

QH
541.5
.R4
J64
1997

Ecological Effects of Reservoir Operations on Blue Mesa Reservoir

Annual Progress Report

May 1, 1996-April 30, 1997

Prepared by

Brett M. Johnson
Principal Investigator

Jason D. Stockwell
Postdoctoral Fellow

Krista Bonfantine
Research Assistant

Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, CO 80523



Colorado Division of Wildlife
RESEARCH CENTER LIBRARY
317 West Prospect Rd.
Fort Collins, CO 80526
USA

QH
541.5 Ecological effect
.R4 of reservoir
J64 operations on Blu
1997 Mesa Reservoir |
annual progress

DATE DUE

QH
541.5 Ecological effect
.R4 of reservoir
J64 operations on Blu
1997 Mesa Reservoir |
annual progress

BDDW015 770

DATE	ISSUED TO



**COLORADO DIVISION OF WILDLIFE
RESEARCH CENTER LIBRARY**

317 West Prospect
Fort Collins, CO 80526 USA
(970) 472-4353

**Ecological Effects of Reservoir Operations
on Blue Mesa Reservoir**

Annual Progress Report

May 1, 1996-April 30, 1997

Prepared by

Brett M. Johnson
Principal Investigator

Jason D. Stockwell
Postdoctoral Fellow

Krista Bonfantine
Research Assistant

Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, CO 80523



TABLE OF CONTENTS

Acknowledgments	3
Summary	4
Introduction	5
Study Site	7

Part 1.

Reservoir Limnology

Methods

Overview	7
Physicochemical Limnology	7
Primary Production	8
Zooplankton	8
Sampling	8
Sample Processing	8

Results and Discussion

Physicochemical Limnology	9
Reservoir Operations	9
Temperature	9
Dissolved Oxygen	10
Secchi Disc	10
Primary Production	10
Chlorophyll a	10
Zooplankton	11
Large versus small mesh nets	11
The Zooplankton Community	12

Part 2.

Fishery Investigations

Methods

Vertical Gill Netting	13
Diet and Growth Analysis	13
Hydroacoustics	14

Results and Discussion	
Vertical Gill Netting	14
Diet and Growth Analysis	14
Hydroacoustics	15
 Part 3.	
Reservoir Thermal Ecology	
Methods	
Thermal Stratification Model	15
Bioenergetics Modeling	16
Results and Discussion	
Thermal Stratification Model	16
Bioenergetics Modeling	17
Conclusions from Modeling	17
 Recommendations for Future	17
 Literature Cited	19
 List of Tables	21
 Tables	22
 List of Figures	27
 Figures	31
 Appendices	77
Appendix A: Experimental vertical gill netting	77
Appendix B: Bioenergetics-based kokanee foraging model	89

ACKNOWLEDGMENTS

The authors acknowledge the continued advice and assistance of Patrick Martinez (Aquatic Researcher, Colorado Division of Wildlife). Steve McCall (U.S. Bureau of Reclamation, Grand Junction Projects Office) coordinated the project. Graduate student Paul Weiss and Professor Darrel Fontane of the CSU Civil Engineering Department are assisting with the thermal modeling; their efforts are greatly appreciated. We thank Rick Harris and Lynn Cudlip (National Park Service, Curecanti National Recreation Area) for their logistical support and for providing housing, storage, and lab space, and the occasional field assistant. Steve Hiebert (U.S. Bureau of Reclamation) and Gordon Mueller (National Biological Service) helped us get up to speed on vertical gill netting, hydroacoustics and entrainment sampling. We appreciate the cooperation and assistance of Sherman Hebein and Dan Brauch (Aquatic Biologists, Colorado Division of Wildlife) and Dave Langlois (Senior Aquatic Biologist, Colorado Division of Wildlife). We are grateful for the help of Parker Schuerman, Rich Scholtz, Jason Garner, Lance Clarke, Shawny Mawhorter, Rob Bringuel, and Adam Craig, who assisted with field sampling, laboratory analyses and data processing. Dave Shuler aged and performed backcalculations on kokanee scales collected in 1989-1996.

The project is supported by a contract from the U.S. Bureau of Reclamation, Grand Junction Projects Office, and by financial and logistic support of the Colorado Division of Wildlife. Some capital equipment for this project was provided by College of Natural Resources, Colorado State University.

SUMMARY

- As in 1993-1995, reservoir discharge and surface elevation were above the longterm average during 1996, due to above average inflow.
- Mean reservoir surface temperature in summer 1996 was about equal to the longterm average in Sapinero and above average in Cebolla and Iola.
- Thermal profiles throughout the 1996 field season were similar to 1995, although the thermocline tended to be deeper in 1996.
- Metalimnetic oxygen minima occurred in Sapinero throughout the 1996 field season.
- Water clarity was slightly higher in 1996 than 1995. There was a stronger negative relationship between chlorophyll concentration and secchi depth than in previous years.
- Peak epilimnetic chlorophyll-a concentration occurred in June of 1996, at 5-11 $\mu\text{g/l}$, depending on basin. As in previous years, the concentration showed a steady decline over the summer.
- As in past years, most large *Daphnia* (≥ 1.0 mm) were in the top 10 m of the water column.
- In 1996, abundance of *D. pulex* increased slightly compared to 1995, while *D. galeata* decreased by more than half.
- Abundance of *Leptodiptomus* more than tripled in 1996 compared to 1994 and 1995, while *Bosmina* decreased by approximately 50%.
- Kokanee continued to feed almost exclusively on large *Daphnia pulex* in Blue Mesa. Their high diet selectivity suggests an abundant food supply for planktivores.
- Based on experimental vertical gill netting, the pelagic fish community during summer 1994-1996 is dominated by kokanee salmon.
- At night in August and September about 94% of kokanee were distributed below 12 m in the water column.
- Lake trout were usually captured in gill nets at depths that corresponded to a water temperature of 10°C.
- Rainbow trout occupied shallower water than kokanee in all months. Rainbow were captured in VGN in the top 12 m in August and in the top 18 m in September.
- Backcalculated growth rates of kokanee have changed little since the 1960's.

- Backcalculated growth rates of rainbow trout have declined steadily since 1989.
- CE-THERM accurately predicted 1996 BMR temperature profiles using parameters fitted to 1994 calibration data, and hence the model should be a valuable tool for predicting relative effects of climate and water operations on BMR thermal structure.
- New reservoir operation regimes should have little effect on reservoir thermal structure during average climatic conditions. A thinner and warmer epilimnion is predicted under new operations and warm, dry weather.
- A bioenergetics-based foraging model for kokanee was refined and calibrated for use in Blue Mesa Reservoir. The model uses food and temperature profiles to predict growth and daily migration behavior of kokanee.
- Bioenergetics modeling suggests that kokanee growth may increase slightly under warmer epilimnion temperatures, but predation risk to lake trout may increase.

INTRODUCTION

With the increasing demand for water in the western United States to serve an expanding range of purposes, it is reasonable to expect reservoir operations to be altered. Retention time, volume, morphometrics, and other reservoir characteristics will likely change. These physical changes could have important ecological consequences that could alter reservoir productivity, biotic communities, and ultimately the quality of the sport fisheries that can be sustained (Figure 1, 2).

Reservoir operations can have direct and indirect effects on reservoir productivity through a variety of mechanisms (Figure 3). Direct effects of water level management on reservoir productivity include reduced nutrient loading and internal recycling, retention times, and altered angler access to the fishery (boat access and distribution/catchability of fish). Indirect effects can alter food web interactions in two basic ways. 1) Water level influences interactions by changing epilimnetic, metalimnetic, and hypolimnetic volumes, and hence altering the density of organisms in each limnetic stratum. 2) Water level also influences epilimnetic warming which has implications for species interactions, altering zooplankton community composition, plankton production, consumption rates of planktivores, competition among planktivores, and predation rates of piscivores. This effect on reservoir thermal structure can be expected to have important consequences for productivity and sport fish yields.

Reservoir retention time, volume, basin morphometry, and climate interact to determine the thermal structure of reservoirs. Thermal structure is a critically important ecological factor in

aquatic systems because it determines physiological rates of poikilothermal (cold-blooded) inhabitants. Thus, temperature drives production of food organisms as well as the consumption rates of predators. In addition, thermal structure controls internal nutrient cycling, and can isolate or concentrate predators and prey. Both have profound implications for reservoir productivity. While creel survey information is critical to assessing how a particular reservoir operation scheme affects yield of sport fish, it provides little insight into how the observed changes were brought about, nor does it suggest strategies that can optimize water management and reservoir productivity.

This study seeks to provide a better understanding of the mechanisms and pathways by which reservoir operations can impact reservoir productivity and the quality of the fishery the reservoir supports. This knowledge will be valuable for assessing ecological and fishery implications of alternative reservoir operation strategies in the future. The approach is fivefold: 1) Assemble historic hydrographs and limnology data from Blue Mesa Reservoir (BMR) and determine relationships among surface elevation, storage, mean water column temperature, and thermocline depth. 2) Conduct a standardized limnological assessment program at sites throughout the reservoir, sampling temperature-dissolved oxygen profiles, chlorophyll, and zooplankton, and estimate zooplankton production rates. 3) Determine seasonal diet, depth distributions and growth of kokanee and rainbow trout using hydroacoustics and vertical gillnetting. 4) Incorporate sport fish diet, distribution, growth rate information into bioenergetics models to estimate consumption demand and population production. 5) Help assess potential entrainment of young-of-year kokanee using hydroacoustics to determine distribution during high discharges in late May, and by assisting with drift net sampling below the dam during the same period.

This report documents the fourth year of progress on the research project investigating the influence of reservoir water operations on ecosystem structure and function in Blue Mesa Reservoir, Gunnison County, Colorado. The primary goal of the work in 1993 was to characterize the physicochemical and biological limnology of the reservoir. In 1994 and 1995, the objectives were to 1) continue monitoring seasonal changes in physicochemical and biological limnology of the reservoir, 2) investigate potential effects of dam operations on stratification patterns in the upper and lower basins of the reservoir, 3) quantify spatial and temporal patterns of zooplankton distribution and abundance, 4) obtain abundance estimates of pelagic fish stocks, 5) determine diet composition of kokanee salmon and rainbow trout, and 6) estimate growth, condition, and depth distribution of sport fishes. In 1995 we concentrated our zooplankton sampling on Sapinero basin to gather population parameters needed to estimate *Daphnia* production, and on modeling the impact of fish predation on zooplankton biomass.

In 1996 our objectives were to continue standardized limnological and fishery monitoring, gather data to calibrate and validate the reservoir thermal model, and develop a bioenergetics-based foraging model for kokanee to study effects of thermal regime on growth and behavior of kokanee.

STUDY SITE

Blue Mesa Reservoir is a mesotrophic, 3,700 ha (9,180 ac), 32 km (20 mi) long impoundment in southwestern Colorado. The earthen dam forming Blue Mesa was constructed in 1965 to store and control heavy spring flows of the Gunnison River, and rises 104 m (342 ft) above the streambed of the river. Two 40,000 kilowatt generating units operate at the base of the dam. The lake is one of three reservoirs in the Curecanti Unit of the Colorado River Storage Project, providing water for irrigation, power generation, and recreation. With a storage capacity of $1.16 \times 10^9 \text{ m}^3$ (940,700 ac-ft), Blue Mesa is the largest reservoir in Colorado. Most of the reservoir is within the National Park Service's Curecanti National Recreation Area.

The fish community in BMR consists primarily of kokanee salmon (*Oncorhynchus nerka*), rainbow trout (*O. mykiss*), lake trout (*Salvelinus namaycush*), brown trout (*Salmo trutta*), cutthroat trout (*Oncorhynchus clarki*), longnose sucker (*Catostomus catostomus*), and white sucker (*Catostomus commersoni*). The lake supports an extremely popular and productive kokanee salmon fishery. For example, in 1993, the lake received over 612,000 angler-hours of fishing effort (ice and openwater angling; S. Hebein, CDOW, Gunnison, pers. comm.). About 340,000 fish were harvested, of which 75.3% (255,772 fish) were kokanee salmon, and 18.5% (83,898 fish) were rainbow trout. Angler caught kokanee were among the largest in Colorado with a mean length of 320 mm. In recent years kokanee catch rates and fishing pressure have dropped, but growth rates remain near the maximum observed for kokanee salmon anywhere.

Part 1. Reservoir Limnology

METHODS

Overview

Data were collected once a month from June to September 1996. Sampling was performed at a single reference station in each of the three main basins: Sapinero (lower), Cebolla (central), and Iola (upper) basins. Our objectives were to acquire information on: 1) BMR limnological parameters (temperature and dissolved oxygen profiles, secchi depth, chlorophyll *a* biomass); 2) depth-stratified zooplankton abundances; 3) fish community composition; 4) kokanee growth rates and population age structure; 5) kokanee diets; 6) kokanee abundance (hydroacoustics); 7) kokanee vertical distributions; and 8) inflow and outflow water temperatures (Table 1).

In 1996, data on zooplankton and limnological parameters were collected at the same reference stations as in 1993-1995 (Figure 4). In addition to zooplankton data, salmonid lengths, weights, scales, otoliths and stomach samples were obtained from angler's catches throughout the summer. Vertical gill netting data were collected in August and September. Thermographs were deployed in June in the BMR dam tailwater and the five main tributaries to the reservoir. Stream temperature data were collected continuously until September 13.

Physicochemical Limnology

Reservoir water operations data were obtained from USGS Water Resources Bulletins,

Colorado Division of Wildlife Research Reports (Wiltzius 1974), and USBR databases and reports.

Historic data on temperature and dissolved oxygen profiles were obtained from Wiltzius (1971) and Cudlip et al. (1987). In 1996, vertical profiles of temperature and dissolved oxygen concentrations were recorded once a month at each reference station. Temperature and dissolved oxygen profiles were obtained using a YSI Model 58 digital meter with 60 m probe cable. Measurements were taken at one meter intervals from 0 to 20 m and at 5 m intervals from 20 to 55 m of depth. Additionally, a temperature profile of the Gunnison River inflow to BMR was taken at the Highway 149 bridge on 24 July to compare with temperature recorded on a temperature logger at the same location.

Secchi depth measurements were made with a standard 200 mm white and black limnological secchi disc (Wetzel and Likens 1991) by averaging two replicate readings taken on the shaded side of the boat.

Primary Production

Chlorophyll water samples were obtained using either a van Dorn sampler (at depths of 1,2,4,6,8,10,12,14,17.5 and 25 m) or a 10-m integrated water column sampler. Some 10-m integrated samples were prefiltered through a 35 μm mesh sieve to separate them into edible and inedible (to *Daphnia*) fractions of total chlorophyll concentration. Water samples were filtered through glass microfiber filter paper (Whatman GF/F) using a vacuum pump (Soranno and Knight 1993). The filter papers were frozen on dry ice and stored frozen until they were extracted and processed. Samples were analyzed for chlorophyll-a by the 24-hr methanol extraction (Holm-Hanson and Riemann 1978, Marker et al. 1980, Riemann 1980, Soranno and Knight 1993) and fluorometry method (Lind 1979, Soranno and Knight 1993, Axler and Owen 1994) using a Turner Designs Model 450 fluorometer.

Zooplankton

Sampling

Zooplankton were collected by oblique tows using a Wildco model 37-315 Clarke-Bumpus plankton sampler with 130-mm diameter opening and several mesh sizes. In June, July, and September, zooplankton were collected with a 153- μm mesh net in the 0-10 and 10-30-m depth strata at each reference station. A net with a mesh size of approximately 1,000x600 μm was used in June to sample larger zooplankton at each reference station in the 0-5, 5-10, 10-15, 15-20, and 20-30 m strata. A 500- μm mesh net was used to sample larger zooplankton in these same depth-strata at each reference station for the remainder of the field season (July, August, and September). Most samples consisted of single replicates, although on a few occasions two or three replicates were collected. All samples were taken between the hours of 0700 and 1300, and preserved in 8% sugared, buffered formalin.

Sample Processing

Samples from the 153- μm mesh net were identified and enumerated as in previous years

(Johnson et al. 1995, 1996). *Daphnia* were identified to species, while copepods and other cladocerans were identified to genus. Each sample was diluted to provide approximately 50-60 *Daphnia* per 1-ml aliquot subsample. Aliquots were placed in a Sedgwick-Rafter counting cell where all taxa were identified and enumerated (Lind 1979, Soranno and Knight 1993) under a compound microscope. Egg counts and body length measurements were taken for *Daphnia* species only. Up to three aliquots were examined per sample. Subsampling was terminated if 20 measurable *D. pulex* were encountered before the third aliquot. Zooplankton abundances were computed as number per liter.

Samples collected with the 1,000x600 and 500- μ m mesh nets were processed in the same fashion as the 153- μ m mesh net. However, only *Daphnia* were counted and measured. Egg counts were also recorded. Subsampling was terminated when 50 measurable *Daphnia* had been encountered, or three aliquots examined. When a sample contained low numbers of *Daphnia*, total counts were made using a plexiglass plankton wheel mounted on a dissecting scope. *Daphnia* were then placed in a Sedgwick-Rafter counting cell and measured under the compound microscope.

RESULTS AND DISCUSSION

Physicochemical Limnology

Reservoir Operations

Mean daily discharge (cubic feet per second; CFS) from BMR was above the long-term average (1972-1992) during water year (WY) 1996. Mean daily discharge peaked at around 2,500 CFS during June. During the pre-reoperation period of 1976-1992 peak discharge also occurred on average during July; however, a spring to early summer peak in discharge is less distinct during this period (Figure 5). Mean surface elevation of the reservoir was higher in all months of WY 1996 than the long-term mean (Figure 6). Monthly inflow (ac-ft) peaked during May 1996 at about 325 ac-ft (Figure 7). The temporal pattern of inflow was similar in 1993-1996, but the magnitude of inflow was highest in 1995.

Temperature

In 1996, mean water temperature in each basin exceeded the 20-year average (Figure 8). Mean temperature in Sapinero (19.1°C) was slightly higher than the long-term mean (18.8°C). However, mean temperatures in the other two basins (20.7 and 19.7°C in Cebolla and Iola, respectively) were approximately 1°C higher than the long-term average (19.4 and 18.8°C, respectively).

Sapinero was not thermally stratified in early June (Figure 9). The water column was weakly stratified in Cebolla (Figure 10), but isothermal in Iola (Figure 11), at this time. Temperature profiles for the remaining months showed fairly strong thermal stratification in Sapinero and Cebolla (range of epilimnion temperature 17-20°C, thermocline depth 7-14 m; Figures 9-10). Thermal profiles from Iola basin during this time period were similar to the top 20 m of the other two basins (Figure 11). In general, stratification patterns in 1996 were similar to 1995, although the thermocline tended to be slightly deeper in 1996.

On 24 July, the thermal profile at the Highway 149 bridge (where the Gunnison River empties into Blue Mesa) was similar to the thermal profile of the reference station in Iola. However, the thermocline was slightly shallower (7 m; Figure 12) at Highway 149 compared to Iola (10 m; Figure 11). Temperatures recorded by the logger at 149 bridge were the lowest of all loggers deployed (Figure 13); all loggers were placed in depths >7m to ensure they would be underwater all season, but this depth probably does not accurately reflect inflow temperatures. Regression models that predict stream inflow temperatures from weather data are preferable in this highly fluctuating reservoir.

Dissolved Oxygen

Dissolved oxygen levels were generally high (> 6 mg/l) in the 0-10 m stratum in all three basins throughout the season (Figures 14-16). However, metalimnetic oxygen minima occurred in Sapinero in August and September. Dissolved oxygen dropped to nearly 4 mg/l, but then increased to >6 mg/l at greater depths. In Cebolla, DO generally fluctuated between 4 and 6 mg/l from July-September at depths greater 14 m, with a minimum of < 3 mg/l in September. Dissolved oxygen levels were generally > 6 mg/l in Iola, except for near bottom in August and September when DO decreased to approximately 4 mg/l.

Secchi Depth

As in previous years, water transparency increased through the season in 1996 at all stations (Figure 17). In general water transparency was greater in 1996 than in 1995 but slightly lower than during 1994. Transparency was more variable in 1993-1996 than the average observed by Cudlip et al. (1987) during 1983-1985 (Figure 18).

There is considerable variability inherent in secchi depth readings between observers and the method is sensitive to sampling conditions; however, there is a trend towards increasing water clarity in the available data. Whether this trend is real or artifactual is unknown at present. If the pattern is real then it could indicate either an increase in grazing pressure by the zooplankton community, lower input or mixing of inorganic material that causes turbidity, or reduced nutrient availability for primary production. The chlorophyll and zooplankton sampling we have undertaken should prove very helpful in determining an explanation for changes in the secchi depth data.

Primary Production

Chlorophyll a

As in 1995, calibrations of the fluorometer using a spectrophotometer and known dilution concentrations of a chlorophyll standard produced the required linear relationship between true chlorophyll concentration and the F_b-F_a fluorometer readings with R^2 values > 0.99. Further, the strong relationship held for all fluorometer gain settings we tested, which encompassed the entire range of gains we anticipate needing for sample processing.

Chlorophyll concentration was highest the first week of June in all three basins. In both Sapinero and Cebolla, this concentration was higher than any date in either 1994 or 1995 (Figure

19). As in 1994 and 1995, chlorophyll concentration declined steadily after the June peak in Sapinero and Cebolla, but was slightly more variable in Iola. The fraction of total chlorophyll of edible size ($<35\mu\text{m}$) for most crustacean zooplankton comprised a slightly smaller fraction of the total chlorophyll than in previous years but remained lowest in Iola. This difference may be due to bluegreen algae blooms which occur in Iola basin.

In general, integrated samples were sufficient to show temporal trends in chlorophyll concentration. Chlorophyll concentrations were variable throughout the epilimnion and metalimnion in all three basins. The only metalimnetic peak in chlorophyll concentration was seen in Cebolla in early June (Figures 20-22). Aside from identifying this peak, sampling at discrete depths did not provide a great deal of information to supplement the integrated samples. We concluded that discrete sampling is not necessary for general estimates of chlorophyll concentration.

Secchi depth is sometimes used as a convenient and inexpensive surrogate for chlorophyll measurements (Cole 1983). At BMR there was a weak negative relationship evident between secchi depth and chlorophyll concentration in 1994 and a strong negative relationship in 1996 (Figure 23). The relationship was not apparent in 1995 when inflow was much higher than past study years. Variation in inorganic turbidity and in the size composition of the phytoplankton community may be responsible for the lack of correspondence between secchi depth and chlorophyll (Edmondson 1980). When inflow is low, secchi depth may provide an adequate estimate of primary producer biomass.

There does not appear to be a trend in conductivity in Sapinero basin since dam construction (Figure 24). This suggests that the nutrient status of the reservoir may not have declined greatly in the three decades since impoundment.

Zooplankton

Large versus small mesh nets

The size frequency distributions of *Daphnia* collected in the three nets were consistent with expectations. As the mesh size increased, so did the size distribution (Figure 25). The modal length of *Daphnia* caught in the $153\text{-}\mu\text{m}$ mesh net was 1.1 mm (range 0.9-2.1 mm), compared to 1.3 mm (0.9-2.5 mm) for the $500\text{-}\mu\text{m}$ mesh net and 1.9 mm (1.1-2.5 mm) for the $1,000\times 600\text{-}\mu\text{m}$ mesh net.

The purpose for using the larger-sized mesh was to better estimate abundances of the large *D. pulex* that are selectively preyed upon by kokanee (Johnson et al. 1996). Sampling by depth-strata showed that large *Daphnia* are primarily found in the top 15 m of the water column in both Sapinero and Cebolla from July through September (Figure 26).

Results from the $153\text{-}\mu\text{m}$ net show that even though abundances of large *Daphnia* are greatest

near the surface (Figure 27), mean length of *D. pulex* is much greater in Sapinero in June and July in the 10-30 m stratum (1.75 and 1.5 mm, respectively) than in the 0-10 m stratum (1.1 and 1.25 mm, respectively; Figure 28). Conversely, mean length of *D. pulex* is greater in the 0-10 m stratum (1.6 mm) versus mean length in the 10-30 m stratum (1.45 mm) in September (Figure 28). Mean length of *D. pulex* in Cebolla for both 0-10 and 10-30 m strata for all sampling dates ranged between 1.1 and 1.45 mm (Figure 28). Across all strata and sampling dates, mean length *D. pulex* was always greater than *D. galeata*. Differences between the two *Daphnia* species accounts for the size-selective feeding behavior of kokanee (Johnson et al. 1996).

The depth distributions of large *Daphnia* can now be used, in conjunction with thermal profiles and fish growth estimates from 1996, to further evaluate/calibrate our bioenergetics-based foraging model for kokanee (Stockwell and Johnson, In press; Appendix B).

The Zooplankton Community

During the 1996 field season a total of 68 zooplankton samples were collected across all mesh sizes, depth strata, and sampling dates. Six taxonomic groups of crustacean macrozooplankton were identified: the cyclopoid copepod *Diacyclops*; the calanoid copepod *Leptodiaptomus*; and the cladocera *Bosmina*, *Ceriodaphnia*, *D. pulex*, and *D. galeata*. Results from 1996 are biased when compared to previous years because we did not take samples in May or August with the 153- μ m mesh net. Ignoring this bias, the zooplankton community in 1996, as in 1993-1995, continued to be dominated by the copepod *Diacyclops* (Figure 29). When abundance estimates from the 0-10 m stratum were averaged across all basins and sampling dates, *Diacyclops* was more than four times more abundant than any other species in 1993, and greater than two times more abundant than any other species in 1994-1996 (Figure 29). *Daphnia pulex* relative abundance increased in 1996 while *D. galeata* decreased. The calanoid copepod *Leptodiaptomus* increased by more than a factor of three compared to 1995. Conversely, *Bosmina* decreased by more than 50%.

The overall abundance of zooplankters in 1996 was highest in June (77 ind/l), and similar to estimates from June 1994 (Figure 30). Abundances in July and September were about 50% of June abundances (30-33 ind/l), and were closer to estimates for those same months in 1995 (Figure 30). In June, *Diacyclops* was more abundant in 1996 (45 ind/l) than in previous years (33 and 25 ind/l in 1994 and 1995, respectively), while *Bosmina* and *D. galeata* were both less abundant than in the two previous years. In July, the most notable differences between 1996 and previous years were the occurrence of *Leptodiaptomus* and copepod nauplii, and the virtual absence of *D. galeata*. Abundances of taxonomic groups in September were similar to 1995.

The high abundance of *Leptodiaptomus* in Iola was primarily responsible for the large increase of this taxonomic group in 1996 (Figure 31). We also found the large increase in copepod nauplii in 1996 was a result of their high abundances in Iola, followed by Cebolla and then Sapinero (Figure 31). The overall decrease in *D. galeata* in 1996 was a result of lower abundances in all three basins.

Part 2. Fishery Investigations

METHODS

Vertical Gill Netting

Vertical gill netting was conducted during three dates in mid-August in all three basins to gather diet and growth information, and to complement hydroacoustic surveys performed by CDOW personnel. We netted on one date in mid-September in Cebolla basin, again to obtain diet and growth information. A gang of three nets was fished during nighttime hours at a midlake station (Table 2). Nets floated on the surface and extended to within about 1-2 m of the lake bottom. Nets measured 60 m long and 3 m wide and were constructed with two mesh sizes (0.5 in, 0.75 in, 1.0 in, 1.25 in, 1.5 in, or 2.0 in) per net. Depth at which each fish was caught was recorded. Gill net caught fish were measured and weighed. Otoliths, scales and stomachs were removed from all kokanee and a subsample of other salmonids.

Diet and Growth Analysis

Kokanee stomach samples were obtained during August-September from vertical gill net sampling and by sampling the angler catch at cleaning stations at each lake basin during June and July. Stomachs were excised and preserved in 10% formalin. Kokanee samples were grouped into three size classes (<250 mm, 250-349 mm, or >349 mm); approximately five stomachs from fish of each size class from each date and sampling location were aggregated for analysis.

Proportions (by volume) of fish, macroinvertebrate, and zooplankton were visually estimated. Non-zooplankton prey were preserved for future analysis. The zooplankton contents were diluted to a density that would yield approximately 20-30 measurable zooplankters. One aliquot was placed in a Sedgwick-Rafter cell and all identifiable organisms were counted. Cladocerans of genera *Ceriodaphnia*, *Bosmina*, *Diaphanosoma*, were all lumped into a group called "other *Daphnia*" and counted as such. *Daphnia* were identified to species if possible. The first 10 specimens of each *Daphnia* species encountered were measured. When there was only one species of *Daphnia* present the first 20 individuals of that species was measured. Only *Daphnia* with an intact carapace were measured. If after counting the entire slide 10 measurements of each *Daphnia* species was not obtained we went back through the slide and measured *Daphnia* (the ones that were passed over because they were not identifiable to species) until a total of 20 *Daphnia* measurements were taken and recorded. Copepods were counted but not identified further because of their rarity in diets.

We took scale samples from kokanee sampled in vertical gill nets, and from a stratified (by length) sample of fish in anglers' creels. A complete complement of otoliths across all kokanee sizes was also taken. Scales were pressed onto acetate slides and examined in a microfiche reader at about 36X. Each scale was read by two trained scale readers. Annuli were determined and scale radii were measured to develop a scale-body length relationship. We transformed the scale/body length data and fit a Fraser-Lee function that we used in backcalculations (Everhart and Youngs 1981). Scale samples obtained by CDOW in 1989, and scales obtained by CSU in 1994 and 1996 were read by CSU undergraduate Dave Shuler. Historic data on kokanee backcalculated length at age were obtained from Wiltzius (1971, 1974).

Hydroacoustics

No hydroacoustics surveys were conducted by CSU in 1996. Data from the 1995 survey were analyzed during 1996. A BioSonics ES-105 dual beam echosounder and 420 kHz with 6/15° transducer mounted in a towed body were used to collect hydroacoustic data at night during the new moon on 23-24 July 1995. Transects (Table 3) coincided with those employed by CDOW on the same nights. Data were recorded on a digital audio tape recorder and processed using BioSonics Echo Signal Processing software, by Richard Thorne of BioSonics, Seattle, Washington.

RESULTS AND DISCUSSION

Vertical Gill Netting

Kokanee salmon comprised between 84-91% of all fish captured in experimental vertical gill nets (Figures 32-33, Appendix A), a similar fraction to that observed in 1994 and 1995. About 3% of the catch in August was brown trout, 7.4% lake trout, and suckers and rainbow trout together comprised 6% of the August catch (Appendix A). In September, 32 kokanee were sampled and only one brown trout and two rainbow trout. In all months over 97% of the catch was of fish <450 mm (Figures 32-33, Appendix A).

About 60% of the fish caught in August were taken in water ≤ 20 m deep (Appendix A). Kokanee were nearly normally distributed throughout the water column between 10-40 m with the mode at about 20 m in August. During September fish were distributed throughout the water column between 1-45 m, with a mode at 25 m (Appendix A), which was deeper than observed in September 1995. As was observed in previous years, rainbow trout were usually caught in water ≤ 10 m deep. Five lake trout were caught between 20 and 50 m in August. The cumulative temperature distribution of summertime lake trout catches since 1994 showed that lake trout are usually found at a depth that corresponds to a temperature of about 10°C (Figure 34). Behavioral thermoregulation to a temperature of 10°C has been observed in other lake trout populations (Stewart et al. 1983).

Diet and Growth Analysis

The preferred prey of kokanee in most lakes is large *Daphnia* spp. (Finnell and Reed 1969; Rieman and Bowler 1980; Schneidervin 1985). Blue Mesa kokanee of all sizes were highly selective for their preferred prey at all basins, through the entire season. Just as in 1994 and 1995, in June and July 1996 kokanee consumed mostly zooplankton, and of that at least 98% was large *Daphnia*. Kokanee were also selective for the larger individuals from zooplankton populations. Kokanee in BMR fed almost exclusively on *Daphnia* over 1.5 mm in length in 1994 and 1995; in 1996 mean length of daphnids in stomachs from all sizes of kokanee ranged 1.62-1.90 mm. Only 1.5% of the *Daphnia* observed in stomachs was <1.0 mm in length.

The extreme selectivity of kokanee for only large individuals of a single species of

zooplankton, when high densities of other species and size classes were present, suggests that the kokanee population is not food limited, and that during summer kokanee abundance is well below the food-imposed carrying capacity of the lake.

Based on scale samples, the backcalculated mean length-at-age of kokanee has changed little since the reservoir was impounded (Figure 35, Table 4). Growth of age-1 kokanee appeared to be greatest in 1989 and least in 1966-69. It appears that growth of rainbow trout to age-1 and age-2 has declined steadily since the reservoir formed (Figure 36). We have yet to compare scale ages with those obtained from otoliths so these conclusions should be considered preliminary until this validation exercise is completed.

Hydroacoustics

Results of hydroacoustics surveys conducted during the June and July 1995 survey are provided in Figures 37-40. Because of the high frequency of the system and the low threshold employed, noise from zooplankton in the top 8 m was excessive. Thus, we presented fish densities from 8 m to the bottom. In July, fish densities (fish/1,000 m³) were similar the three basins. Fish density was highest in the 16-18 m stratum in each basin, about 4-6 m shallower than in the August 1994 survey.

Target strengths generally increased with depth in each basin. Smallest mean target strengths always occurred in depths of 2-10 m. Many of the targets acquired in the 2-10 m strata are probable zooplankton concentrations rather than fish. Zooplankton sampling showed maximum plankter densities in the top 10 m of the water column in all basins during July. Target strengths were similar across depths from 12-48 m at about -48dB, and highest below 48 m, presumably because lake trout dominate the fish assemblage at these depths.

Results of mid-day and nighttime sonar surveys showed a bimodal depth distribution (modes at 20 and 34 m) during day and a vertical migration to shallower water (about 18 m) at night (Figure 41).

Part 3. Reservoir Thermal Ecology

METHODS

Thermal Stratification Model

We parameterized and calibrated a reservoir thermal stratification model called CE-THERM (Environmental Laboratory 1986) for Blue Mesa Reservoir. The basic framework of CE-THERM is a heat budget and hydrodynamic equations that distribute the heat in the water column. The heat budget requires the following primary inputs: quantity and temperature of water inflow and outflow, daily meteorologic data (wind, cloud cover, air temperature, etc.), and water quality parameters (water transparency and total dissolved solids, suspended solids, etc.). Insolation, conduction, evaporation, diffusion and entrainment are among the physical processes that are explicitly incorporated in the model (Figure 42). A regression model relating air and tributary

temperatures (developed by Paul Weiss, CSU Civil Engineering graduate student) was developed and was used to generate predictions for the 1994 stratified period. In 1995 and 1996 we deployed temperature loggers at input streams and at the reservoir outflow to refine estimates of aquatic thermal inputs and outputs.

We developed four scenarios (Table 5) to simulate relative effects of climate and water operations on the Blue Mesa thermal regime: 1) average weather conditions and traditional operations (both based on pre-1993 longterm averages, 2) average weather and new operations (releases to mimic the pre-dam hydrograph in the Gunnison River below Lake Fork), 3) warm, dry weather (reduced inflow and cloud cover, increased air and inflow temperatures) and traditional operation, and 4) warm, dry weather and new operations.

Bioenergetics Modeling

During 1996, we modified and calibrated an existing bioenergetics-based foraging model for kokanee (Stockwell and Johnson, In press; Appendix B). The model was originally developed by Bevelhimer and Adams (1993) to evaluate the effects of different migration strategies on kokanee growth in a North Carolina lake. We modified the model to incorporate a corroborated respiration function and a more realistic foraging function. The model uses inputs of vertical gradients of temperature and food (*Daphnia* abundances) to evaluate trade-offs (in terms of optimizing growth) between maximizing kokanee consumption in food rich surface waters and minimizing metabolic costs in colder, deeper waters. Calibration of the modified model shows fairly good agreement with Blue Mesa field data (temperature, *Daphnia* abundances, and kokanee growth; Appendix B). The utility of the model is that, when coupled with the reservoir stratification model CE-THERM, it allows quantitative predictions of changes in kokanee behavior and subsequent growth as a result of alternative dam operation schedules and climate conditions.

RESULTS AND DISCUSSION

Thermal Stratification Model

Model parameterization and calibrations using all available 1994 data are complete, and we were able to obtain close agreement between simulated and observed temperature profiles. The model with these coefficients was used to predict 1996 stratification at biweekly intervals with considerable success (Figure 43). Some refinements of parameters are still needed (e.g., better data on wind speed and direction, and air light extinction coefficients).

During “normal” weather conditions the high spring and summer releases from the “new operations” scenario resulted in a <9 m lower surface elevation during the growing season but the predicted thermal structure of the reservoir was similar regardless of the water operation regime (Figure 44). In a warm and dry year (lower initial surface elevation, lower inflows, increased air temperatures and increased insolation) maximum temperature of the epilimnion was about 2°C warmer in both operations scenarios. Stratification was predicted to be stronger and the volume of the epilimnion smaller in the new operations scenario.

Bioenergetics Modeling

The bioenergetics-based kokanee model will be published in the October or November 1997 issue of Canadian Journal of Fisheries and Aquatic Sciences. A manuscript is attached as Appendix B, which shows results of field calibration and simulations. Overall, model growth estimates for kokanee bounded the observed growth for all age-classes and dates we examined. Furthermore, migration strategies generated by the model to optimize growth were consistent with our current knowledge of kokanee diel vertical migration. These general results suggest the model can be used as an effective tool to examine potential changes in kokanee growth and behavior resulting from new dam operation schedules.

Preliminary results from the modeling suggests the increased surface temperatures and stronger thermocline in dry and warm years with large spring releases will not inhibit kokanee growth, and that kokanee growth may even be slightly enhanced (Figure 45). However, increased growth might have a cost of increased predation risk to piscivorous lake trout. Under the extreme scenario, the proportion of lake trout habitat $\leq 10^{\circ}\text{C}$ greatly increases, and the distance between lake trout and kokanee habitat decreases. This scenario is likely to increase spatial overlap between predator and prey, and therefore place kokanee at a greater risk to predation (Figure 46).

Conclusions from Modeling

Blue Mesa Reservoir's thermal regime appears to be relatively insensitive to changes in operations under "normal" climatic conditions. Preliminarily, it appears that reservoir managers have considerable latitude for new operations without negative thermal consequences for kokanee salmon growth, but predation risk has not been adequately evaluated. Effects of reoperation on nutrient dynamics have not been addressed. This approach could also be applied to examine effects of climate on fish production, predation demand, and carrying capacity.

RECOMMENDATIONS FOR FUTURE

The following are important next steps that derive from our work at Blue Mesa during 1993-1996. However, no funding is currently available to pursue these goals.

Blue Mesa has been one of the top kokanee salmon fisheries in the world, and a significant proportion of the Colorado's coldwater fishery resource. There are indications that the BMR fish assemblage is changing. Kokanee abundance is declining, while piscivorous lake trout have apparently increased dramatically.

- Continue to gather information on fish abundance, diet, and growth rates.
- Creel survey information will be needed to obtain information on kokanee mortality rates.
- The sampling program implemented in 1994 to gather fish stomach samples and growth

information from angler caught fish should be continued.

- Hydroacoustics surveys for estimating fish abundance and distribution, and vertical gillnetting for “groundtruthing” hydroacoustics data, species identification and to provide diet samples should be continued.
- Estimate kokanee encounter rates with piscivorous lake trout.

We should continue with work predicting the importance of climate on reservoir structure and function by implementing the reservoir thermal model that predicts thermal structure from weather data, inflow volume and temperatures, and discharge patterns. Continuing to refine links between direct physical effects of reservoir reoperation with the ecological implications via bioenergetics modeling approaches will be insightful. This framework is allowing us to study to potential interplay between direct anthropogenic and climatic influences in determining reservoir trophic dynamics and productivity, and also to forecast some implications of global climatic change for reservoir management.

- Continue our collaboration with national experts in reservoir thermal modeling at the CSU Civil Engineering Department to study reservoir operations influences on the thermal structure of the lake and its food web
- Evaluate CE-THERM’s heat budget algorithms (evaporation, insolation) for low humidity, high elevation reservoirs.
- Test CE-THERM thermal predictions in a warm, dry year. Additional study years with a wider range of environmental conditions than have already been observed would strengthen the evaluation of this approach. Field sampling could be planned as late as March in a given year to insure that field effort occurs during a dry year.
- Test foraging model’s predictions of kokanee migratory behavior
- Perform multi-reservoir comparisons to examine the influence of basin morphometry on thermal and trophic responses to climate and operations.

A wealth of data and understanding of reservoir patterns and processes has accumulated during this project. Blue Mesa is serving as a proving ground for modeling techniques being implemented to link physical and biological processes. As western reservoir water management policies and objectives change, these techniques could prove to be invaluable for assessing ecological responses to reservoir reoperation.

LITERATURE CITED

- Axler, R.P. and C.J. Owen. 1994. Measuring chlorophyll and phaeophytin: whom should you believe? *Lake and Reservoir Management* 8:143-151.
- Cole, G.A. 1983. *Textbook of Limnology*. Third Edition. Waveland Press, Inc. Prospect Heights, Illinois.
- Cudlip, L.S., R.D. French, and D. Hickman. 1987. Blue Mesa Reservoir, Colorado: a historical review of its limnology, 1965-1985. U.S. Bureau of Reclamation Technical Report 85-9, Denver, CO.
- Edmondson, W.T. 1980. Secchi disc and chlorophyll. *Limnology and Oceanography* 25:378-379.
- Holm-Hansen, O. and B. Rieman. 1978. Chlorophyll a determination: improvements in methodology. *Oikos* 30:438-447.
- Johnson, B.M., Wise, M.J., Counard, C.J., and Szerlong G. 1995. Ecological effects of reservoir operations on Blue Mesa Reservoir. Annual Progress Report to U.S. Bureau of Reclamation. 153 pp.
- Johnson, B.M., Wise, M.J., Herwig, B., Szerlong, G., Faber, D., and Byall, B. 1996. Ecological effects of reservoir operations on Blue Mesa Reservoir. Annual Progress Report to U.S. Bureau of Reclamation. 124 pp.
- Lind, O.T. 1979. *Handbook of common methods in limnology*, second edition. C.V. Mosby, Co., Saint Louis, MO.
- Marker, A.F.H., E.A. Nusch, H. Rai, and B. Rieman. 1980. The measurement of photosynthetic pigments in freshwater and standardization of methods: conclusions and recommendations. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 14:91-106.
- Rieman, B. 1980. A note on the use of methanol as an extraction solvent for chlorophyll a determination. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 14:70-78.
- Soranno, P.A. and S.E. Knight. 1993. *Methods of the Cascading Trophic Interactions Project*. University of Wisconsin, Center for Limnology, Madison, WI.
- Stockwell, J.D. and B.M. Johnson. In press. Refinement and calibration of a bioenergetics-based foraging model for kokanee (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.*
- Wetzel, R.G. and G.E. Likens. 1991. *Limnological Analyses*. Springer-Verlag, New York.

Wiltzius, W.J. 1974. Final Report: Post-impoundment Fishery Investigations, Curecanti Unit, Upper Colorado Storage Project, Colorado Division of Wildlife, Fort Collins, Co.

Wiltzius, W.J. 1971. Job Completion Report: Post-impoundment Fishery Investigations, Curecanti Unit, Upper Colorado Storage Project, Colorado Division of Wildlife, Fort Collins, Co.

LIST OF TABLES

- Table 1. Overview of sampling conducted on Blue Mesa Reservoir in 1996.
- Table 2. Location of standard sampling stations on Blue Mesa Reservoir visited during 1994, 1995, 1996. GPS coordinates were recorded using Garmen GPS-75 without differential correction
- Table 3. Standardized transects used during hydroacoustics surveys at Blue Mesa Reservoir during June, August, and October 1994 and July 1995.
- Table 4. Backcalculated mean lengths at age for kokanee from Blue Mesa Reservoir. Backcalculations performed using the transformed Fraser-Lee method, $v=0.7073$. N Obs is the number of fish of a given age in the sample; N is the number of scale measurements at a given annulus obtained from the sample.
- Table 5. Climate and reservoir operations scenarios used in CE-THERM simulations of the Blue Mesa thermal regime.

Table 1. Overview of sampling conducted by CSU on Blue Mesa Reservoir in 1996.

Parameter	Approach	Methods
Temperature	Profiles	Once a month, from June-September, at each reference station in each basin. Once at Highway 149 bridge in July.
Dissolved oxygen	Profiles	Once a month, from June-September, at each reference station in each basin.
Secchi depth	Measurements	Once a month, from June-September, at each reference station in each basin.
Chlorophyll	0-10 m Integrated	Once a month, from June-September, at each reference station in each basin.
	Profiles	Once at each reference station in each basin in June, July, and September.
Zooplankton	Depth-stratified Samples	153 μm mesh: 0-10, 10-30 m in June, July, and September at each station in each basin 500 μm mesh: 0-5, 5-10, 10-15, 15-20, 20-30 m in July, August, and September at each station in each basin 3 replicates 0-5 m in Cebolla in July; 40, 50 m in Sapinero in July 1,000x600 μm mesh: 0-5, 5-10, 10-15, 15-20, 20-30 m in June at each station in each basin 3 replicates 0-5 m in Cebolla in July
Fish (salmonids) size, spp, depths	Vertical Gill Nets (six meshes)	11 sets: one-two nights per basin in June, July, September.
Diet	Sampling	at fish cleaning stations every two weeks at each basin.
Abundance	Hydroacoustics	Lakewide Survey - three basins during 23-24 July
Diel Vertical Migration	SONAR Transects	in Sapinero on 28 June
Stream Temperatures	Loggers	Maintained temperature loggers in the Gunnison River input (Highway 149), Lake Fork, Cebolla Creek, Soap Creek, and the dam tailwater June-September

Table 2. Location of sampling stations established on Blue Mesa Reservoir and visited during 1994, 1995, and 1996. GPS coordinates were recorded using Garmen GPS-75 without differential correction.

Station Name	Purpose	Depth (m)	Waypoint Name	GPS Coordinates (UTM)		
				Zone	Easting	Northing
Iola Basin	Zooplankton, chlorophyll, temp-DO profiles, secchi	20	IOLAZP	13 S	0317192	4260939
Iola VGN	Vertical gill nets	21	IOLVGN	13 S	0317379	4260984
Cebolla Basin	Zooplankton, chlorophyll, temp-DO profiles, secchi		CEBZP	13 S	0308310	4261123
Cebolla VGN	Vertical gill nets	50	CEBVGN	13 S	0308329	4261032
Cebolla Arm VGN	Vertical gill nets	23	none	13 S	0308400	4257900
Sapinero Basin	Zooplankton, chlorophyll, temp-DO profiles, secchi		SAPZP	13 S	0298077	4259910
Sapinero VGN	Vertical gill nets	54	SAPVGN	13 S	0297774	4259573

Table 3. Standardized transects used during hydroacoustics surveys at Blue Mesa Reservoir during June, August, and October 1994 and July 1995.

Lake Basin	Waypoint Name	UTM Zone	UTM Easting	UTM Northing	Transect Length (m)	Approx. time (min.)
Iola	DOW017	13 S	0319284	4261659	Start	0
	DOW018	13 S	0318334	4260700	1350	14
	DOW019	13 S	0317055	4261339	1430	17
	DOW020	13 S	0316129	4260128	1524	16
	DOW021	13 S	0313657	4259509	?	27
Cebolla	DOW107	13 S	0310067	4259394	Start	0
	DOW108	13 S	0309284	4260817	1624	17
	DOW007	13 S	0307782	4261437	1666	18
	DOW109	13 S	0307404	4259814	1603	18
	DOW110	13 S	0306220	4260894	1582	16
	DOW111	13 S	0305332	4259585	2970	20
Sapinero	DOW010	13 S	0302448	4260294	Start	0
	DOW011	13 S	0301536	4261506	1517	19
	DOW012	13 S	0300093	4260623	1692	18
	DOW013	13 S	0299306	4262244	1802	26
	DOW014	13 S	0298977	4260700	1579	17
	DOW015	13 S	0297348	4259580	1977	21
	DOW016	13 S	0298700	4258534	1709	?

Table 4. Backcalculated mean lengths at age for kokanee from Blue Mesa Reservoir. Backcalculations performed using the transformed Fraser-Lee method, $v=0.7073$. N Obs is the number of fish of a given age in the sample; N is the number of scale measurements at a given annulus obtained from the sample.

Year	Actual Age	N Obs	Backcalculation Age	Mean Length	N	Std Error
1989	1	3	1	186.8	3	5.72
	2	132	1	199.9	132	2.02
			2	269.8	132	2.64
	3	44	1	186.4	44	3.54
			2	262.7	44	4.59
			3	326.1	44	3.83
1994	1	18	1	177.2	18	5.99
	2	15	1	199.2	15	9.01
			2	285.9	15	7.49
	3	1	1	175.5	1	.
			2	290.6	1	.
			3	326.0	1	.
1995	1	66	1	167.2	66	3.56
	2	124	1	165.5	124	3.05
			2	247.3	123	4.58
	3	54	1	169.3	54	3.80
			2	260.2	54	6.57
			3	330.5	54	5.27
	4	5	1	158.1	5	10.7
			2	242.1	5	12.1
			3	322.4	5	17.1
			4	366.8	5	14.5

Table 5. Climate and reservoir operations scenarios used in CE-THERM simulations of the Blue Mesa thermal regime.

CE-THERM Model Input	Average Weather, Traditional Operations (Figure 44a)	Average Weather with New Operations (Figure 44c)	Warm, Dry Weather, Traditional Operations (Figure 44b)	Warm, Dry Weather with New Operations (Figure 44d)
INITIAL CONDITIONS				
Start Date	May 22 (Day of year = 142)			
End Date	September 23 (Day of year = 266)			
Initial Temp. Profile	1994-95 Mean			
Initial Surf. Elev. (m)	1969-92 Mean (83 m above bottom)		1969-92 Mean minus 1SD (77 m above bottom)	
WEATHER				
Air Temperature (°C)	1992-1996 Mean		1992-96 Mean + 4 °C	
Dewpoint (°C)			1992-1996 Mean	
Sky Cover (0-1)			1992-96 Mean minus 50%	
Wind (km•h ⁻¹)			1992-1996 Mean	
Barometric Pressure (mb)				
WATER BUDGET				
Inflow Volumes (m ³ •s ⁻¹)	1969-92 Mean		1969-92 mean minus 1SD	
Inflow Temperatures (°C)	Regression with 1992-96 Mean Air Temperatures		Regression with 1992-96 Warmer Air Temperatures	
Outflow Volumes (m ³ •s ⁻¹)	1969-92 Mean	Mimic Natural Hydrograph	1969-92 Mean	Mimic Natural Hydrograph

LIST OF FIGURES

- Figure 1. Conceptual figure depicting mechanisms linking reservoir operations to reservoir productivity and fish yield.
- Figure 2. Conceptual figure showing abiotic and biotic linkages between reservoir operations and sport fish yields.
- Figure 3. Direct and indirect effects of reservoir operations on food web dynamics in Blue Mesa Reservoir.
- Figure 4. Map of Blue Mesa Reservoir showing locations of stations sampled in 1996.
- Figure 5. Mean daily discharge from Blue Mesa Reservoir in water year 1994 (WY94), WY 95, and WY 96, and the mean daily discharge for the period 1976-1992 (upper panel); and the difference between 1996 discharge and the longterm mean (lower panel).
- Figure 6. Surface elevation of Blue Mesa Reservoir in water year 1993 (WY93) through water year 1996 (WY96) and the mean surface elevation for the period 1966-1979.
- Figure 7. Monthly inflow (thousands of ac-ft) into Blue Mesa Reservoir in water years 1993-1996.
- Figure 8. July surface temperatures in the three main lake basins on Blue Mesa Reservoir in 1996, and nine previous years. Dashed lines indicate long-term mean.
- Figure 9. Blue Mesa Reservoir temperature profiles ($^{\circ}\text{C}$) at the Sapinero station during the 1996 field season.
- Figure 10. Blue Mesa Reservoir temperature profiles ($^{\circ}\text{C}$) at the Cebolla station during the 1996 field season.
- Figure 11. Blue Mesa Reservoir temperature profiles ($^{\circ}\text{C}$) at the Iola station during the 1996 field season.
- Figure 12. Blue Mesa Reservoir temperature profile ($^{\circ}\text{C}$) where Gunnison River enters Iolo Basin (Highway 149) bridge during July 1996.
- Figure 13. Mean daily temperatures recorded by loggers submerged at four tributaries and the outlet of Blue Mesa Reservoir during 1996.

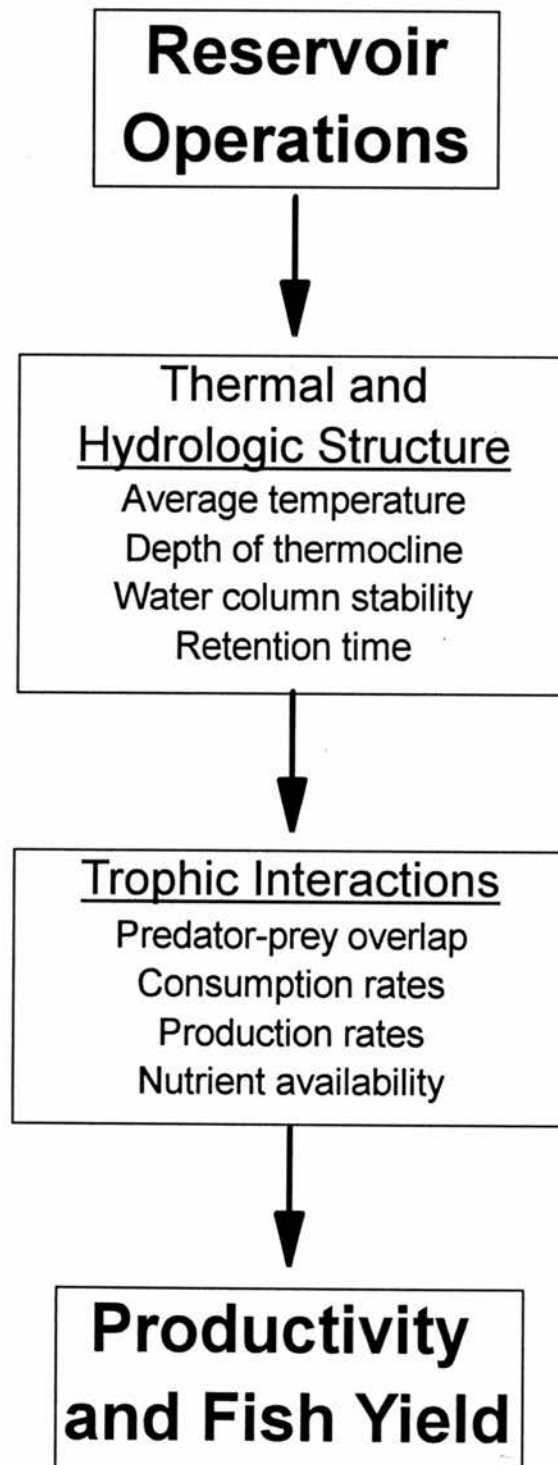
- Figure 14. Dissolved oxygen (mg/l) profiles taken during the 1996 field season at the Sapinero station.
- Figure 15. Dissolved oxygen (mg/l) profiles taken during the 1996 field season at the Cebolla station.
- Figure 16. Dissolved oxygen (mg/l) profiles taken during the 1996 field season at the Iola station.
- Figure 17. Seasonal secchi depth (m) in the three main basins in Blue Mesa Reservoir from 1994-1996.
- Figure 18. Secchi depth values (m) from the three main lake basins in Blue Mesa Reservoir from 1994-1996 and the mean secchi readings at the three basins during 1983-1985 (from Cudlip et al. 1987) and 1993 (Johnson 1994).
- Figure 19. Chlorophyll-a concentration ($\mu\text{g/l} \pm 2\text{SE}$; $n=1$ per date in 1996) in 0-10 m integrated samples in three stations in Blue Mesa Reservoir from 1994-1996. Concentrations from the edible fraction ($<35\mu\text{m}$; open circles) are shown for 1995 and 1996.
- Figure 20. Chlorophyll-a concentration ($\mu\text{g/l}$) by depth during summer 1996 at the Sapinero station.
- Figure 21. Chlorophyll-a concentration ($\mu\text{g/l}$) by depth during summer 1996 at the Cebolla station.
- Figure 22. Chlorophyll-a concentration ($\mu\text{g/l}$) by depth during summer 1996 at the Iola station.
- Figure 23. Relationship between secchi depth (m) and chlorophyll-a concentration ($\mu\text{g/l}$) at three stations in Blue Mesa Reservoir during 1994-1996.
- Figure 24. Conductivity of Blue Mesa surface water in Sapinero (open circles) and Cebolla (closed circles) basins during three time periods: 1960's (Wiltzius 1971), 1980's (Cudlip et al. 1987) and 1990's (M. Malick, NPS, pers. comm.).
- Figure 25. Size-frequency distributions of *Daphnia* caught in three different sized meshes during the 1996 field season.
- Figure 26. Abundances of large *Daphnia* (≥ 1.0 mm) by depth in Sapinero and Cebolla. NS indicates the depth stratum was not sampled.

- Figure 27. Abundances by depth strata for the nine zooplankton taxa/stages sampled from Blue Mesa Reservoir averaged over all stations and sampling dates. Data from the 15-30 m stratum in 1994 and the 10-30 m stratum in 1995 and 1996 are from Sapinero and Cebolla only.
- Figure 28. Mean length of *D. pulex* and *D. galeata* in each 0-10 and 10-30 m strata through the field season in 1996. *Daphnia* were captured with the 153- μ m net.
- Figure 29. Relative abundance of the eight zooplankton taxa/stages sampled in the top 10 m of the water column of Blue Mesa Reservoir. Abundances were averaged over all stations and sampling dates (May-September) from 1994-1996. Note that 1996 data do not include data from May or August.
- Figure 30. Abundances of nine zooplankton taxa/stages in the 0-10 m of the water column averaged by month from 1994-1996.
- Figure 31. Abundances of nine zooplankton taxa/stages in the 0-10 m depth stratum averaged over all times for three stations in Blue Mesa Reservoir from 1994-1996.
- Figure 32. Length-frequency of brown trout (LOC), kokanee (KOK), longnose sucker (LGS), lake trout (MAC), and rainbow trout (RBT) sampled in experimental vertical gill nets in August 1996.
- Figure 33. Length-frequency of brown trout (LOC), kokanee (KOK), longnose sucker (LGS), lake trout (MAC), and rainbow trout (RBT) sampled in experimental vertical gill nets in September 1996.
- Figure 34. Temperature-frequency distribution of lake trout sampled by vertical gillnets during the stratified periods of 1994-1996.
- Figure 35. Mean backcalculated length at age of kokanee from six time periods in Blue Mesa Reservoir.
- Figure 36. Mean backcalculated length at age of rainbow trout from four time periods in Blue Mesa Reservoir.
- Figure 37. Fish density (fish/1,000 m³) and target strength (dB) by depth strata averaged by transects in Sapinero basin in July, 1995. Data from 0-8 m were eliminated due to high noise.
- Figure 38. Fish density (fish/1,000 m³) and target strength (dB) by depth strata averaged by transects in Cebolla basin in July 1995. Data from 0-8 m were eliminated due

to high noise.

- Figure 39. Fish density (fish/1,000 m³) and target strength (dB) by depth strata averaged by transects in Iola basin in July 1995. Data from 0-8 m were eliminated due to high noise.
- Figure 40. Fish density (fish/1,000 m³) and target strength (dB) by depth strata averaged across all transects by lake basin in July 1995. Data from 0-8 m were eliminated due to high noise.
- Figure 41. Fish density (fish/1,000 m³) and target strength (dB) by depth strata by transect during mid-day and nighttime hydroacoustics surveys in Sapinero in July, 1995. Data from 0-8 m were eliminated due to high noise.
- Figure 42. Schematic representation of the processes modeled in CE-THERM reservoir thermal model.
- Figure 43. Observed (solid lines) and predicted (dotted lines) temperature profiles. Predictions in 1994 were results after calibrating model to match 1994 profiles as closely as possible. Predictions in 1996 were made using all parameterizations establishing during the calibration to 1994 data, and thus are real model predictions.
- Figure 44. Reservoir content and thermal structure in response to four climate and operations scenarios (Table 5) modeled with CE-THERM.
- Figure 45. Kokanee growth (bars) and diel migration ranges (arrows) under normal weather and traditional reservoir operations versus growth and migration under warm, dry weather and new reservoir operations, predicted with the model in Appendix B.
- Figure 46. Increase in kokanee predation risk in response to higher lake trout consumption rates and proportionately more of the reservoir's volume habitable by lake trout during warm, dry weather and new reservoir operations.

Mechanisms linking reservoir operations to reservoir productivity and fish yield



Abiotic-Biotic Linkages Between Reservoir Operations and Sport Fisheries

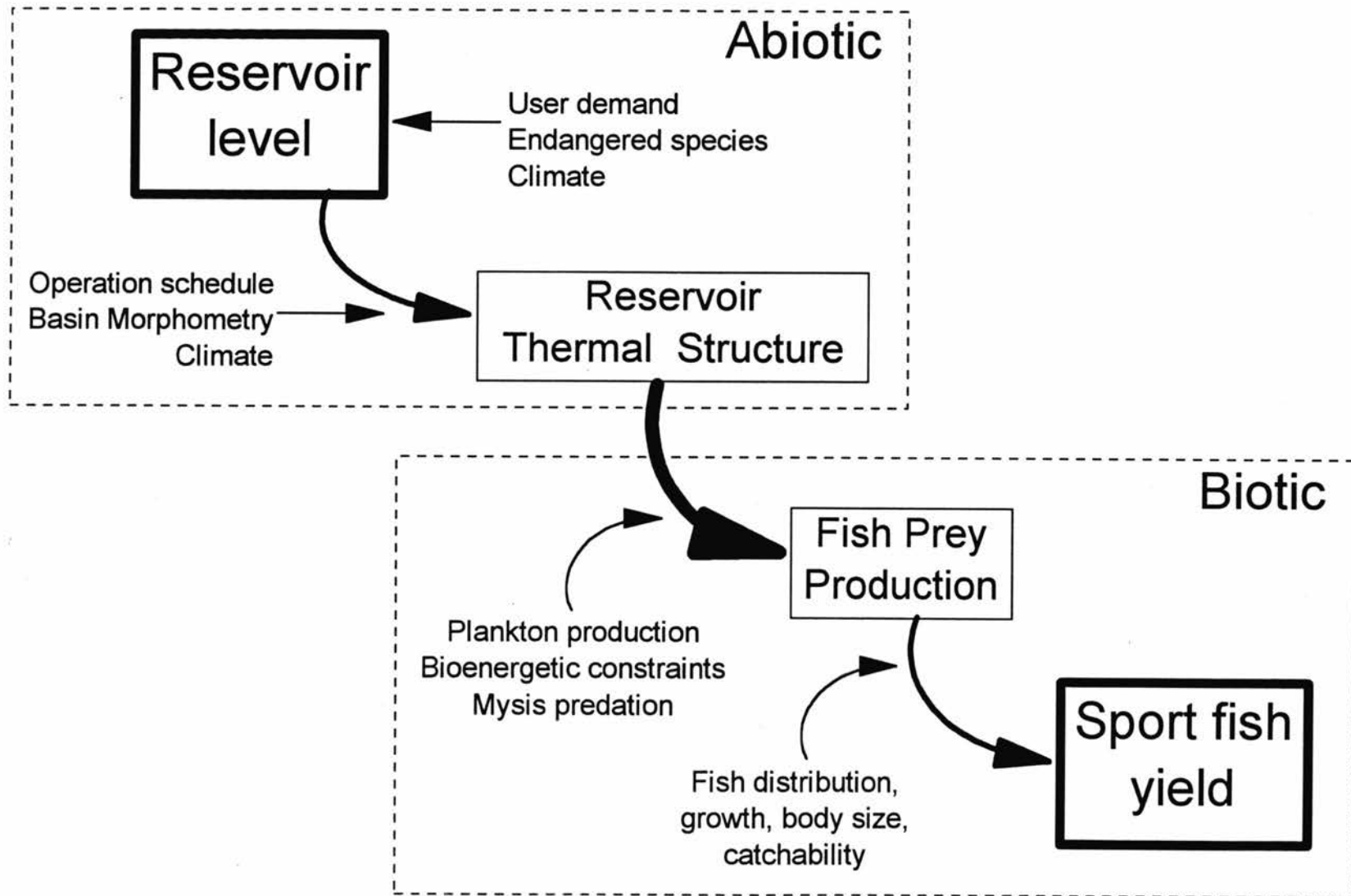


Figure 2.

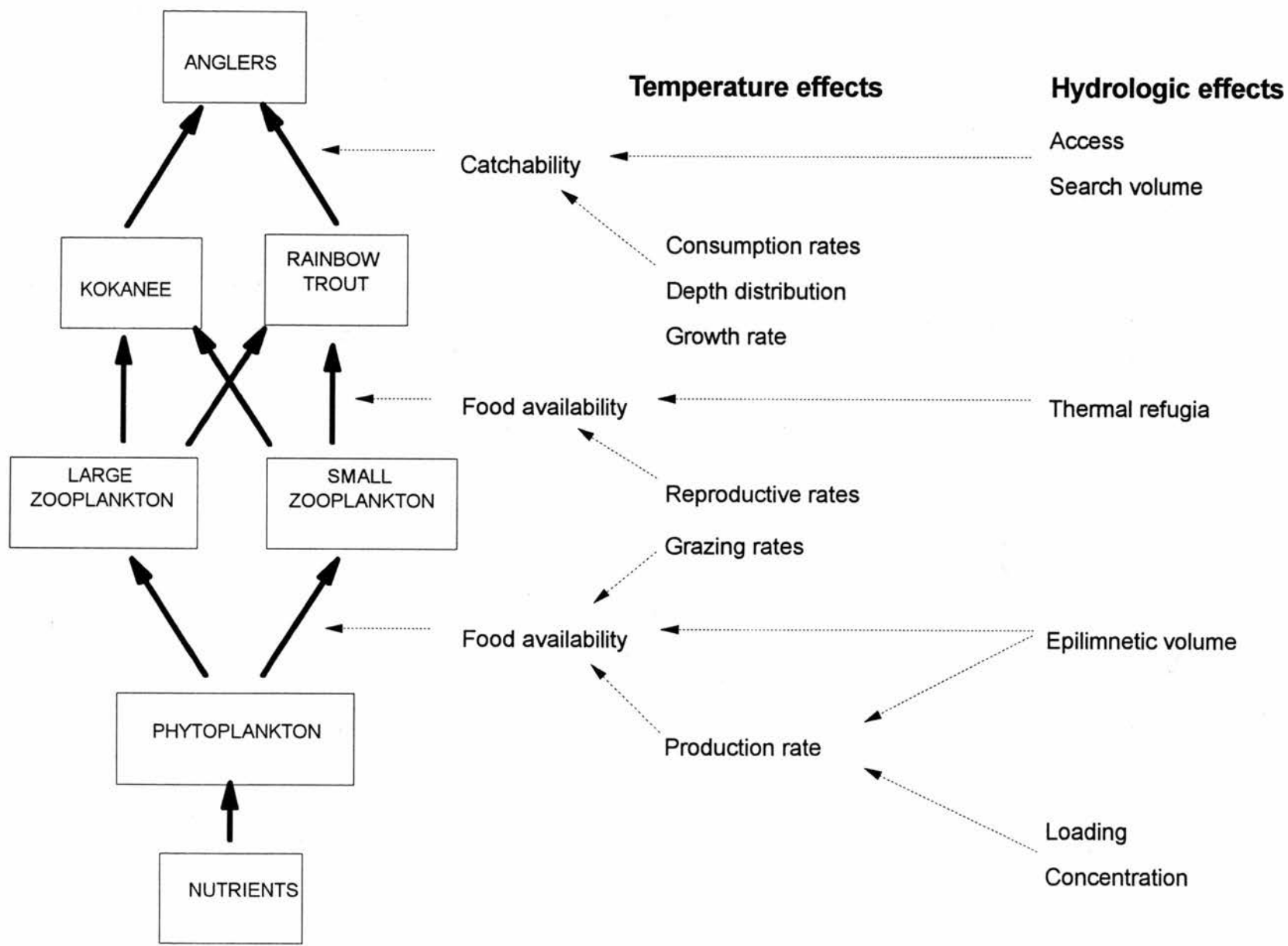


Figure 3.

Blue Mesa Reservoir

Gunnison County, CO

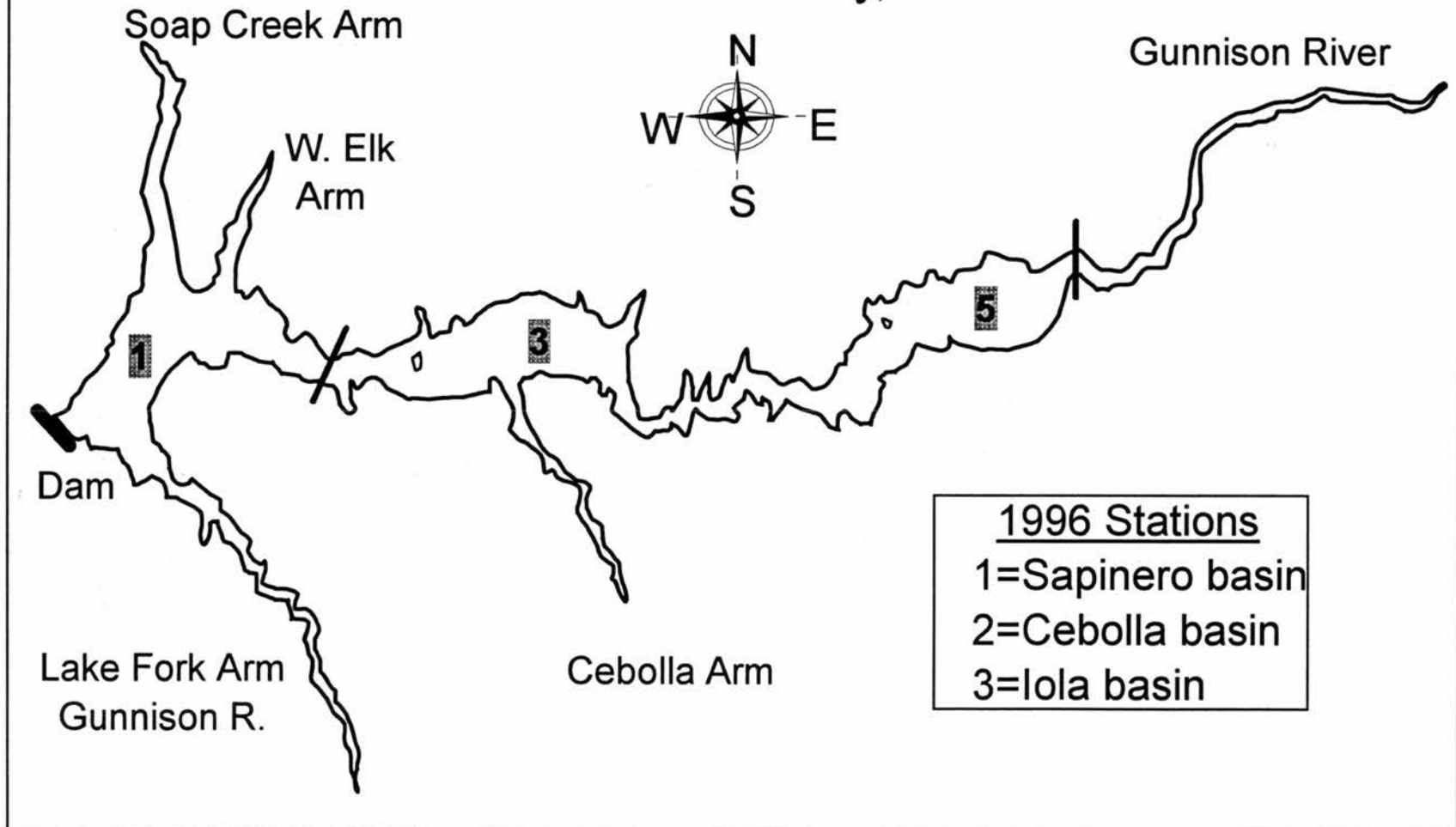
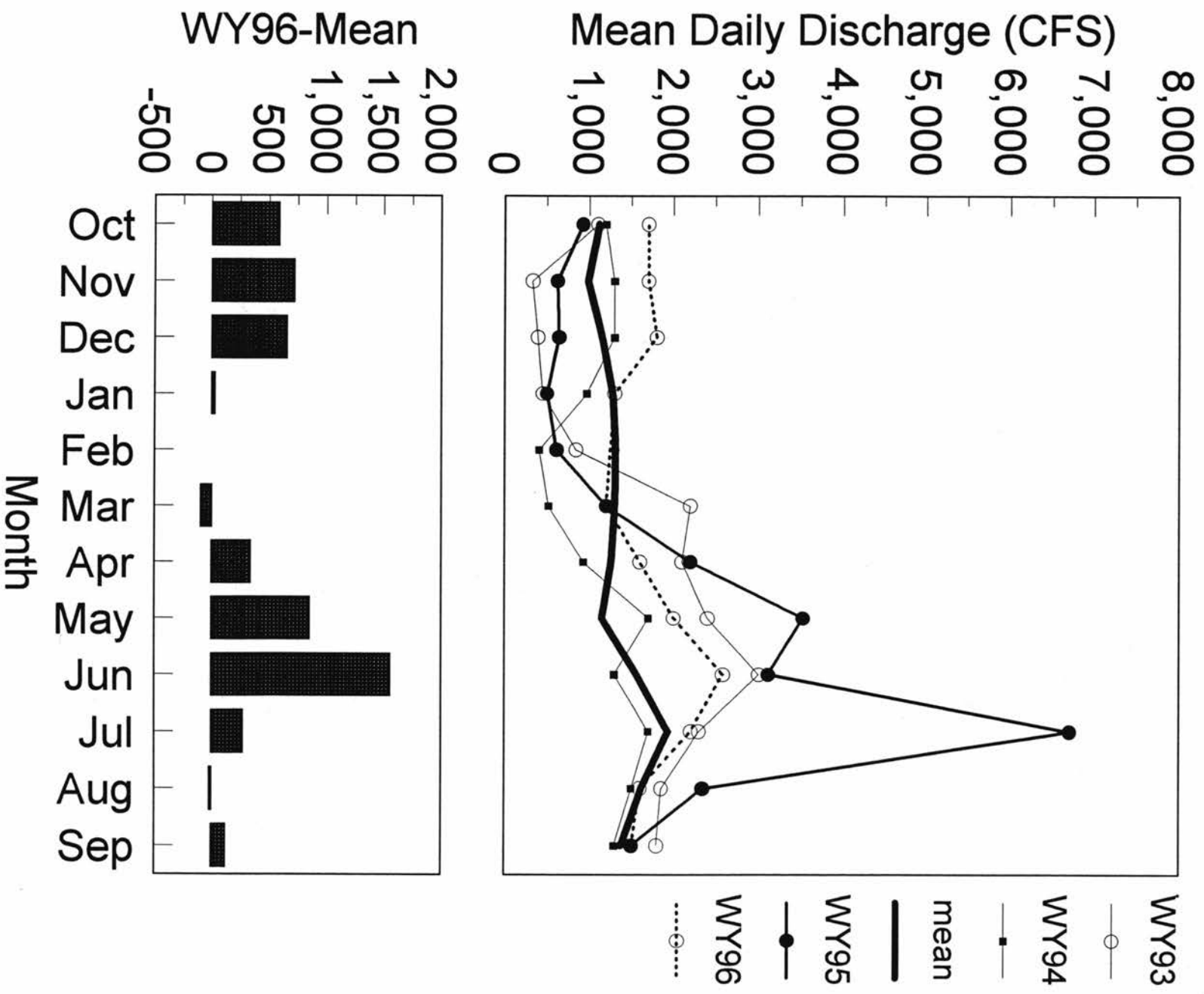


Figure 4.

Figure 5.



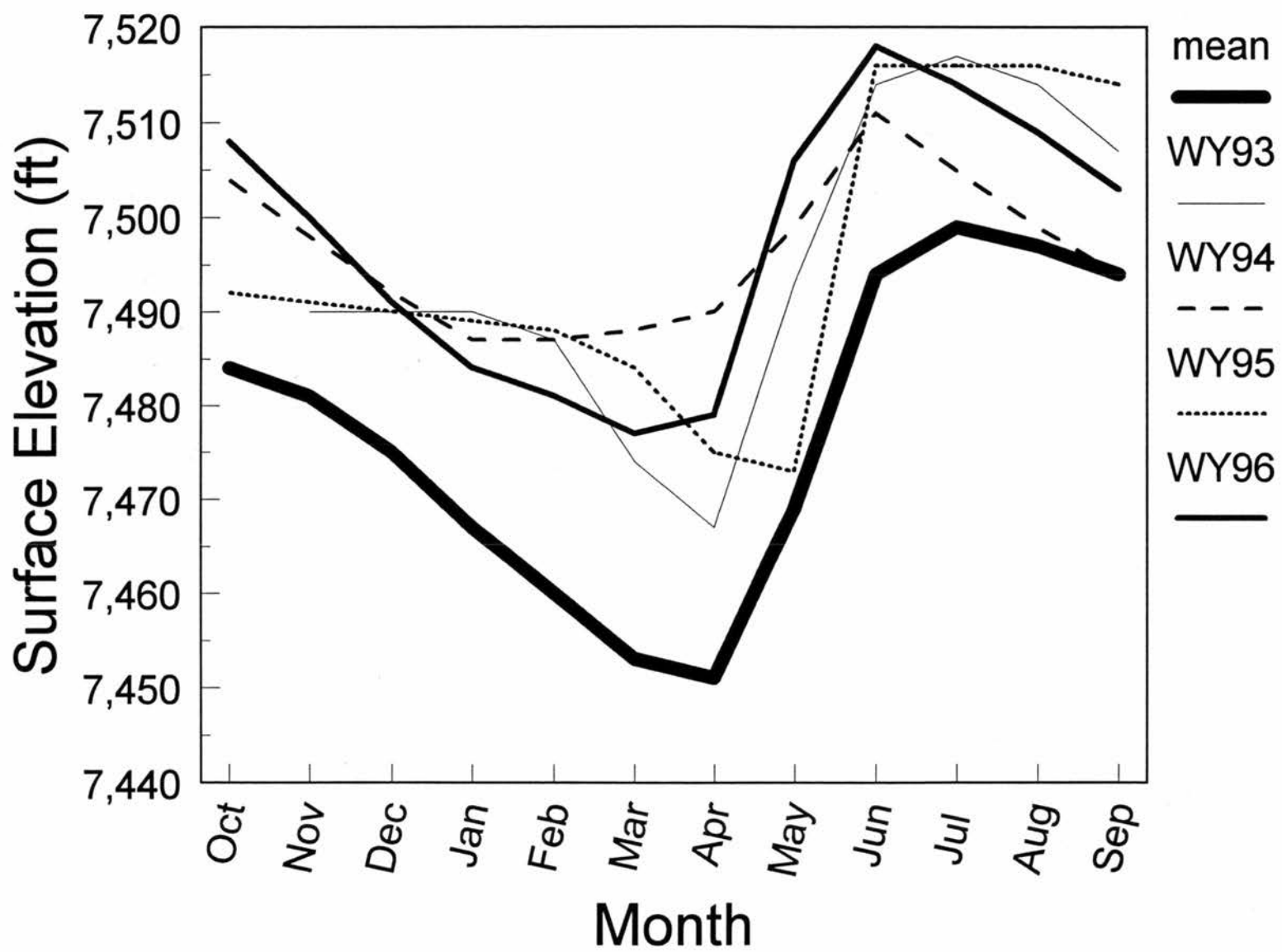


Figure 6.

Figure 7.

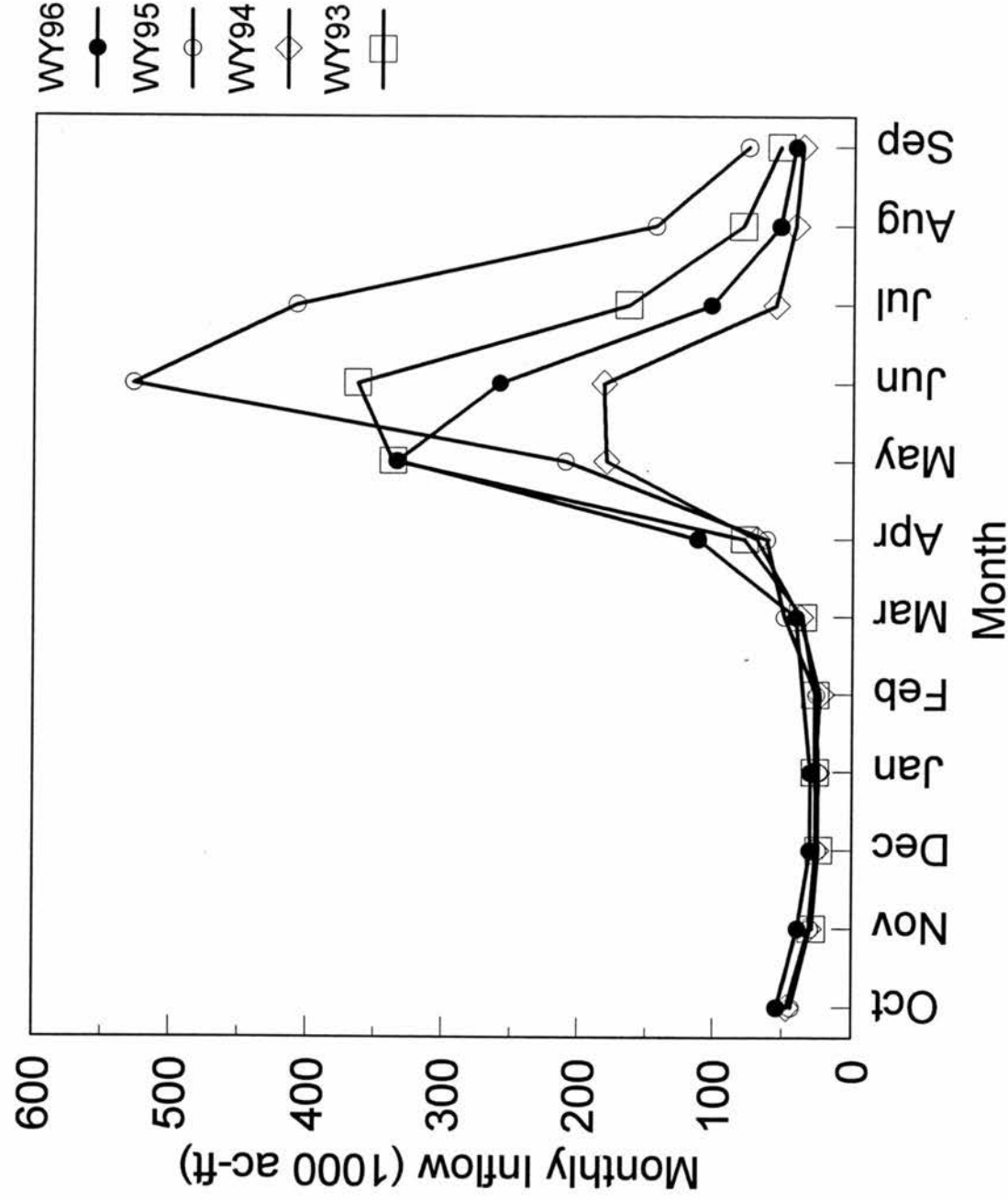


Figure 8.

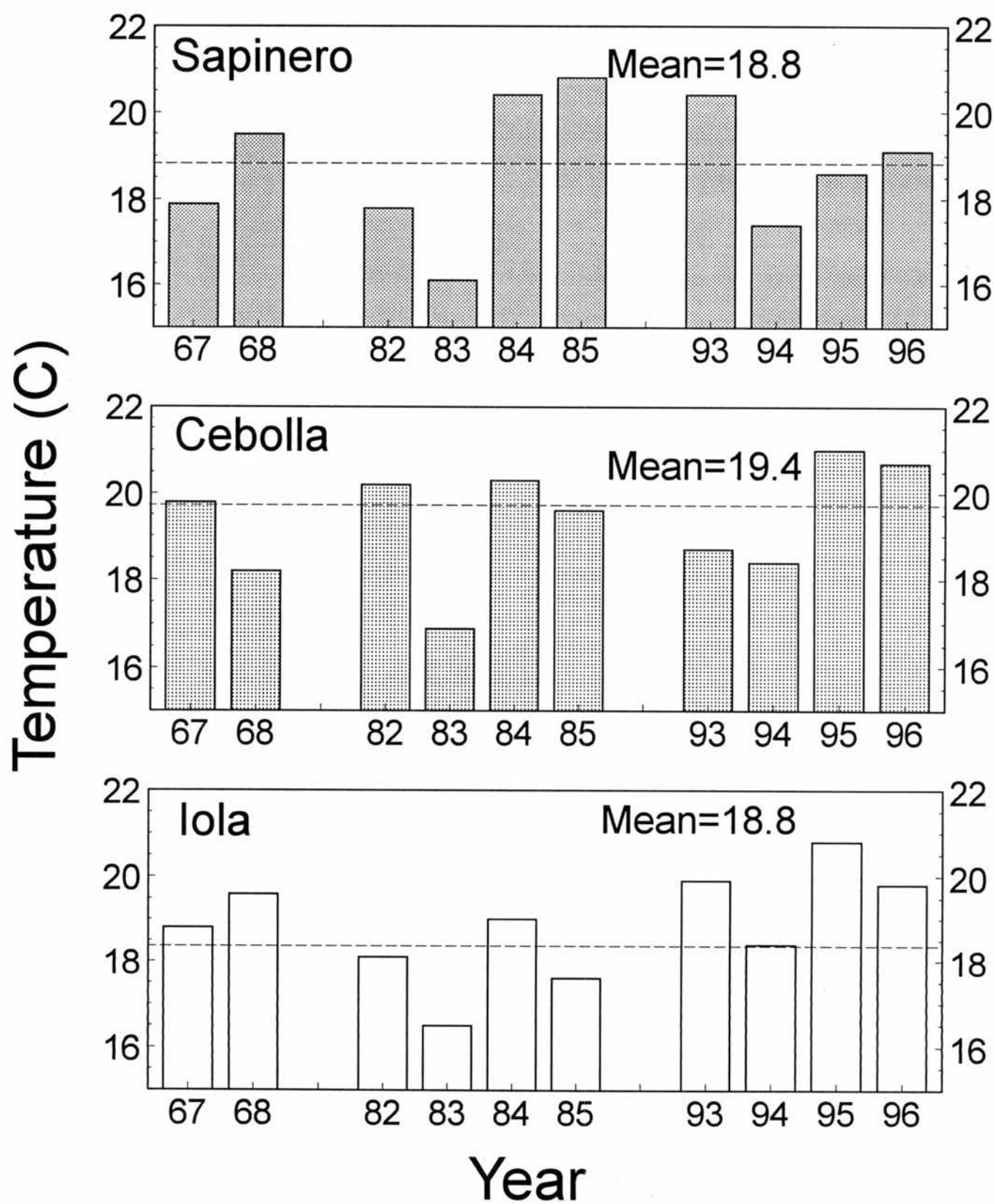


Figure 9.

Sapinero 1996

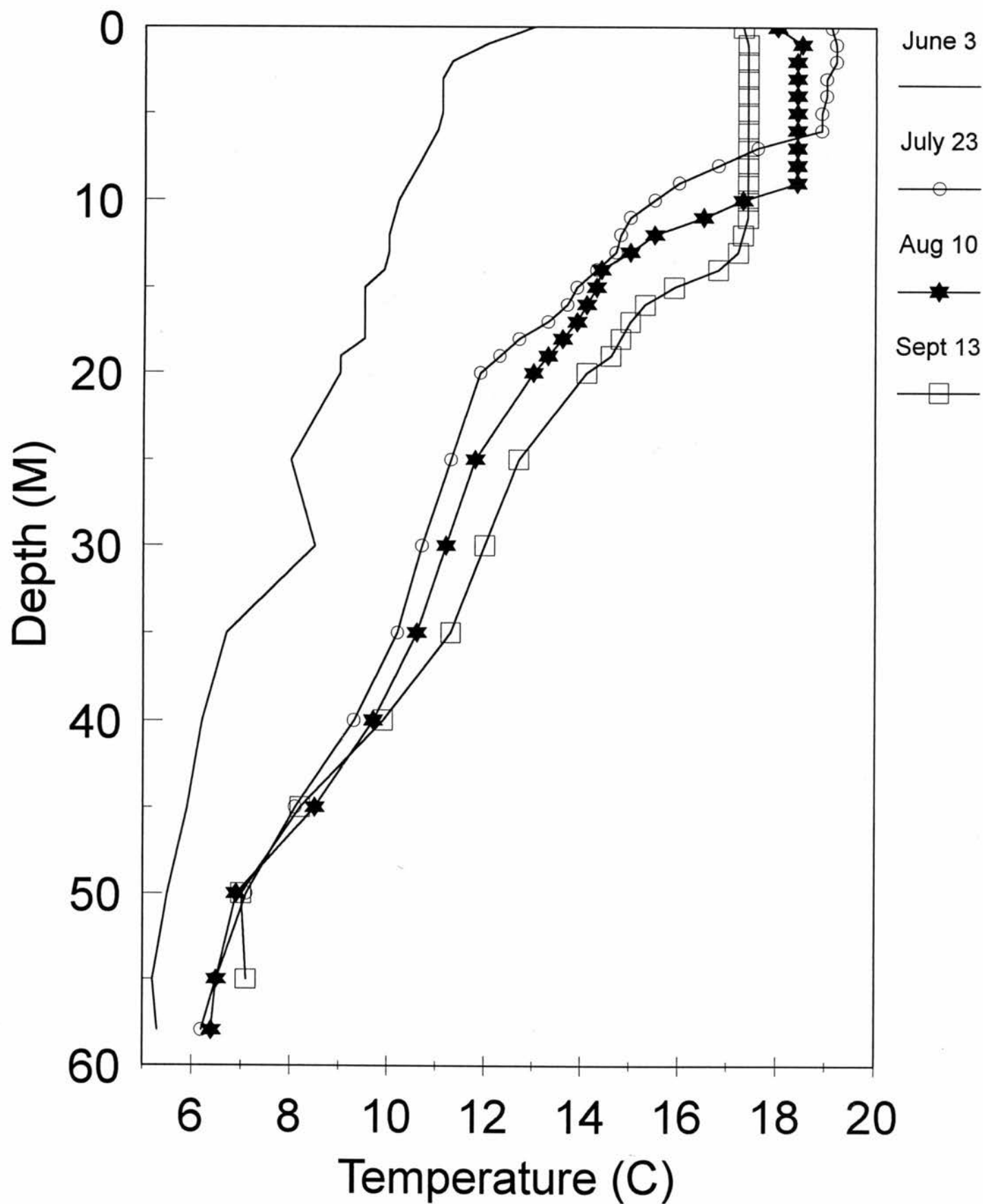


Figure 10.

Cebolla 1996

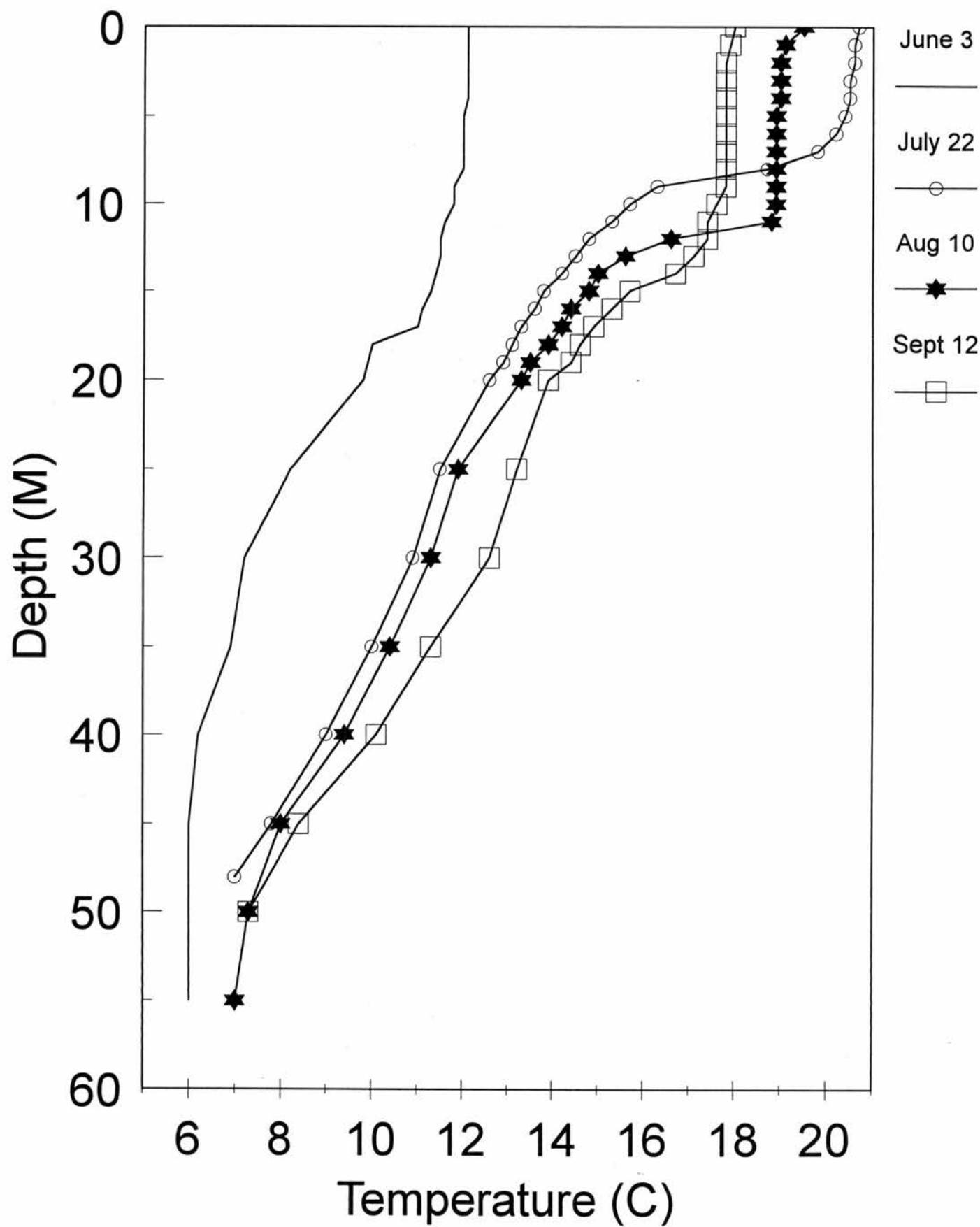


Figure 11.

Iola 1996

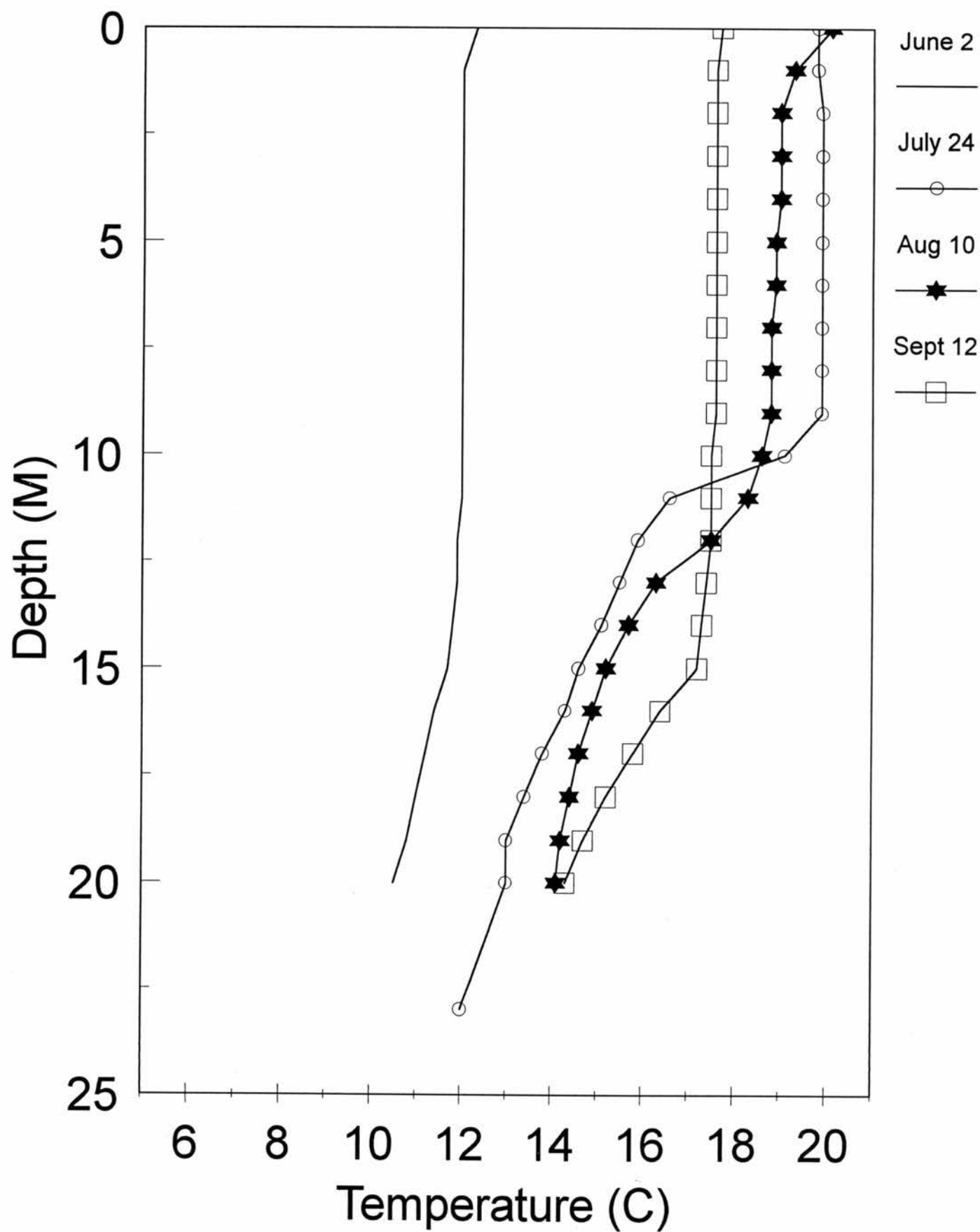
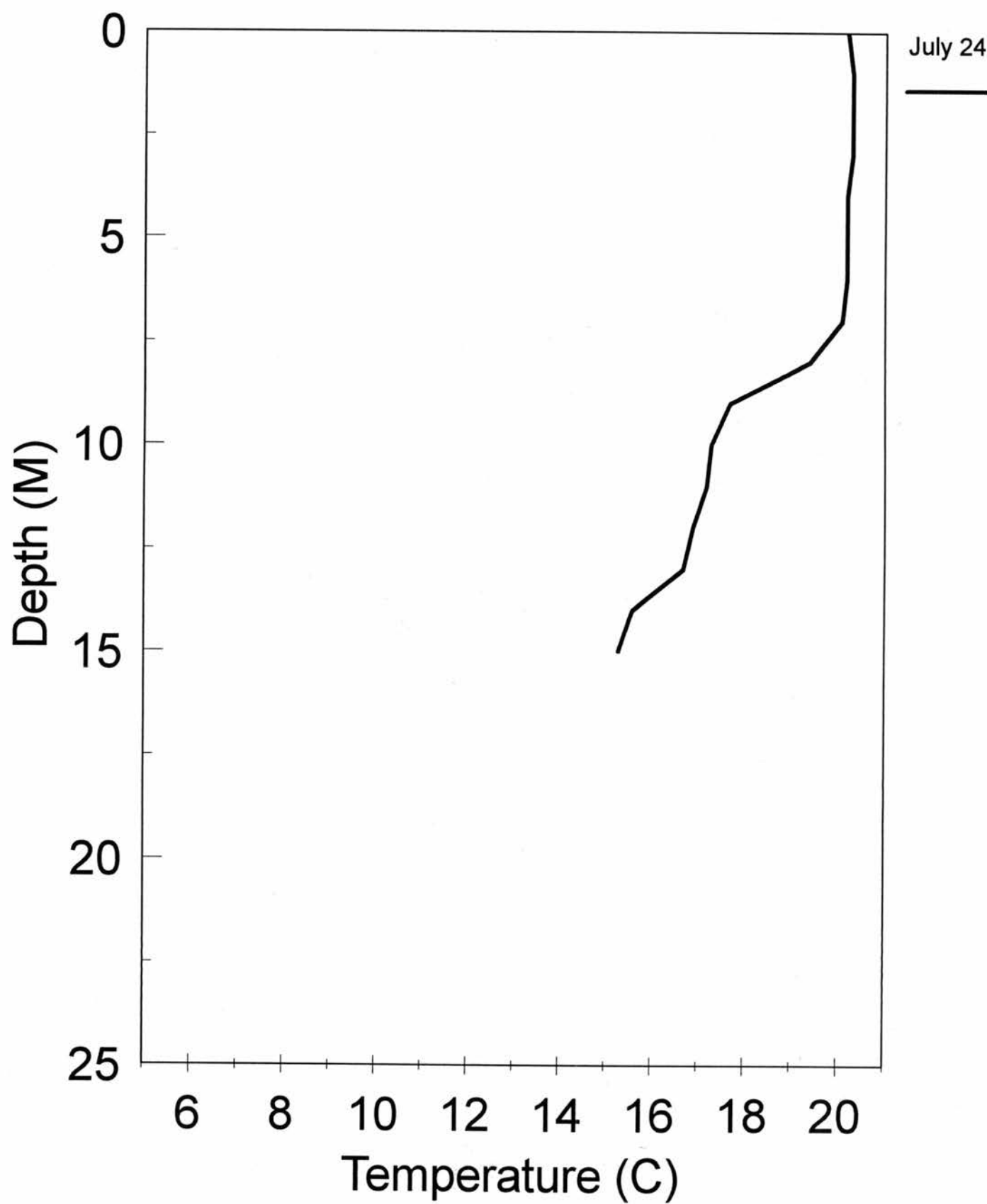


Figure 12.

Hwy 149
1996



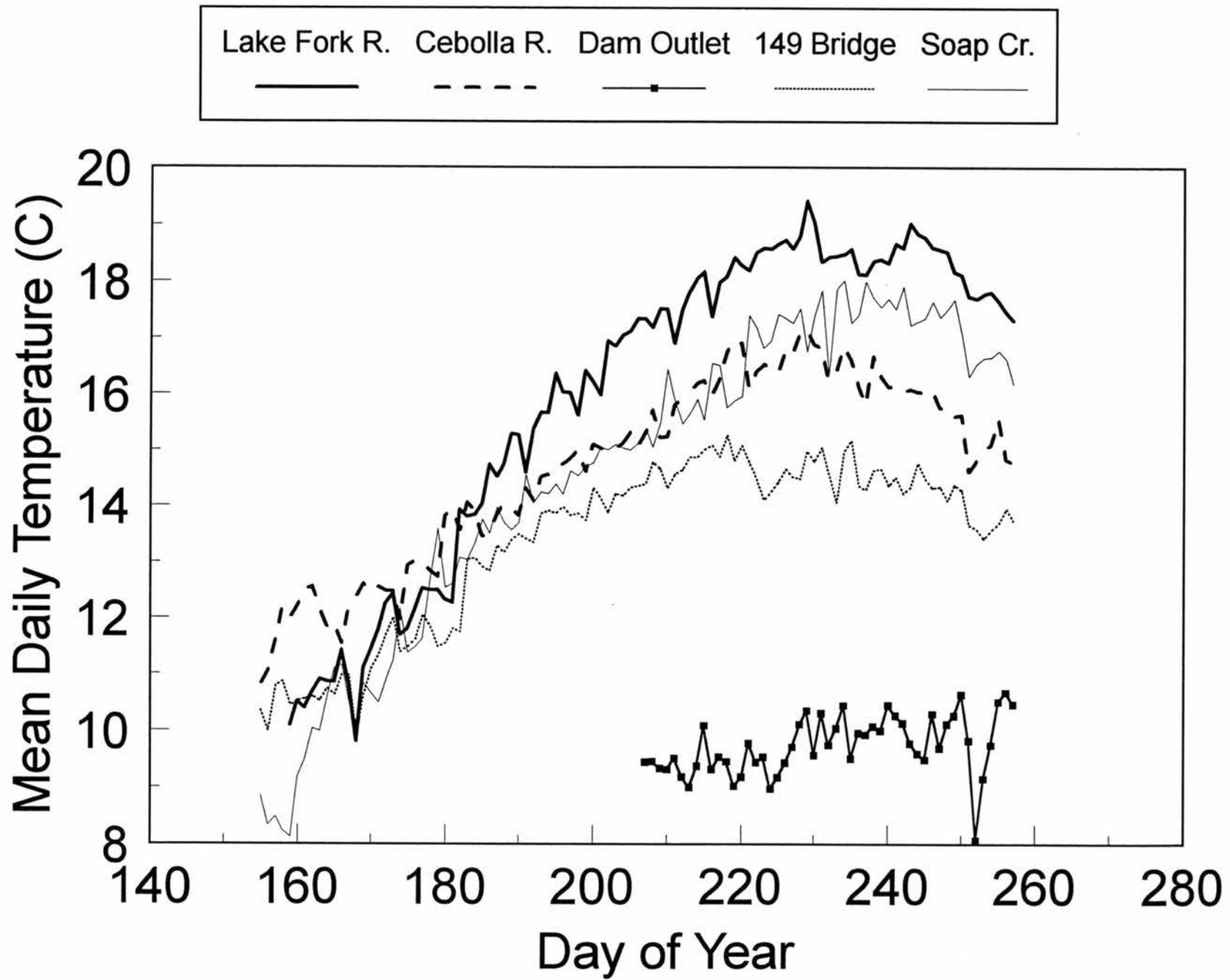


Figure 13.

Figure 14.

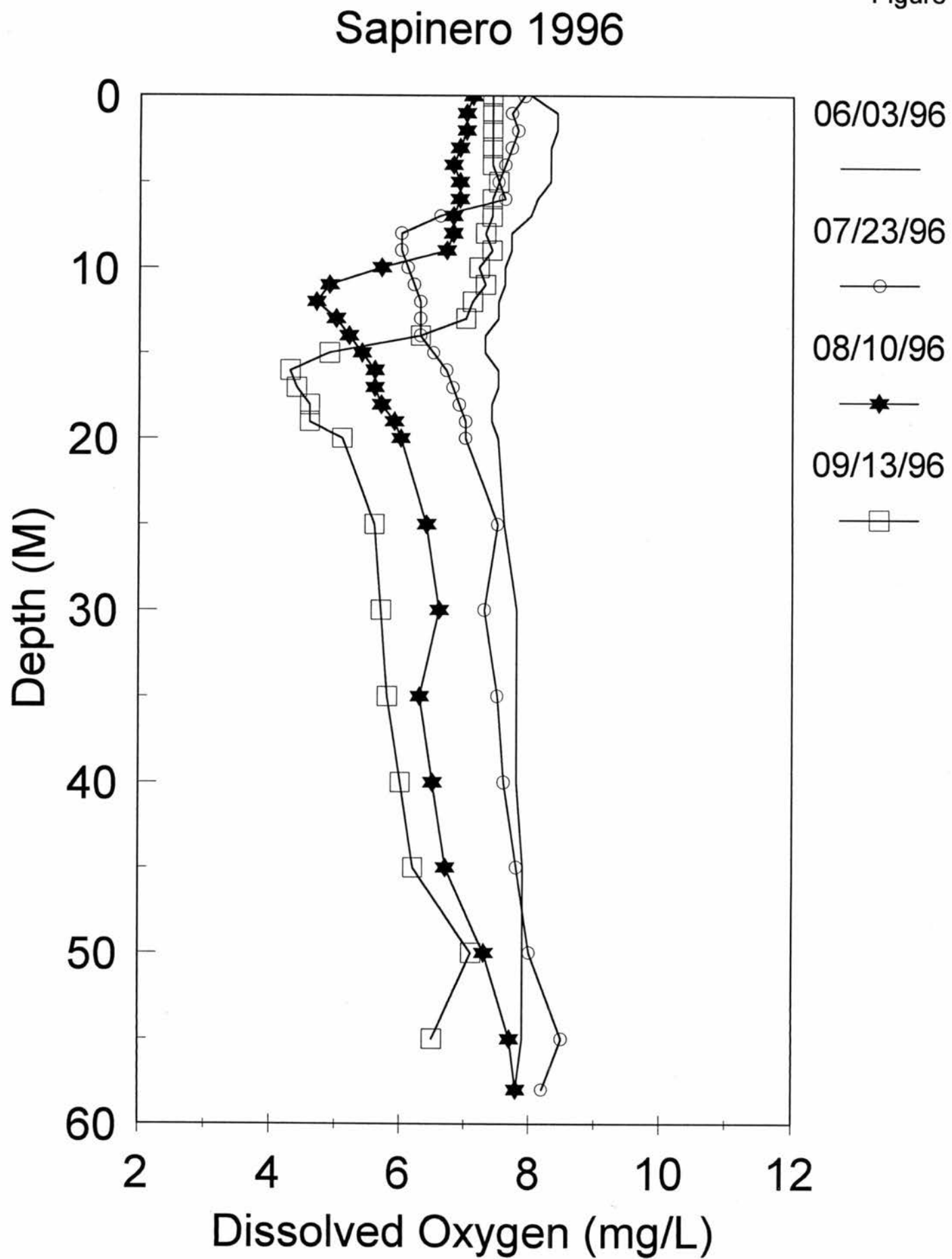


Figure 15.

Cebolla 1996

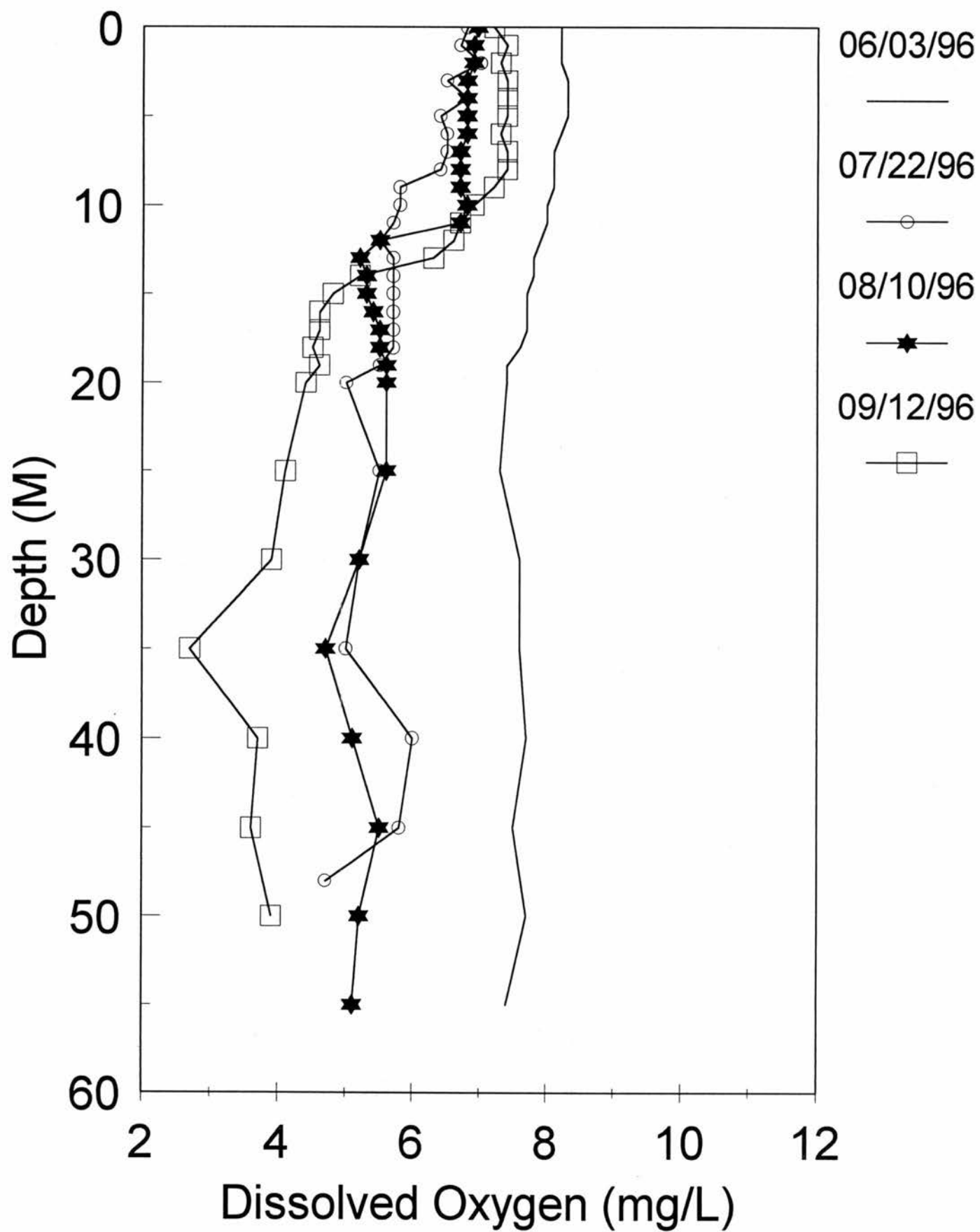


Figure 16.

Iola 1996

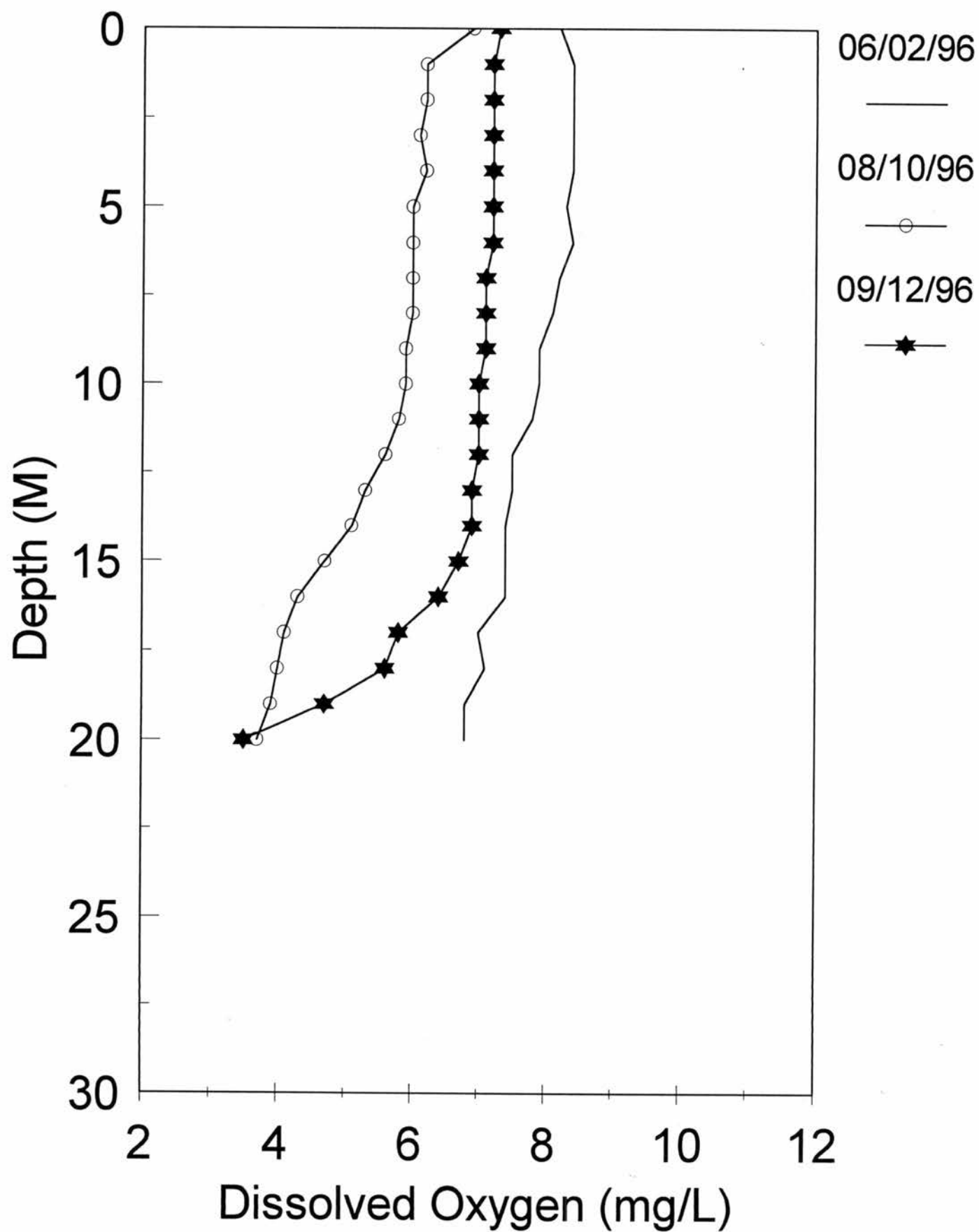


Figure 17.

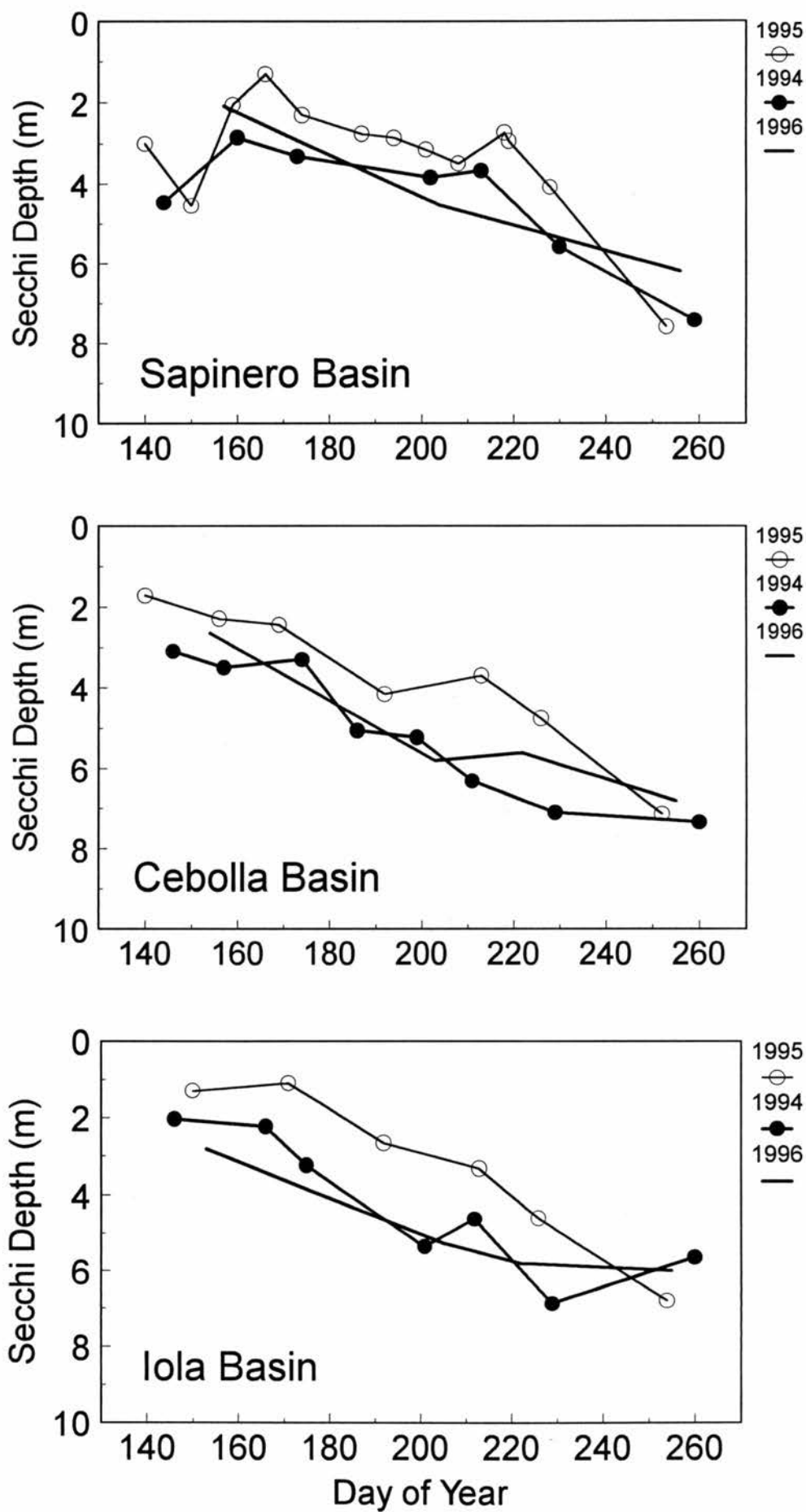
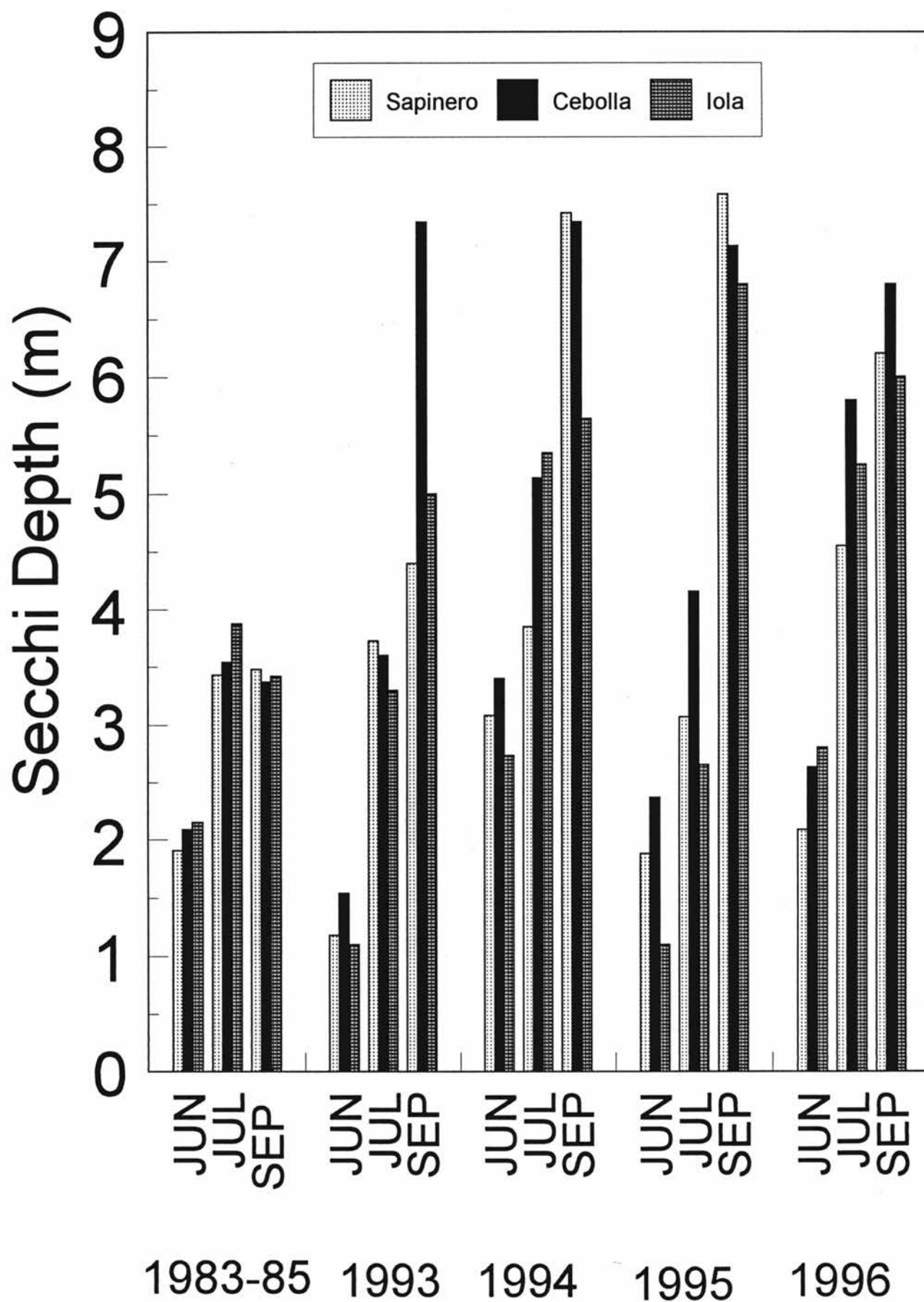
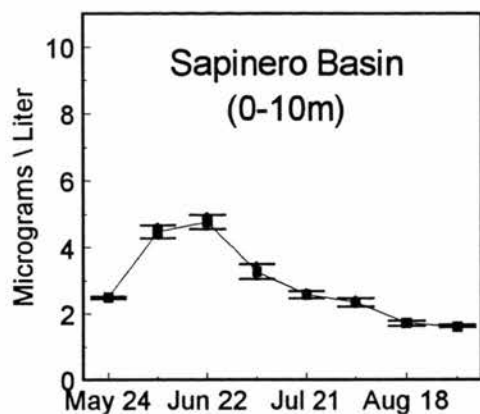


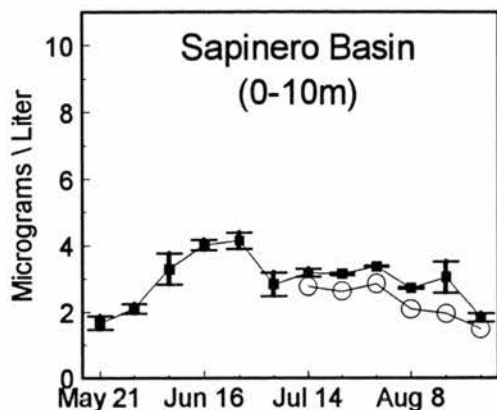
Figure 18.



1994



1995



1996

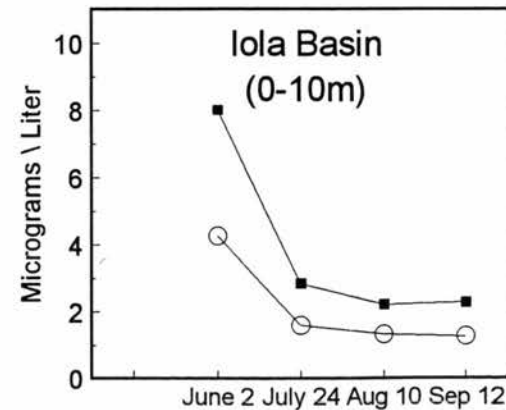
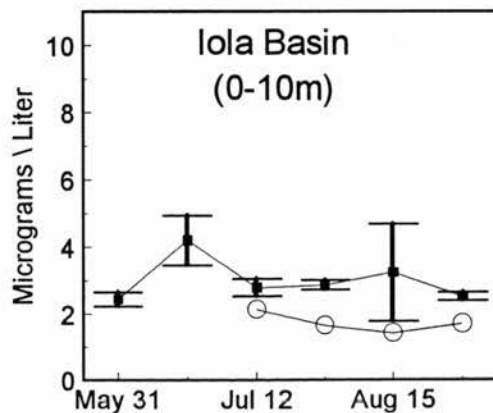
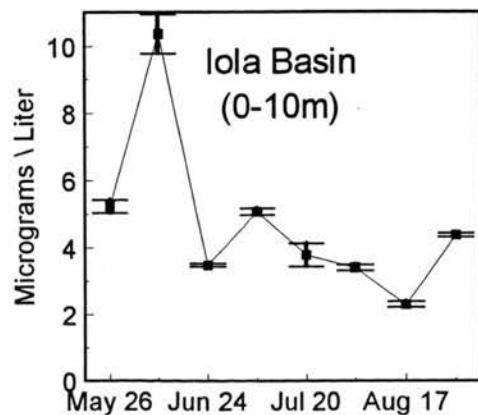
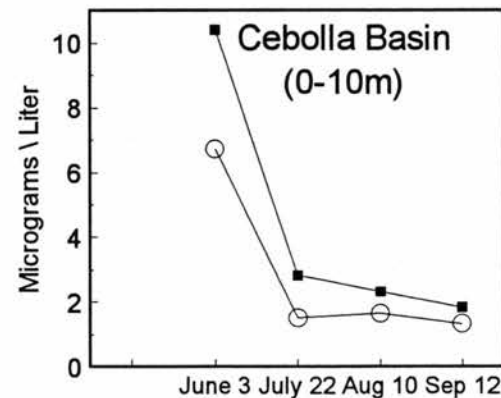
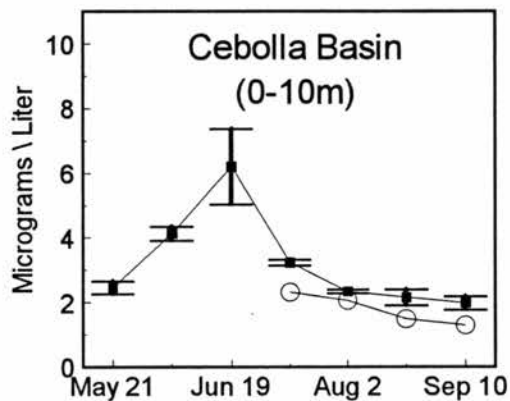
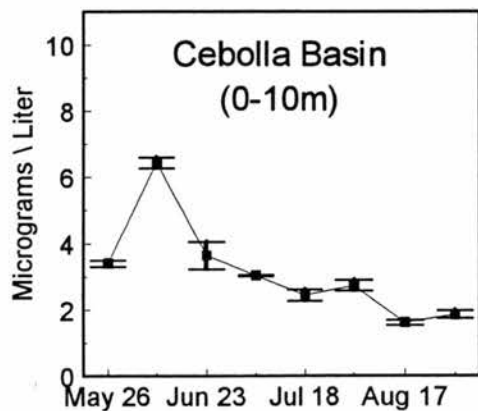
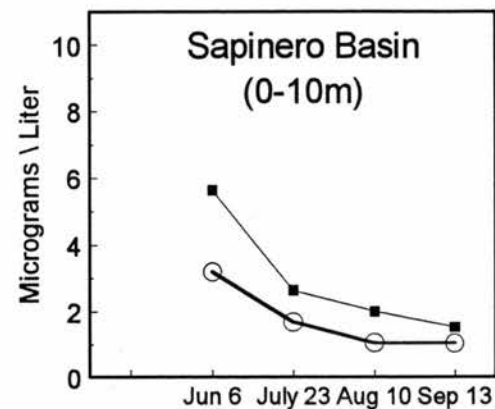


Figure 19.

Sapinero Basin, 1996

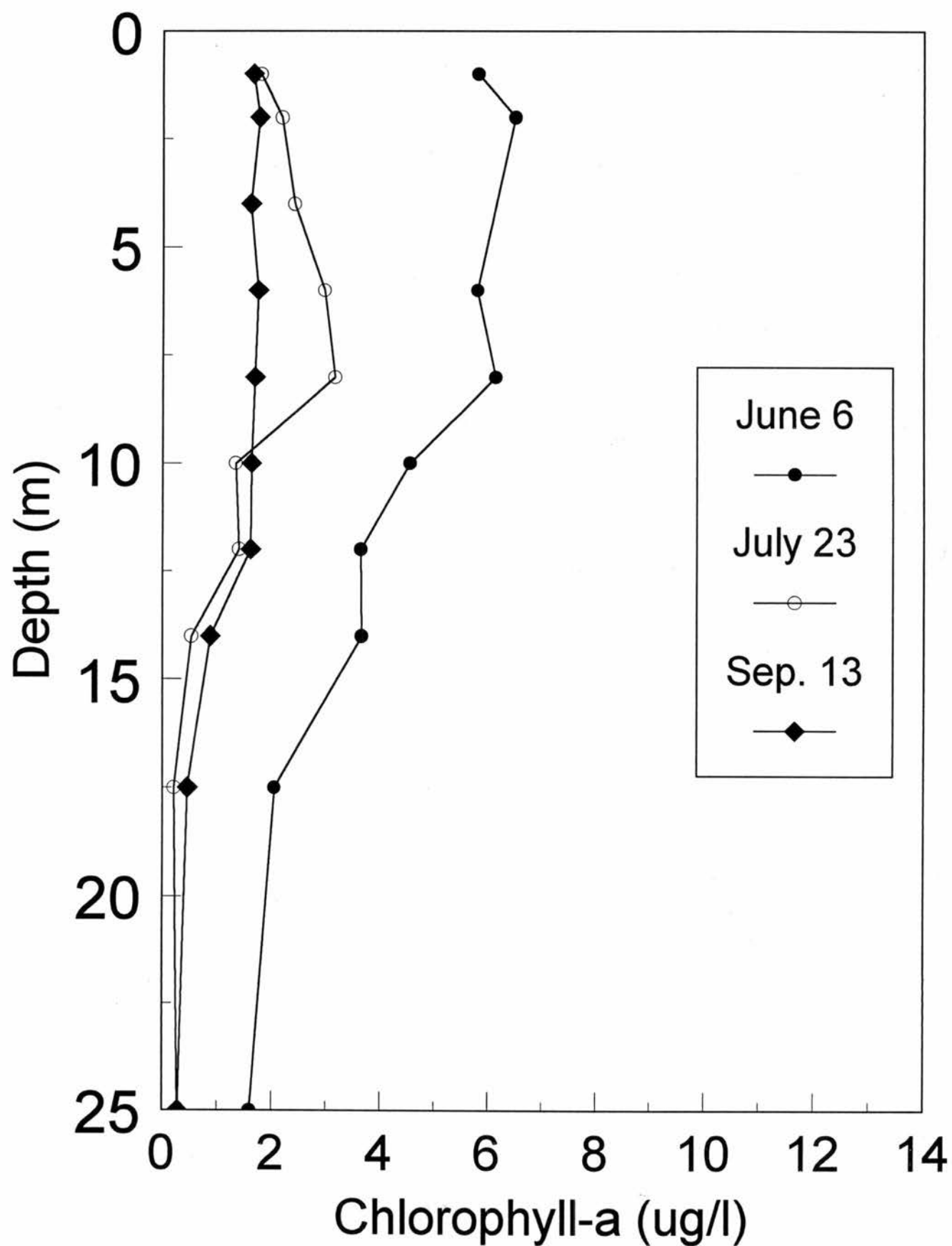


Figure 21.

Cebolla Basin, 1996

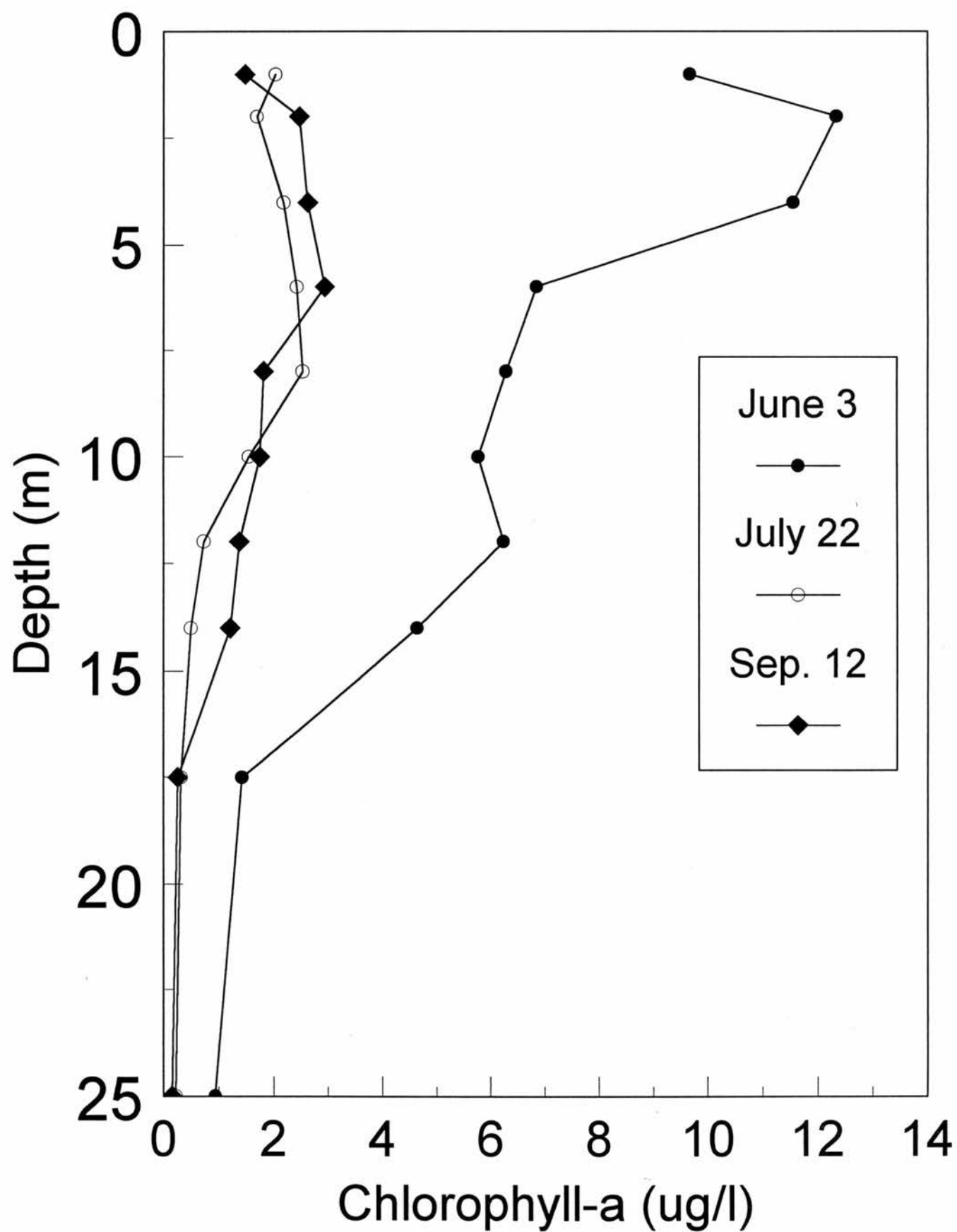
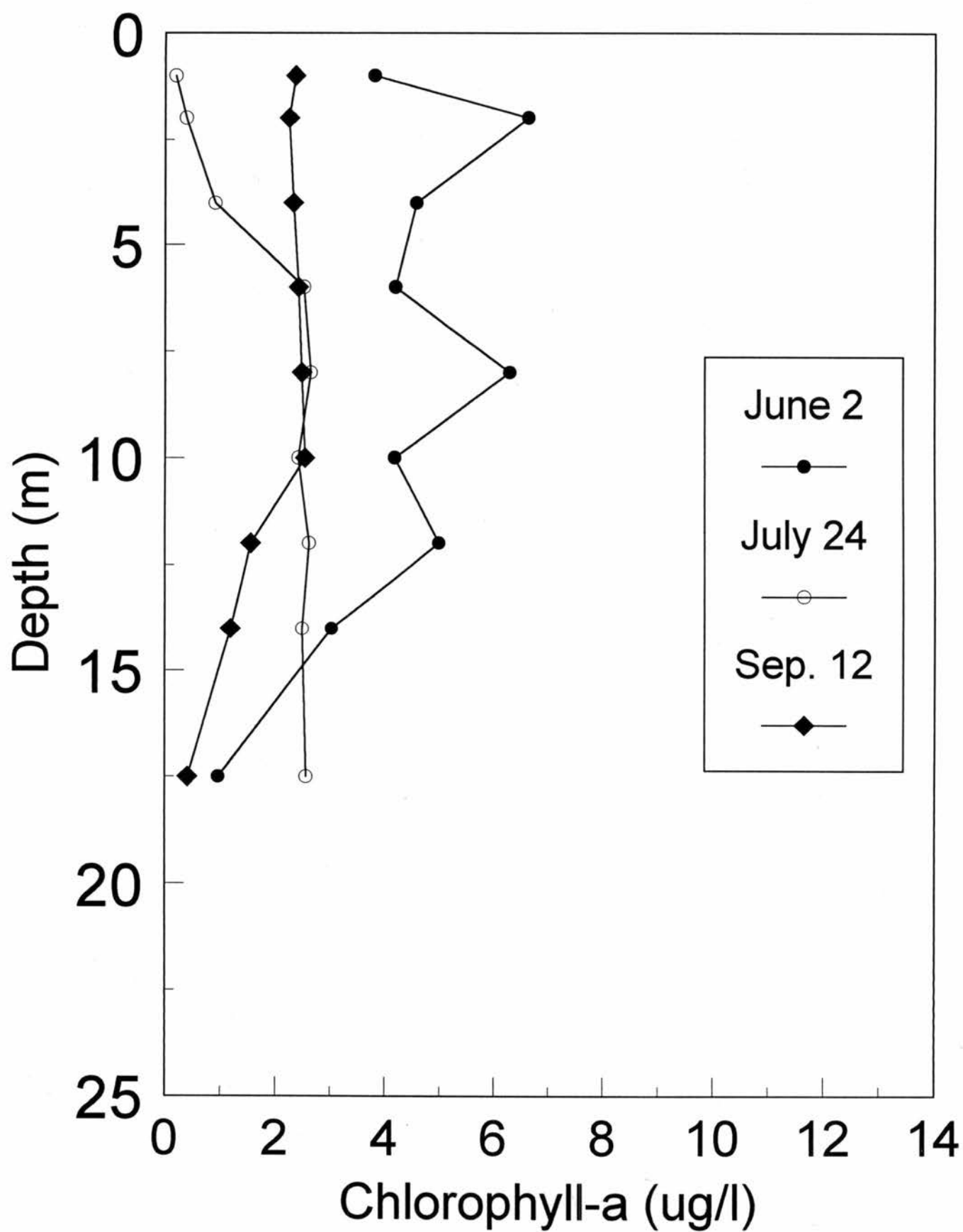


Figure 22.

Iola Basin, 1996



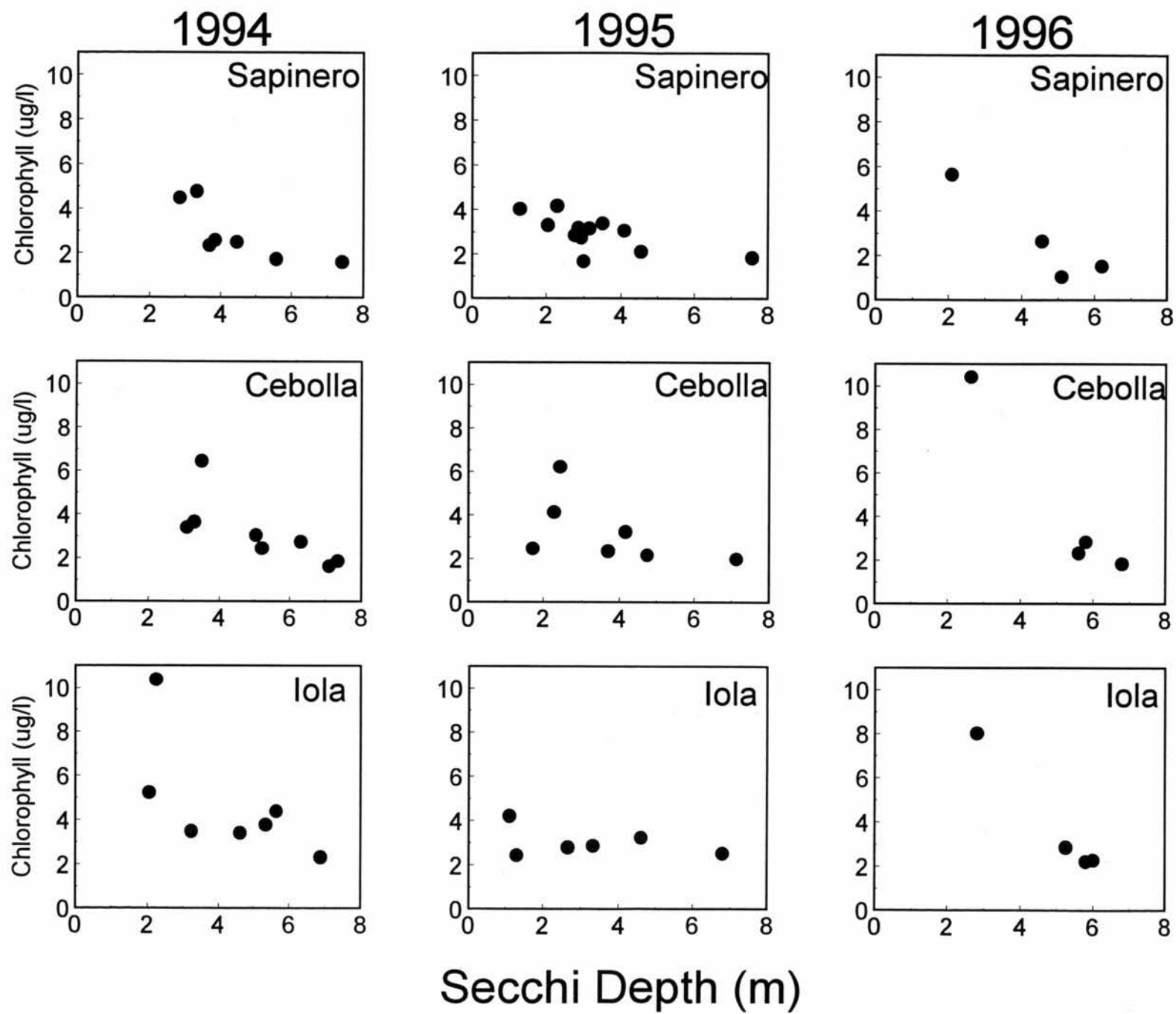


Figure 23.

Figure 24.

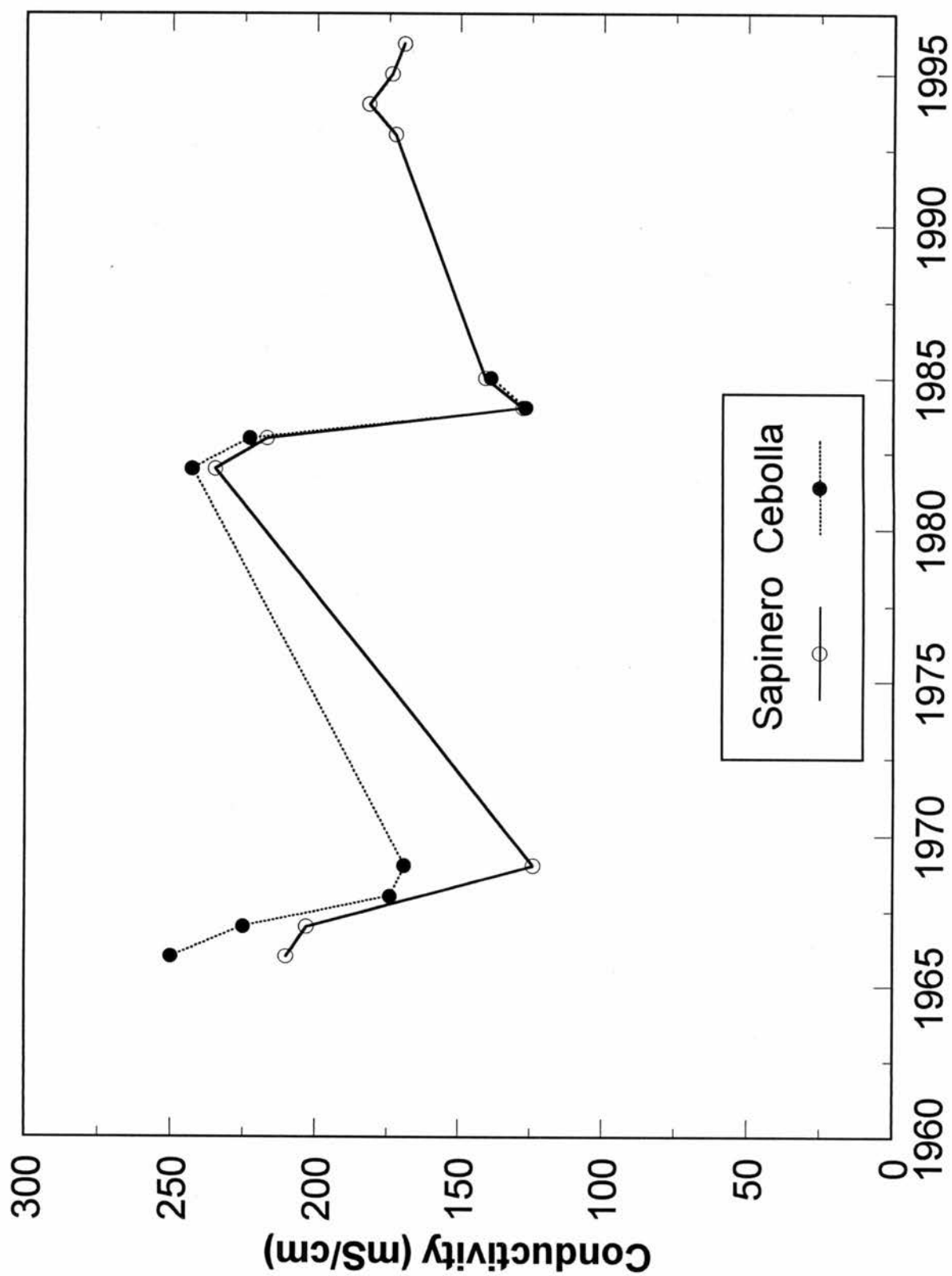
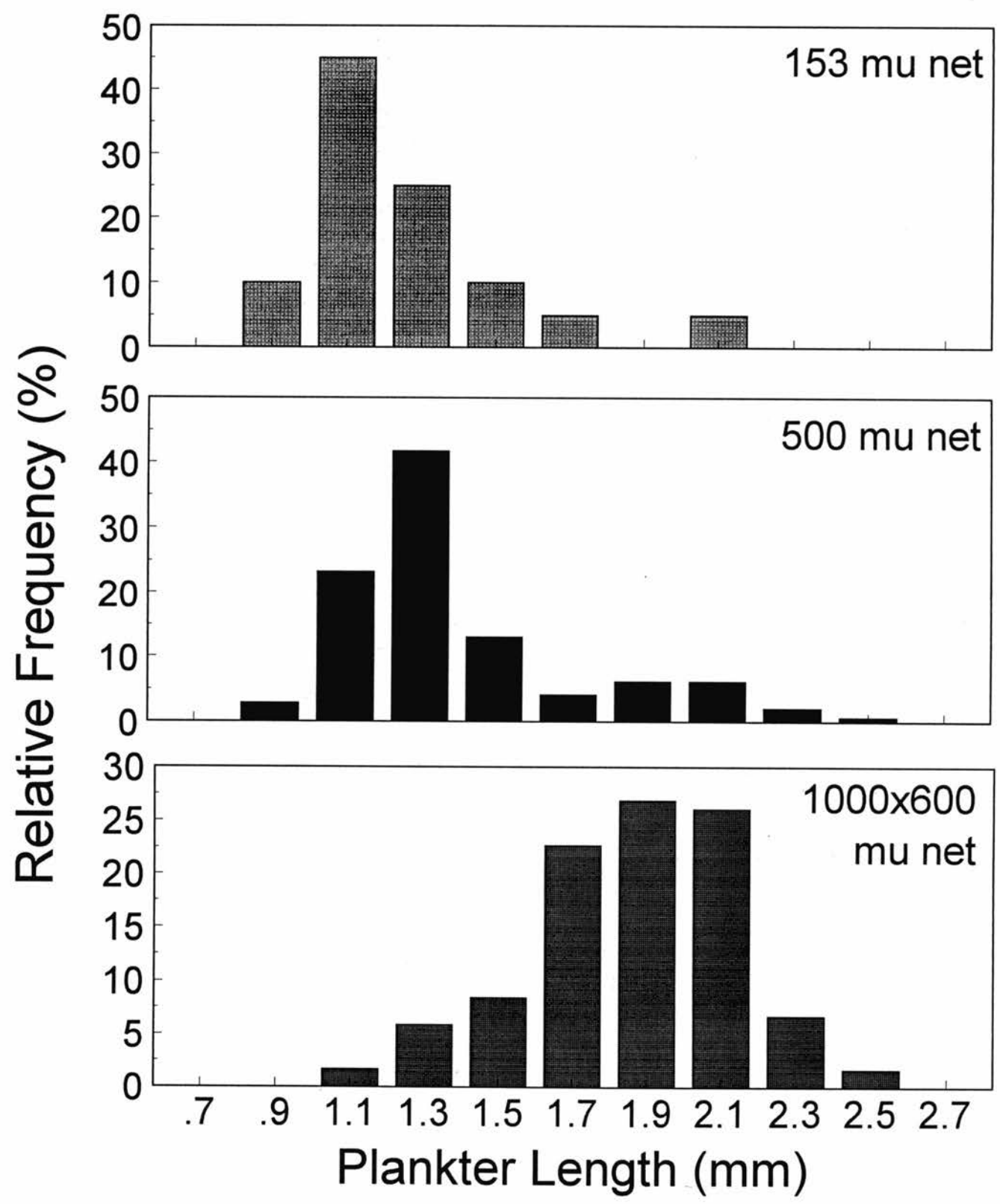
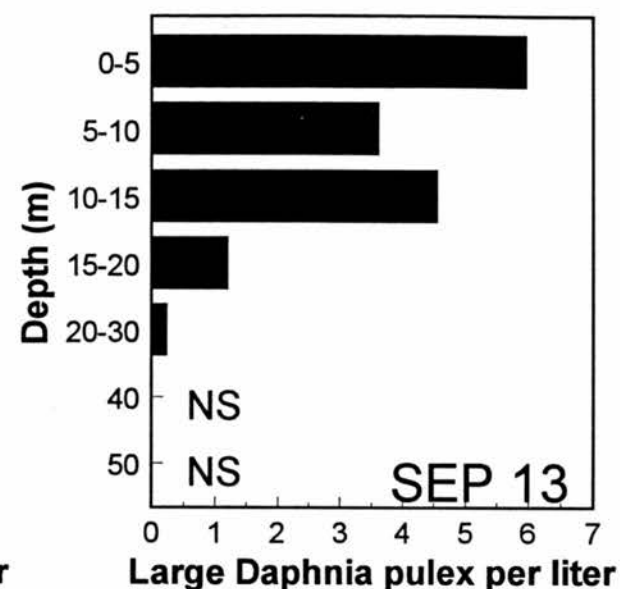
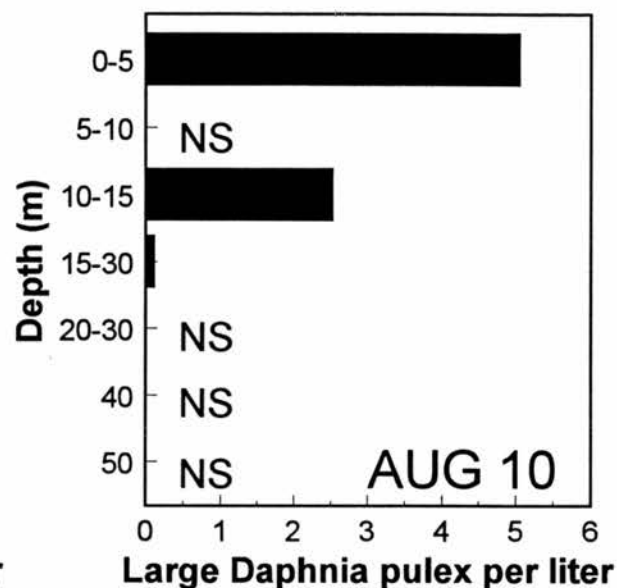
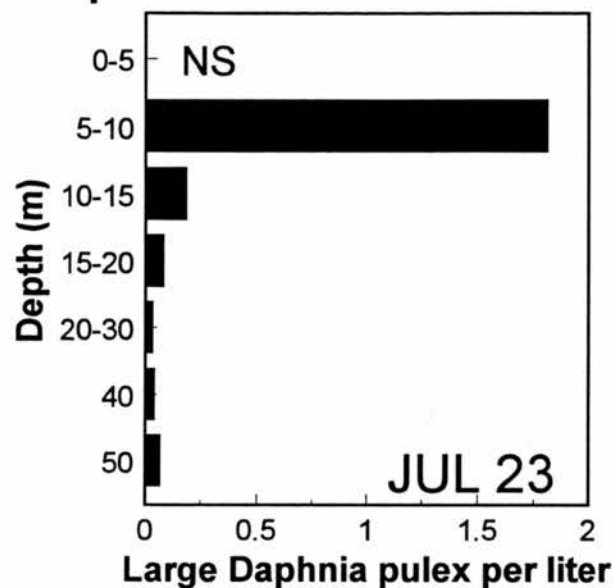


Figure 25.



Sapinero



Cebolla

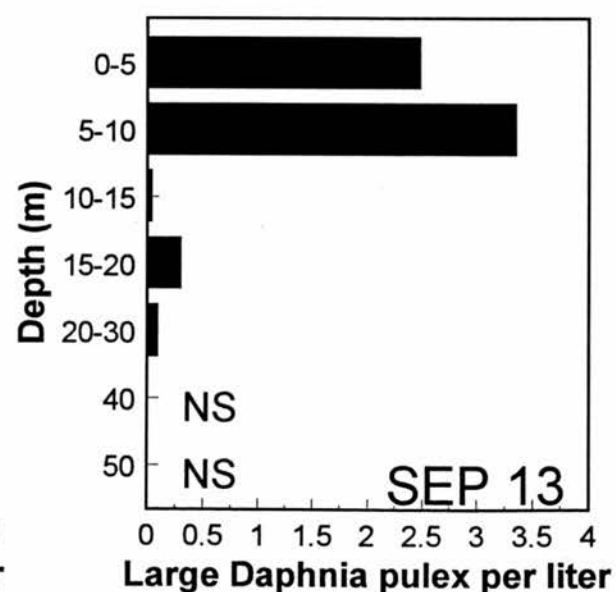
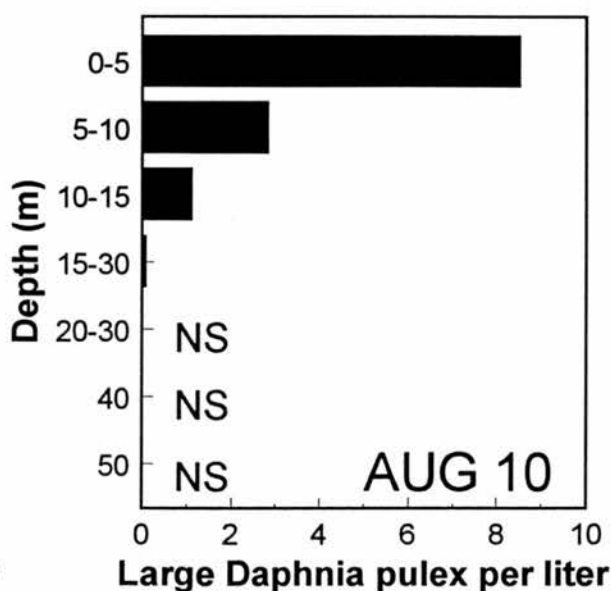
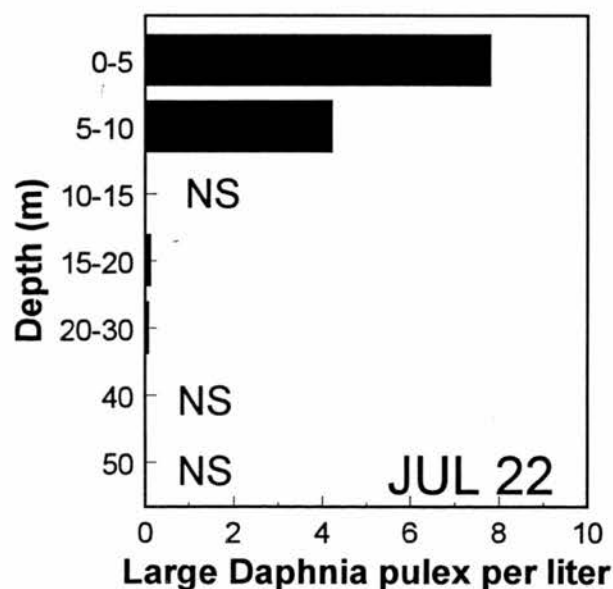


Figure 26.

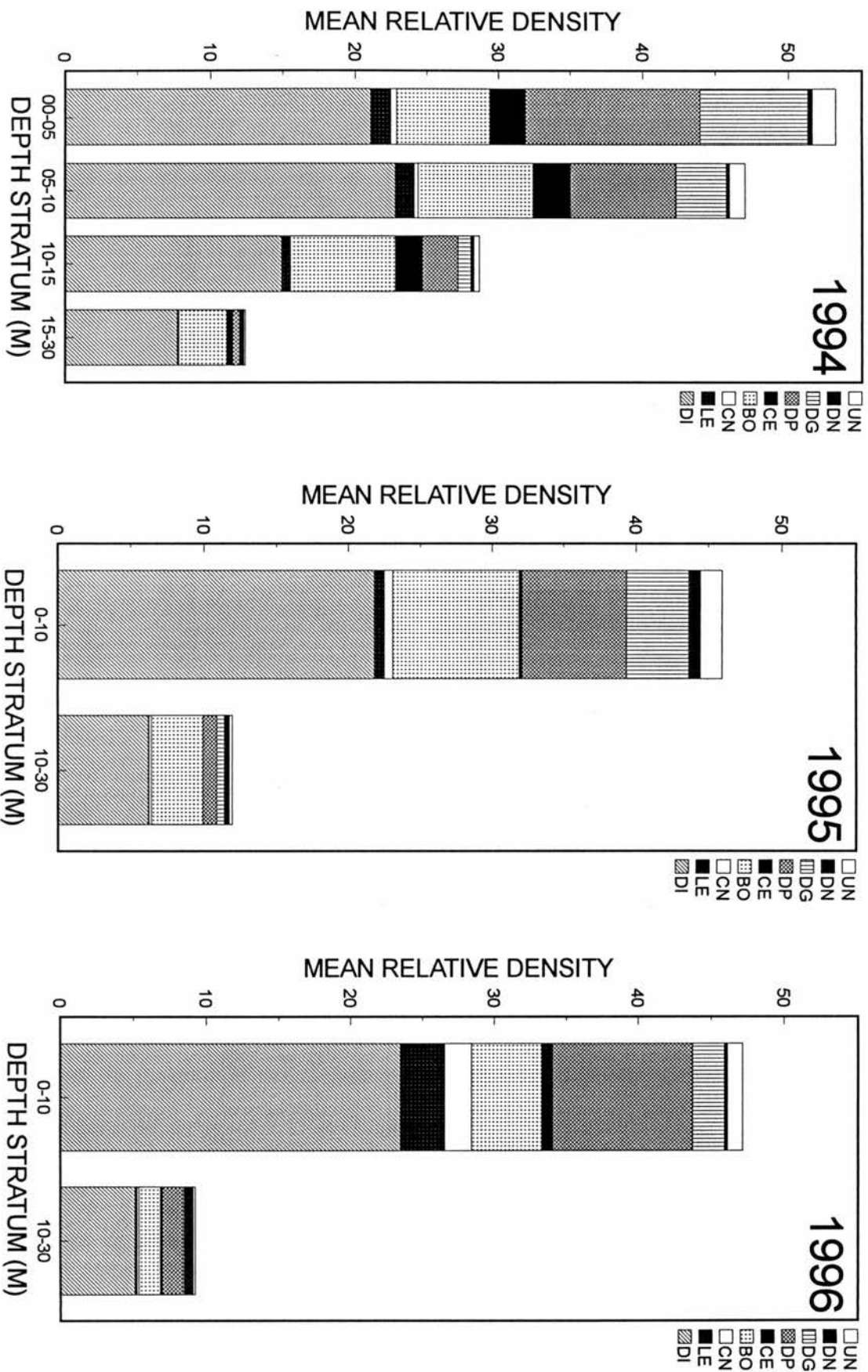


Figure 27.

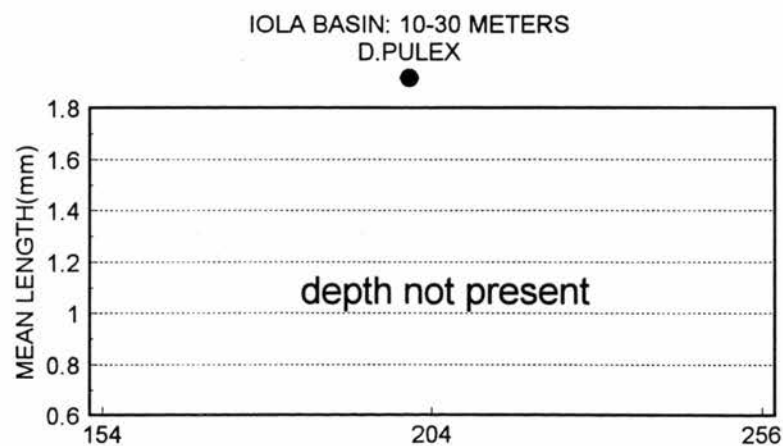
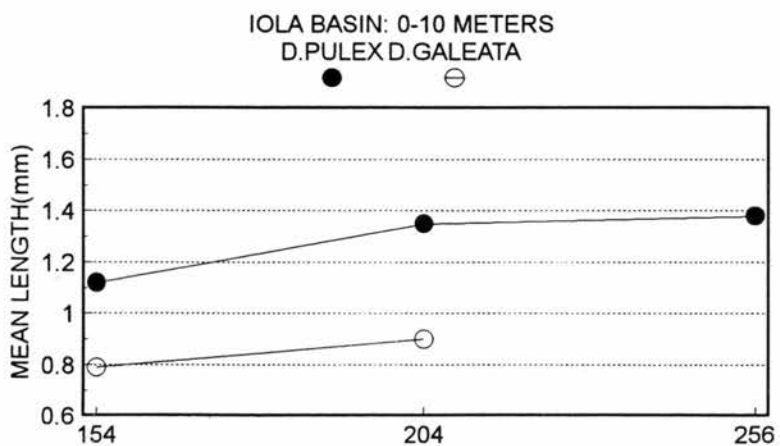
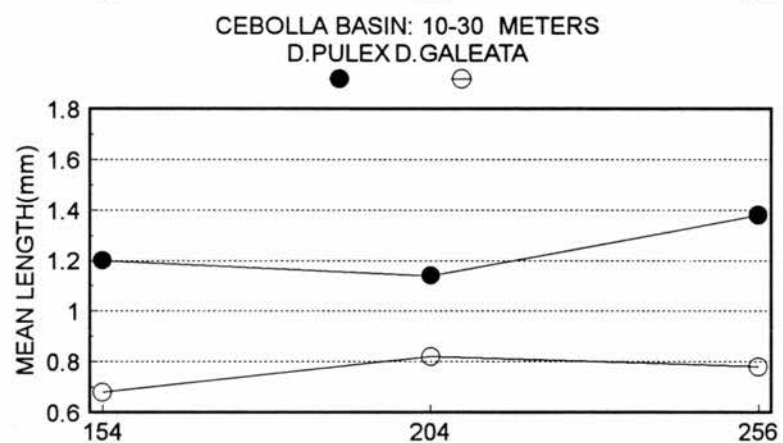
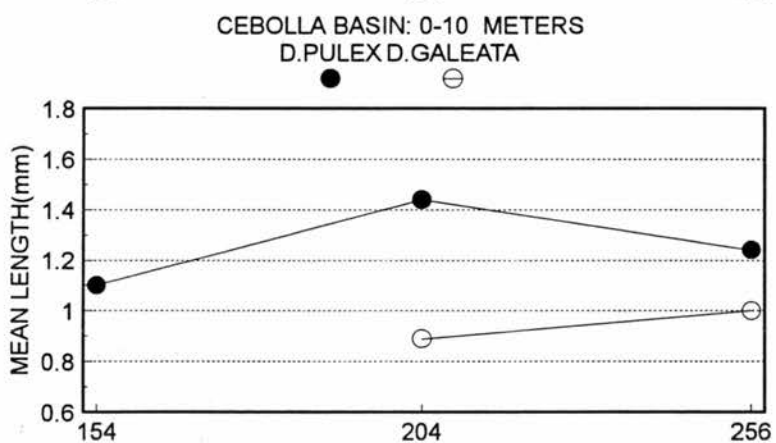
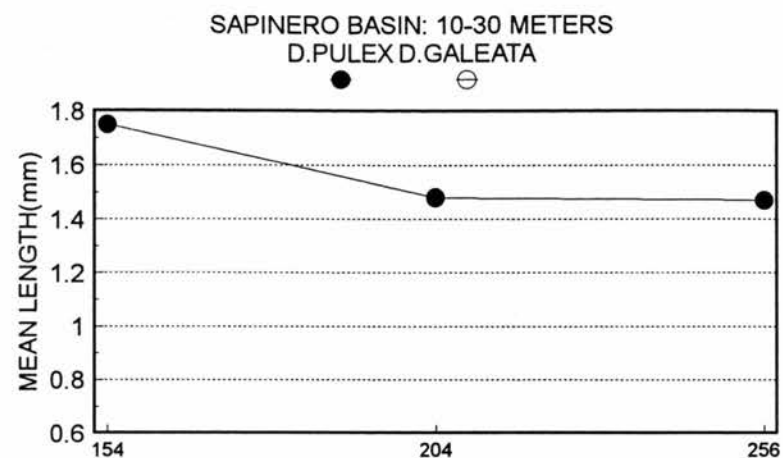
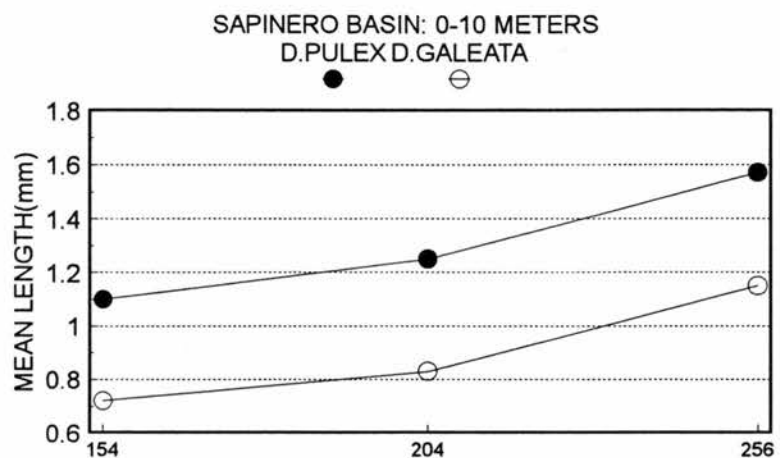
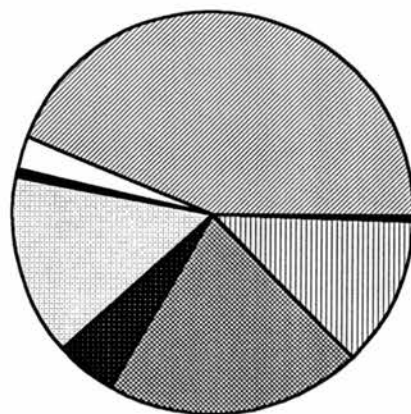


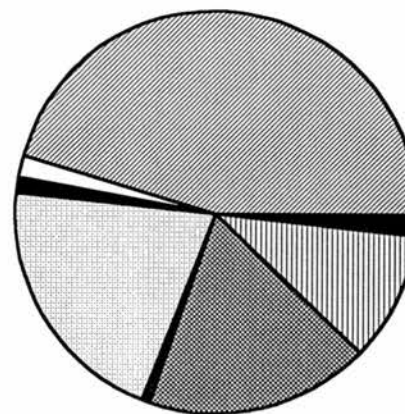
Figure 28.

Zooplankton Community Composition

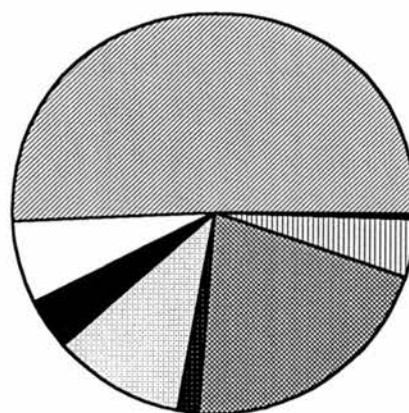
All dates, basins, for the 0-10m stratum



1994



1995



1996



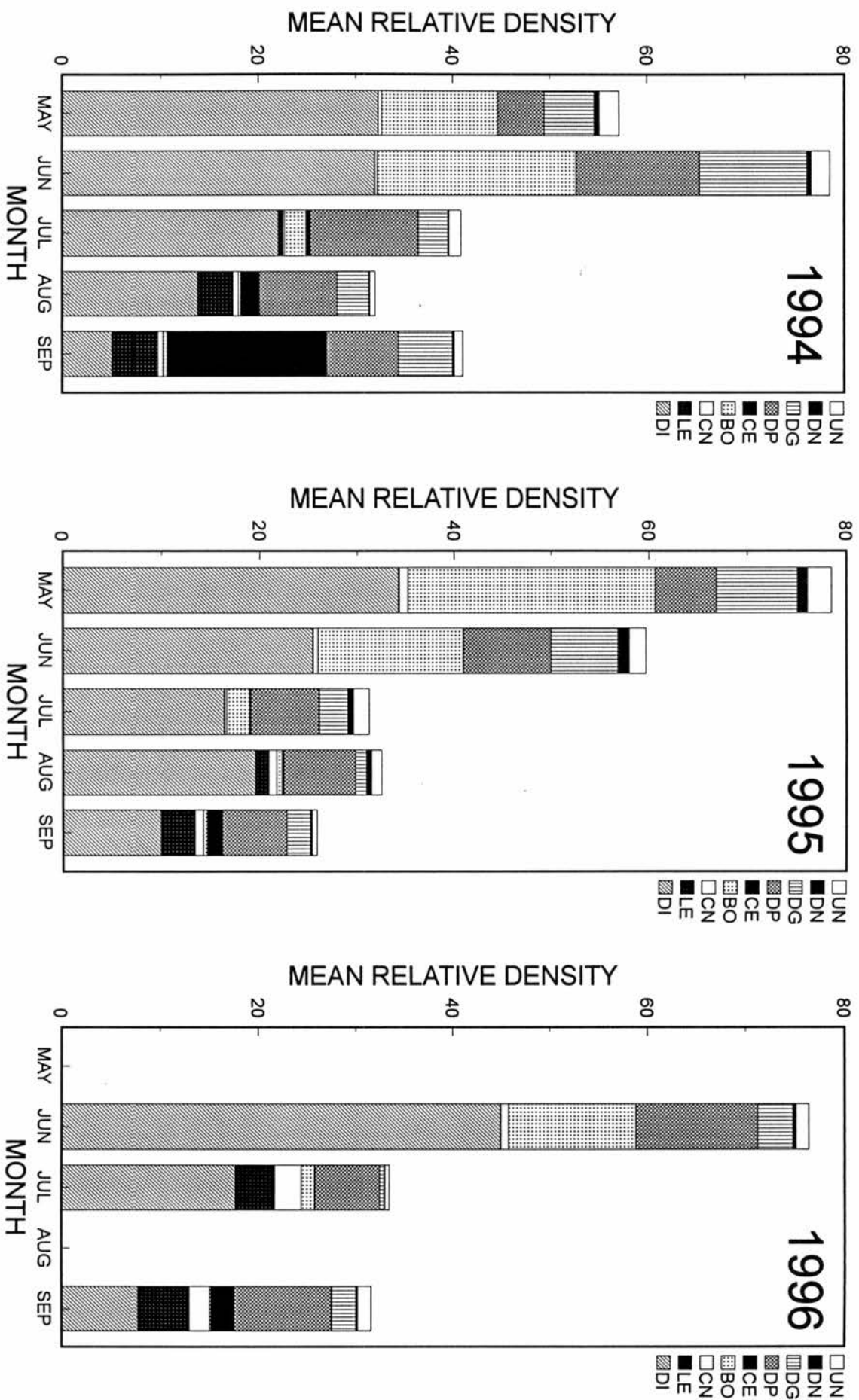


Figure 30.

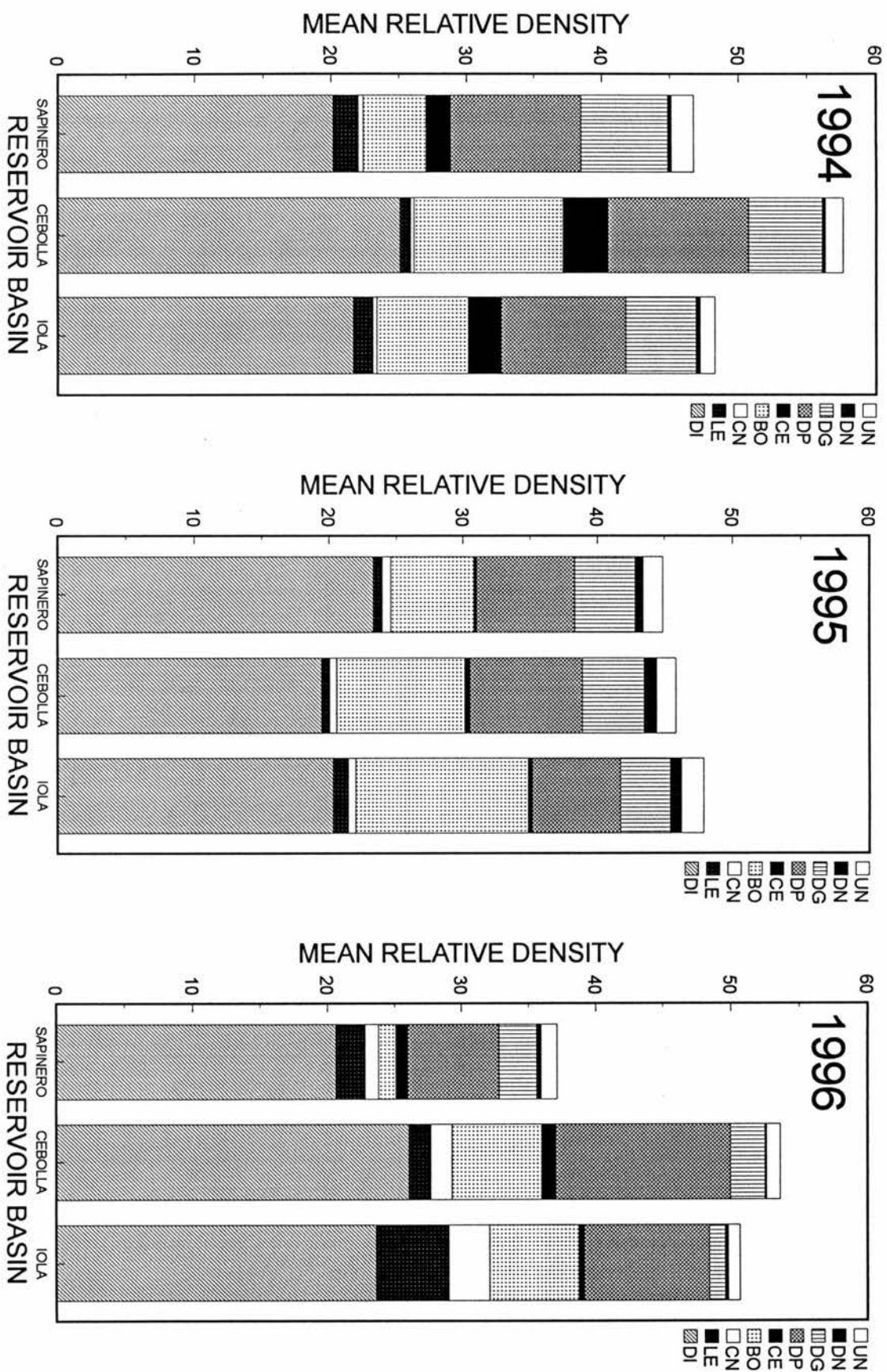
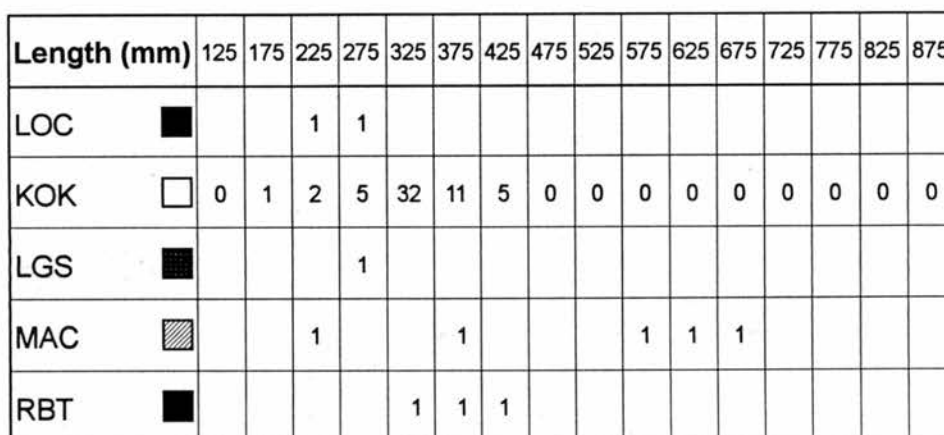


Figure 31.

Length-frequency of fishes in VGN Blue Mesa Reservoir - August 1996



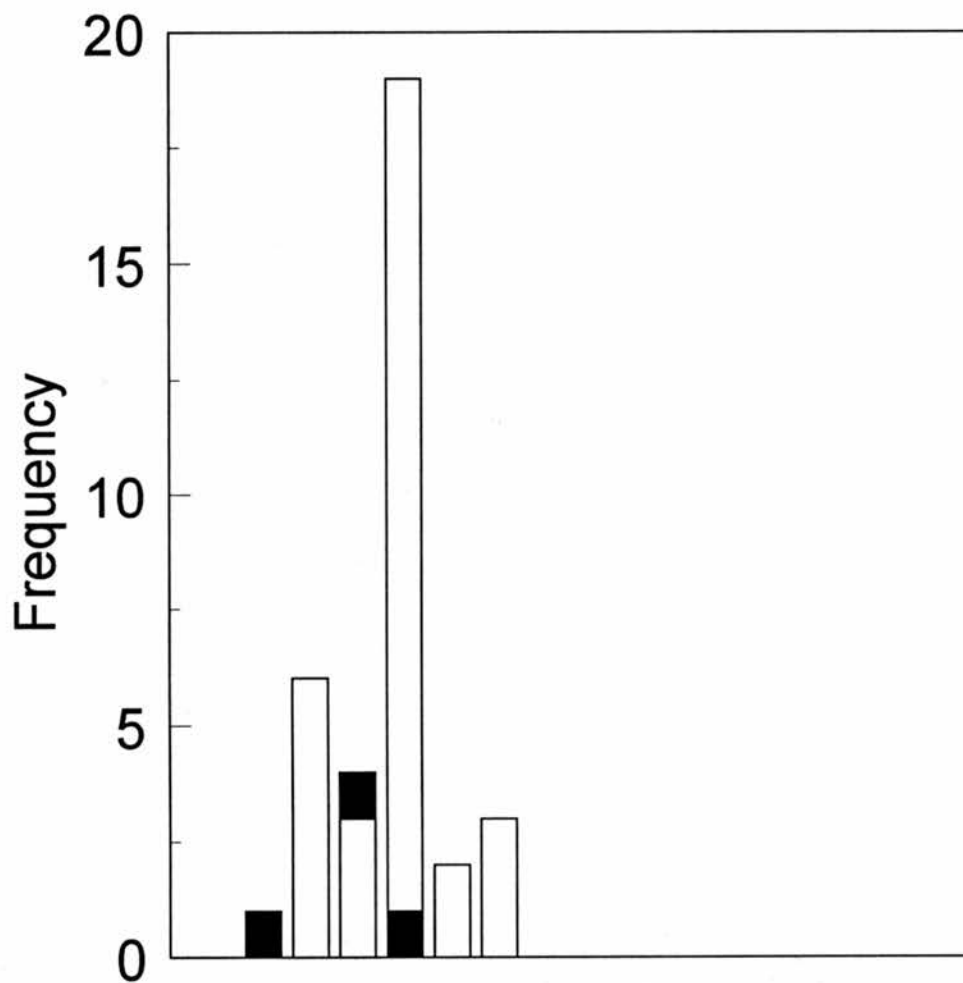
[illegible]

Figure 34.

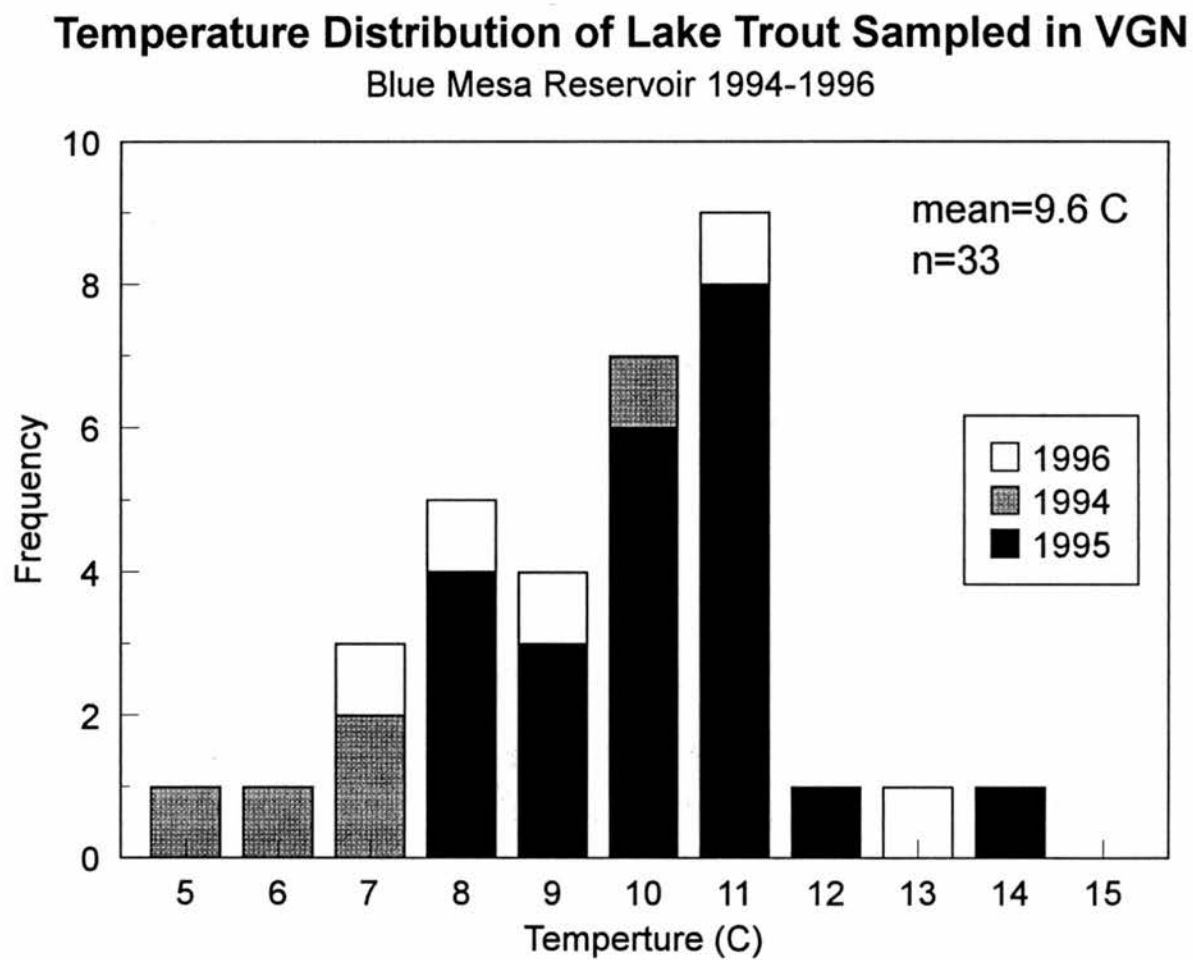


Figure 35.

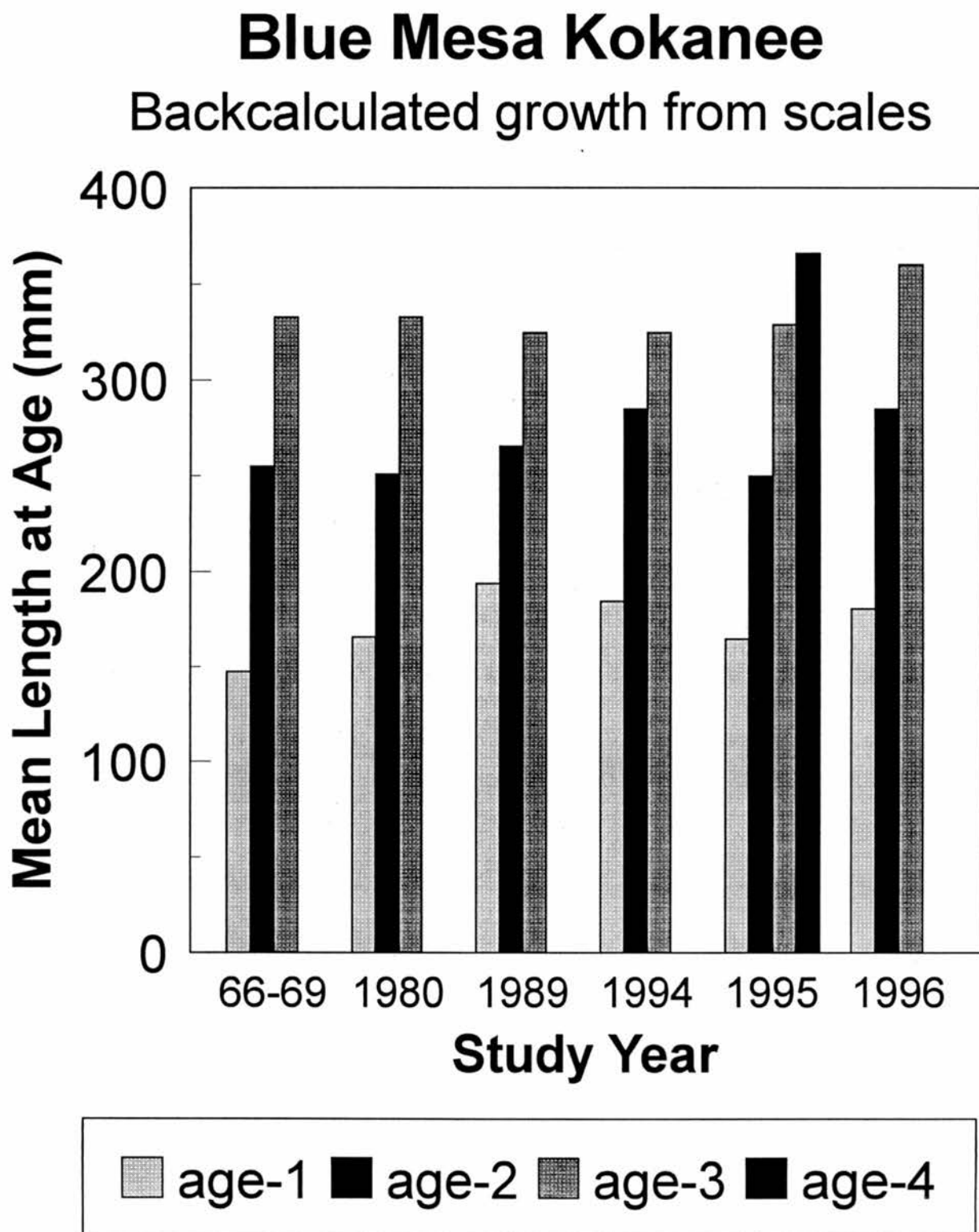


Figure 36.

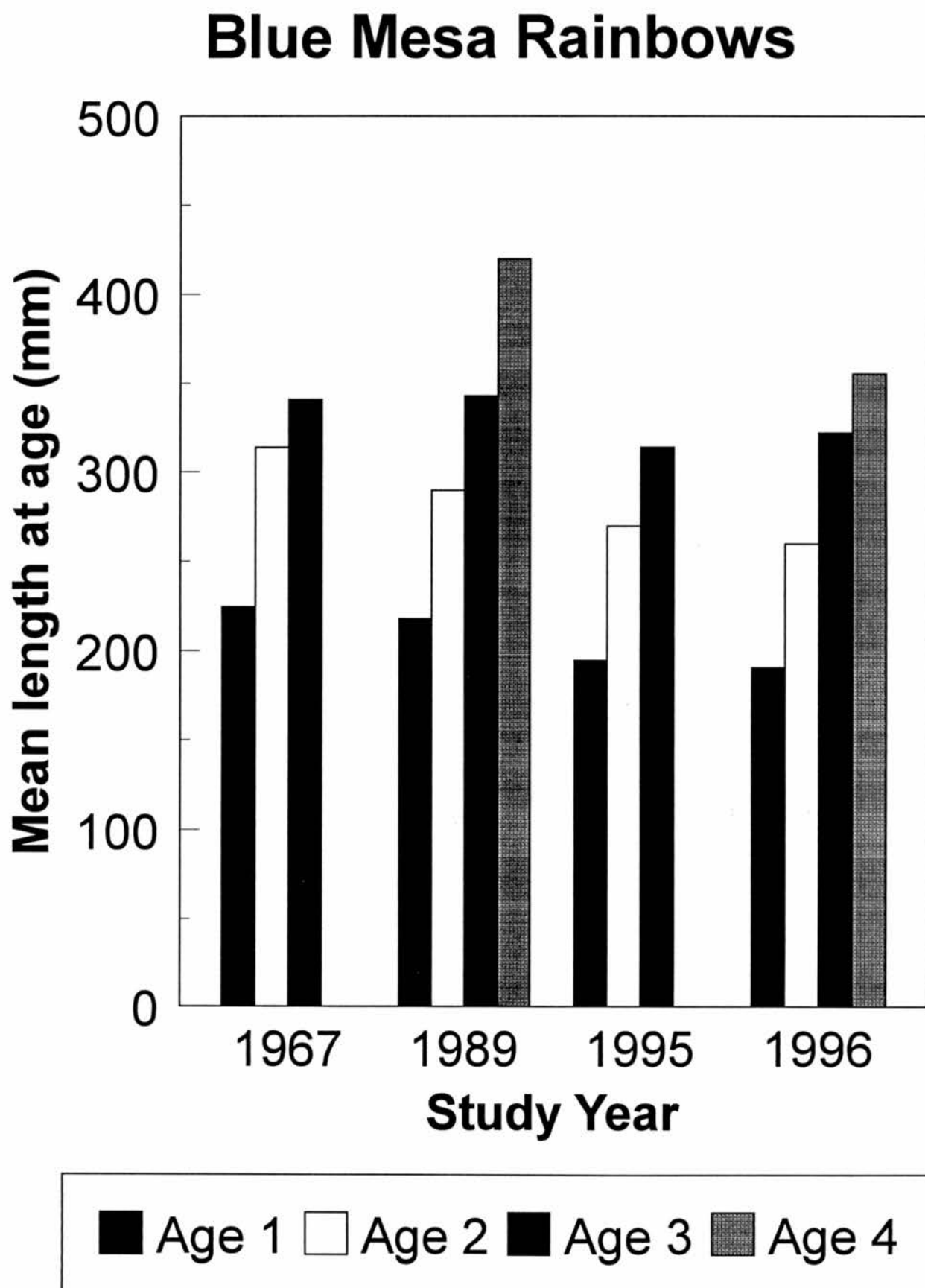


Figure 37.

Sapinero Sonar Survey - Jul 24 1995

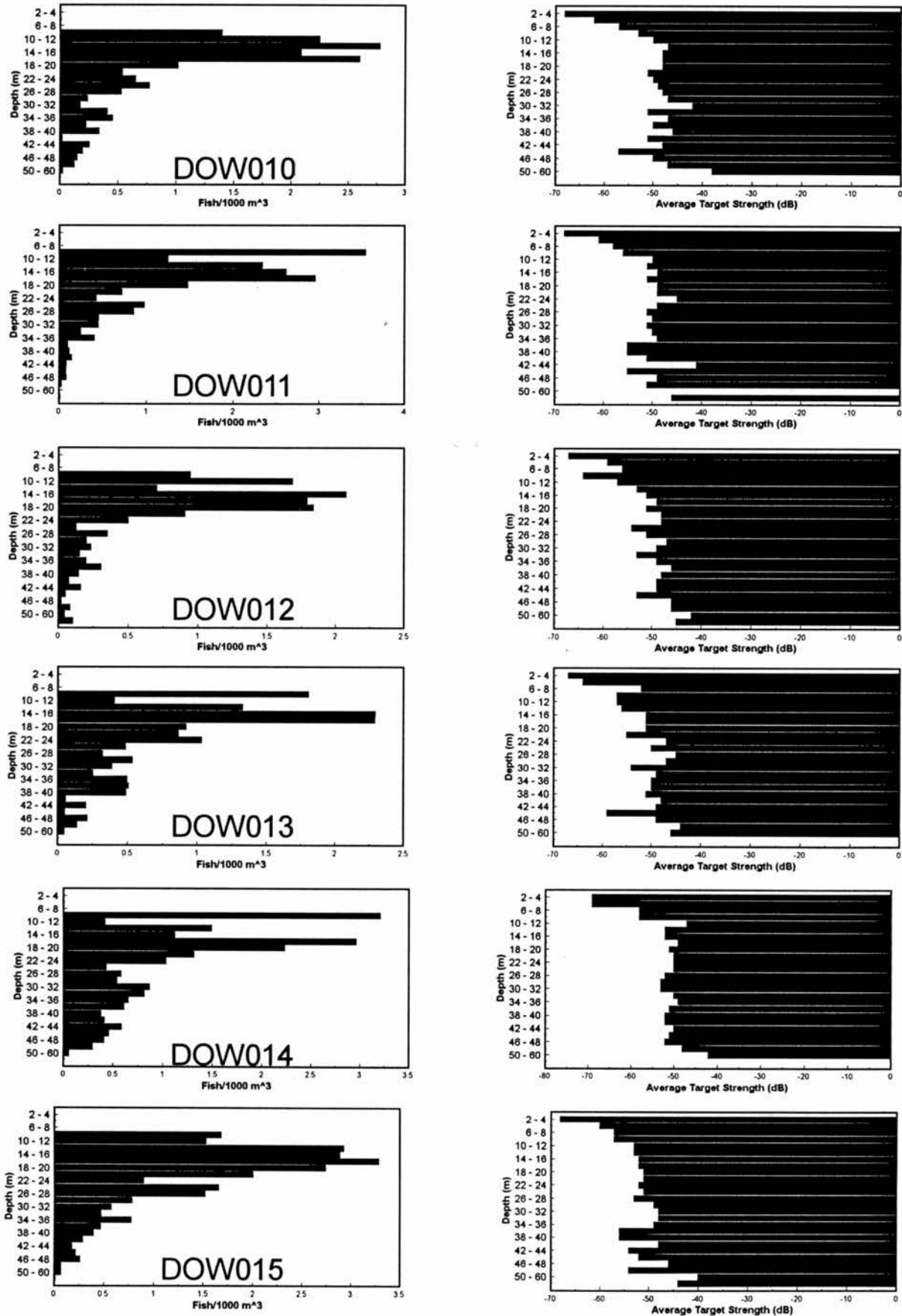


Figure 38.

Cebolla Sonar Survey - Jul 23-24 1995

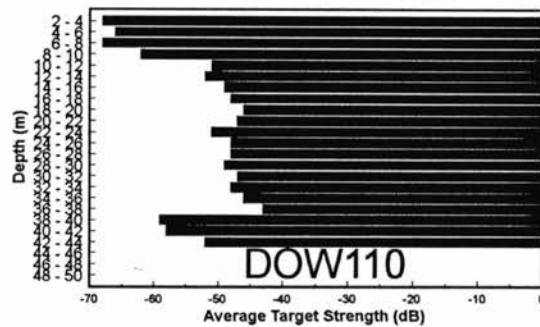
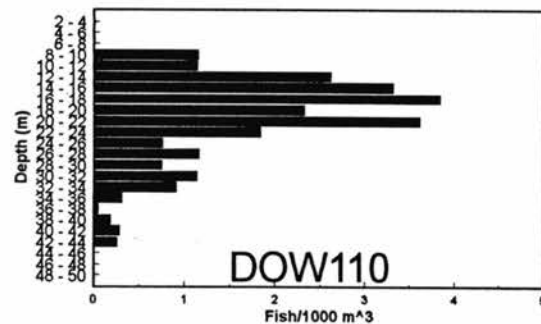
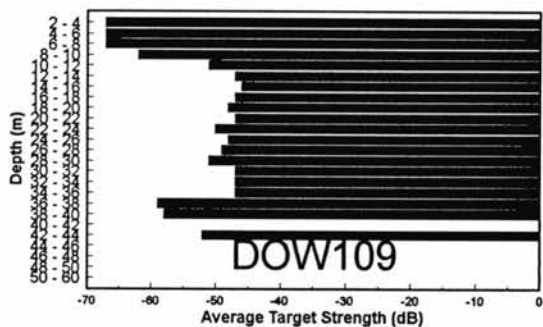
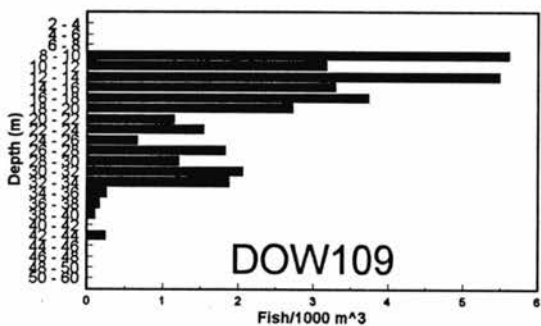
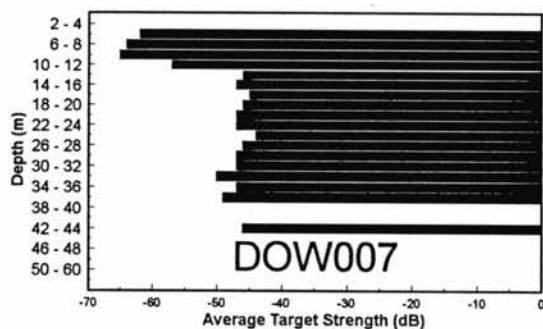
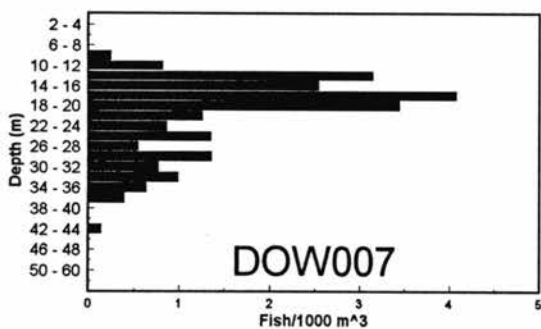
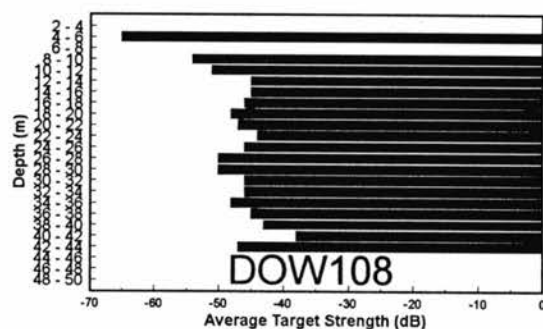
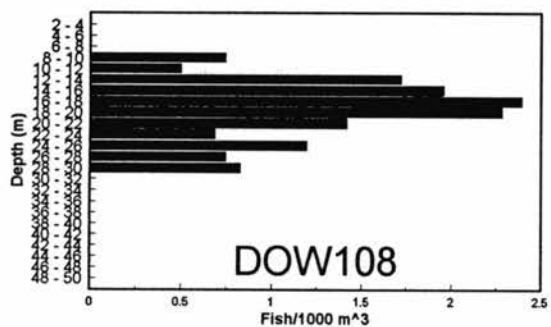
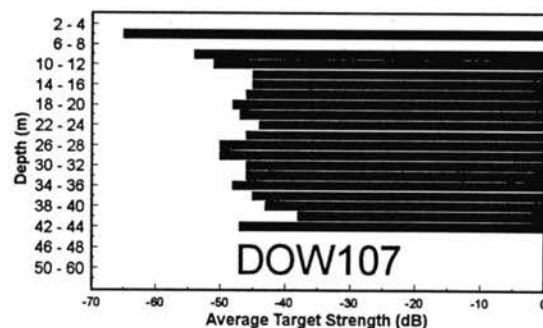
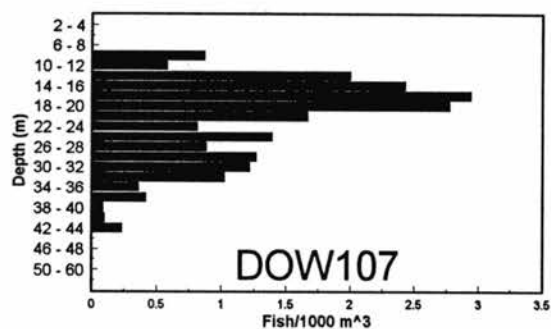


Figure 39.

Iola Sonar Survey - Jul 24, 1995

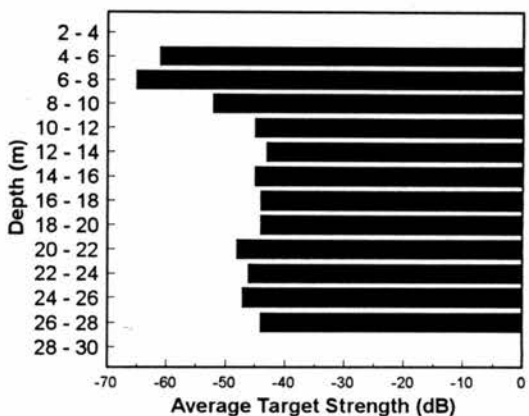
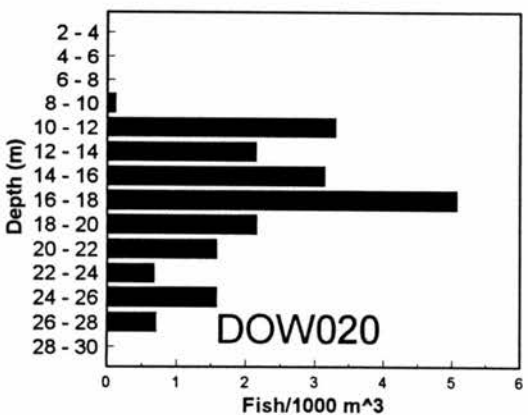
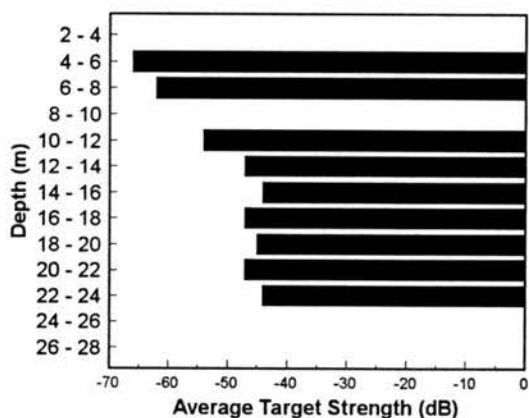
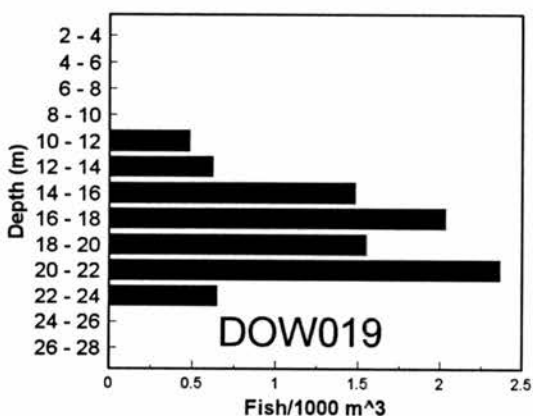
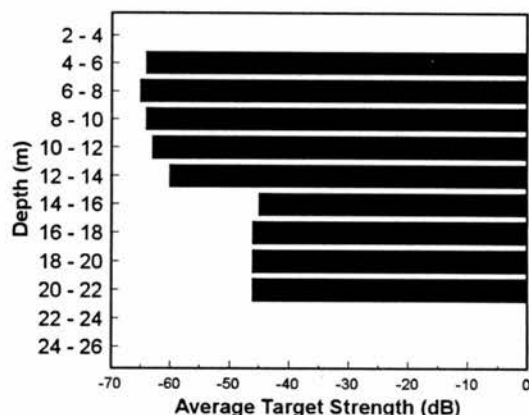
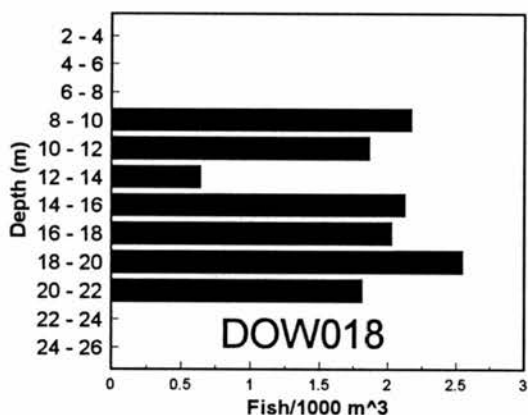
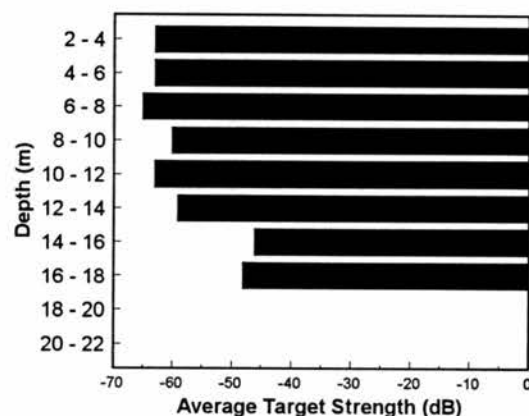
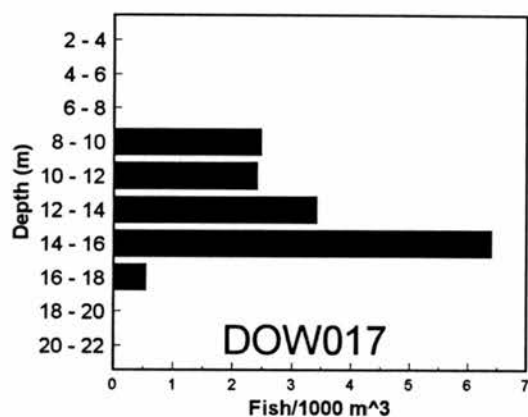
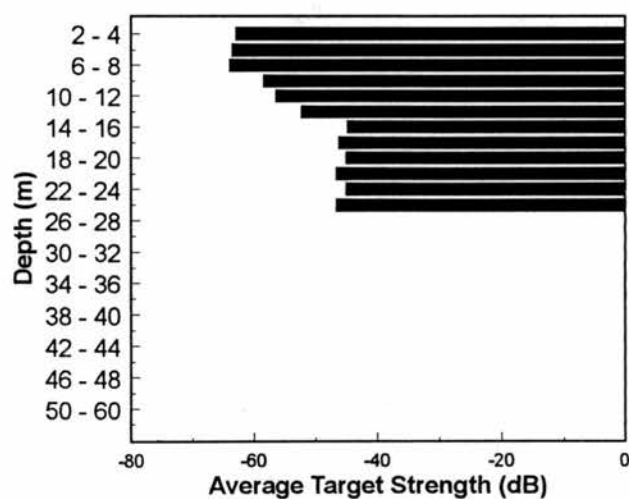
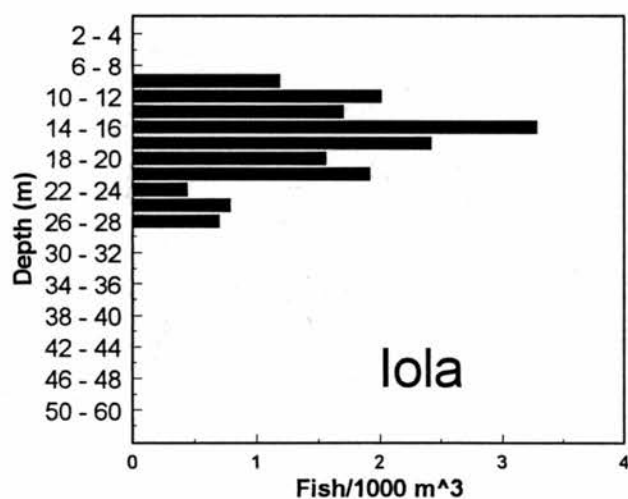
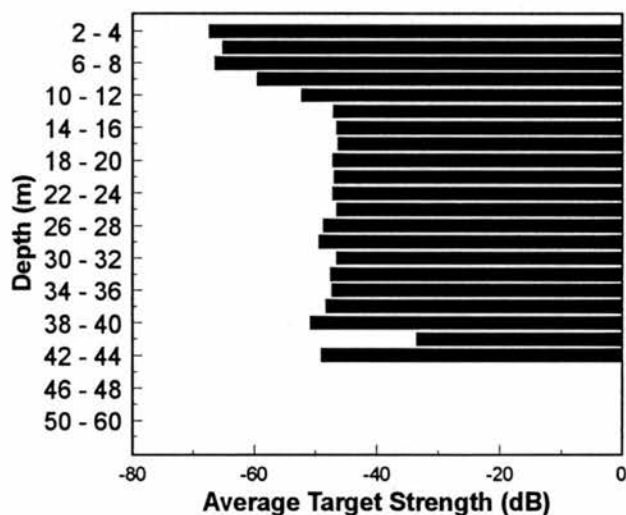
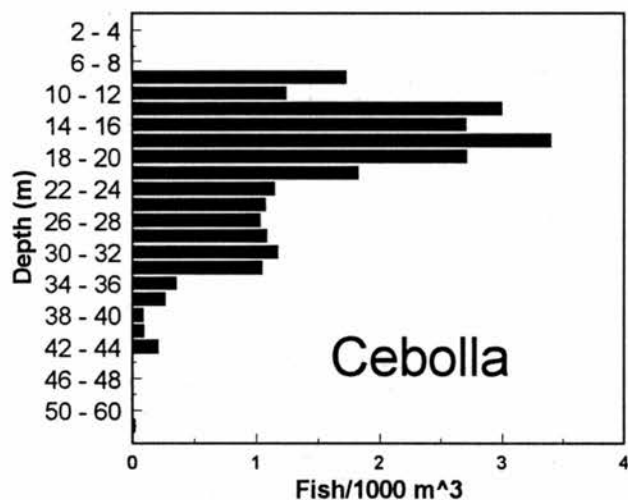
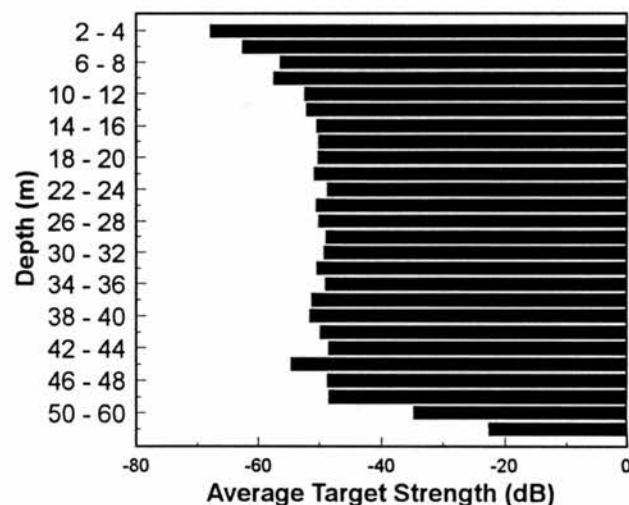
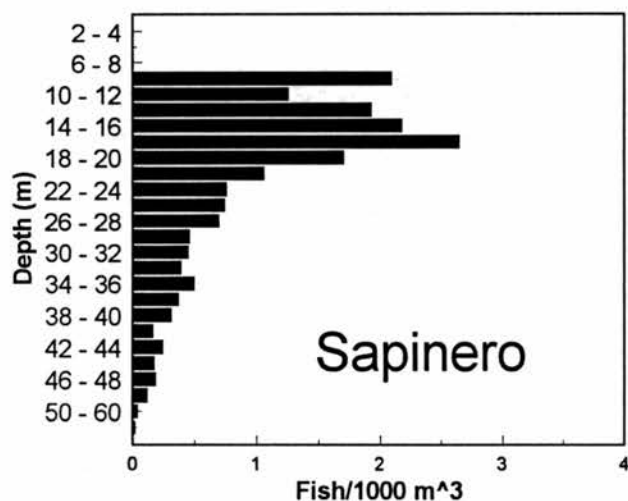
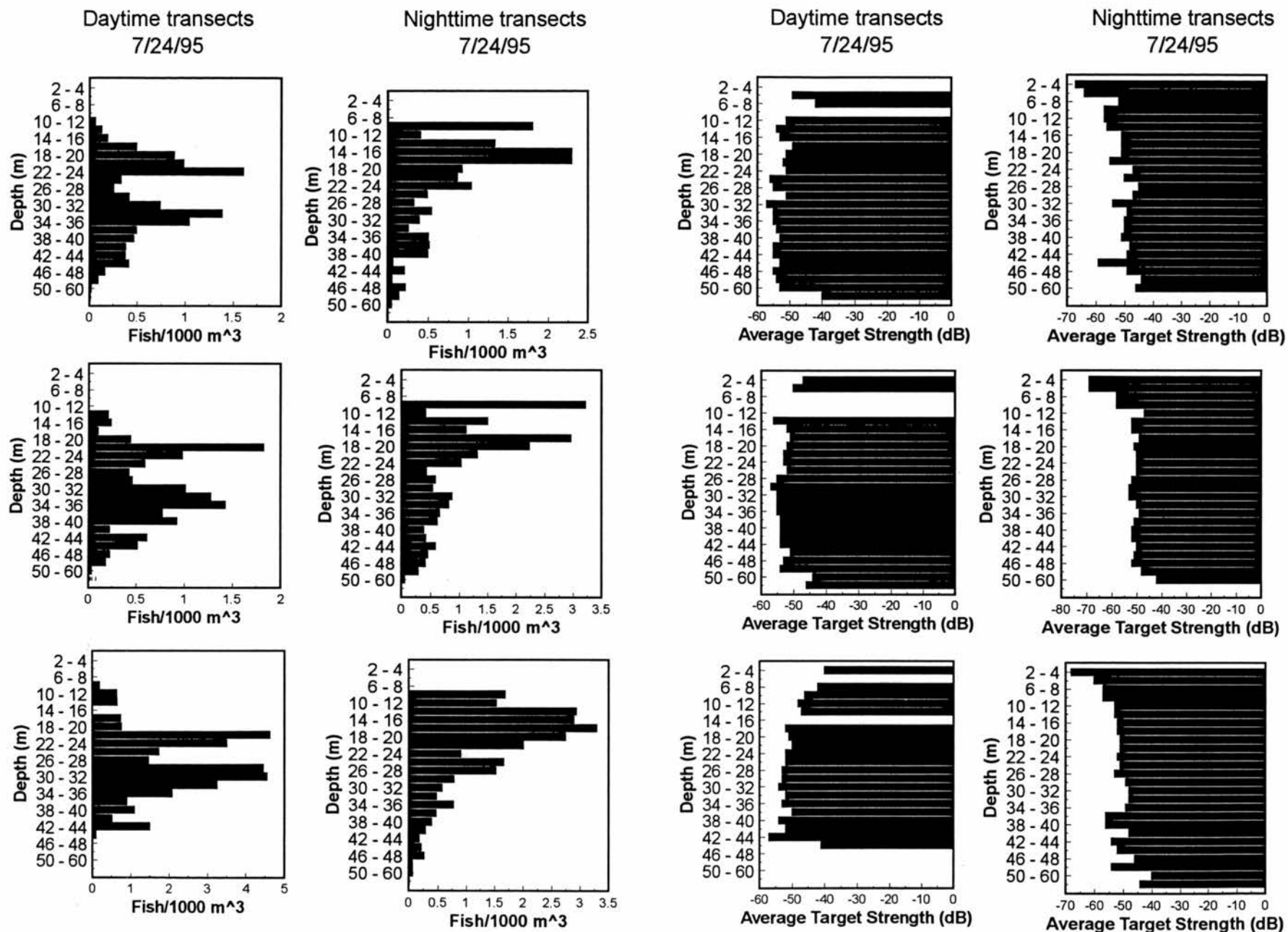


Figure 40.

Sonar Survey - Jul 23-24 1995

Mean of All Transects by Basin

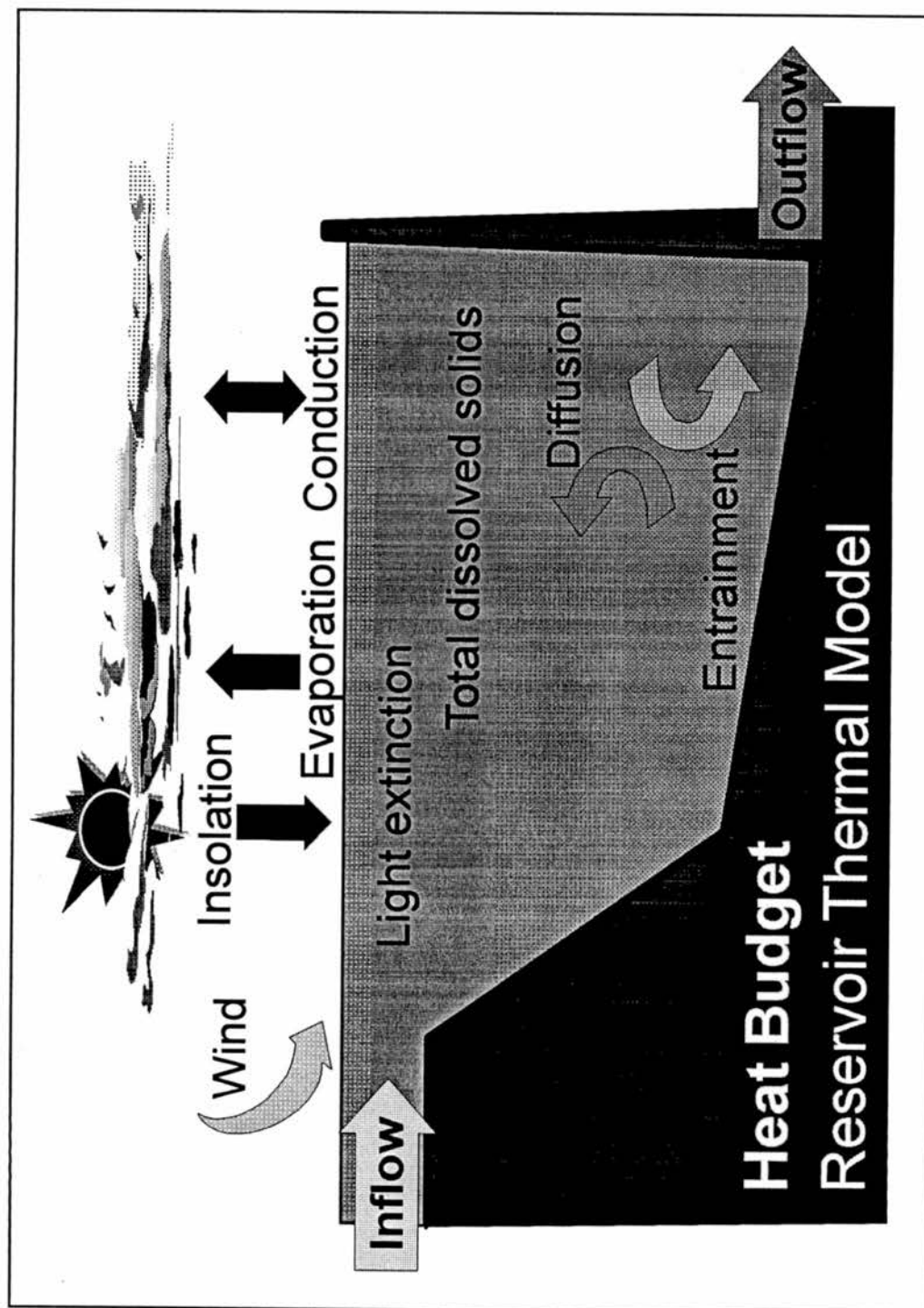




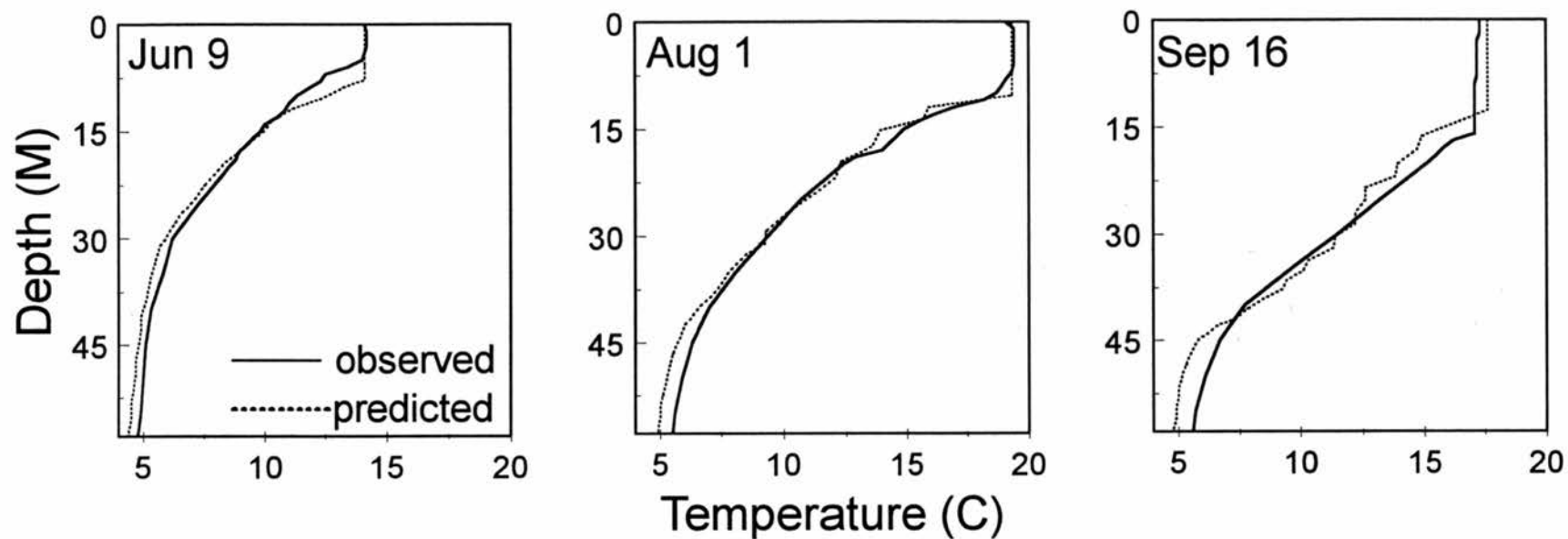
Sapinero

Figure 41.

Figure 42.



Calibration with Observed Data - 1994



Prediction with Independent Data - 1996

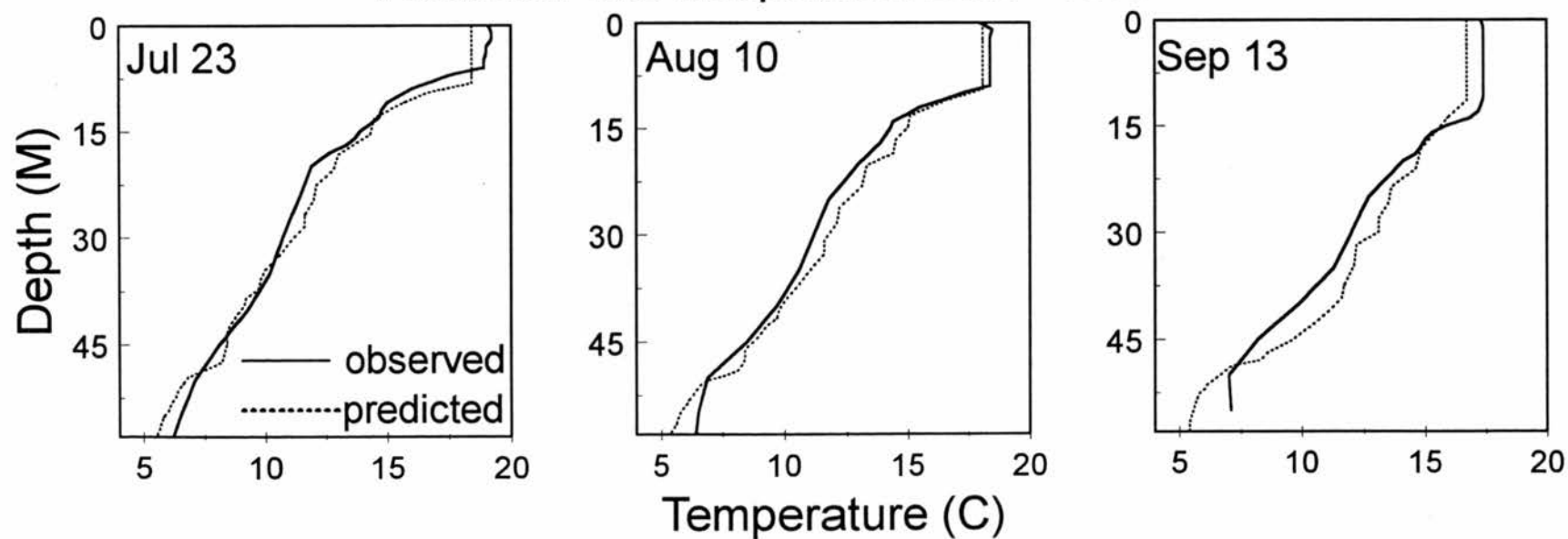
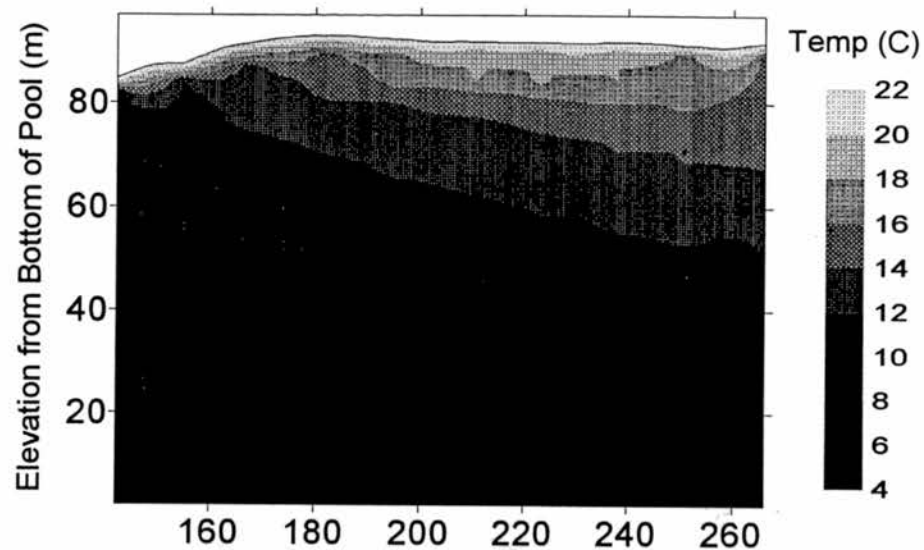
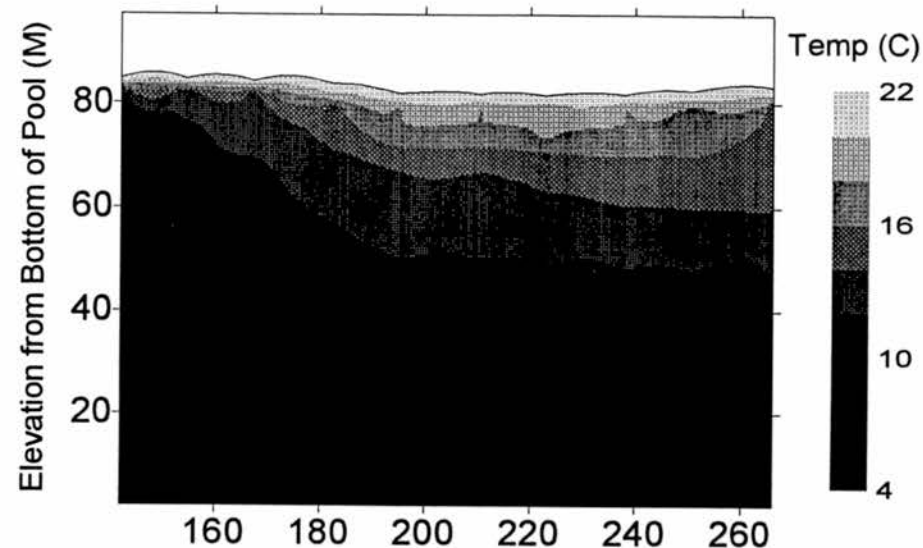


Figure 43.

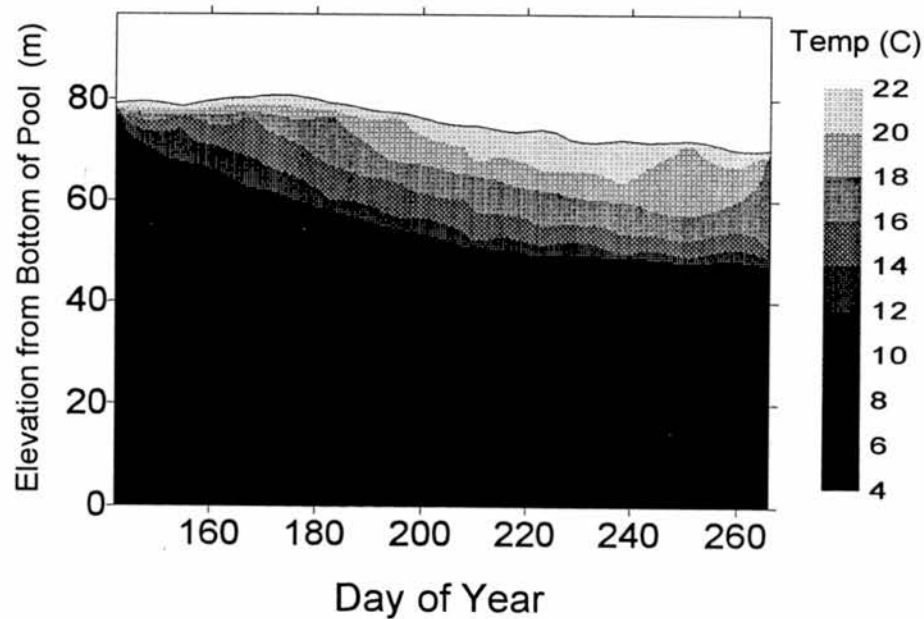
(a) Traditional Operations, Average Weather



(c) New Operations, Average Weather



(b) Traditional Operations, Warm and Dry Weather



(d) New Operations, Warm and Dry Weather

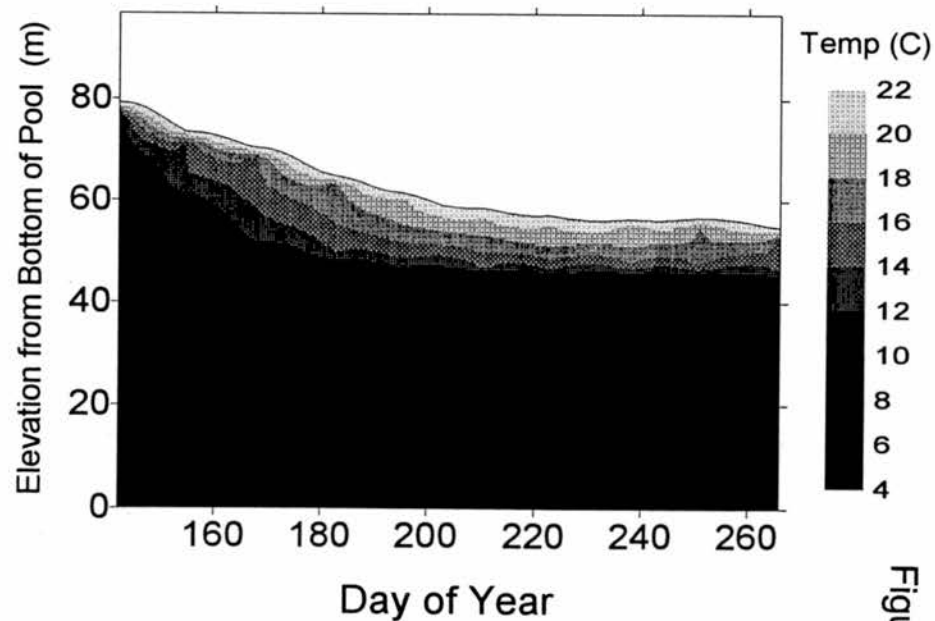


Figure 44.

Age-1 Kokanee Responses

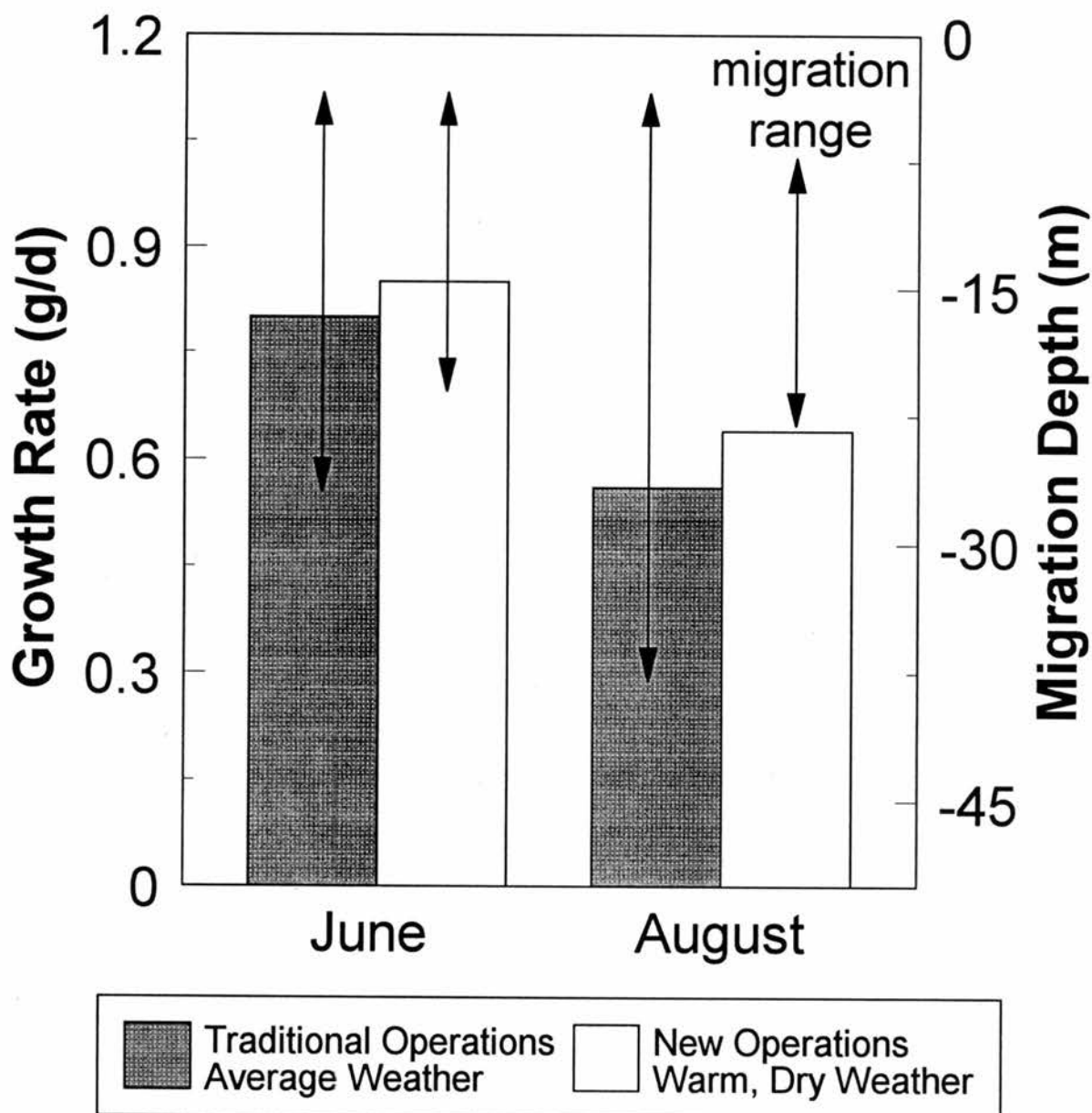
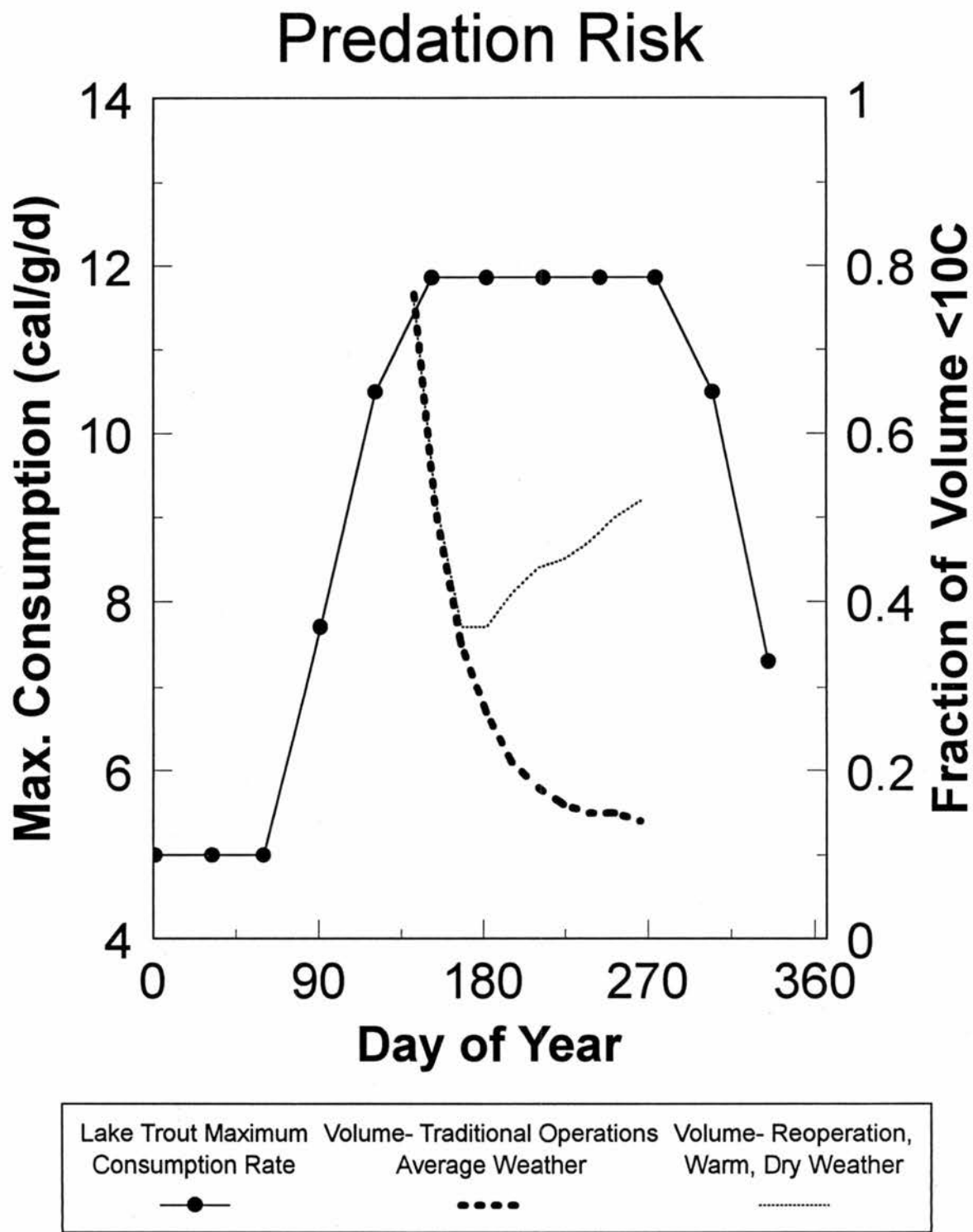


Figure 46.



APPENDIX A.
Experimental Vertical Gill Net Results

Table A1. Capture frequencies of fishes sampled in vertical gill nets during August and September 1996 at Blue Mesa Reservoir.

Month	SPP	Cumulative Frequency	Cumulative Percent	Frequency	Percent
August	KOK	56	83.6	56	83.6
	LGS	1	1.5	57	85.1
	LOC	2	3.0	59	88.1
	MAC	5	7.5	64	95.5
	RBT	3	4.5	67	100.0
Sept	KOK	32	91.4	32	91.4
	LOC	1	2.9	33	94.3
	RBT	2	5.7	35	100.0

[illegible]

----- SPP=KOK MONTH=8 -----					
TRUEDEP Midpoint		Freq	Cum. Freq	Percent	Cum. Percent
0	e	0	0	0.00	0.00
5	e	0	0	0.00	0.00
10	e****	4	4	7.41	7.41
15	e*****	9	13	16.67	24.07
20	e*****	21	34	38.89	62.96
25	e*****	9	43	16.67	79.63
30	e*****	6	49	11.11	90.74
35	e**	2	51	3.70	94.44
40	e***	3	54	5.56	100.00
45	e	0	54	0.00	100.00
	eaaaaeaaaaeaaaaeaaaaea				
	5 10 15 20				
	Frequency				

----- SPP=KOK MONTH=9 -----					
TRUEDEP Midpoint		Freq	Cum. Freq	Percent	Cum. Percent
0	e****	2	2	6.25	6.25
5	e	0	2	0.00	6.25
10	e****	2	4	6.25	12.50
15	e**	1	5	3.13	15.63
20	e****	2	7	6.25	21.88
25	e*****	12	19	37.50	59.38
30	e*****	5	24	15.63	75.00
35	e*****	5	29	15.63	90.63
40	e**	1	30	3.13	93.75
45	e****	2	32	6.25	100.00
50	e	0	32	0.00	100.00
	eaaaaeaaaaeaaaaeaaaaae				
	2 4 6 8 10 12				
	Frequency				

Table A4. Depth distribution (m) of lake trout (MAC) sampled in nighttime experimental vertical gill net sets at Blue Mesa Reservoir during 1996. SPP=species, TRUEDEP=depth where fish was captured.

----- SPP=MAC MONTH=8 -----

TRUEDEP Midpoint		Freq	Cum. Freq	Percent	Cum. Percent
0	é	0	0	0.00	0.00
5	é	0	0	0.00	0.00
10	é	0	0	0.00	0.00
15	é	0	0	0.00	0.00
20	é*****	1	1	20.00	20.00
25	é	0	1	0.00	20.00
30	é	0	1	0.00	20.00
35	é*****	1	2	20.00	40.00
40	é*****	1	3	20.00	60.00
45	é*****	1	4	20.00	80.00
50	é*****	1	5	20.00	100.00
55	é	0	5	0.00	100.00
60	é	0	5	0.00	100.00
	é				
	éaaaaaaaaaaaaaaaaaaaaaé				
	1				

Frequency

Table A5. Depth distribution (m) of rainbow trout (RBT) sampled in nighttime experimental vertical gill net sets at Blue Mesa Reservoir during 1996. SPP=species, TRUEDEP=depth where fish was captured.

----- SPP=RBT MONTH=8 -----					
TRUEDEP Midpoint		Freq	Cum. Freq	Percent	Cum. Percent
0	é*****	2	2	66.67	66.67
5	é	0	2	0.00	66.67
10	é*****	1	3	33.33	100.00
15	é	0	3	0.00	100.00
20	é	0	3	0.00	100.00
	é				
	èààààààààààààààààààè				
	1 2				
	Frequency				
----- SPP=RBT MONTH=9 -----					
TRUEDEP Midpoint		Freq	Cum. Freq	Percent	Cum. Percent
0	é	0	0	0.00	0.00
5	é*****	1	1	50.00	50.00
10	é	0	1	0.00	50.00
15	é*****	1	2	50.00	100.00
20	é	0	2	0.00	100.00
	é				
	èààààààààààààààààààè				
	1				
	Frequency				

[illegible]

SPP-VOK MONTH-9

[illegible]

Table A8. Length-frequency of brown trout (LOC) sampled in experimental vertical gillnets fished at Blue Mesa Reservoir during August and September, 1996. TLENGTH is fish total length, SPP=species.

TLENGTH		Cum.		Cum.	
Midpoint	Freq	Percent	Percent	Freq	Percent
150	0	0.00	0.00	0	0.00
170	0	0.00	0.00	0	0.00
190	0	0.00	0.00	0	0.00
210	0	0.00	0.00	0	0.00
230	1	50.00	50.00	1	50.00
250	0	0.00	50.00	0	0.00
270	1	50.00	100.00	1	50.00
290	0	0.00	100.00	0	0.00
310	0	0.00	100.00	0	0.00
330	0	0.00	100.00	0	0.00
350	0	0.00	100.00	0	0.00
370	0	0.00	100.00	0	0.00
390	0	0.00	100.00	0	0.00
410	0	0.00	100.00	0	0.00
430	0	0.00	100.00	0	0.00
450	0	0.00	100.00	0	0.00

TLENGTH		SPP=LOC MONTH=9			
Midpoint		Freq	Percent	Cum. Percent	
150	é	0	0.00	0.00	
170	é	0	0.00	0.00	
190	é	0	0.00	0.00	
210	é	0	0.00	0.00	
230	é	0	0.00	0.00	
250	é	0	0.00	0.00	
270	é	0	0.00	0.00	
290	é	0	0.00	0.00	
310	é	0	0.00	0.00	
330	é	1	100.00	100.00	
350	é	1	0.00	100.00	
370	é	0	0.00	100.00	
390	é	0	0.00	100.00	
410	é	0	0.00	100.00	
430	é	0	0.00	100.00	
450	é	0	0.00	100.00	

Frequency

1

Table A9. Length-frequency of rainbow trout (RBT) sampled in experimental vertical gillnets fished at Blue Mesa Reservoir during August and September, 1996. TLENGTH is fish total length, SPP=species.

----- SPP=RBT MONTH=8 -----					
TLENGTH			Cum.		Cum.
Midpoint		Freq	Freq	Percent	Percent
150	é	0	0	0.00	0.00
170	é	0	0	0.00	0.00
190	é	0	0	0.00	0.00
210	é	0	0	0.00	0.00
230	é	0	0	0.00	0.00
250	é	0	0	0.00	0.00
270	é	0	0	0.00	0.00
290	é	0	0	0.00	0.00
310	é	0	0	0.00	0.00
330	é	0	0	0.00	0.00
350	é*****	2	2	66.67	66.67
370	é	0	2	0.00	66.67
390	é	0	2	0.00	66.67
410	é	0	2	0.00	66.67
430	é*****	1	3	33.33	100.00
450	é	0	3	0.00	100.00
	é				
	éaaaé				
		1	2		
		Frequency			
----- SPP=RBT MONTH=9 -----					
TLENGTH			Cum.		Cum.
Midpoint		Freq	Freq	Percent	Percent
150	é	0	0	0.00	0.00
170	é	0	0	0.00	0.00
190	é*****	1	1	50.00	50.00
210	é	0	1	0.00	50.00
230	é	0	1	0.00	50.00
250	é	0	1	0.00	50.00
270	é*****	1	2	50.00	100.00
290	é	0	2	0.00	100.00
310	é	0	2	0.00	100.00
330	é	0	2	0.00	100.00
350	é	0	2	0.00	100.00
370	é	0	2	0.00	100.00
390	é	0	2	0.00	100.00
410	é	0	2	0.00	100.00
430	é	0	2	0.00	100.00
450	é	0	2	0.00	100.00
	é				
	éaaaé				
			1		
		Frequency			

TLENGTH		SPP=MAC MONTH=8			
Midpoint		Freq	Cum. Freq	Percent	Cum. Percent
150	é	0	0	0.00	0.00
170	é	0	0	0.00	0.00
190	é	0	0	0.00	0.00
210	é	0	0	0.00	0.00
230	é	0	0	0.00	0.00
250	é	0	0	0.00	0.00
270	é*****	1	1	20.00	20.00
290	é	0	1	0.00	20.00
310	é	0	1	0.00	20.00
330	é	0	1	0.00	20.00
350	é	0	1	0.00	20.00
370	é	0	1	0.00	20.00
390	é*****	1	2	20.00	40.00
410	é	0	2	0.00	40.00
430	é	0	2	0.00	40.00
450	é	0	2	0.00	40.00
470	é	0	2	0.00	40.00
490	é	0	2	0.00	40.00
510	é	0	2	0.00	40.00
530	é	0	2	0.00	40.00
550	é	0	2	0.00	40.00
570	é*****	1	3	20.00	60.00
590	é	0	3	0.00	60.00
610	é	0	3	0.00	60.00
630	é*****	1	4	20.00	80.00
650	é*****	1	5	20.00	100.00
670	é	0	5	0.00	100.00
690	é	0	5	0.00	100.00
710	é	0	5	0.00	100.00
éaaaé					

1

Frequency

Table A11. Mean Fulton's condition factor ($K \times 10,000$) for fish sampled in experimental vertical gill nets at Blue Mesa Reservoir during 1996. MN=month, N=number of fish included in the mean.

Species	MN	N Obs	Mean	N	Std Dev
Kokanee	8	56	0.1044832	56	0.0069736
	9	32	0.1047965	32	0.0094033
Longnose sucker	8	1	0.0974854	1	.
Brown trout	8	2	0.0966310	2	0.0009528
	9	1	0.0937512	1	.
Lake trout	8	5	0.0821524	2	0.0069088
Rainbow trout	8	3	0.0927315	3	0.0047440
	9	2	0.1135037	2	0.0007763

APPENDIX B.
Manuscript

Stockwell, J. D. and B. M. Johnson. 1997.

Refinement and calibration of a bioenergetics-based foraging model for
kokanee (*Oncorhynchus nerka*).

Canadian Journal of Fisheries and Aquatic Sciences
(In press).

Abstract

Results from a mechanistic, bioenergetics-based foraging model for kokanee (*Oncorhynchus nerka*) were compared with results from a corroborated standard model. Daily growth estimates from the mechanistic model were 239% higher than estimates from the standard model at temperatures $\geq 12^{\circ}\text{C}$, and 42% lower at temperatures $\leq 8^{\circ}\text{C}$. The mechanistic model was then modified by incorporating a different respiration function and a new size- and temperature-dependent functional response. Although sensitive to prey and predator size, prey handling time, and feeding duration, results from the modified model were comparable to the standard model. Using observed vertical profiles of temperature and prey densities, model growth estimates for kokanee from Blue Mesa Reservoir, Colorado bounded observed growth under realistic ranges of model parameters. The model also made the following four predictions: seasonal and annual ontogenetic shifts in 1) foraging and 2) migration strategies; 3) very low prey handling times ($0.33 \text{ s} \cdot \text{Daphnia}^{-1}$) for larger fish, suggesting that kokanee may be capable of gulp/filter feeding; and 4) higher daily maximum consumption rates for smaller kokanee than previously hypothesized. The revised model provides a mechanistic means to forecast anthropogenic and climatic thermal effects on fish behavior and growth.

Introduction

Bioenergetics models (Hewett 1989; Hewett and Johnson 1992) have proven to be an invaluable tool in fisheries ecology. The elegance of these models (collectively called the "Wisconsin" model; Ney 1990) has been their use of fundamental thermodynamics to uncover important ecological insights. For example, the Wisconsin model has been used to explicitly predict physiological effects of body size (e.g., Post 1990), behavioral thermoregulation with changes in body size and food availability (e.g., Crowder and Magnuson 1983), and contaminant accumulation and elimination dynamics (e.g., Madenjian et al. 1993). Overall, these models have defined constraints on growth via temperature, body size, and feeding rate (e.g., Rice et al. 1983; Luecke et al. 1996). The Wisconsin model has also been useful for management purposes including determination of stocking densities (e.g., Stewart et al. 1981) and harvest rates (e.g., Carline et al. 1984; Johnson et al. 1992). For a complete review of the Wisconsin model, see Trans. Am. Fish. Soc. 122(5).

Up to now, these models have performed well at predicting direct effects of environmental change on the consumption and growth of fishes. However, there are no explicit mechanisms for linking consumers with their prey (but see Madenjian et al. 1993). Feeding rate or growth is a required input to solve the energy budget. However, many environmental problems will affect predators indirectly through effects on their prey. For example, eutrophication, nutrient abatement, chemical pollution, thermal pollution, and climate change can affect production of lower trophic levels (e.g., Schindler et al. 1985; McQueen et al. 1986; Carpenter and Kitchell 1993; Porter et al. 1996, Zagarese et al. 1994). To predict the impact of these environmental effects, feeding rate needs to be an explicit, predicted function within the modeling framework.

0 Incorporation of an explicit feeding function is also important because studies of predator-
 prey relationships are making a transition from aggregated population level analyses of predator
 demand and prey supply (e.g., Stewart et al. 1981; Stewart and Ibarra 1991; Eby et al. 1995; Rand
 et al. 1995) to more detailed, spatially-explicit models of predator-prey interactions (e.g., Mason et
 al. 1995). These latter models scale up from individuals to populations while accounting for spatial
 5 heterogeneity in the biotic (e.g., prey distributions) and abiotic (e.g., temperature, light, and dissolved
 oxygen) environments.

 In this paper, we refine and calibrate a spatially-explicit, bioenergetics-based foraging model
 for kokanee salmon (*Oncorhynchus nerka*) (Bevelhimer 1990; Bevelhimer and Adams 1993) by
 incorporating an explicit and improved feeding function to link predator dynamics to prey density.
 10 Kokanee are well suited for this type of modeling approach because 1) they are extremely selective
 in their diet (e.g., Vinyard et al. 1982), 2) their prey are usually vertically stratified (e.g., Lampert
 1989), and 3) they exhibit strong diel vertical migrations through a range of temperatures (e.g.,
 Finnell and Reed 1969). Our goal was to develop a realistic and predictive model that could be used
 to study possible climatic and anthropogenic thermal effects on growth and production of kokanee.
 15 In addition to its utility for applied issues, the model provides a framework for examining basic
 foraging ecology of kokanee and other planktivorous fishes.

Methods

 We first describe the model of Bevelhimer and Adams (1993) and outline the comparison we
 20 make with the Wisconsin model. Results of this comparison are presented to introduce and justify the

refinements to Bevelhimer and Adams' model. We then outline further comparisons between the modified model and the Wisconsin model, and a preliminary sensitivity analysis of the modified model. Finally, we describe parameterization and calibration of the modified model using field data.

General model description

We adopted the bioenergetics model for kokanee developed by Bevelhimer and Adams (1993), from here on referred to as the "B&A" model. The B&A model was originally developed to test the growth maximization hypothesis for kokanee (Bevelhimer and Adams 1993). This hypothesis predicts that kokanee undergo diel migrations to maximize their net energy assimilation by maximizing food consumption and minimizing metabolic costs. Alternatively, Eggers (1978; sockeye) and Johnston (1990; kokanee) suggest diel migration by juveniles is a result of predator avoidance, whereas Clark and Levy (1988; sockeye) propose that migration results from a trade-off between predation risk and energetic efficiency. Results from Bevelhimer and Adams (1993) support the growth maximization hypothesis when kokanee and their prey are thermally segregated - vertical migration can be energetically advantageous under these conditions.

The B&A model is based on the bioenergetics mass balance equation (Kitchell et al. 1977):

$$[1] \quad G = C - (R + F + U),$$

where G = specific growth rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$), C = specific rate of consumption, R = specific rate of respiration (including basal and active metabolism, and specific dynamic action), F = specific rate of egestion, and U = specific rate of excretion. The B&A model differs from the Wisconsin model in

0 four important features: the B&A model 1) is constructed to estimate growth from consumption, 2)
models consumption as a type II functional response, modified by a temperature-dependent digestion
function, 3) is rescaled for a 30-min time step, and 4) allows fish to vertically migrate. Data
requirements for a 24-h simulation include vertical profiles of water temperature and prey density,
initial fish mass, time fish spends in each depth stratum, feeding status (feeding or not feeding) during
5 each 30-min time step, and mean prey size. A factorial combination of depths and feeding durations
is used to examine resultant growth from a suite of possible migration strategies for each given set
of environmental conditions.

Estimates of consumption and growth rates, and gross conversion efficiency from Bevelhimer
and Adams (1993) were within the range expected for similarly sized kokanee feeding at high rations
10 (Brett 1979). However, these model estimates have not been directly compared to field estimates or
results from other models. For the more mechanistic B&A model to be applied to the same range of
basic and applied questions that the Wisconsin model has proven useful, calibration and corroboration
are critical next steps.

To run a simulation, a fish of a given size is placed in a particular depth stratum with a
15 corresponding water temperature, prey density, and mean prey size. If the fish is feeding, the amount
of food consumed is determined as a function of prey density at that depth. At the end of the first 30-
min period, fish growth is determined by subtracting energetic losses from energy consumed (see
Table 1 of Bevelhimer and Adams (1993) for model equations), and the fish moves (or stays) to the
next depth stratum as indicated by model input. Any food remaining in the stomach at the end of the
20 time step is carried over to the next 30-min time step. Food consumed during this next time step,

0 dependent on feeding status and prey density at that depth, is added to any undigested food in the
stomach. If the amount of food in the stomach would exceed the stomach capacity (Table 1;
Bevelhimer and Adams 1993), then the fish is considered satiated, and consumption during the 30-
min period is set at the stomach capacity. As a result, food intake during a 30-min time step can be
lower than the amount determined by the functional response. The process of calculating growth is
5 repeated for this and all subsequent time steps. At the end of 24 h, growth is summed over all time
steps to provide an estimate of daily growth. Each 24-h simulation was run until a steady-state
(ending stomach content mass equal to beginning stomach content mass) was reached (Bevelhimer
and Adams 1993). Results from the steady-state runs were used in the analyses.

The Wisconsin model was also used to examine the bioenergetics of kokanee. This model has
10 been corroborated with independently derived estimates of consumption and energy budgets for three
populations of juvenile sockeye salmon (anadromous form of kokanee; Beauchamp et al. 1989).
Therefore, we were interested in any departures of the B&A model results from the Wisconsin model
results for a 24-h simulation, and we attempted to refine the B&A model to reconcile these
differences.

15 We evaluated the B&A model by comparing the daily scope for growth (energy available to
a fish after accounting for all energetic losses) and specific rates of consumption, respiration, egestion
and excretion of a 500-g kokanee to the Wisconsin model. The standard simulation of Bevelhimer
and Adams (1993) was initially used for the B&A model. Inputs to the model for the standard
simulation include 1) feeding duration of 12 h, 2) feeding swimming speed of $20 \text{ cm}\cdot\text{s}^{-1}$, and 3) 2.25-
20 mm prey (*Daphnia* sp). The model was run for 24 h over a range of temperatures ($4\text{-}25^{\circ}\text{C}$).

Maximum scope for growth was estimated by setting prey density to a saturation level (10^6 *Daphnia*·m⁻³) where the fish could feed at maximum rate (73 *Daphnia*·min⁻¹; Hyatt 1980). For the Wisconsin model (Hewett and Johnson 1992), parameters were taken from Beauchamp et al. (1989), with proportion (P) of maximum consumption (C_{\max}) set to 1.0. Growth and specific rates of consumption and losses were estimated over the same range of temperatures as the B&A model. The same *Daphnia* and kokanee caloric contents were used in each model (Table 1).

Results from the comparison of the two models showed a large discrepancy in daily scope for growth estimates. Daily scope for growth from the B&A model was an average of 42% lower than the Wisconsin model at temperatures $\leq 8^\circ\text{C}$, and an average of 239% higher at temperatures $\geq 12^\circ\text{C}$ (Fig. 1a). The B&A model predicted positive growth across all temperatures (4 - 25°C), with an optimum growth of $4.03\text{ g}\cdot\text{day}^{-1}$ at 16°C . The Wisconsin model predicted positive growth for temperatures $\leq 18^\circ\text{C}$, with an optimum growth of $3.17\text{ g}\cdot\text{day}^{-1}$ at 8°C (Fig. 1a).

The discrepancy in growth estimates can be attributed to much lower active respiration rates in the B&A model (Fig. 1b,c). Across all temperatures examined, respiration estimates from the B&A model were, on average, 43% lower than estimates from the Wisconsin model. The B&A model also estimated higher consumption rates and showed a plateau in consumption at higher temperatures (Fig. 1b), whereas the Wisconsin model predicted lower consumption rates as well as a drop in consumption at temperatures $> 18^\circ\text{C}$ (Fig. 1c).

All other components of the energy budget used in the B&A model (egestion and excretion; Bevelhimer and Adams 1993) were the same functions used in the Wisconsin model (Beauchamp et al. 1989). We therefore modified the respiration and consumption functions of the B&A model to

produce growth estimates comparable to the corroborated Wisconsin model.

Modified B&A model

Respiration - The respiration function of Beauchamp et al. (1989; from Hewett and Johnson 1992):

$$[2] \quad R = 0.00143 \cdot M^{-0.209} \cdot e^{(0.086 \cdot T)} \cdot ACTIVITY \cdot oxycal \cdot \frac{t}{t_{day}},$$

where R = respiration ($\text{cal} \cdot \text{g}^{-1} \cdot \text{t}^{-1}$), M = mass (g), T = temperature ($^{\circ}\text{C}$), $ACTIVITY = e^{(0.0234 \cdot VEL)}$ and is the increment for active metabolism, $VEL = 9.9 \cdot e^{(0.0405 \cdot T)} \cdot M^{0.13}$ and is the optimal swimming speed ($\text{cm} \cdot \text{s}^{-1}$), $oxycal$ = oxycaloric conversion factor ($\text{cal} \cdot \text{g}^{-1} \text{O}_2$), t = model time step (min), and t_{day} = length of day (min), was substituted into the B&A model (Table 1). Respiration was divided by 48 to convert from the daily time step of Beauchamp et al. (1989) to the 30-min time step of Bevelhimer and Adams (1993).

Functional response - Experiments have demonstrated that young sockeye from the Pacific northwest stop feeding as water temperature approaches their upper tolerance limit ($\geq 23^{\circ}\text{C}$; Donaldson and Foster 1940; Brett 1952; Brett et al. 1969). We therefore concluded that the asymptote in consumption at the highest temperatures in the B&A model (Fig. 1b) was inappropriate for western North American stocks. To correct this, the amount of *Daphnia* biomass consumed in each time step was modified by Thornton and Lessem's (1978) temperature function (Beauchamp et al. 1989; Table 1). Application of the Thornton and Lessem function was scaled with reference to

0 10°C because the functional response used in the B&A model was derived at this temperature (Hyatt
1980; Bevelhimer and Adams 1993). Furthermore, the function was applied to the biomass of
Daphnia consumed, and not the number consumed, because the function coefficients were derived
using biomass measurements (Beauchamp et al. 1989).

Sensitivities of the Wisconsin model parameters are well known (Kitchell et al. 1977; Bartell
5 et al. 1986). Therefore, we did not perform sensitivity analyses on the components of the modified
B&A model shared with the Wisconsin model. However, we did perform a preliminary sensitivity
analysis of the modified B&A model on the unshared components. The new model was run using two
sizes of kokanee (100 and 500 g), three feeding durations (6, 12, and 18 h), and three prey sizes
(1.75, 2.25, and 2.75 mm). Results were compared with the Wisconsin model across the same
10 temperature range and maximum feeding rates used in the initial comparison.

Results from this comparison suggested one of two possibilities: either 1) there should be
large differences in time spent foraging (~6 h) between 100 and 500-g fish, or 2) there are
shortcomings in the consumption function. For the latter, consumption is the only plausible function
to criticize as respiration, egestion, and excretion are identical in both models, and differences in SDA
15 are both minimal and dependent on the amount of food consumed. Furthermore, the functional
response used in the B&A model (Hyatt 1980) was derived from feeding experiments using a single
size-class of kokanee (15 g) at 10°C, and did not include the possibility of size-dependence in
foraging rate. Because work on other fishes suggests predator size can influence their functional
response (Werner 1977; Miller et al. 1992, 1993; Walton et al. 1994), we pursued modification of
20 the functional response.

We scaled the functional response to predator size through volume searched using the following form of a Holling type II functional response:

$$[3] \quad C = \frac{E \cdot Z}{1 + E \cdot Z \cdot h} \cdot 60 \quad ,$$

where C is consumption ($Daphnia \cdot min^{-1}$), E is volume searched (m^3), Z is *Daphnia* density (m^{-3}), and h is handling time ($s \cdot Daphnia^{-1}$; Table 1). Volume searched, E , was taken from Gerritsen and Strickler (1977):

$$[4] \quad E = \frac{\pi \cdot R_d^2}{3} \cdot \frac{(3 \cdot v^2 + u^2)}{v} \quad ,$$

where R_d is the reaction distance of kokanee to their prey (m), v is kokanee swimming speed ($m \cdot s^{-1}$), and u is *Daphnia* swimming speed ($m \cdot s^{-1}$; Table 1). Kokanee swimming speed is size- and temperature-dependent and is determined from the VEL component of the respiration function (Eq. 2; Table 1). We assumed that during feeding 100% of the *Daphnia* encountered by kokanee are ingested (Hyatt 1980, Vinyard et al. 1982).

To calibrate the functional response, Equations 3 and 4 were used to predict consumption at the prey densities, fish size (15 g), and water temperature (10°C) used in the experiments of Hyatt (1980). Handling time was taken from the maximum consumption observed by Hyatt ($\approx 50 Daphnia \cdot min^{-1}$ or $1.2 s \cdot Daphnia^{-1}$). Predictions from Equations 3 and 4 under these conditions were then compared to the results of Hyatt (1980).

The new functional response scales for body size in two ways. First, increased body size

0 increases swimming speed, thus directly influencing the volume searched E (Eq. 4). The second
possible influence is handling time differences among fish size-classes. No handling time data were
available so a range of values were used (Table 1). Reaction distance was assumed to be constant
across the size-classes because the literature suggests reaction distances in other visually feeding
planktivorous fishes increase greatly during very early development, but then diminish beyond a
5 certain size - usually within the first year of life (e.g., Breck and Gitter 1983; Rahmann et al. 1989;
Wahl et al. 1993). Therefore, the mean reaction distance of 15-g kokanee from Hyatt (1980) was
assumed to represent the reaction distance of larger fish (Table 1). We examined the sensitivity of the
functional response to changes in fish body size (i.e., volume searched) and handling time.

10 **Model Parameterization and Simulations**

Growth estimates from the modified model were dependent on model inputs (predator and
prey sizes, feeding duration, handling time). As a result, various combinations of model inputs could
be used to generate growth estimates similar to the Wisconsin model. We therefore compared
estimates of growth from the modified B&A model with observed growth of age-1, -2, and -3
15 kokanee from Blue Mesa Reservoir, Gunnison, CO (Cudlip et al. 1987). Inputs to the model included
observed vertical profiles of temperature and *Daphnia* densities from 1994, mean prey size from
kokanee stomachs sampled in 1995, and observed masses of fish from 1995. Limnological data from
1994 were used because these data were collected at a finer spatial and temporal resolution than in
1995. However, much more fish growth data were available from 1995 than 1994. Because
20 comparisons of temperature profiles, prey densities and distributions, and kokanee growth collected

0 in both years showed similar patterns (Johnson et al. 1995, 1996), we assumed results would not be compromised by using input from the two different years.

For simulations of each age-class, a range of feeding durations and handling times were used. The goal was not necessarily to match modeled growth with observed - inputs can be adjusted to generate matching results. Rather, the goal was to bound the estimates using a more mechanistic
5 approach than the more commonly used Wisconsin model. Incorporating feeding mechanisms should then clarify which factors are most important to understanding kokanee growth, and how these factors might direct future field and laboratory work.

Blue Mesa Reservoir (BMR) is a mesotrophic, 3 700 ha, 32 km long impoundment in southwestern Colorado with a storage capacity of $1.16 \times 10^9 \text{ m}^3$. The fish community of BMR is
10 relatively simple, consisting of primarily kokanee, rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), and longnose sucker (*Catostomus catostomus*). Kokanee is the dominant fish species. However, the population has been steadily declining over the past three years with a concomitant increase in the lake trout population (Sherman Hebein, Colorado Division of Wildlife, unpublished data).

15 Thermal profiles of BMR were obtained using a Yellow Springs Instruments Model 58 meter with a 60-m probe cable. Measurements were taken at 1-m intervals from 0 to 20 m and at 5-m intervals from 20 to 55 m, from May through September 1994.

Zooplankton were collected by oblique tows using a Wildco model 37-315 Clark-Bumpus plankton sampler with a 130-mm diameter opening and a 153- μm net. The flowmeter on the Clark-
20 Bumpus sampler was calibrated using a Schwaiffer water velocity meter. Two replicate samples were

0 taken from each of 0-5, 5-10, 10-15, and 15-30-m strata on 21 May 1994. During June-September 1994 three replicate samples were collected every two to three weeks from each of 0-5, 5-10, and 10-15-m strata, and two replicates from the 15-30-m stratum. All samples were taken between the hours of 09:00 and 12:00, and preserved in 8% sugared, buffered formalin.

5 A 1-mL aliquot was taken from each sample using a Hensen-Stempel pipette. The aliquot was placed in a Sedgwick-Rafter cell where all *Daphnia* were identified to species and enumerated (Lind 1979; Soranno and Knight 1993) under a compound microscope. The first 24 individuals encountered in each sample were measured with an ocular micrometer to the nearest 0.01 mm. Two aliquots from each replicate sample were processed.

10 Densities of *Daphnia* ≥ 1.0 mm in each stratum (m^{-3}) were used as prey input to the model because 1) kokanee feed exclusively on *Daphnia* in BMR (97% *D. pulex* and 3% *D. galeata*; Johnson et al. 1995, 1996), and 2) the original functional response used by Bevelhimer and Adams (1993) was a function of the density of *Daphnia* ≥ 1.0 mm (Hyatt 1980).

15 Mean length of each age-class of kokanee in 1995 was estimated from otolith samples obtained on 8 June (age-1, $n=11$; age-2, $n=20$; age-3, $n=8$) and 26 July (age-1, $n=22$; age-2, $n=33$; age-3, $n=16$) from fish sampled in vertical gill nets and angler's creels (Martinez 1996). Mean length at the end of the growing season was estimated from backcalculations (age-1, $n=123$; age-2, $n=54$; Johnson et al. 1996) and from otoliths of fish in the spawning run (age-3, $n=163$; Martinez 1996). Wet masses were computed using a length-mass regression ($r^2 = 0.95$, $n=228$) developed from all fish sampled in vertical gill nets during June through September (Johnson et al. 1996). We computed the
20 instantaneous daily growth rate (G) and interpolated masses (M) between fish sampling dates using

the formula:

$$[5] \quad M_1 = M_0 \cdot e^{Gt}$$

where M_1 = final mass (g), M_0 = initial mass, and t = number of days between sampling dates (for G) or number of days to the interpolated mass (for M). We estimated daily growth rates (DGR; g·d⁻¹) on limnological sampling dates from the equation:

$$[6] \quad DGR = \frac{M_0 \cdot e^{Gt} - M_0}{t}$$

where M_0 = mass at the start of the day, and $t = 1$ d.

Vertical profiles of temperature and *Daphnia* (≥ 1.0 mm) densities from a reference station in Sapinero Basin, the largest and most downstream basin of BMR, were used as inputs to the model (Table 1). Three dates were chosen from the 1994 sampling period to represent seasonal fluctuations in temperature and prey availability. Because mature BMR kokanee typically begin their spawning migration in September, we did not use September sampling dates for the simulations.

Temperature data on each limnological sampling date, t_{lim} , were averaged into seven depth strata: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, and 30-50 m. *Daphnia* densities from the zooplankton sampling were assigned to these strata accordingly. The observed densities from the 15-30-m strata were consistently low and were assigned to each of the 15-20, 20-25, 25-30, and 30-50-m strata. The 30-50-m stratum was used to allow kokanee access to deeper, colder water despite no routine zooplankton sampling at these depths. Few *Daphnia* were found in zooplankton samples collected from 40 and 50 m in July 1994 and 1996 (BMJ, unpublished data), indicating extrapolation of

Daphnia densities from the 15-30-m stratum to these depths is a reasonable assumption. Additionally, data from experimental vertical gill nets set in BMR in 1994 and 1995 show that kokanee do reside at these depths at times (Johnson et al. 1995, 1996).

Daphnia do not vertically migrate in BMR (Johnson et al. 1995). Therefore, the vertical distribution of *Daphnia* used as model input for each 24-h simulation was held stationary.

Fish were allowed to locate at two depths (feeding and non-feeding periods) in each 24-h simulation. Depths were the mid-points of the strata identified above (2.5, 7.5, 12.5, 17.5, 22.5, 27.5, and 40 m). All possible migration strategies were evaluated (7 depth strata = 28 different migration strategies). The migration strategy that maximized growth on each limnological sampling date (t_{lim}) was noted, and that growth was used in the comparison with the observed growth estimates on that date.

The mean size of *Daphnia* in the diets of BMR kokanee in 1995 (1.68 mm; Johnson et al. 1996) was used to convert consumption from numbers to biomass (Table 1). Mean size consumed did not differ across the season or age-classes (BMJ, unpublished data). Initial masses of each kokanee age-class were determined for day $t_{lim}-1$ using Equation 5. Very little information on kokanee feeding duration and prey handling times was available in the literature, but initial growth estimates from the model appeared to be sensitive to these parameters. We performed simulations at seven different feeding durations (4, 6, 8, 10, 12, 14, and 16 h) and five different handling times (0.33, 0.5, 0.67, 1.0, and 1.2 s $\cdot Daphnia^{-1}$) to evaluate the sensitivity of the modified model to these parameters. We used observed growth $\pm 20\%$ as our criteria for determining which combinations of feeding durations and handling times were realistic.

Results

Modified B&A model

For a 500-g kokanee under standard simulation conditions, application of the respiration function of Beauchamp et al. (1989) and the Thornton and Lessem (1978) temperature function greatly improved the performance of the B&A model when compared to the Wisconsin model. The combination of higher respiration rates (identical to the Wisconsin model) and the decline in consumption at higher temperatures (Fig. 1d) brought estimates of scope for growth in line with estimates from the Wisconsin model for temperatures $> 10^{\circ}\text{C}$ (Fig. 1a). Growth estimates at low temperatures were still less than the Wisconsin model - a result of lower consumption in the modified B&A model at these temperatures (Fig. 1d).

Scope for growth varied considerably with fish size and feeding duration when prey size (2.25-mm *Daphnia*) was held constant (Fig. 2a,b). For a 500-g kokanee, a 12-h feeding duration best fit growth estimates from the Wisconsin model (mean squared error, $\text{MSE} = 0.82$; Fig. 2a). A 6-h feeding period resulted in lower estimates across the entire temperature range ($\text{MSE} = 3.97$), while an 18-h feeding period resulted in higher estimates ($\text{MSE} = 5.85$; Fig. 2a). Temperature for optimum growth also shifted with changes in feeding duration. The more feeding duration was restricted, the lower the optimum temperature (Fig. 2a). This is expected from the B&A model - as food becomes limited, simulated fish minimize energy costs by using colder water (Bevelhimer and Adams 1993). This has also been demonstrated empirically (Crowder and Magnuson 1983). For the 100-g kokanee, a 6-h feeding duration best matched growth estimates from the Wisconsin model ($\text{MSE} = 0.10$; Fig. 2b). Feeding periods of 12 and 18 h both overestimated scope for growth ($\text{MSE} = 1.27$ and 4.27 ,

0 respectively). Again, a decrease in optimum temperature for growth occurred with decreasing feeding durations (Fig. 2b).

When prey size and feeding duration were varied simultaneously, and fish were held at their optimum temperature for growth, results differed for the two fish sizes. Increasing prey size from 1.75 to 2.75 mm (an increase in *Daphnia* mass of nearly 400%) for the 100-g fish resulted in relatively small increases in growth (average across feeding durations = 12%; Fig. 2d). Much larger increases occurred when feeding time was increased from 6 to 18 h (average across prey sizes = 218% increase). For the 500-g fish, an increase in prey size from 1.75 to 2.75 mm translated to an average increase in growth of 458% (Fig. 2c). Increasing feeding duration for the larger fish also increased growth rates by over one order of magnitude (average of 1033%; Fig. 2c).

10 Estimates of consumption ($Daphnia \cdot min^{-1}$) from the functional response using Equations 3 and 4 for a 15-g kokanee, feeding at 10°C with a handling time of 1.2 s $Daphnia^{-1}$, fell within the 95% confidence intervals of the experimental data of Hyatt (1980; Fig. 3a). Consequently, we assumed that the new functional response (Eqs. 3 and 4) was adequate to describe foraging of a 15-g kokanee under these conditions, and that it could then be scaled for body size effects via size-dependent search volume. A complete list of equations used in the modified B&A model is listed in Table 1.

Consumption rate estimates from the new functional response were much more sensitive to handling time than fish body size (Fig. 3b). The asymptote of consumption rate decreased by 70% (from 166 to 49 $Daphnia \cdot min^{-1}$) when handling time was increased 260% (from 0.33 to 1.2 s $Daphnia^{-1}$), whereas there was very little difference in consumption rate with a 90% reduction in

body size (from 573 to 59 g; Fig. 3b).

Model Calibration

Surface temperatures in Sapinero Basin in 1994 ranged from a low of 13°C on 21 May to a high of 20°C on 18 August (Fig. 4). Hypolimnetic temperatures generally stayed near 5°C throughout the season. Despite these vertical gradients, a strong thermocline was not apparent on any of the sampling dates (Fig. 4).

The abundance of *Daphnia* ≥ 1.0 mm in the upper 10-m of the water column remained high throughout the season, accounting for 91% of all *Daphnia* in this size-class in the water column (Fig. 4). Maximum densities never fell below 9 100 m⁻³ (21 May), while the highest recorded density exceeded 17 300 m⁻³ (21 July; Fig. 4). These maximum densities were well above densities required to saturate the functional response for each handling time (Fig. 3).

Growth rates of kokanee collected from BMR in 1994 and 1995 were relatively high. Mean length of BMR kokanee at age-1 (170 mm; Johnson et al. 1996) was greater than backcalculated length at age-1 reported in other lakes throughout the western United States (range = 78-156 mm, n = 8; Bjornn 1961; Bowler 1976; Bowler 1979; Cordone et al. 1971; Clark and Traynor 1972; Hanzel 1974a,b). Age-2 and -3 BMR kokanee each had the second largest length at age (264 and 335 mm, respectively; Johnson et al. 1996) when compared to similarly aged fish throughout the west (age-2, range = 154-319 mm, n = 8; age-3, range = 209 - 362 mm, n = 7; Bjornn 1961; Bowler 1976; Bowler 1979; Cordone et al. 1972; Clark and Traynor 1972; Hanzel 1974a,b). Daily growth estimates of BMR kokanee ranged from 0.41 to 1.39 g·day⁻¹ for age-1 fish, 0.52 to 2.66 g·day⁻¹ for age-2 fish,

0 and 1.85 to 2.40 $\text{g}\cdot\text{day}^{-1}$ for age-3 fish (Fig. 5). All three age-classes showed a drop in daily growth over the second half of the field season (Fig. 5).

Simulations using the modified model (Table 1) and observed data from BMR (Figs. 4 and 5) corroborated results from earlier evaluations (Figs. 2 and 3). Daily growth estimates from the model indicated that different foraging strategies should be employed by different age-classes, but that these optimal strategies change seasonally with changes in prey and temperature distributions and fish body size.

Early in the growing season (10 June), daily growth estimates of age-1 kokanee were more sensitive to changes in feeding duration than to changes in handling times (Fig. 6a). Using the mean growth rate across all handling times for each of the 4 (0.66 $\text{g}\cdot\text{d}^{-1}$) and 16-h (1.69 $\text{g}\cdot\text{d}^{-1}$) feeding durations (Fig. 6a), the range in daily growth estimates was 163% of the observed growth (0.80 $\text{g}\cdot\text{d}^{-1}$). Using the mean growth rate across all feeding durations for each of the 1.2 $\text{s}\cdot\text{Daphnia}^{-1}$ (1.22 $\text{g}\cdot\text{d}^{-1}$) and 0.33 $\text{s}\cdot\text{Daphnia}^{-1}$ (1.39 $\text{g}\cdot\text{d}^{-1}$) handling times, the range in daily growth estimates was only 21% of the observed growth. Similar comparisons for age-2 and -3 kokanee showed that modeled growth of age-2 fish was also more sensitive to feeding duration than to handling time (90 versus 36%, respectively; Fig. 6b), whereas modeled growth of age-3 fish was more sensitive to handling time than to feeding duration (151 versus 127%, respectively; Fig. 6c). Based on observed daily growth estimates ($\pm 20\%$), model simulations for 10 June suggest that age-1 kokanee should feed between 4 and 6 $\text{h}\cdot\text{d}^{-1}$, age-2 between 12 and 16 $\text{h}\cdot\text{d}^{-1}$, and age-3 between 8 and 16 $\text{h}\cdot\text{d}^{-1}$, depending on the handling time (Fig. 6).

20 The model also indicated a progression in kokanee migration strategies for 10 June. Age-1

0 fish were predicted to feed at the surface and migrate the least, age-2 fish were predicted to feed at or near the surface and migrate slightly deeper than age-1 fish, and age-3 fish were predicted to feed below the surface and migrate the deepest (Fig. 6). Within each age-class, foraging occurs higher in the water column and migration distances decrease with increases in feeding durations and/or decreases in handling times (Fig. 6).

5 Daily growth estimates from the modified B&A model for age-1 kokanee during the middle of the growing season (21 July) were again more sensitive to feeding duration than to handling time. Increasing feeding duration from 4 to 16 h changed daily growth by 135% compared to observed growth, whereas decreasing handling time from 1.2 to 0.33 *s·Daphnia*⁻¹ changed daily growth by 47% (Fig. 7a). Results (not shown) from simulations using the starting mass for age-1 fish on 10 June (60
10 g) for the 21 July input data (Fig. 4) were qualitatively similar to growth estimates from 10 June. This indicates that the increasing (decreasing) sensitivity of growth rates to handling time (feeding duration) for age-1 fish is a result of increased body size rather than differences in the prey and temperature distributions on the two dates. Model growth rate estimates for age-2 fish on 21 July were nearly equally sensitive to changes in feeding duration and handling time (71 versus 61%,
15 respectively; Fig. 7b). Age-3 fish were more sensitive to handling time than to feeding duration (140 versus 96%, respectively; Fig. 7c), similar to simulation results for 10 June (Fig. 6c).

Comparisons of modeled growth estimates with observed estimates ($\pm 20\%$) on 21 July show that an increase in the amount of time spent feeding (compared to 10 June) was necessary for all age-classes to bound observed growth (Fig. 7). Age-1 fish needed to feed 6 to 12 $\text{h}\cdot\text{d}^{-1}$ to grow the
20 observed $1.39 \pm 0.28 \text{ g}\cdot\text{d}^{-1}$, age-2 fish 14 to 16 $\text{h}\cdot\text{d}^{-1}$ to grow $2.66 \pm 0.53 \text{ g}\cdot\text{d}^{-1}$, and age-3 fish 10 to

0 16 h·d⁻¹ to grow 2.4 ± 0.48 g·d⁻¹ (Fig. 7). If the handling time of age-3 fish was restricted to ≥ 0.5
 s·*Daphnia*⁻¹, their modeled growth would only approach the observed estimate if they fed for 16 h·d⁻¹,
 demonstrating the importance of an accurate handling time estimate for larger fish (Fig. 7c).
 Furthermore, simulations using the Wisconsin model for age-1 and -2 kokanee on this date show that
 these fish could not reach their observed growth when allowed to feed at maximum consumption (P
 5 = 1.0) at their optimum temperature (Fig. 7a, b).

In general, results from the modified B&A model also show that age-1 fish should forage at
 and migrate to deeper depths on 21 July than on 10 June. Age-1 fish will also feed closer to the
 surface and migrate less with increased feeding durations and/or decreased handling times. The
 migration strategy of age-2 fish was to feed and migrate deeper than on 10 June. However, their
 migration strategy generally remained unchanged on 21 July regardless of feeding duration or
 10 handling time (Fig. 7b). The migration strategy of age-3 fish on 21 July remained unchanged with
 feeding duration, but changed drastically with different handling times. For example, these fish
 migrated from 7.5 to 40 m with a handling time of 0.33 s·*Daphnia*⁻¹. At the highest handling times,
 they did not migrate, remaining at 40 m depth (Fig. 7c).

15 Results from model simulations for 18 August show that growth of age-1 fish was still more
 sensitive to feeding duration than to handling time (442% versus 212%, respectively; Fig. 8a), but
 that the difference was smaller than previous dates. Model growth of age-2 and -3 fish was more
 sensitive to changes in handling time than to changes in feeding duration (398% versus 336%,
 respectively, for age-2; 142% versus 24%, respectively, for age-3; Fig. 8b, c). Depending on handling
 20 time, age-1 kokanee needed to feed between 6 and 14 h·d⁻¹ to bound the observed growth rate, age-2

0 between 6 and 16 $\text{h}\cdot\text{d}^{-1}$, and age-3 between 12 and 16 $\text{h}\cdot\text{d}^{-1}$ (Fig. 8). The required feeding duration of age-2 fish dropped dramatically - a result of the substantial drop in the observed growth rates (from > 2.5 to $< 1.0 \text{ g}\cdot\text{d}^{-1}$; Fig. 5b).

Optimal migration strategies for 18 August, when surface water temperature was highest, show that age-1 fish will feed at and migrate to deeper depths than on 21 July. However, migration strategies within this age-class did not change very much with feeding duration or handling time (Fig. 5 8a). Migration strategies for age-2 and -3 fish are similar to their respective migration patterns on 21 July (Fig. 8b,c).

Discussion

10 In this study, we have modified the original B&A model to provide comparable results to the corroborated Wisconsin model, and to calibrate the new model using field observations. The process of evaluating the sensitivity of the model and identifying combinations of inputs that bounded observed growth uncovered some interesting predictions about the foraging ecology of kokanee. First, the model predicted an ontogenetic shift in foraging strategy when kokanee reached approximately 300 g. Foraging strategies of kokanee $< 300 \text{ g}$ should be to increase their feeding time, while strategies for fish $> 300 \text{ g}$ should be to reduce their handling times. This shift in feeding strategy is a result of changing stomach capacities of the fish. If we assume that consumption of larger prey is equivalent to more efficient consumption of smaller prey, then the preliminary sensitivity analysis (Fig. 2c, d) demonstrates the relationship between stomach capacity and foraging strategy. While 15 feeding on the smallest prey sizes (1.75 mm), the stomach capacity of smaller fish was reached 20

quickly while consuming at maximum rates. The only way to increase consumption (i.e., growth) is to spend more time feeding. Conversely, larger fish were not limited by stomach capacity while feeding on 1.75-mm *Daphnia*. Therefore, increasing prey size to 2.25 mm (or increasing the rate at which 1.75-mm *Daphnia* are consumed) resulted in a much larger increase in growth.

Second, the model results suggested that age-3 kokanee required very short handling times (0.33 s·*Daphnia*⁻¹) to allow sufficient consumption rates to match their observed daily growth later in the season. Laboratory observations made by Hyatt (1980) demonstrated that age-0 kokanee are particulate feeders. However, it is difficult to accept that kokanee could feed on 3 *Daphnia*·s⁻¹ with this feeding mode. Such a short handling time suggests the ability to forage by gulping and/or filtering, and simple calculations show that this hypothesis is tenable. Mouth gape area measurements made on adult kokanee (mean mass 511.2 g) collected from BMR averaged 0.0004 m² (JDS, unpublished data). At 10°C, these fish have an optimum swimming speed of 0.33 m·s⁻¹ (Beauchamp et al. 1989, Table 1). Using mean prey density of 17 500 *Daphnia*·m⁻³ (maximum observed densities in BMR; Fig. 4), and the equation

$$[4] \quad \text{HandlingTime} = \frac{1}{\text{MouthArea} \cdot \text{SwimmingSpeed} \cdot \text{PreyDensity}},$$

potential *in situ* handling time is estimated to be 0.43 s·*Daphnia*⁻¹. Given the integrated nature of zooplankton samples collected by the Clarke-Bumpus, it is likely that kokanee can experience much higher densities than 17 500 *Daphnia*·m⁻³ in BMR. Consequently, handling time could easily reach 0.33 s·*Daphnia*⁻¹.

While Hyatt (1980) did not observe filter feeding in kokanee during feeding experiments using

0 *Daphnia* spp., maximum prey densities used in his experiments were 2 000 m⁻³, compared to epilimnetic densities of 9 000 to 17 500 m⁻³ in BMR. We are not aware of any other studies that have specifically examined the foraging behavior of kokanee at such high zooplankton densities. Some studies have indicated that prey intake by other planktivorous fishes can be maximized by switching from particulate to filter feeding when prey concentrations exceed some critical threshold (e.g.,
5 Gibson and Ezzi 1992).

Third, when allowed to feed for 16 h (midsummer day length) in the modified model, age-1 BMR kokanee were predicted to have maximum growth rates nearly double the maximum scope for growth estimate (at the optimum temperature) from the Wisconsin model (Figs. 6a-8a). In this case, only a small portion of the difference (~10%) can be attributed to the energetic efficiency of vertical
10 migration - smaller fish are more tolerant of warmer water and therefore not as restricted in their upper thermal range compared to larger fish. Rather, the differences in predicted growth rates are a result of the differences in maximum consumption rate in each model.

The discrepancy points out the need to accurately extrapolate from laboratory feeding experiments to feeding behavior in the field. This is an important issue given the exciting
15 technological advances in spatially-explicit modeling of predator-prey interactions (Brandt et al. 1992; Mason and Patrick 1993, Mason et al. 1995). We suspect that feeding rate predictions differ due to different time scales used in each model. In the modified B&A model, fish feed in 30-min time steps. Maximum consumption over 24 h is determined by feeding duration, stomach capacity, and gastric evacuation rate. Additionally, the functional response was derived at a 1-min time scale with fasted
20 fish, and therefore motivation to feed is maximal in the model as long as there is any unfilled stomach

0 volume. Because satiation does not enter directly into the calculation of *in situ* feeding rate, long feeding durations may predict unrealistic daily consumption rates in the modified model. However, Godin (1981) experimentally demonstrated that feeding rates of juvenile pink salmon (*O. gorbuscha*), after satiation, were approximately equal to their gastric evacuation rate. More work is needed to determine the importance of satiation on the functional response of age-1 and older kokanee .

5 In the Wisconsin model, maximum daily consumption rate was derived from feeding experiments where fish were fed excess rations three times a day (Brett et al. 1969, Brett 1971). It is not clear how scaling three distinct feeding bouts to 24 h might affect maximum daily consumption estimates, compared to a more continuous feeding regime typical of a pelagic planktivore. Furthermore, results of feeding experiments using pelleted food may not be applicable to fish in the
10 wild (Beauchamp et al. 1989). Beauchamp et al. (1989) state that their model of maximum consumption should be considered an hypothesis. In light of our results, we hypothesize that maximum consumption rates of age-1 kokanee (< 150 g) can be considerably higher than previously predicted by the Wisconsin model.

15 Alternatively, Luecke and Brandt (1993) found that rainbow trout increased the mass of *Daphnia* in their stomachs by reducing (squeezing out) the water content of their prey. This effectively doubled the energy density of the *Daphnia*. If kokanee are capable of this, then our model would overestimate the feeding durations and/or underestimate the prey handling times required to bound observed growth. It would also explain why growth estimates from the Wisconsin model required a $P > 1.0$ to approach observed growth of age-1 and -2 kokanee in July. However, even
20 doubling growth estimates from our modified model for age-3 kokanee in August would still require

0 a feeding rate of 3 *Daphnia*·s⁻¹ to approach observed growth.

Finally, the model predicted ontogenetic shifts in migration strategies at both seasonal and annual time scales - consistent with expectations from the bioenergetics principle that thermal optima are mass-dependent. As the growing season progressed, age-1 fish in the modified model fed at greater depths and migrated longer distances. Age-2 and -3 fish showed similar but weaker patterns
5 for the first half of the growing season. Across age-classes, the model demonstrated that older fish tend to feed at and migrate to greater depths at any given point in time.

For all simulations, we kept kokanee reaction distance constant (0.08 m) regardless of feeding depth. This is an unlikely assumption given the changes in light level with depth at both diurnal and seasonal time scales. Based on secchi depths for Blue Mesa Reservoir on the three simulation dates
10 (2.9, 3.9, and 5.6 m for June, July, and August, respectively; BMJ, unpublished data), calculated changes in percentage transmission of surface light from a depth of 2.5 to 12.5 m as a function of secchi depth (Wetzel 1983), and measured reaction distances of several fish species over a range of light intensities (O'Brien 1979), we reduced kokanee reaction distance to 0.04 m and ran several simulations across the three simulation dates. Decreased reaction distance did not affect model
15 growth rates of smaller kokanee because their smaller stomach capacities were saturated at the high prey densities. However, model growth rates of fish that were predicted to maximize growth by feeding at 12.5-m depth (age-2 kokanee in August, and age-3 model kokanee in July and August) were reduced two to five times. Consequently, the optimum migration strategies in these cases shifted to feeding depths of < 10 m, where light levels and reaction distances would be presumably greater.
20 However, growth rates would be lower than initial simulations (reaction distance 0.08 m) because

0 of warmer temperatures at these feeding depths. This is particularly important to note for age-3 fish
in August, where the gap between observed and model growth would widen, enforcing the notion
that these fish might have to feed at a greater rate and/or for longer periods of time. Future
modifications to the functional response to include the effects of light levels on reaction distance
would add another level of sophistication to the model, and might provide more insights into the
5 foraging ecology of kokanee.

We have been sampling kokanee with both experimental vertical gill nets and sonar since 1993
to examine diets and to estimate population abundances. The sampling designs employed do not
provide adequate temporal resolution and coverage to appropriately test our model predictions of
migratory behavior. Other studies have found similar differences between day and night vertical
10 distributions of kokanee (e.g., Finnell and Reed 1969; Maiolie and Elam 1996), although these
patterns are not ubiquitous and may even be reversed (e.g., Chapman and Fortune 1963; Levy 1991).
A comprehensive series of diel surveys in BMR is planned for the 1997 field season to corroborate
model predictions.

The model predictions, while not fully tested in this study, demonstrate the predictive
15 capabilities that are possible by adding more ecological realism to the bioenergetics framework.
Despite enjoying wide use, application, and in a few cases corroboration (Hanson et al. 1993; Ney
1993), the Wisconsin model lacks some of this ecological realism. Ecosystem managers need
predictive models to forecast individual responses and community and ecosystem consequences of
natural and anthropogenic environmental change. In reservoirs, climate and water management
20 interact to determine stratification patterns, with obvious implications for lentic biota. In response to

0 the increasing demand on reservoir water in the western United States to serve an expanding range
of purposes, traditional reservoir operation schedules are being changed. Large releases to simulate
natural floods for downstream habitat restoration (Wuehrich 1996), periodic releases to help
transport salmon smolts to the ocean (Berggren and Filardo 1993), and spring releases to mimic a
natural snowmelt hydrograph and improve spawning conditions for endangered Colorado River fishes
5 (Tyus 1992) all are significant departures from historic operations. Few, if any studies have addressed
the upstream (reservoir) effects of these new operation strategies.

Our intent in further developing the B&A approach was to generate a modeling framework
that was sufficiently realistic and accurate to predict effects of seasonal variation in vertical gradients
of temperature and prey density on kokanee growth, behavioral response, and population
consumption demand. It is reasonable to hypothesize that changing reservoir operations could alter
10 temperature and prey stratification, imposing constraints on kokanee depth distribution, especially
in reservoirs such as BMR that are near the upper thermal limit for kokanee. Consequences might
include reduced access to predominately epilimnial zooplankton resources, reduced scope for growth,
and increased spatial and temporal overlap with, and hence, predation risk from the primary piscine
15 predator, the lake trout (e.g., Martinez and Wiltzius 1995). The modeling framework further
developed here provides the means to predict the effects of reservoir stratification scenarios on fish
behavior and growth, and as such, could be a powerful tool for understanding the ecological effects
of anthropogenic environmental change.

Acknowledgments

Mark Bevelhimer graciously provided a copy of his spreadsheet kokanee model. Krista Bonfantine, Blake Byall, Cory Counard, Derrek Faber, Brian Herwig, Glenn Szerlong, Mike Wise, and a host of other excellent student helpers collected and/or processed the data for Blue Mesa Reservoir. Patrick Martinez of the Colorado Division of Wildlife provided field assistance, and supplied kokanee growth data. Rick Harris (NPS), Steve Hiebert (USBR), and Gordon Mueller (USGS-BRD) provided logistical support in the field. Comments by Dave Beauchamp, Mark Bevelhimer, Jim Kitchell, Patrick Martinez, Doran Mason and an anonymous reviewer greatly improved earlier versions of this manuscript. This study was supported by funds from the U.S. Bureau of Reclamation, Grand Junction Projects Office, Colorado.

References

- Bartell, S.M., Breck, J.E., Gardner, R.H., and Brenkert, A.L. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. *Can. J. Fish. Aquat. Sci.* **43**:160-168.
- Beauchamp, D.A. , Stewart D.J., and, Thomas, G.L. 1989. Corroboration of a bioenergetics model for sockeye salmon. *Trans. Am. Fish. Soc.* **118**:597-607.
- Berggren, T.J., and Filardo, M.J. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River Basin. *N. Am. J. Fish. Manage.* **13**:48-63.
- Bevelhimer, M.S. 1990. Habitat selection by kokanee salmon and smallmouth bass in thermally heterogeneous environments: the importance of growth maximization to diel habitat shifts. Ph.D. thesis, University of Tennessee, Knoxville, TN.
- Bevelhimer, M.S., and Adams, S. M. 1993. A bioenergetic analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka*. *Can. J. Fish. Aquat. Sci.* **50**:2336-2349.
- Bjornn, T.C. 1961. Harvest, age structure, and growth of game fish populations from Priest and Upper Priest Lakes. *Trans. Am. Fish. Soc.* **90**:27-31.
- Bowler, B. 1976. Lake Pend Oreille kokanee life history studies. Idaho Department of Fish and

Game. Lake and Reservoir Investigations, Job Performance Report F-53-R-11; Job IV-e.

Bowler, B. 1979. Kokanee life history studies in Priest Lake. Idaho Department of Fish and Game. Lake and Reservoir Investigations, Job Completion Report. F-73-R-1; Job III.

Brandt, S.B., Mason, D.M., and Patrick, E.V. 1992. Spatially-explicit models of fish growth rate. Fisheries 17:23-35.

Breck, J.E., and Gitter M.J. 1983. Effect of fish size on the reaction distance of bluegill (*Lepomis macrochirus*) sunfish. Can. J. Fish. Aquat. Sci. 40:162-167.

Brett, J.R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Bd. Canada 9:265-323.

Brett, J.R. 1971. Satiation time, appetite, and maximum food intake of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 28:409-415.

Brett, J.R. 1979. Environmental factors and growth. In Fish physiology. Vol. 8. Edited by W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York., pp. 599-675.

Brett, J.R. and T.D.D. Groves. 1979. Physiological energetics. In Fish physiology. Vol. 8. Edited by

W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York., pp. 279-352.

Brett, J.R., and Higgs, D.A. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. J. Fish. Res. Board Can. **27**:1767-1779.

Brett, J.R., Shelbourn, J.E., and Shoop C.T. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Bd. Canada **26**:2363-2394.

Carline, R.F., Johnson, B.L., and Hall, T.J. 1984. Estimation and interpretation of proportional stock density for fish populations in Ohio impoundments. N. Am. J. Fish. Manage. **4**:139-154.

Carpenter, S.R., and Kitchell, J.F. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge.

Chapman, D.W., and Fortune, Jr., J. 1963. Ecology of kokanee salmon. Oregon Game Commission, Res. Div. Rep. pp. 11-42.

Clark, C.W., and Levy, D.A. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Am. Nat. **131**:271-290.

Clark, J.H., and Traynor, J.J. 1972. Kokanee (*Oncorhynchus nerka*) in Helena Valley Reservoir. Proceedings of the Montana Academy of Sciences **32**:48-56.

Cordone, A.J., Nicola, S.J., Baker, P.H., and Frantz, T.C. 1971. The kokanee salmon in Lake Tahoe. Calif. Fish and Game **57**:28-43.

Crowder, L.B., and Magnuson, J.J. 1983. Cost-benefit analysis of temperature and food resource use: a synthesis with examples from fishes. *In* Behavioral energetics: the cost of survival in vertebrates. Edited by W.P. Aspey and S.I. Lustick. Ohio State University Press, Columbus, Ohio. pp. 189-221.

Cudlip, L.S., French, R.D., and Hickman, D. 1987. Blue Mesa Reservoir, Colorado: a historical review of its limnology, 1965-1985. U.S. Bureau of Reclamation Technical Report 85-9.

Donaldson, L.R., and Foster, F.J. 1940. Experimental study of the effect of various water temperatures on the growth, food utilization, and mortality rates of fingerling sockeye salmon. Trans. Am. Fish. Soc. **70**:339-346.

Dumont, H.J., Vand de Velde, I., and Dumont, S. 1975. The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos of continental waters. Oecologia **19**:75-97.

Eby, L.A., Rudstam, L.G., and Kitchell, J.F. 1995. Predator responses to prey population dynamics: an empirical analysis based on lake trout growth rates. *Can. J. Fish. Aquat. Sci.* **52**:1564-1571.

Eggers, D.M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. *Limnol. Oceanogr.* **23**:1114-1125.

Elliott, J.M., and Persson, L. 1978. The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* **47**:977-991.

Finnell, L.M., and Reed, E.B. 1969. The diel vertical movements of kokanee salmon, *Oncorhynchus nerka*, in Granby Reservoir, Colorado. *Trans. Am. Fish. Soc.* **98**:245-252.

Gerritsen, J., and Strickler, J.R. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Board Can.* **34**:73-82.

Gibson, R.N., and I.A. Ezzi. 1992. The relative profitability of particulate- and filter-feeding in the herring, *Clupea harengus* L. *J. Fish Biol.* **40**:577-590.

Godin, J.-G. J. 1981. Effect of hunger on the daily pattern of feeding rates in juvenile pink salmon, *Oncorhynchus gorbuscha* Walbaum. *J. Fish. Biol.* **19**:63-71.

Hansen, M.J., Boisclair, D., Brandt, S.B., Hewett, S.J., Kitchell, J.F., Lucas, M.C., and Ney, J.J. 1993. Applications of bioenergetic models to fish ecology and management: where do we go from here? Trans. Am. Fish. Soc. **122**:1019-1030.

Hanzel, D.A. 1974*a*. Age and growth analysis of fishes of Flathead Lake - kokanee. Montana Dept. Fish and Game, Job Progress Report F-33-R-8; Job I-b.

Hanzel, D.A. 1974*b*. Age and growth analysis of fishes of Flathead Lake - kokanee. Montana Dept. Fish and Game, Job Progress Report F-33-R-8; Job I-b.

Hewett, S. W. 1989. Ecological applications of bioenergetics models. Am. Fis. Soc. Symp. **6**:113-120.

Hewett, S.W., and Johnson, B. L. 1992. Fish bioenergetics model 2. An upgrade of a generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute, Madison, WI.

Hyatt, K.D. 1980. Mechanisms of food resource partitioning and the foraging strategies of rainbow trout (*Salmo gairdneri*) and kokanee (*Oncorhynchus nerka*) in Marion Lake, British Columbia. Ph.D. thesis. University of British Columbia, Vancouver, B.C.

Johnson, B. M., Stewart, R. S., Gilbert, S. J., Luecke, C., and Kitchell, J. F. 1992. Forecasting the effects of gamefish stocking and harvest regulations on the planktivore community in a eutrophic lake. N. Am. J. Fish. Manage. **12**:797-807.

Johnson, B.M., Wise, M.J., Counard, C.J., and Szerlong G. 1995. Ecological effects of reservoir operations on Blue Mesa Reservoir. Annual Progress Report to U.S. Bureau of Reclamation. 153 pp.

Johnson, B.M., Wise, M.J., Herwig, B., Szerlong, G., Faber, D., and Byall, B. 1996. Ecological effects of reservoir operations on Blue Mesa Reservoir. Annual Progress Report to U.S. Bureau of Reclamation. 124 pp.

Johnston, N.T. 1990. A comparison of the growth of vertically-migrating and nonmigrating kokanee (*Oncorhynchus nerka*) fry. Can. J. Fish. Aquat. Sci. **47**:486-491.

Kitchell, J.F., Stewart, D.J., and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Can. J. Fish. Aquat. Sci. **34**:1922-1935.

Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. Functional Ecology **3**:21-27.

0 Levy, D.A. 1991. Acoustic analysis of diel vertical migration behavior of *Mysis relicta* and kokanee (*Oncorhynchus nerka*) within Okanagan Lake, British Columbia. Can. J. Fish. Aquat. Sci. **48**:67-72.

Lind, O.T. 1979. Handbook of common methods in limnology, second edition. C.V. Mosby Co., St. Louis, Missouri.

5 Luecke, C., and Brandt, D. 1993. Estimating the energy density of daphnid prey for use with rainbow trout bioenergetics models. Trans. Am. Fish. Soc. **122**:386-389.

10 Luecke, C., W.A. Wurtsbaugh, P. Budy, H.P. Gross, and G. Steinhart. 1996. Simulated growth and production of endangered Snake River sockeye salmon. Fisheries **21**:18-25.

Madenjian, C.P., Carpenter, S.R., Eck, G.W., and Miller, M.A. 1993. Accumulation of PCBs by lake trout (*Salvelinus namaycush*): an individual-based model approach. Can. J. Fish. Aquat. Sci. **50**:97-109.

15 Maiolie, M.A., and Elam, S. 1996. Kokanee depth distribution in Dworshak Reservoir and implications toward minimizing entrainment. Idaho Department of Fish and Game. Dworshak Dam Impacts Assessment and Fisheries Investigation, Annual Progress Report, Project Number 87-99.

20 Martinez, P.J. 1996. Coldwater Reservoir Ecology. Colorado Division of Wildlife, Progress Report,

0 Federal Aid Project F-242R-3.

Martinez, P.J., and Wiltzius, W.J. 1995. Some factors affecting a hatchery-sustained kokanee population in a fluctuating Colorado reservoir. *N. Am. J. Fish. Manage.* **15**:220-228.

5 Mason, D.M., and Patrick, E.V. 1993. A model for space-time dependence of feeding for pelagic fish populations. *Trans. Am. Fish. Soc.* **122**:884-901.

Mason, D.M., Goyke, A., and Brandt, S.B. 1995. A spatially-explicit bioenergetics measure of habitat quality for adult salmonines: comparison between Lake Michigan and Ontario. *Can. J. Fish. Aquat. Sci.* **52**:1572-1583.

McQueen, D.J., Post, J.R., and Mills, E.L. 1986. Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.* **43**:1571-1581.

15 Miller, T.J., Crowder, L.B., and Rice, J.A. 1992. Body size and the ontogeny of the functional response in fishes. *Can. J. Fish. Aquat. Sci.* **49**:805-812.

Miller, T.J., Crowder, L.B., and Rice, J.A. 1993. Ontogenetic changes in behavioural and histological measures of visual acuity in three species of fish. *Env. Biol. Fish.* **37**:1-8.

Ney, J.J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predator and prey. *Reviews in Aquatic Science* **2**:55-81.

Ney, J.J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. *Trans. Am. Fish. Soc.* **122**:736-748.

O'Brien, W.J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. *Am. Sci.* **67**:572-581.

Porter, K.G., Saunders, P.A., Haberyan, K.A., Macubbin, A.E., Jacobsen, T.R., and Hodson, R.E. 1996. Annual cycle of autotrophic and heterotrophic production in a small, monomictic Piedmont lake (Lake Oglethorpe): analog for the effects of climatic warming on dimictic lakes. *Limnol. Oceanogr.* **41**:1041-1051.

Post, J.R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetic models. *Can. J. Fish. Aquat. Sci.* **47**:554-560.

Rahmann, H., Jeserich, G., and Zeutzius, I. 1989. Ontogeny of visual acuity of rainbow trout under normal conditions and light deprivation. *Behaviour* **98**:315-343.

Rand, P.S., Stewart, D.J., Lantry, B.F., Rudstam, L.G., Johannsson, O.E., Goyke, A.P., Brandt, S.B.,

0 O'Gorman, R., and Eck, G.W. 1995. Effect of lake-wide planktivory by the pelagic prey fish
community in Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. **52**:1546-1563.

Rice, J.A., Breck, J.E., Bartell, S.M., and Kitchell, J.F. 1983. Evaluating the constraints of
temperature, activity, and consumption on growth of largemouth bass. Environ. Biol. Fishes **9**:263-
5 275.

Richman, S. 1958. The transformation of energy by *Daphnia pulex*. Ecol. Monogr. **28**:273-291.

Schindler, D.W., Mills, K.H., Malley, D.F., Findlay, D.L., Shearer, J.A., Davies, I.J., Turner, M.A.,
10 Linsey, G.A., and Cruikshank, D.R. 1985. Long-term ecosystem stress: the effects of years of
experimental acidification on a small lake. Science **228**:1395-1401.

Soranno, P.A., and Knight, S.E. 1993. Methods of the cascading trophic interactions project.
University of Wisconsin, Center for Limnology, Madison, Wisconsin.

15 Stewart, D.J., and Ibarra, M. 1991. Predation and production by salmonine fishes in Lake Michigan,
1978-1988. Can. J. Fish. Aquat. Sci. **48**:909-922.

Stewart, D.J., Kitchell, J.F., and Crowder, L.B. 1981. Forage fishes and their salmonid predators in
20 Lake Michigan. Trans. Am. Fish. Soc. **110**:751-763.

Thornton, K.W., and Lessem, A.S. 1978. A temperature algorithm for modifying biological rates. Trans. Am. Fish. Soc. **107**:284-287.

Tyus, H. M. 1992. An instream flow philosophy for recovering endangered Colorado River fishes. Rivers **3**:27-36.

Vinyard, G.L., Drenner, R.W., and Hanzel, D.A. 1982. Feeding success of hatchery-reared kokanee salmon when presented with zooplankton prey. Prog. Fish-Cult. **44**:37-39.

Wahl, C.M., Mills, E.L., McFarland, W.N., and DeGisi, J.S. 1993. Ontogenetic changes in prey selection and visual acuity of the yellow perch, *Perca flavescens*. Can. J. Fish. Aquat. Sci. **50**:743-749.

Walton, W.E., Easter Jr., S.S., Malinoski, C., and Hairston Jr., N.G. 1994. Size-related change in visual resolution of sunfish (*Lepomis* spp.). Can. J. Fish. Aquat. Sci. **51**:2017-2026.

Werner, E.E. 1977. Species packing and niche complementarity in three sunfishes. Am. Nat. **111**:553-578.

Wetzel, R.G. 1983. Limnology. Saunders, Philadelphia.

0 Wuethrich, B. 1996. Deliberate flood renews habitats. *Science* **272**:344-345.

Zagarese, H.E., Williamson, C.E., Mislivets, M., and Orr, P. 1994. The vulnerability of *Daphnia* to UV-B radiation in the northeastern United States. *Ergeb. Limnol.* **43**:207-216.

5 **List of Figures**

Figure 1. Comparison of estimates from the B&A, modified B&A, and Wisconsin bioenergetics models for a 500-g kokanee under standard simulation conditions (see text). (A) Scope for growth estimates as a function of temperature for all three models. (B) The energy budget from the B&A model as a function of temperature. Scope for growth is represented by area between total respiration (R) and consumption (C) minus losses curves. (C) and (D) Same as (B) but for the Wisconsin and the modified B&A models, respectively.

Figure 2. (A) Scope for growth estimates for a 500-g kokanee as a function of temperature and feeding duration for the modified B&A model. Scope for growth estimates from the Wisconsin model are also shown. (B) Same as (A) but for a 100-g kokanee. (C) Scope for growth estimates for a 500-g kokanee as a function of feeding duration and prey size for the modified B&A model. (D) same as (C) but for a 100-g kokanee.

Figure 3. (A) Comparison of original (Hyatt 1980) and modified functional responses. Hyatt's (1980) functional response was determined using lab experiments with 15-g kokanee at 10°C. The solid line

describes the functional response by $C=Z/(0.0138 \cdot Z+11.5)$, where C is consumption ($Daphnia \cdot min^{-1}$) and Z is *Daphnia* density (m^{-3}). The dotted line indicates the modified functional response (see Table 1), using a 15-g kokanee at $10^{\circ}C$, with a handling time of $1.2 s \cdot Daphnia^{-1}$. (B) Sensitivity of the modified functional response when fish body size and handling times are varied.

Figure 4. Vertical profiles of temperature and densities of *Daphnia* ≥ 1.0 mm in Sapinero Basin, Blue Mesa Reservoir, 1994. Asterisks indicate data used as inputs to the modified B&A model for comparison of model growth estimates with field observations.

Figure 5. Observed masses and daily growth estimates of (A) age-1, (B) age-2, and (C) age-3 kokanee from Blue Mesa Reservoir, 1995. Exponential growth was used to generate daily growth estimates (see text). Daily observed growth is plotted on limnological sampling dates (Fig. 4) to compare with estimates generated by the modified B&A model.

Figure 6. Daily growth estimates from the modified B&A model for (A) age-1, (B) age-2, and (C) age-3 kokanee, using limnological data from 10 June 1994. Starting masses of kokanee for model simulations, as determined from field observations, were 59.79 g for age-1, 222.87 g for age-2, and 575.07 g for age-3. The horizontal dotted lines represent daily growth from field observations for the same date, while the horizontal dashed lines indicate maximum scope for growth at optimum temperature as predicted by the Wisconsin model. Solid squares connected by vertical lines indicate depths of migration strategies from the modified B&A model that maximized growth for the given

0 feeding duration and handling time.

Figure 7. Same as Figure 6, but for limnological sampling date 21 July 1994. Starting kokanee masses for simulations were 103.38 g for age-1, 314.70 g for age-2, and 666.46 g for age-3. Single solid square for a given feeding duration and handling time indicates migration strategy that maximized growth was to remain at the indicated constant depth for the entire 24-h simulation.

Figure 8. Same as Figure 7, but for limnological sampling date 18 August 1994. Starting kokanee masses for simulations were 121.15 g for age-1, 342.45 g for age-2, and 722.34 g for age-3.

Table 1. The modified B&A model as developed from Bevelhimer (1990) and Bevelhimer and Adams (1993). Sources are as follows: 1) Gerritsen and Strickler (1977), 2) Thornton and Lessem (1978), 3) Beauchamp et al. (1989), 4) Hyatt (1980), 5) Brett (1971), 6) Dumont et al. (1975), 7) Elliott and Persson (1978), 8) Brett and Higgs (1970), 9) Bevelhimer and Adams (1993), 10) Hewett and Johnson (1992), 11) Brett and Groves (1979), 12) Richman (1958). Note that 1 cal = 4.184 J.

Parameter	Value	Source
Consumption (C)		
C (<i>Daphnia</i> ·min ⁻¹)	$[E \cdot Z] / [(1 + (E \cdot Z \cdot h)) \cdot TL \cdot 60]$	
E , volume searched (m ³)	$(\pi \cdot R_d^2) / 3 \cdot (3 \cdot v^2 + u^2) / v$	1
TL , Thornton-Lessem function	$[(0.58 \cdot e^{(0.21 \cdot (T-3))}) / (1 + 0.58 \cdot (e^{(0.21 \cdot (T-3))} - 1)))] \cdot [(0.5 \cdot e^{(0.97 \cdot (24-T))}) / (1 + 0.5 \cdot (e^{(0.97 \cdot (24-T))} - 1))]$	2,3
R_d , reaction distance (m)	0.08	4
v , kokanee swimming speed (cm·s ⁻¹)	$9.9 \cdot e^{(0.0405 \cdot T)} \cdot M^{0.13}$	3
u , <i>Daphnia</i> swimming speed (cm·s ⁻¹)	0	
Z , prey density (<i>Daphnia</i> ·m ⁻³)		
h , handling time (s· <i>Daphnia</i> ⁻¹)	0.33-1.2	
T , temperature (°C)		
M , kokanee mass (wet g)		
stomach capacity (wet g)	$[14.1 - 4.95 \cdot \log_{10}(M)] / 100$ for $M < 253.5$ g; $0.022 \cdot M$ for $M \geq 253.5$ g	5

0	m, <i>Daphnia</i> mass (wet mg)	$0.052 \cdot L_d^{3.012}$	6
	L_d , <i>Daphnia</i> length (mm)		
	Digestion (D)		
	D (cal·t ⁻¹)	$[((C \cdot m - M_0/r) \cdot (1 - e^{-rt})) + (C \cdot m \cdot t)] \cdot E_{dap}$	7
	r, digestion coefficient	$0.0140 \cdot T - 0.0154$	8
5	M_0 , initial stomach content mass (wet g)		
	t, model time step (min)	30	9
	Respiration (R)		
	R (cal·g ⁻¹ ·t ⁻¹)	$0.00143 \cdot M^{-0.209} \cdot e^{(0.086 \cdot T)} \cdot \text{ACTIVITY} \cdot \text{oxycal} \cdot t/t_{day}$	3
	ACTIVITY	$e^{(0.0234 \cdot \text{VEL})}$	3
10	VEL	$9.9 \cdot e^{(0.0405 \cdot T)} \cdot M^{0.13}$	3
	oxycal, oxycaloric conversion factor (cal·g ⁻¹ O ₂)	3241	
	t_{day} , length of day (min)	1440	
	Egestion (F)		
	F (cal·t ⁻¹)	$0.455 \cdot T^{-0.222} \cdot D$	10
15	Excretion (U)		
	U (cal·t ⁻¹)	$0.0233 \cdot T^{0.580} \cdot (D - F)$	10
	Specific Dynamic Action (SDA)		

0	SDA (cal·t ⁻¹)	0.14·(D-F)	11
	Energy Density		
	E _{dap} (cal·wet g ⁻¹ <i>Daphnia</i>)	586	12
	E _{kok} (cal·wet g ⁻¹ kokanee)	1.851·M+1250 for M ≤ 196 g; 0.1254·M+1588 for M > 196 g	10

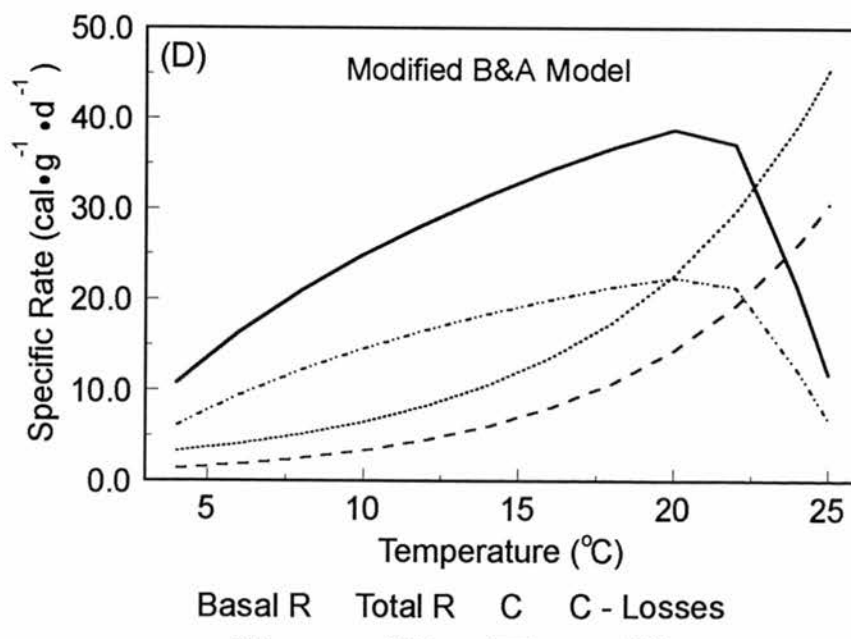
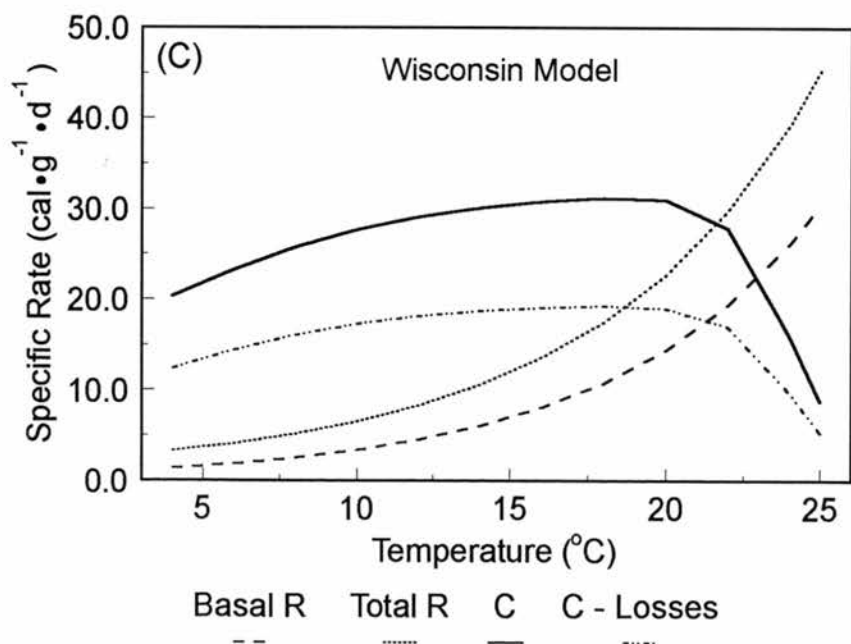
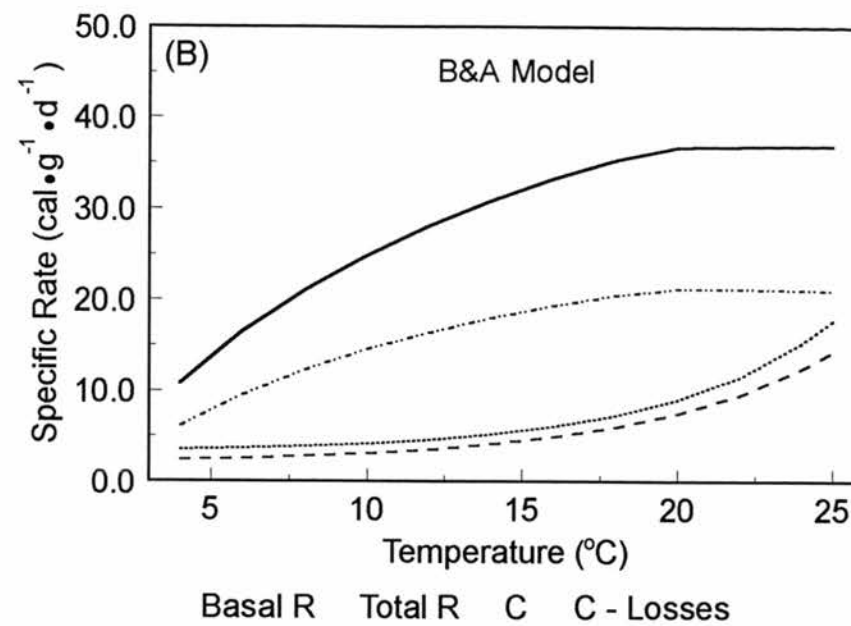
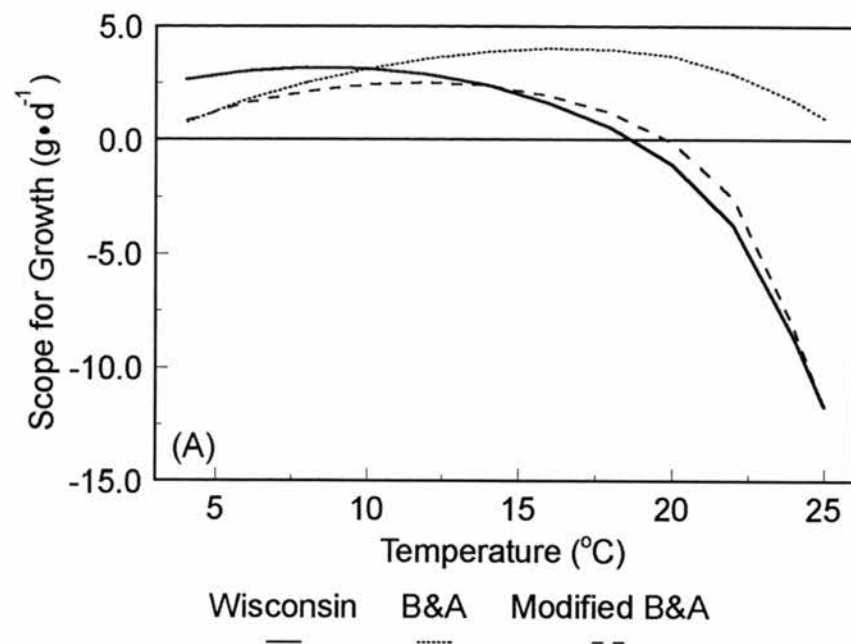


Fig. 1

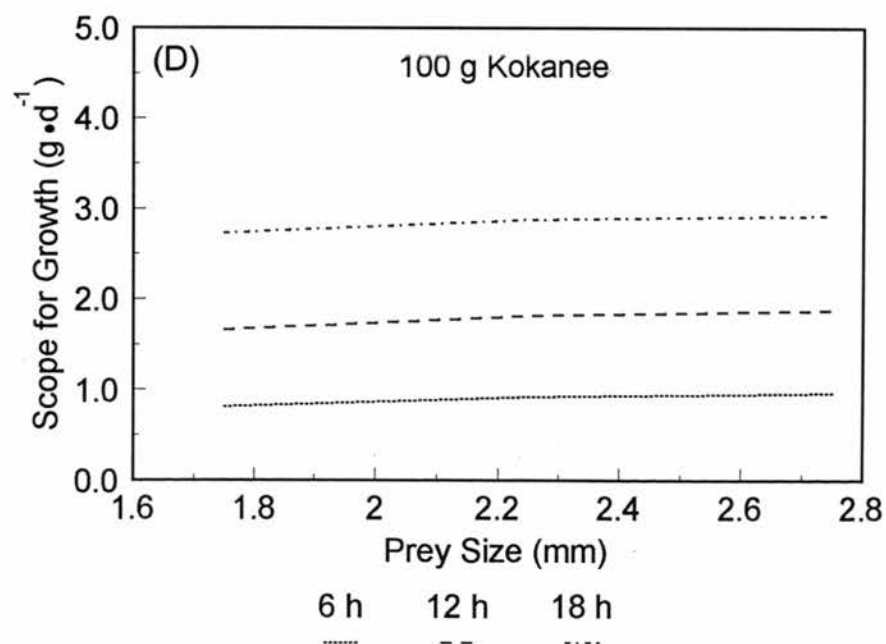
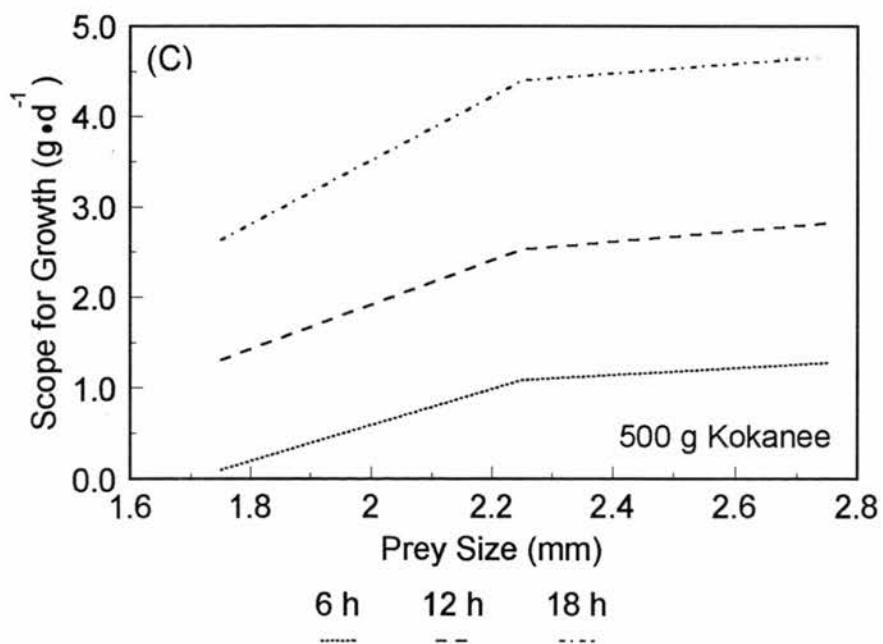
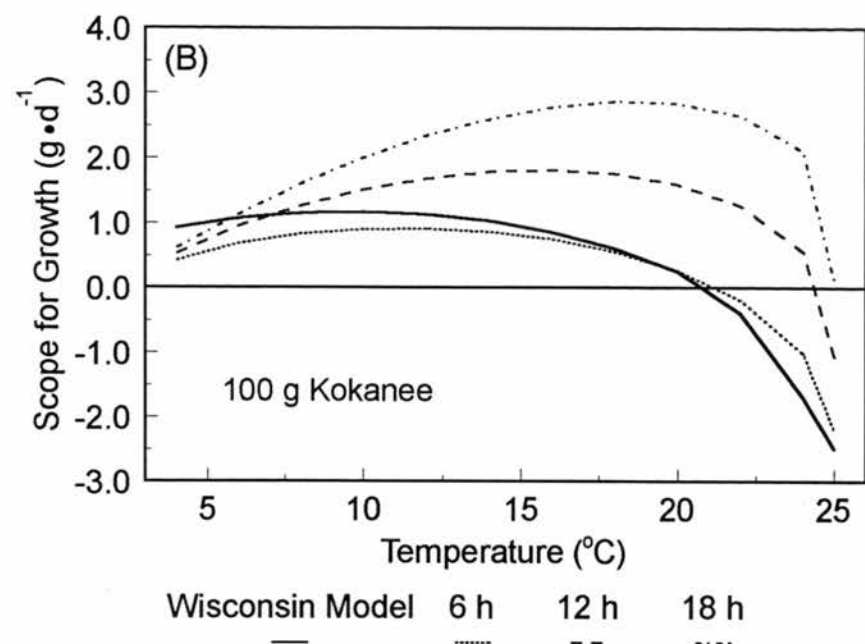
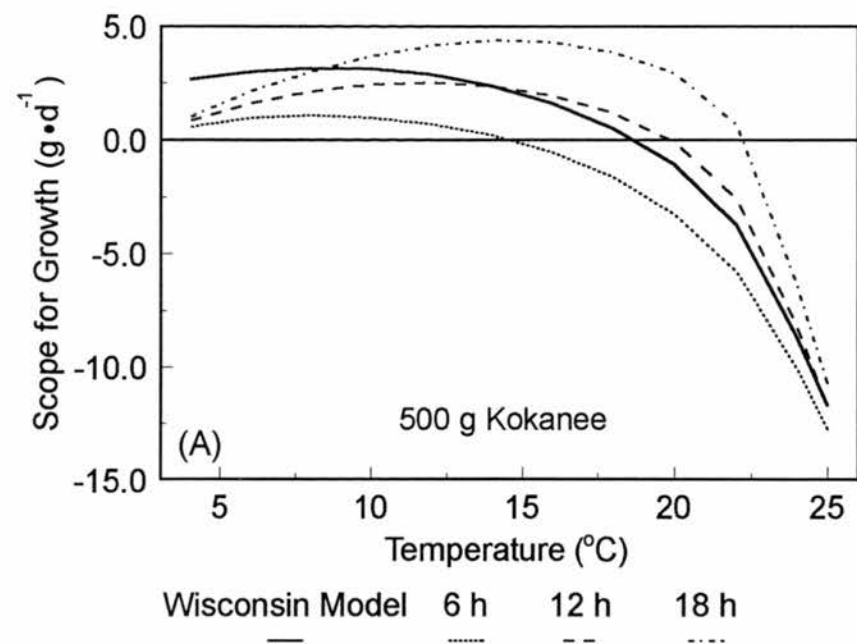


Fig. 2

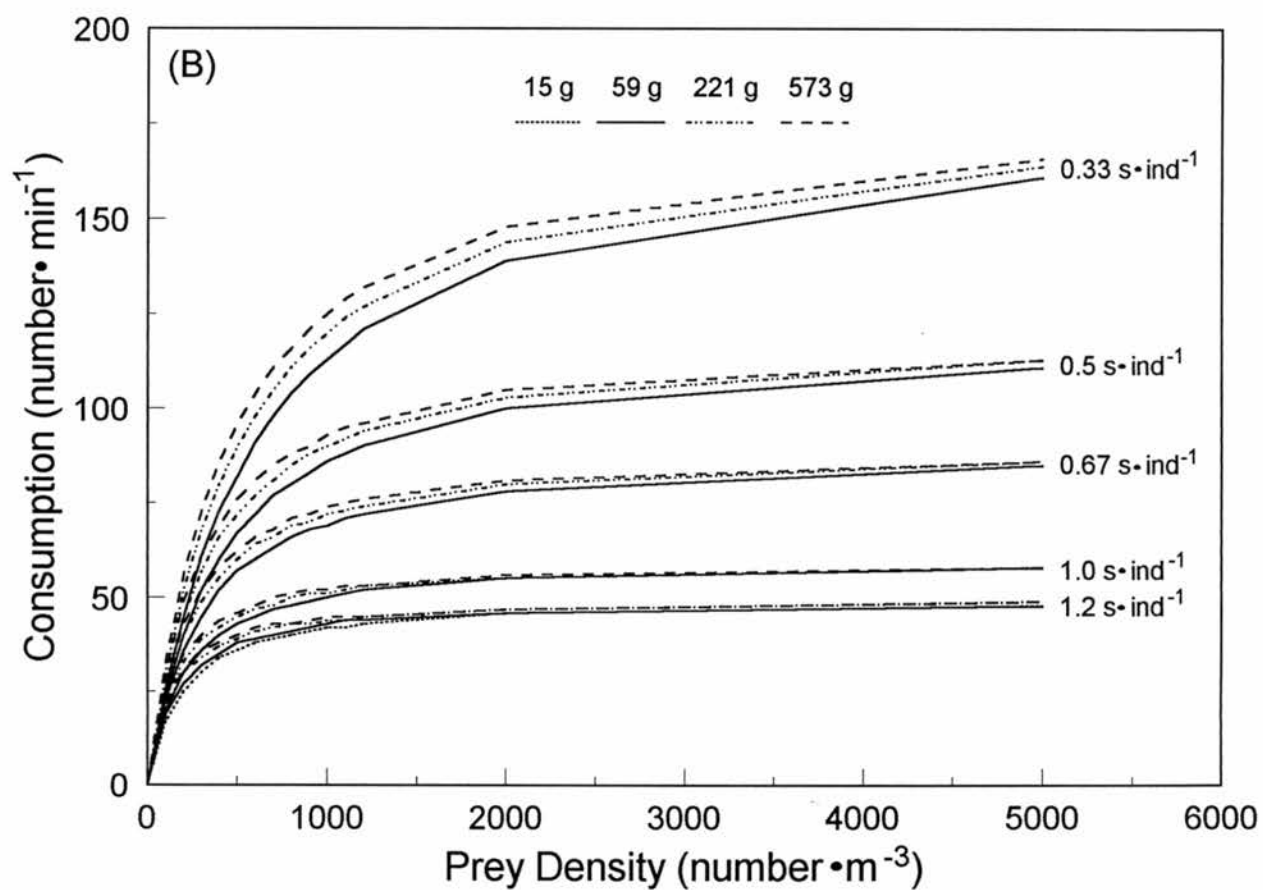
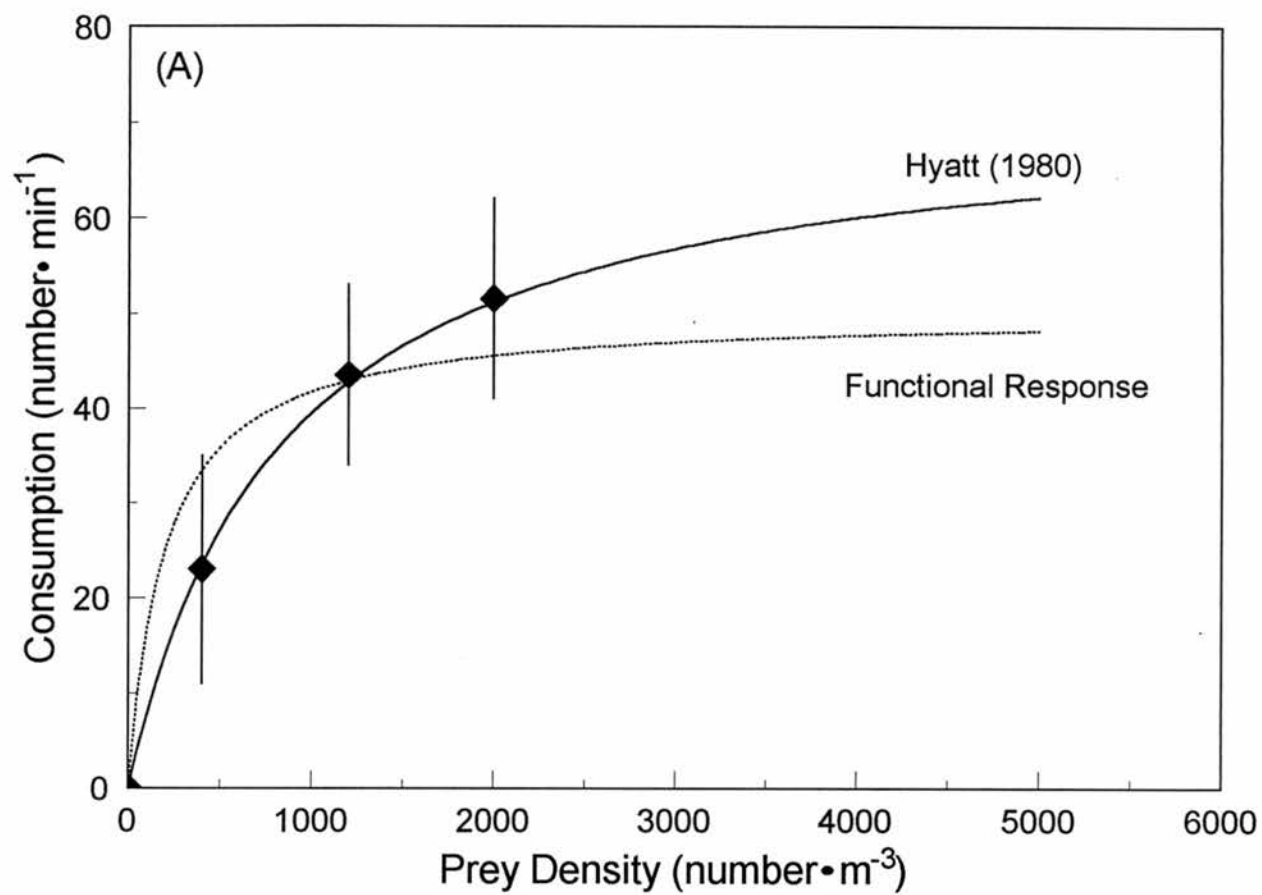


Fig. 3

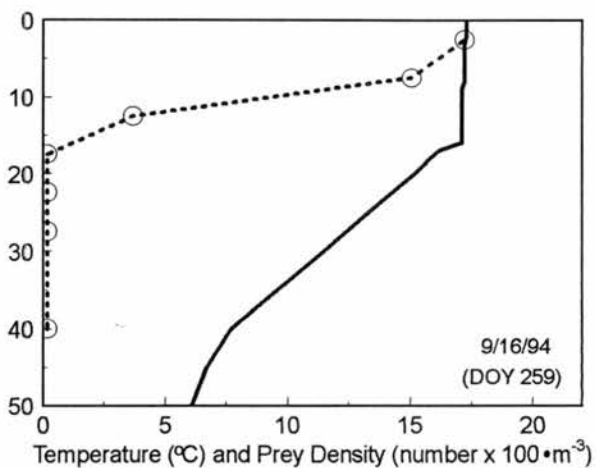
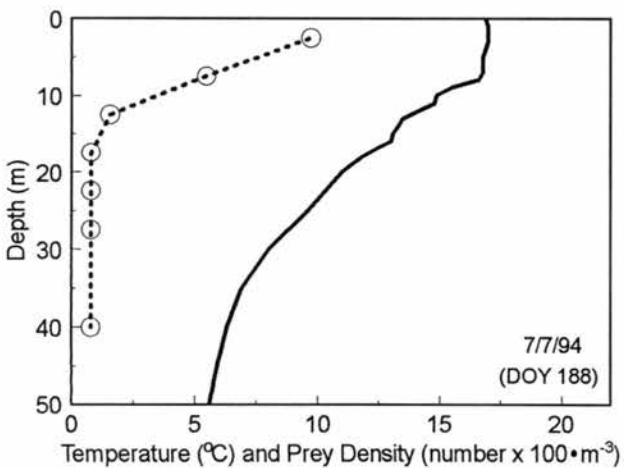
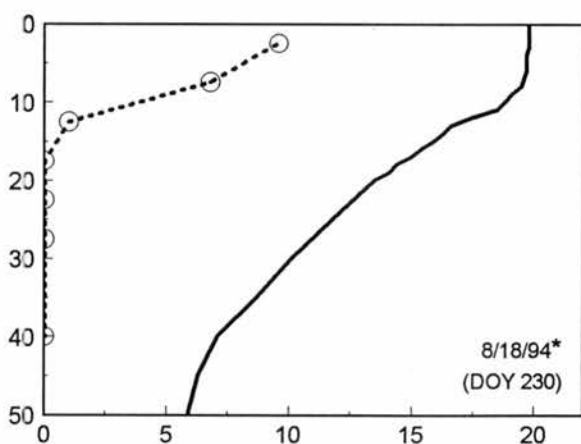
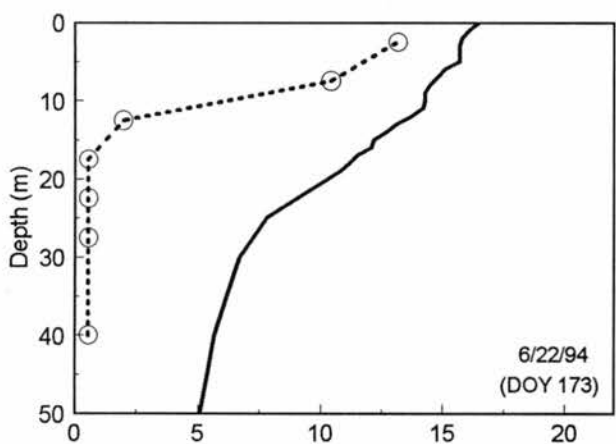
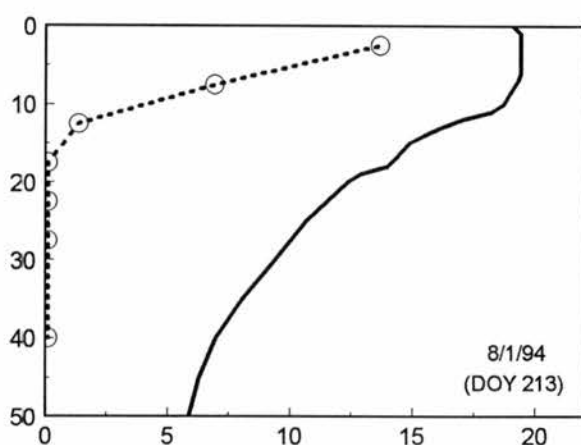
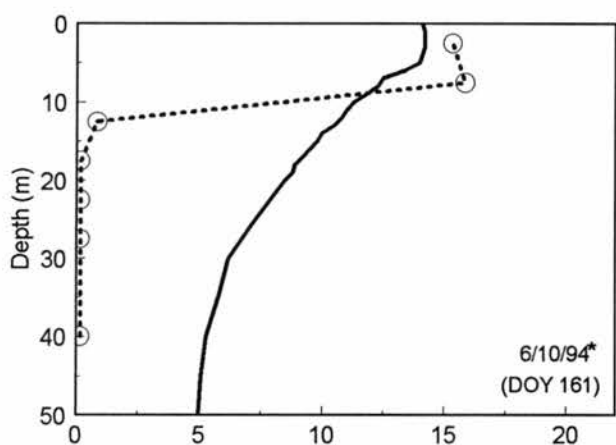
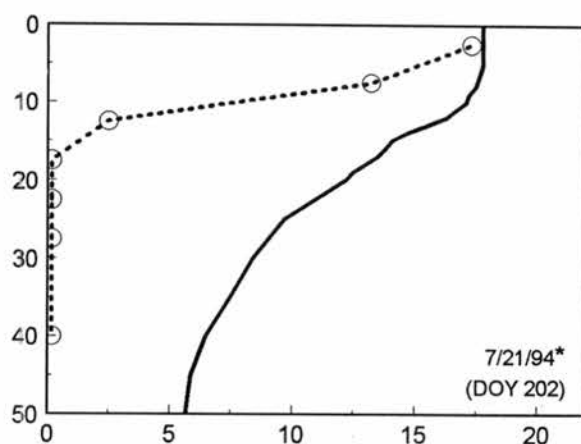
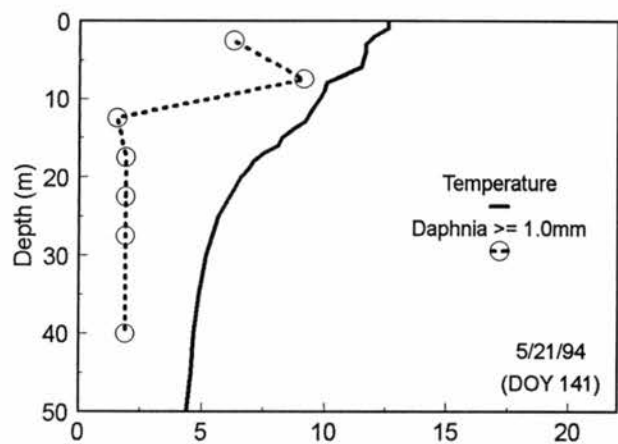


Fig. 4

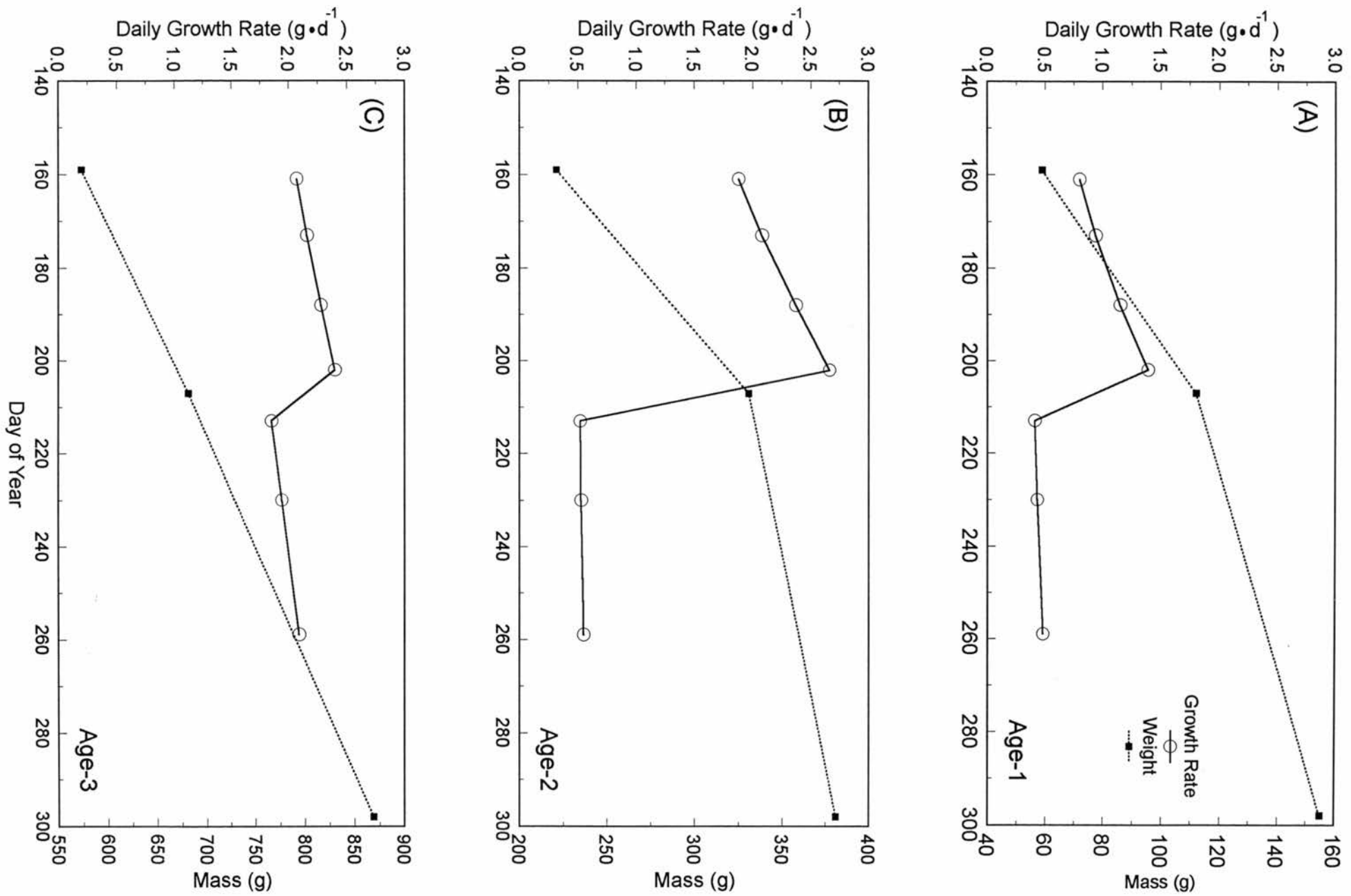


Fig. 5

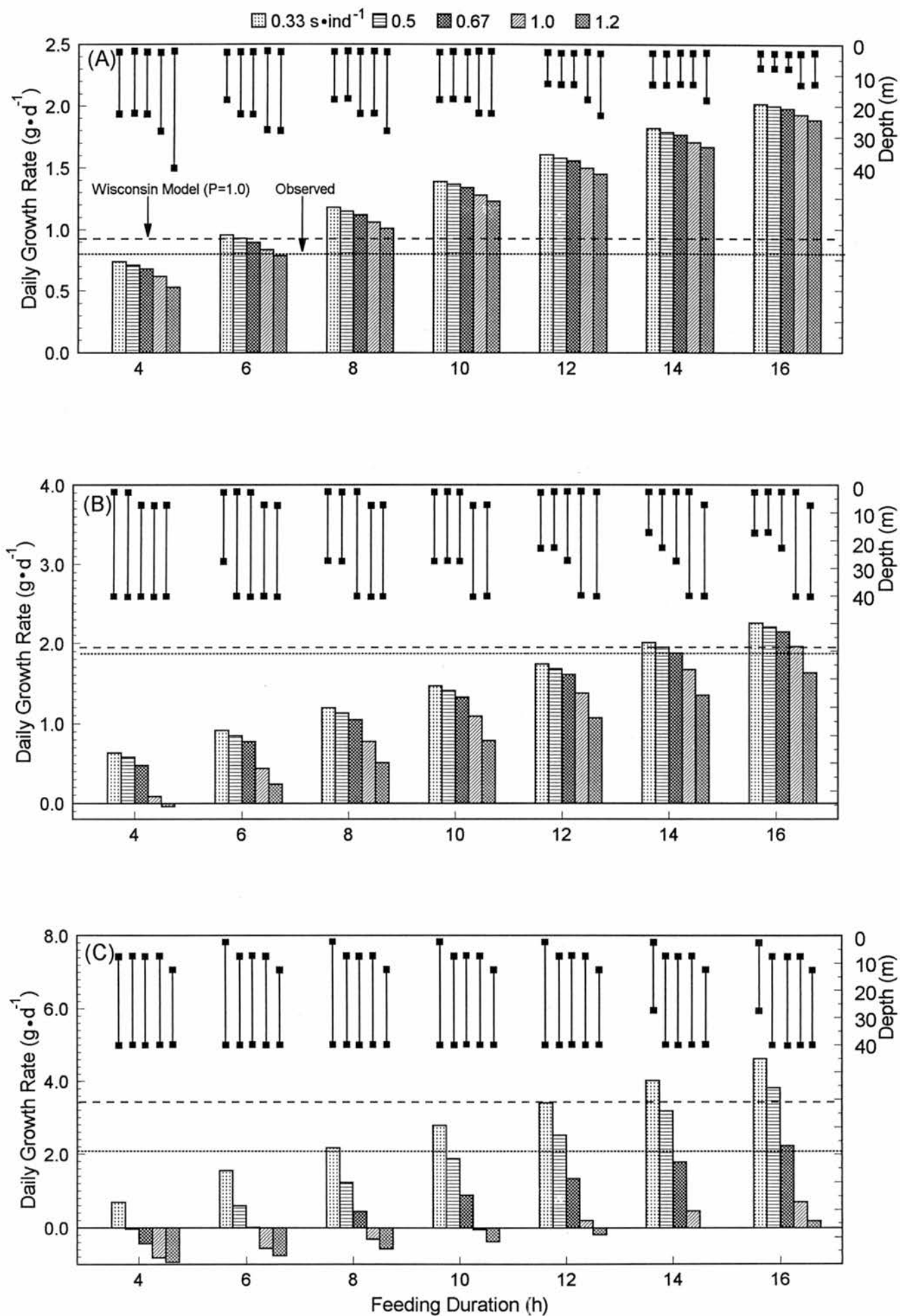


Fig. 6

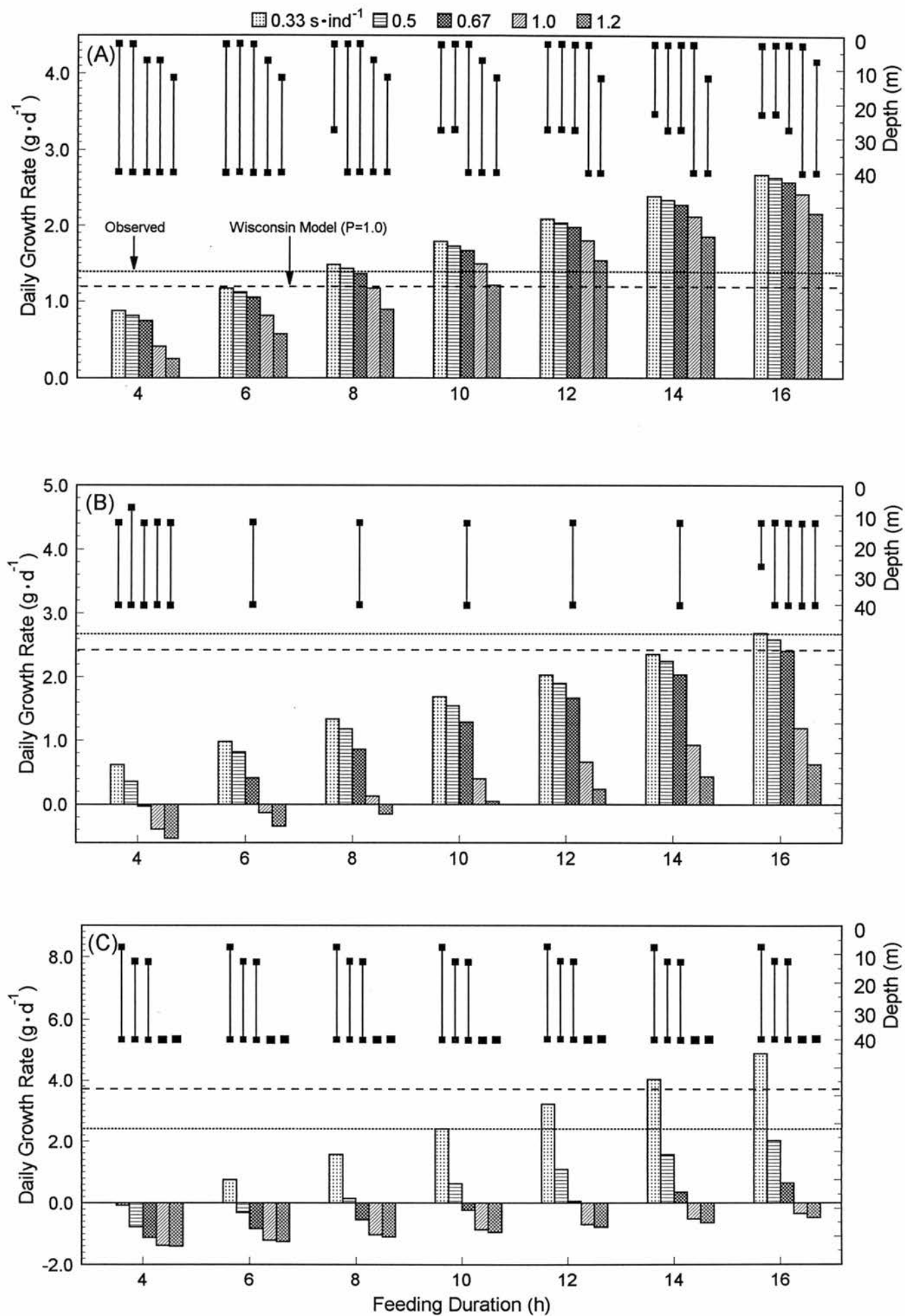


Fig. 7

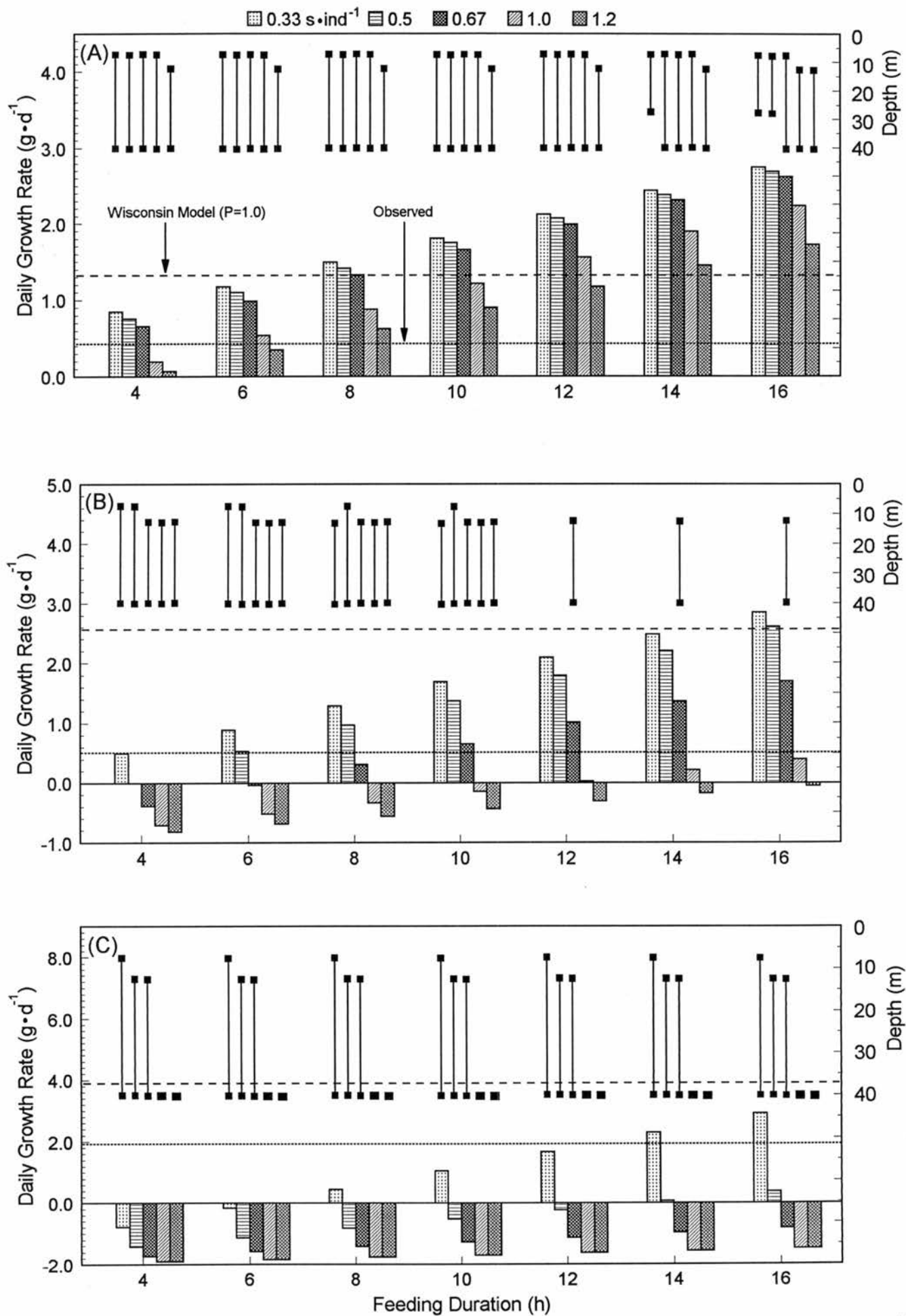


Fig. 8

