data. However, based on published information combined with observations during the 10-year study, the following explanation is offered.

Changes in the amount of primary production were part of long-term fluctuations in amount of primary production in the lake system (see Fig. 36 in the Phytoplankton section). These fluctuations corresponded to long-term fluctuations in chlorophyll and phytoplankton cell biovolume. Fluctuations in primary production were probably influenced by changes among years in the amount of upwelling of nutrient-rich waters from the deep-lake during winter and spring (McManis 1992). High biomasses of rotifers and *Bosmina* and an absence of *Daphnia* during the period of low primary production in 1985 was probably related to nutritional needs, feeding abilities and the

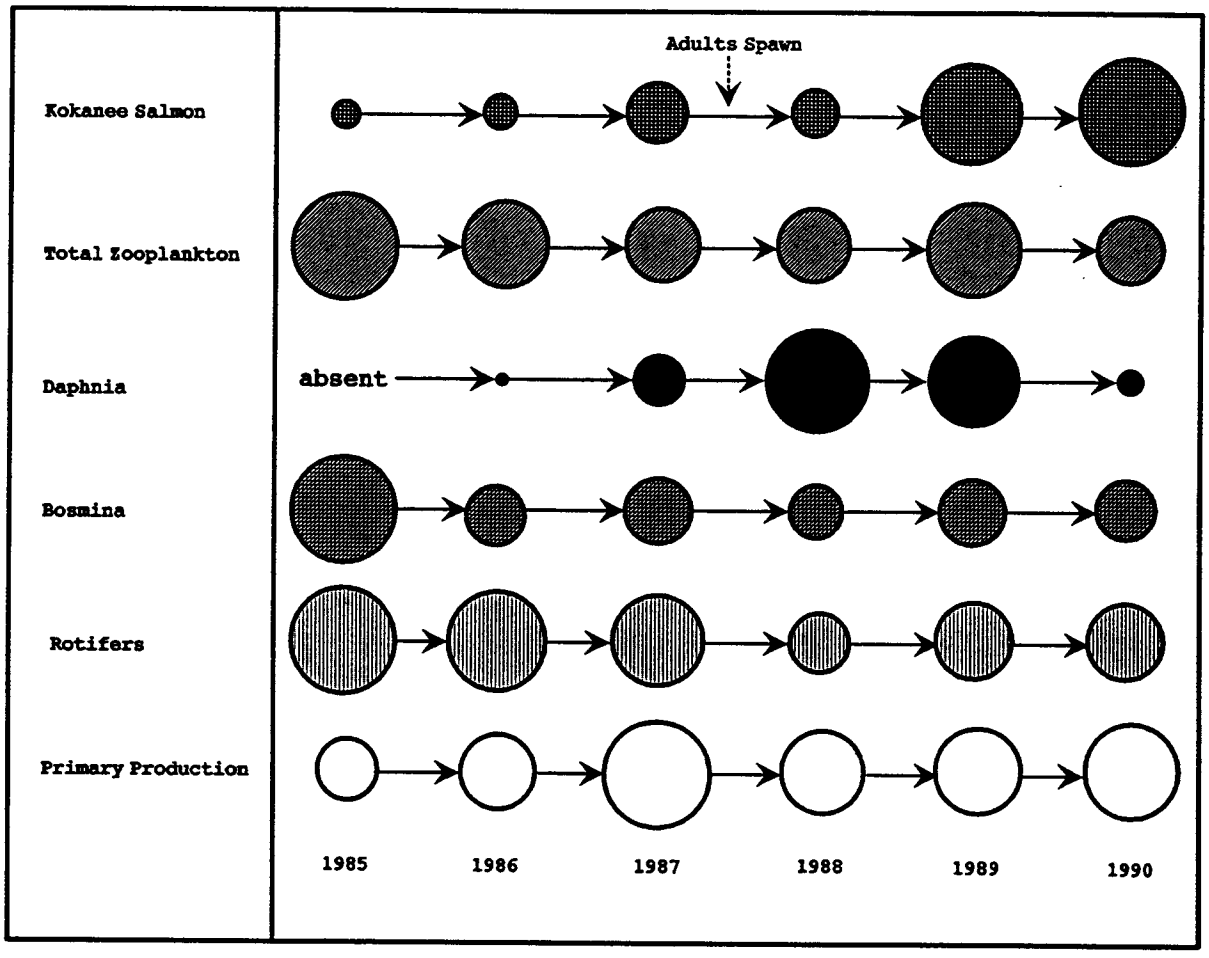


Figure 10. Simple model of the temporal patterns of major variables of the pelagic food web between 1985 and 1990. The size of the circles are in proportion to maximum biomass of each variable through time. The largest circle for each variable has a value of 100% of the maximum.

food threshold concentrations of these organisms. The latter refers to the densities of food at which metabolic losses equal assimilation. Rotifers have been shown to develop high biomasses in unproductive lakes because of their relatively low food threshold concentrations (DeMott 1989). *Bosmina* can exist at relatively high biomasses in unproductive lakes because it filter feeds and does so efficiently on large-bodied flagellated phytoplankton (DeMott 1982). Similarly, *Daphnia* populations have low densities when prey densities are low due to *Daphnia's* high food threshold concentrations (DeMott 1989). *Daphnia* appeared in the lake as primary production increased in 1986, which suggested that the nutritional base improved for *Daphnia.* Although *Daphnia* was low in biomass in 1986, its presence in the strata of 80-120 m coincided with a dramatic shift in the distribution and biomass of *Bosmina* from a depth stratum of 40-120 m in 1985 to a depth stratum of 40-80 m in 1986. This shift was maintained through 1990 (see Zooplankton section). These shifts in the distribution and biomass of *Bosmina* may have resulted from competitive interactions with *Daphnia* (DeMott 1989). Similarly, the reduction in the biomass of rotifers after 1986 may have been due to competitive interactions and mechanical interference from *Daphnia* (DeMott 1989) because many of the dominant rotifer taxa inhabited the 80-120 m stratum.

The increase in kokanee salmon biomass between 1985 and 1987 was due to increased mean weights of a dominant 1984 year class of fish. The low biomass of kokanee salmon in 1988 occurred because most of this year class spawned and died during the winter of 1987-88. This decline in kokanee biomass coincided with the period of highest biomass of *Daphnia.* The large increase in *Daphnia* biomass in 1988 was

probably related to a reduction in predation by kokanee on *Daphnia*. The increase in kokanee salmon biomass between 1988 and 1990 was due to an increase in the mean weights of 1987, 1988, and 1989 year classes. The large reduction in *Daphnia* biomass between 1988 and 1990 probably was due to predation by the kokanee salmon rather than a reduction in the food base because primary production was at moderate levels compared to the level in 1985 when *Daphnia* was absent. Although the absence of *Daphnia* in 1985 was probably associated with a period of low primary production, as mentioned above, the absence of *Daphnia* in 1985 may have also been influenced by predation from adult kokanee salmon before the salmon spawned and died in 1984.

Briefly stated, the pelagic food web in Crater Lake appears to be controlled by both bottom-up and top-down processes (McQueen and Post 1988). Upwelling of nutrients from the deep-lake appears to control the amount of primary production, which in turn effects the food supply of *Daphnia*. During periods of very low primary production, *Daphnia* biomass is reduced or absent, whereas rotifer and *Bosmina* biomasses are high. An increase in primary production is associated with increased *Daphnia* biomass and reductions in the biomasses of rotifers and *Bosmina*, as well as a restriction in the distribution of *Bosmina*. At high levels of primary production *Daphnia* biomass increases in the absence of high biomasses of kokanee salmon. When high biomasses of kokanee salmon are present, *Daphnia* biomass is reduced greatly relative to the level of primary production.

Benthic Flora and Fauna

For the descriptive analysis of organisms associated with benthic communities in Crater Lake, it is convenient to divide the bottom area into four major zones based on

their location relative to the lake surface (Fig. 11.). The **Supralittoral Zone**, which includes the narrow area between the water surface and 1 m above the surface level, is a wave splash zone that consists of rock faces, pumice boulders, and cobble or gravel beaches (Table 1). The **Eulittoral Zone**, a zone under the influence of wave action, is located between the water surface and a depth of 5 to 10 m and represents and area of maximum habitat diversity and complexity. Dominant habitats in this zone include rock faces, areas of boulder and cobble talus, pumice deposits, sand pockets between boulders, and woody debris. The **Sublittoral Zone** is the part of the euphotic zone that extends from about 5 m below the water surface to a depth of 120 m. Its lower limit represents the depth of effective light penetration and the lower distributional limit for bryophytes. Our classification system recognized two subzones within the Sublittoral Zone, the **Ooze Subzone** between the depths of 5 m and 30 m and the **Moss Subzone** between depths of 30 m and 120 m. The former subzone is characterized by rock faces and boulder islands with accumulations of flocculent detrital material (ooze) in pockets between the rock formations, whereas the latter subzone consists of dense stands of aquatic moss. The region below the depth of 120 m is designated as the **Profundal Zone**, a large area that includes steep rock faces and a talus slope, the **Caldera Slope Subzone**, and a sediment plain, the **Abyssal Plain Subzone.**

An inventory of the common invertebrate animals was compiled during the 10-year study of Crater Lake (Table 1). Estimates of seasonal and annual variations in the production and biomass of the dominant benthic animals are not yet available and represent a priority for future research. Dominant invertebrates in the Supralittoral Zone are saldids, springtails, hydrophilid beetles, and midges; whereas the Eulittoral Zone supports populations of snails, caddisflies, mayflies, alderflies, midges, and mites.

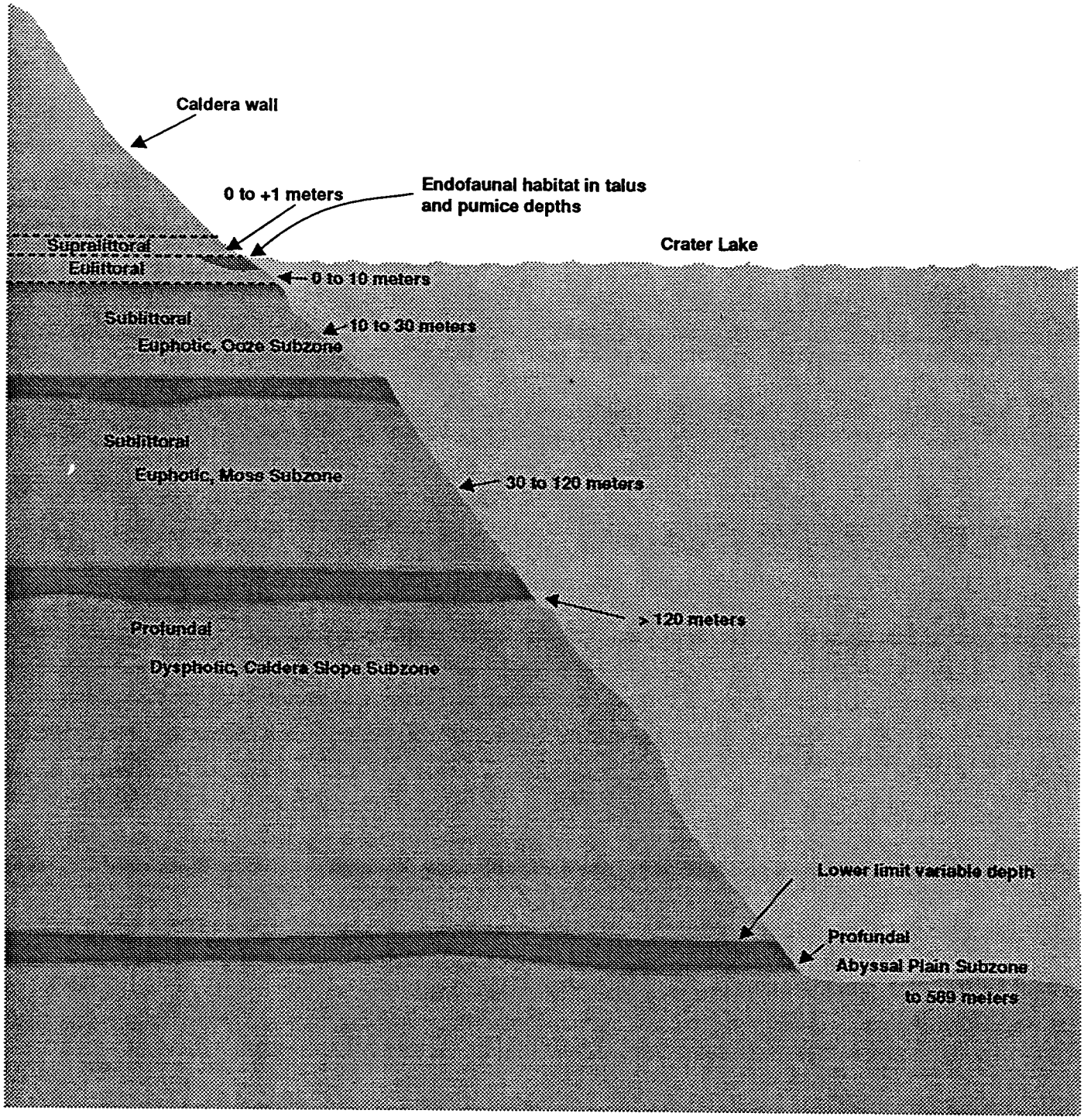


Figure 11. A diagram of the major benthic habitat zones along the sides of the caldera wall on the bottom of Crater Lake.

Table 1. Summary of benthic habitat types and associated benthic organisms found in the different depth zones of Crater Lake.

ZONE/SUBZONE	DEPTH RANGE	DOMINANT HABITATS	COMMON INVERTEBRATES		COMMON VEGETATION	
			Common Name	Scientific Name	Common Name	Scientific Name
SUPRALITTORAL Wave Splash Zone	0 to +1 Meters	Rock face; Pumice boulder; Cobble or gravel beach	Saldids, Springtails, Hydrophilid beetles, and Midges	Saldidae, Collembola, Hydrophilidae, and Chironomidae	Green Algae, Blue-green, algae, Colonial chrysophytes, and Diatoms	*Ulothrix, Calothrix, Nostoc, Hydrurus, Gomphonema, Cymbella, Diatoma*
EULITTORAL Wave Action Zone	0 to - 10 Meters	Maximum habitat complexity: Rock face, Boulder/cobble talus, Sand pockets between boulders, Macophyte beds, Woody debris, and Possible extensive endofaunal habitat in talus and pumice deposits	Maximum invertebrate species richness and density: Snails, Caddisflies, Mayflies, Alderflies, Midges, and Mites	Gastropoda, Trichoptera, Ephemeroptera, Sialidae, Chironomidae, and Acari	Green Algae, Blue-green algae, Diatoms, and Aquatic vascular plants	*Mougeotia, Zygnema, Spirogyra, Nostoc, Gomphonema, Cymbella, Epithemia, Achnanthes, Fragilaria, Melosira, Navicula, Rhoicosphenia, Synedra, Myriophyllum, Ranunculus*
SUBLITTORAL Depths with sufficient light for photosynthetic organisms						
A. Euphotic, Ooze Subzone	-5 to -30 Meters	Boulder islands with flocculent detrital material (ooze) in pockets, Rock faces	Species richness and density less than in Eulittoral Zone, Insect taxa decrease in dominance with increasing depth	Same as eulittoral zone	No samples from this region; flora assumed to consist of Green Algae, Blue-green Algae, and Diatoms	No observations from this zone
B. Euphotic, Moss Subzone	-30 to -120 Meters	Extensive beds of aquatic moss	Midges, Mites, Clams, Worms, and Microcrustaceans	Chironomidae, Acari, Sphaeriidae, Oligochaeta, Nematoda, Ostracoda, Copepoda	Moss, and epiphytic Green Algae, Blue-green Algae, Yellow-green Algae, and Diatoms	*Drepanocladus, Cladophora, Bulbochaete, Mougeotia, Oedogonium, Rhizoclonium, Spirogyra, Cosmarium, Staurastrum, Nostoc, Tribonema, Vaucheria, Coccoeis, Cymbella, Epithemia, Fragilaria, Gomphonema, and Melosira*
PROFUNDAL Depths below which light is insufficent to support the growth of bryophytes						
A. Dysphotic, Caldera Slope Subzone	< -120 meters	Rock face and talus slopes	Nothing known, invertebrate species richness and density assumed to be low	Unknown	Green Algae, Blue-green Algae, Yellow-green Algae, and Diatoms	*Oedogonium, Nostoc, Cymbella, Epithemia, Melosira, and Vaucheria*
B. Abyssal Plain Subzone	to -589 meters	Sediment plain	Midges, Worms, and Microcrustaceans	Heterotrissocladius, Oligochaeta, Nematoda, Copepoda, and Ostracoda	Green Algae, Blue-green Algae, Yellow-green Algae, and Diatoms	*Oedogonium, Nostoc, Cymbella, Epithemia, Melosira, and Vaucheria*

The Eulittoral Zone also represents a region of maximum invertebrate density and diversity. The Sublittoral Zone contains many of the same taxa as the Eulittoral Zone, but in comparison, has lower species richness and density. In general, the dominance of insect taxa decreases with increasing depth, while the relative abundances of midges, mites, clams, worms, and microcrustaceans increase. Invertebrate species richness and density is low in the Profundal Zone. Limited sampling indicates that midges, worms, and microcrustaceans do occur in very low densities in the Abyssal Plain Subzone down to the deepest depths of the lake.

The benthic vegetation in Crater Lake is dominated by algae and the aquatic moss *Drepanocladus aduncus*. Two species of aquatic vascular plants (*Ranunculus aquatilus* and *Myriophyllum spicatum*) are found in the Eulittoral Zone near the outlets of several springs on the caldera wall. Green algae, particularly species of *Mougeotia, Zygnema,* and *Cladophora,* and the cyanobacterium *Nostoc* are often visible in the Eulittoral Zone from the shoreline around the lake and from a boat in the vicinity of Wizard Island. Diatoms and *Ulothrix zonata* are abundant in the lower reaches of many of the springs, and dense mats of stalked diatoms (*Gomphonema* and *Cymbella*) may slough off nearshore rocks and float out into the lake. The abundance of *Nostoc*, a nitrogen-fixing bacterium, in the Eulittoral Zone suggests that this organism may have a role in the process of nutrient recycling, particularly during thermal stratification when the epilimnion is sealed off from any nutrient inputs from the hypolimnion. Below the Eulittoral Zone, aquatic vegetation is particularly abundant between the depths of 25 and 80 m, a region where *Drepanocladus* reaches its maximum population density. Numerous species of green algae, yellow-green algae, cyanobacteria, and diatoms grow

epiphytically on the moss and on small rocks in the vicinity of the moss bed. The maximum depth of algal growth is still unknown, although living cells were observed in samples from depths below 120 m.

The presence of a relatively large biomass of autotrophic organisms between the depths of 30 m and 120 m indicates that benthic assemblages may have a significant effect on the nutrient dynamics of Crater lake. Undoubtedly, the nutrient demand and detrital inputs of the benthic moss and associated algae have at least a local impact in some regions of the lake. Unfortunately, estimates of moss and algal primary production and biomass are very difficult to obtain at such great depths and are not likely to become available in the near future.

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Long-term Monitoring Program

Gary L. Larson, C. David McIntire, and Mark Buktenica

One of the goals of the 10-year limnological study of Crater Lake was to develop a long-term monitoring program (see Introduction section). Results from the 10-year study demonstrated the dynamic nature of components important to the ecology of the lake system, such as deep-water circulation, nutrients, water level, clarity, productivity, abundances of plant and animal plankton, and abundances of fish. All of these components exhibited cyclic patterns. Although an extensive limnological data base was assembled during the 10-year study, the program was of insufficient length to characterize the periodicities and amplitude of the cyclic phenomena. Additional studies of the lake are required and, thus, the long-term monitoring program required by Public Law 97-250 is particularly appropriate and meaningful. The long-term monitoring program described in the following is recommended. The goal of the program is to continue to develop a reliable data base on physical, chemical, and biological components of the lake system from which the status and dynamics of the lake can be assessed through time.

Access to the lake was a major consideration in the design of the monitoring program. The lake can be reached by foot via the Cleetwood trail during summer and early fall (June through September). The lake only can be reached in winter and spring by helicopter or by descending and ascending the caldera wall. Accessibility and sampling in winter, spring, and late fall (October - November) is further restricted by frequent periods of poor weather. Recognizing these limitations and the difficulty of working on Wizard Island in winter, researchers should sample the lake at monthly

intervals between June and September, when the lake is accessible by foot and when boats can be moored on the lake, and should also strive to sample the lake during periods of good weather at other times of the year. Although weather conditions at any given time in the park are not predictable from year to year, sampling should be attempted each year in January and April to match the "off-season" sampling periods established in the 10-year program. The off-season data are considered essential to evaluate seasonal changes in the lake system. January and April samples would provide estimates of the amount of deep-water circulation, concentrations of nutrients, primary productivity, and characteristics of the phytoplankton and zooplankton communities. Sampling from June through September would provide information on the limnological conditions of the lake during the period of thermal stratification. With the few exceptions noted below, samples should be taken at Station 13 (see Study Area and Facilities sections) to be consistent with the major sampling site used over the last 10 years. Physical, chemical, and biological characteristics of the lake should be sampled using the protocol described below.

Recommended Procedures and Methods

Temperature

Temperature should be measured at a depth of 1 cm with a hand thermometer and also with a conductivity-temperature-depth (CTD) probe from the lake surface to a depth of 550 m. These measurements should be made once in January, once in April, and at weekly intervals from June through September. Temperature profiles at Stations 11 and 23 should be taken in August to compare with the August temperature profile at Station 13.

Optical

Secchi disk (20 cm in diameter) clarity readings and transmissometer profiles from the lake surface to 550 m should be taken once in January, once in April, and at weekly intervals from June through September. Photometer readings should also be taken once in January, once in April, and at monthly intervals from June through September. In August of each year, Secchi disk clarity readings, and photometer and transmissometer profiles should be taken at Stations 11 and 23 to compare with the August readings and profiles recorded at Station 13.

Water Quality

Water samples for measurement of total alkalinity, pH, specific conductance, and dissolved oxygen samples should be collected once in January, once in April, and at monthly intervals between June and September. Water samples for the analyses should be collected using Van Dorn-style samplers with collections at the lake surface and at depths of 5, 10, 20, 60, 100, 200, 300, 400, 500, and 550 m.

Nutrients

Water samples for measurement of total phosphorus, orthophosphate, nitrate-nitrogen, total Kjeldahl-nitrogen, and ammonia-nitrogen should be collected once in January, once in April, and at monthly intervals between June and September with collections at the lake surface and at depths of 20, 60, 100, 200, 300, 400, 500, and 550 m. Additional samples for measurement of nitrate-nitrogen should be collected at depths of 225, 250 and 275 m on each sampling date. Water samples for measurement of trace elements (calcium, sodium, magnesium, and chloride), silica, and sulfate-sulfur should be collected during winter and spring trips and in August at the lake surface and

at depths of 20, 60, 100, 200, 300, 400, 500, and 550 m.

Chlorophyll, Primary Production, and Phytoplankton

Water samples for the analysis of chlorophyll concentration, primary productivity, and phytoplankton community structure should be collected once in January, once in April, and at monthly intervals from June through September. Samples for the estimation of chlorophyll concentration and phytoplankton species composition, cell density, and biovolume should be collected at the lake surface and at depths of 5, 10, 20, 30, 40, 60, 80, 100, 120, 140, 160, 180, 200, 225, 250, 275, and 300 m. Samples to evaluate rates of primary production should be measured at the lake surface and at depths of 5, 10, 20, 30, 40, 60, 80, 100, 120, 140, 160, and 180 m. Water samples for measurements of chlorophyll concentration and rates of primary production should be differentially filtered for picoplankton.

Zooplankton

Samples for analysis of species composition, density, and biomass of zooplankton should be collected once in January, once in April, and at monthly intervals between June and September. The collection net should be a vertical-haul 0.5-m-diameter number-25 closing net. Samples should be collected from depth intervals of 0-20 m, 20-40 m, 40-60 m, 60-80 m, 80-100 m, 100-120 m, 120-160 m, 160-200 m, and 200-300 m. One set of samples should be collected at night in August each year to determine patterns of diel vertical migration.

Benthic Macroinvertebrates

Samples of benthic macroinvertebrates should be collected annually in August at

selected littoral and deep-water sites to determine species composition and relative abundances. Littoral samples should be collected using SCUBA gear and bottom dredges. Dredges also should be used for the deep-water samples.

Fish

Species composition of fish communities and concurrent estimates of relative abundance and biomass, length, weight, age, condition, and diet should be determined at selected sampling sites in January, again in April, and at monthly intervals from June through September. In January and April, samples should be collected in the littoral area using gill nets. In summer and fall, samples along the littoral zone should be collected monthly using hook-and-line gear and gill nets. Also, samples in the pelagic zone in summer and fall should be obtained with down-rigger gear.

Caldera Springs

Water samples should be collected at five caldera springs (numbers 20, 38, 39, 42 and 48) to evaluate nutrient inputs to the lake. Samples from these inlet streams could serve to indicate potential anthropogenic contamination from visitor facilities on the caldera rim. Temperature data and water quality samples (pH, alkalinity, and specific conductance) should be collected once in January, once in April, and at monthly intervals between June and September. Nitrate-nitrogen samples should be collected on each trip. Samples for measurement of total phosphorus, orthophosphate, total Kjeldahl-nitrogen, ammonia-nitrogen, trace elements, silica, sulfate-sulfur, and bacteria (total coliform, fecal coliform, and fecal streptococcus) should be collected in August.

Bulk Atmospheric Deposition and Chemistry

Total atmospheric deposition should be measured annually using two rocket collectors, one located on the caldera rim near Rim Village and another on the west side of Wizard Island. Annual assessment of the amount of precipitation at these two sites should be compared to precipitation data from the rocket collector maintained by the U.S. Geological Survey near Cleetwood Cove. Nutrient concentrations in bulk atmospheric deposition should be determined at weekly intervals using samples from a collector located near Rim Village.

Water Level

Temporal changes in the elevation of the lake should continue to be recorded using the gaging station of the U.S. Geological Survey at Cleetwood Cove.

Sample and Data Management

All biological samples should be archived in the park museum collection following standard procedures of the National Park Service. Field collection sheets should be duplicated, and one copy should be archived at the park and the other archived at the Cooperative Park Studies Unit at Oregon State University. Physical, chemical and biological data should be entered into computer files in a timely manner. All data should be archived at the park and at the Cooperative Park Studies Unit. Annual reports should be prepared in a format consistent with the report produced during the 10-year study.

Additional Studies

Several specific studies are recommended to enhance the general monitoring

effort.

Zooplankton. Copepods and chydorid crustacean zooplankton taxa were discovered in the stomach contents of kokanee salmon captured in 1990-91. These taxa have not been found in the zooplankton samples collected at Station 13. These results suggest that the kokanee may have fed along the littoral zone of the lake. A survey of the zooplankton community in the littoral zone is recommended.

Periphyton and Macrophytes. Little is known about the periphyton and macrophytes in Crater Lake. Surveys of both types of plant communities are recommended.

Moss. Initial studies of the distribution of deep-water moss in Crater Lake were conducted in 1989. Additional studies are recommended to assess the horizontal and vertical distributions, productivity, and nutrient uptake of the moss throughout the lake basin.

Amphibians. Little is known about the distributions and abundance of these species at Crater Lake. A study of this is recommended.

Crayfish. Very little is known about this non-native species of crayfish in Crater Lake. A study of the distribution and abundance of the crayfish population in Crater Lake is recommended.

Spring Discharge. Little is known about the discharge of springs in the caldera. A study of the temporal changes in the amount of discharge at selected springs is recommended.

Boats. Approximately 1,500 gallons of gasoline are used by tour and research boats each summer on Crater Lake. A study of effects of boat engine exhaust, gasoline, and oil on the lake is recommended.

As the nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural and cultural resources. This includes fostering wise use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for enjoyment of life through outdoor recreation. The department assesses our energy and mineral resources and works to ensure that their developement is in the best interest of all our people. The department also promotes the goals of the Take Pride in America campaign by encouraging stewardship and citizen responsibility for the public lands and promoting citizen participation in their care. The department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

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