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

Annual Progress Report

May 1, 1997-April 30, 1998

Prepared by

Brett M. Johnson  
Principal Investigator

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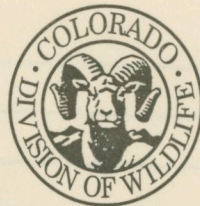
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## ACKNOWLEDGMENTS

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) and Ron Sutton (U.S. Bureau of Reclamation, Salt Lake City) coordinated the project. Professor Darrel Fontane of the CSU Civil Engineering Department assisted with the thermal modeling. We also thank Rick Harris and Matt Malick of the National Park Service for their logistical support. 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 Brady Allen, Kathleen Apakupakul, Krista Bonfantine, Dan Brauch, Tom Cady, Daren Carlisle, Daren Chacon, Gregg Chenu, Jason Garner, Sture Hansson, Josh Hobgood, Steve Johnson, Shawndra Mawhorter, Tim Sundlov, Ron Sutton, and Joe Zendt for their tireless help in the field and lab. Steve Johnson and Doran Mason provided valuable guidance with processing of sonar data. Krista Bonfantine processed zooplankton samples and aged fish. 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 1993-1996, reservoir discharge and surface elevation were above the longterm average during 1997, likely due to another year of above average inflow.
- Mean surface temperature in July 1997 was below the longterm average in Sapinero.
- Thermal stratification in August 1997 was similar to 1996 and 1995, although the thermocline was slightly shallower and the epilimnion was warmer in 1997.
- Metalimnetic oxygen minima observed in Sapinero throughout the 1995 and 1996 field seasons was not as pronounced in 1997.
- Water clarity in 1997 was within the range of variability observed from 1993 to 1996.
- As in past years, most large *Daphnia* ( $\geq 1.0$  mm) were in the top 10 m of the water column during summer.
- Abundance of *Leptodiptomus* appeared to decline in 1997 to 1994 and 1995 levels, while unidentified copepod nauplii were several times more abundant than in previous years. However, the sampling scheme was less comprehensive in 1997 compared with past years.
- 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 continued to be dominated by kokanee salmon.
- Macroinvertebrates, mainly terrestrial insects, were always important in rainbow trout diets, especially for small rainbow trout in spring and large rainbow trout in summer. Zooplankton were the dominant prey of small rainbow trout in summer and fall, and of large rainbow trout in fall.
- Growth rate of kokanee has remained relatively constant during the study, and is among the fastest growth of kokanee anywhere.
- Based on hydroacoustics and creel surveys, kokanee abundance continued to decline in 1997 to its lowest level since the study began. Greatly increased stocking and higher lake trout harvest mortality are recommended to protect the kokanee stock.
- The bioenergetics-based foraging model for kokanee that we refined and calibrated for use in Blue Mesa Reservoir suggests that bioenergetic and foraging constraints were not sufficient to explain DVM early in the summer, when thermal stratification was weak. However, these constraints could explain observed patterns later in the summer, when optimal thermal habitat for kokanee was spatially segregated from food-rich surface waters.

## INTRODUCTION

This report documents the fifth year of progress on a 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 we continued standardized limnological and fishery monitoring, gathered data to calibrate and validate the reservoir thermal model, and developed a bioenergetics-based foraging model for kokanee to study effects of thermal regime on growth and behavior of kokanee.

In 1997, our main emphasis was performing three diel surveys to evaluate the predictive capabilities of the bioenergetics-based foraging model for kokanee we developed in 1996. We monitored kokanee vertical distributions during each survey, as well as observed growth across the growing season to compare with model predictions of kokanee growth and behavior. These comparisons are presented in a draft manuscript (Stockwell and Johnson, In Review) appended to this report. Other accomplishments during this project are summarized in Tables 1-2.

### Part 1. Reservoir Limnology

#### METHODS

##### **Overview**

Data were collected once a month from June to August 1997 during the new moon at a single reference station in Sapinero Basin. Additionally, we sampled limnological parameters and zooplankton in Sapinero, and collected fish from a reference station in Cebolla Basin in early May 1997. Our objectives were to acquire information on: 1) BMR limnological parameters (temperature and dissolved oxygen profiles, secchi depth); 2) depth-stratified zooplankton abundances; 3) fish community composition; 4) kokanee growth rates and population age structure; 5) kokanee abundance (hydroacoustics); 6) kokanee diel vertical distributions across the growing season (hydroacoustics and vertical gill nets); 7) inflow water temperatures; and 8) diet and stable isotope samples of fishes.

In 1997, data on zooplankton and limnological parameters were collected at the same Sapinero (June to August) and Cebolla (early May) reference stations as in 1993-1996 (Figure 1). In addition to temperature, dissolved oxygen, secchi depth, and zooplankton data, salmonid lengths, weights, scales, otoliths, stomach weights, and depth distributions were obtained from vertical gill nets. A thermograph was deployed on May 8 in the Gunnison River upstream of Blue Mesa, and was retrieved on August 5.

## 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 1997, vertical profiles of temperature and dissolved oxygen concentrations were recorded once a month at the Sapinero 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. A temperature logger in the Gunnison River at the Cooper Ranch Picnic Area recorded 48 stream temperatures per day during May 8- August 5. 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.

## Zooplankton

### *Sampling*

Zooplankton were collected by oblique tows using a Wildco model 37-315 Clarke-Bumpus plankton sampler (Lind 1979) with 130-mm diameter opening and two mesh sizes. A single tow was made in the 0-5, 5-10, and 10-15-m depth strata using a 500- $\mu$ m mesh on each of 8 May, 31 May, 8 July, and 4 August in Sapinero. We focused our sampling efforts in these strata because data from 1996 indicated that most large *Daphnia* were concentrated in the upper 15 m of the water column. Additionally, a single tow was made using 153- $\mu$ m mesh net from 0-10 m on the latter three dates at the same station. A second replicate was taken in July because of low sampling volume on the first attempt. The larger mesh size was used to more efficiently sample large *Daphnia*, while the smaller mesh was used to compare with samples from previous years. All samples were taken between the hours of 0730 and 1030, and preserved in 8% sugared, buffered formalin.

### *Sample Processing*

Samples from the 153- $\mu$ m 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. Two aliquots were examined per sample. Up to 25 individuals for each of *Daphnia pulex* and *D. galeata* were measured for each sample (two aliquots). Zooplankton abundances were computed as number per liter.

Samples collected with the 500- $\mu$ m mesh net were processed in the same fashion as the 153- $\mu$ 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

Due to above normal precipitation, 1997 inflow to Blue Mesa was above average again, as it was in most previous study years (Figure 2). Thus, Blue Mesa surface elevation remained well above the long term mean all year, except during March and April (Figure 3).

#### *Temperature*

In July 1997, surface water temperature in Sapinero Basin was below the 20-year average (Figure 4). Surface temperature (16.3°C) was 2.5°C lower than the long-term mean (18.6°C).

Water column temperatures in Sapinero decreased from 7.9°C at the surface to 4.7°C at 55 m in early May (Figure 5). Surface waters increased to >12°C on 31 May. Strong thermal stratification was present on 8 July, with the top 10 m at approximately 16°C, and a fairly sharp thermocline at 10-m depth (Figure 5). In early August, surface waters warmed to >19°C from 0-5-m depth. Temperatures at all remaining depths in August were about 1°C warmer than in July (Figure 5). Temperatures in the Gunnison River at the Cooper Ranch Picnic Area, averaged by day, increased from slightly below 8°C on May 8 to slightly above 16°C on August 5 (Figure 6).

#### *Dissolved Oxygen*

Dissolved oxygen levels were generally high (> 6 mg/l) in the 0-10 m stratum throughout the season (Figure 7). There was a slight decrease in metalimnetic oxygen in July (Figure 7), similar to previous years. In August, dissolved oxygen decreased to 3-4 mg/l at depths <35 m (Figure 7).

#### *Secchi Depth*

As in previous years, water transparency increased from early to late summer in Sapinero Basin (Figure 8, 9). In general water transparency in 1997 was within the range of variability observed from 1993 to 1996.

### Zooplankton

#### *500- $\mu$ m Mesh Net*

Because densities of large *Daphnia* ( $\geq 1.0$  mm) were primarily concentrated in the upper 15 m of the water column in 1996, we concentrated our sampling efforts with the 500- $\mu$ m mesh net at these depths in 1997. Overall densities were low in late May, high in July, and intermediate in August (Figure 10). In May, there was no pattern in densities with depth (Figure 10). Densities ranged between 1 and 2 per liter. A strong gradient was apparent in July, where densities were >13 per liter in the 0-5-m stratum, and decreased to 2 per liter in the 10-15-m stratum (Figure 10). In August, densities of large *Daphnia* were approximately 8 per liter in the 0-5-m stratum, and around 4 per liter in each of the 5-10 and 10-15-m strata (Figure 10).

These depth distributions of large *Daphnia* were used as input to evaluate the bioenergetics-based foraging model for kokanee (Stockwell and Johnson In Review; Appendix A) that we developed in 1996 (Stockwell and Johnson 1997).

### *153- $\mu$ m Mesh Net*

Results from the 153- $\mu$ m net show that mean length of *D. pulex* is greater than *D. galeata* on all sampling dates (Figure 11). This is consistent with findings from previous years (Johnson et al. 1996, 1997), and likely accounts for the size-selective predation on *D. pulex* by kokanee (Johnson et al. 1996, Stockwell et al. In Review). Mean length of *D. pulex* increased from 1.15 mm in late May to about 1.3 mm in July and August (Figure 11). Mean length of *D. galeata* increased from <0.8 mm in May, to about 0.9 mm in July, and then to >1.0 mm in August (Figure 11).

Five taxonomic groups of crustacean macrozooplankton were collected with the 153- $\mu$ m mesh net: the cyclopoid copepod *Diacyclops*; the calanoid copepod *Leptodiatomus*; and the cladocera *Bosmina*, *D. pulex*, and *D. galeata*. Unlike 1996, we found no *Ceriodaphnia* present in 1997. Results from 1997 are biased when compared to previous years because we did not take samples from the same months and basins in all years. Ignoring this bias, the zooplankton community in 1997, as in 1994-1996, continued to be dominated by the copepod *Diacyclops* (Figure 12). *Diacyclops* comprised 50% of the zooplankton community. Copepod nauplii, unlike previous years, also constituted a major portion of the zooplankton community composition (20%). The proportion of *D. galeata* was slightly greater in 1997 than previous years, while *D. pulex* and *Bosmina* were slightly lower (Figure 12). *Leptodiatomus*, which showed a relatively strong increase in 1996 compared to 1994-95, was rare in 1997. Again, these comparisons are biased because of incomplete temporal and spatial coverage of 1997 zooplankton sampling. Many of the trends could be artifacts of limited sampling.

The overall abundance of zooplankters in Sapinero in 1997 was highest in late May (83 ind/l), and decreased slightly in July (74 ind/l) and August (55 ind/l) (Figure 13). These abundances are the highest observed for each of the three months from 1994-97. However, they may be an artifact of limited sampling. If we had sampled Cebolla and Iola basins in 1997, then estimates would be lower if zooplankton abundances were lower in these two basins. We also see that the large contribution of copepod nauplii to the the zooplankton community composition (Figure 12) is a result of a large pulse in late May (Figure 13). This observation may have not been recorded in previous years depending on environmental conditions, hatching of nauplii, and sampling dates. We also see that the absence of *Ceriodaphnia* in 1997 may be a result of not sampling in September. Most occurrences of *Ceriodaphnia* in past years was limited to September (Figure 13).

## Part 2. Fishery Investigations

### METHODS

#### **Vertical Gill Netting**

Kokanee were collected with vertical gill nets on 7-8 May, 1-2 June, 8-9 July, and 4-5 August. We used three gangs of experimental vertical gill nets on all sampling dates. These nets floated on the surface, measured 55 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. In May these nets were fished down to 30 m overnight from 19:00 to 07:30 hours at a reference station in Cebolla Basin. All fish sampling for the remainder of the summer was done at the reference station in Sapinero Basin, where limnological parameters were collected. Nets were set down to 45-m depth in June, and 55 m in July and August. In addition to the three gangs of experimental vertical gill nets, we fish an additional 12 gangs of vertical gill nets, each measuring 15 m long and 3 m wide with a single mesh size of 1.0, 1.25, or 1.75 in. In July, we

joined these shorter nets to make them 30 m long, and we only fished three of these gangs in July and August (for a total of six gangs - 3 gangs at 55 m long by 3 m wide, and 3 gangs at 30 m long by 3 m wide).

For June, July, and August, kokanee vertical distributions were monitored over a 24 hour period on each trip. Nets were set and lifted as follows: 1-2 June between 11:30-19:00, 19:00-00:00, 00:00-08:00, and 08:00-13:00 hours; 8-9 July between 19:30-22:30, 22:30-02:00, 02:00-04:45, and 04:45-08:00 hours; and 4-5 August between 18:45-19:30, 21:30-01:00, 01:00-04:30, and 04:30-08:15 hours.

Depth at which each fish was caught was recorded. Gill net-caught fish were measured and weighed. Otoliths, scales and stomachs were removed from most kokanee and a subsample of other salmonids.

### **Diet and Growth Analysis**

Stomach samples obtained from kokanee in diel gill net surveys were used to estimate stomach fullness, prey selection, wet-dry mass ratios of stomach contents, and digestion rate. Kokanee stomachs were extracted immediately and contents were weighed to the nearest 0.1 g. Eight stomachs each in July and August were preserved in 10% formalin for later quantification of prey in the laboratory. *Daphnia* in these samples were measured and their eggs were counted. Contents of other stomachs were frozen on dry ice prior to drying in a 60°C oven. Dried stomach contents were then reweighed on an analytical balance to determine water content for a study examining water extraction by kokanee (Stockwell et al. In Press). Stomach weights were also used to compute feeding chronology and digestion rate (Stockwell and Johnson In Review).

Stomach samples obtained from Blue Mesa rainbow trout during 1995 (n=7), 1996 (n= 5) and 1997 (n=28 stomachs) were analyzed for prey composition by size class (<250 mm TL and >= 250 mm TL) and season (spring, summer and fall). Stomachs were removed from fish captured in experimental gill nets and from samples of the anglers' catch at cleaning stations. Stomachs were preserved in 10% formalin prior to analysis in the laboratory. Contents of each stomach were examined under a dissecting microscope and relative composition (percent by volume) of each prey taxon was estimated by eye. First contents were sorted into three categories: zooplankton, macroinvertebrates, and fish. The zooplankton category was further discriminated into cladocerans and copepods, and macroinvertebrates were classified into Hymenoptera, Chironomid, Coleoptera, Ephemeroptera, Hemiptera, Tricoptera, Amphipoda, and crayfish.

Growth of kokanee was determined from microscopic examination of whole otoliths (DeVries and Frie 1996). Otolith-derived ages were corroborated using the Petersen length-frequency method (DeVries and Frie 1996).

### **Hydroacoustics**

We used an HTI Model 240 split beam 200-kHz echo sounder to repeatedly sample a single transect over a 24 hour period during the new moon of each of June, July, and August. The transect covered approximately 3.2 km, and was located in Sapinero Basin (UTM endpoints: station SAPT1A=13S 0297969 4259716, station SAPT1B=13S 0300630 4261515). Reference point SAPT1A was located near the vertical gill netting station. Sampling times over the course of each diel survey were based on our presumption that kokanee would show strongest vertical migration during dusk and dawn. We therefore sampled these time periods intensively, supplemented by sampling during mid-day and mid-night. Because of technical difficulties, hydroacoustic data were acquired

during the following time periods only: 1 June - 11:13 to 12:15, 19:13 to 22:26; 8 July - 11:56 to 12:54, (9 July) 03:45 to 07:03, 08:33 to 09:38, 11:26 to 11:58; and 4 August - 19:30 to 21:51, (7 August) 09:33 to 11:07.

Additionally, we conducted an abbreviated lakewide sonar survey on 6 -7 August by sampling a subset of CDOW standard transects (Table 4). In Iola Basin, we sampled transects DOW017-DOW018, DOW018-DOW019, DOW019-DOW020, and DOW020-DOW021. In Cebolla Basin, we sampled transects DOW107-DOW108, DOW108-DOW109, and DOW109-DOW110. All transects were sampled between 22:48 and 00:59. Mean fish densities (kokanee sized targets only, -55 to -33 dB) were computed across transects within a basin in 5-m depth strata from near the surface (2 m) to 60 m. Then basin means were averaged to produce lakewide mean fish densities (fish/1000 m<sup>3</sup>) in 5-m depth strata. Reservoir surface elevation on August 6, 1997 was used to compute the volume in each stratum from U.S. Bureau of Reclamation morphometry tables. Mean fish densities in each stratum were multiplied by strata volumes and summed to provide a lakewide abundance estimate.

Sampling rate in June was set at 5 pings/second, but was reduced to 3 pings/second in July and August. Data were recorded on a digital audio tape recorder and processed using HTI software.

## RESULTS AND DISCUSSION

### Vertical Gill Netting

Analysis of kokanee catches in 1997 vertical gill net surveys are presented in Appendix A. Because methods differed in 1997 from past years (shorter net sets in 1997), detailed analyses of catches are not presented. The total 1997 vertical gill net catch of game fishes was comprised of 371 kokanee, 59 brown trout, 38 rainbow trout, 25 lake trout and 4 Snake River cutthroats. After removing stomachs, otoliths, scales, and muscle and liver tissue samples (for stable isotope analysis), edible fish were turned over to CDOW for distribution to area food pantries. Inedible remains were disposed of in the CDOW wildlife landfill near Gunnison, per scientific collection permit guidelines.

### Diet and Growth Analysis

Mass of kokanee stomach contents decreased through the night to near empty in early morning in July and August, indicating age 1-3 kokanee do not feed during the night (Appendix A). Comparison of the digestion function used by Bevelhimer and Adams (1993) and Stockwell and Johnson (1997) with field samples indicated that the model function underestimated gastric evacuation at Blue Mesa (Appendix A). An improved function was derived from the field data for incorporation in the model (Appendix A).

Kokanee diet consisted entirely of *Daphnia pulex*. Kokanee of all ages selected large daphnids (>1.7 mm; Table 5). Rainbow trout diet did not differ greatly by size class (Figure 14) but did appear to differ by season. In spring, before zooplankton become abundant, small (<250mm TL) rainbow trout diet was dominated by macroinvertebrates. Only one large rainbow trout was sampled in spring and it contained mostly unidentified fish remains. In summer, samples sizes of small and large rainbow trout were much greater. Small rainbow trout consumed about 70% zooplankton and 30% macroinvertebrates. Large rainbows consumed 70% macroinvertebrates and 30% zooplankton. Diet of both size classes of rainbow trout in fall was dominated by zooplankton (60% for small and 80% for large rainbow trout), but sample sizes were n=2 fish for both size classes. The zooplankton component of rainbow trout stomachs was entirely cladocerans. Macroinvertebrates were primarily

terrestrial insects (Hymenoptera, Coleoptera, and Hemiptera) but Chironomids were also common (16% of stomachs). Ephemeroptera, Tricoptera, Amphipoda and crayfish were rarely eaten (Table 6).

Kokanee growth rates estimated from otoliths and length-frequency analysis in June-August 1997 (Table 7) were similar to rates estimated from scales and otoliths in previous years (Figure 15). Kokanee growth in Blue Mesa continued to rank among the highest growth rates of any kokanee population in the literature (Luecke and Canning 1996; Martinez 1994, 1995; Rieman and Meyers 1992; Graynoth 1987; Hanzel 1974a, 1974b).

### **Hydroacoustics**

There was a wide range of patterns in kokanee vertical distribution over the course of the field season (Appendix A). In June, age 1 fish were primarily concentrated between 15-25-m depth during daylight hours, although they were also present between 5-15 and 25-45-m strata. Age 2-3 kokanee showed a bimodal distribution at this time, with peaks in the 0-5 and 15-25-m depth strata. Kokanee from all three age-classes appeared to ascend at dusk, forming a thick layer between 5-10 m during the night.

The same general pattern occurred in July (Appendix A). During darkness, kokanee were concentrated in a thick layer between 10 and 20-m depth. At dawn, kokanee were somewhat more dispersed but primarily located between 5 and 20-m depth. During morning and midday, age 1 fish were concentrated between 5-10 and 15-25 m, while age 2-3 fish were scattered throughout the water column.

In August, migration patterns reversed. Mid-morning distributions were located between 5 and 15 m for all ages. At dusk, kokanee occupied a much broader, and deeper range of depths. At dark, vertical distributions were concentrated between 15 and 50 m for age 1 fish, and primarily between 15 and 30 m for age 2-3 fish.

Although we were not able to conduct the complete standardized August hydroacoustics survey performed in previous years, the sampling we did should be quite comparable to past surveys. Abundance of kokanee-sized fish targets in 1997 was lower than that observed during 1994-1996 (Figures 16-19). The low abundance of kokanee estimated from hydroacoustics was supported by creel survey data (D. Brauch, CDOW, Gunnison, CO, unpublished data) which showed that angler effort and catch rate continued an annual decline since 1993 (Figure 20). The extremely low estimated abundance of kokanee in 1997 is of great concern because declines in kokanee at Lake Granby mean that Blue Mesa's kokanee population must be self-sustaining from its own egg supply. The mechanism behind the kokanee decline remains unresolved, but lake trout predation is likely an important factor (Johnson and Martinez in prep).

## **RECOMMENDATIONS**

Blue Mesa has been one of the top kokanee salmon fisheries in the world, and a significant proportion of Colorado's coldwater fishery resource. There are indications that the BMR fish assemblage is changing. Kokanee abundance continued to decline in 1997, while piscivorous lake trout have apparently increased dramatically. Close monitoring is needed to prevent this fishery from collapsing. Based on our work in 1993-1997 we recommend the following:

- Continue to gather information on fish abundance, diet, and growth rates.

- Conduct creel surveys to obtain information on kokanee catch rates and mortality.
- Increase kokanee stocking rates substantially. The system is well below carrying capacity and could sustain at least 3-4 times the current number of kokanee.
- In the absence of zooplankton monitoring, continue the sampling program implemented in 1994 to gather fish stomach samples and growth information from angler caught fish.
- Continue hydroacoustics surveys for estimating fish abundance and distribution, and vertical gillnetting for “groundtruthing” hydroacoustics data, species identification and to provide diet samples.
- Estimate kokanee encounter rates with piscivorous lake trout.

We should continue to work to predict the importance of climate on reservoir structure and function by implementing the reservoir thermal model CE-THERM. 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. We recommend the following:

- 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
- Complete the evaluation of 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.
- Perform multi-reservoir comparisons to examine the influence of basin morphometry on thermal and trophic responses to climate and operations.
- Complete lab experiments on kokanee feeding rate for incorporation into the foraging model we are linking to CE-THERM

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.

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Table 1. CSU accomplishments during Blue Mesa Reservoir Reoperation Study, July 1993- May 1998: Presentations (invited presentations marked with asterisk).

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\*Johnson, B. M. 1998. Effects of dam operations on reservoir food web interactions. Department of Fisheries and Wildlife Departmental Seminar, Utah State University, Logan, UT.

\*Johnson, B. M. and D. Beauchamp. 1998. Continuing Education Workshop: Reservoir Research and Management, Colorado-Wyoming and Bonneville Chapters, American Fisheries Society, Grand Junction, CO.

\*Johnson, B. M., J. D. Stockwell, and D. G. Fontane. 1997. Ecosystem responses to new dam operations in a large montane reservoir. North American Lake Management Society, Houston, TX.

Johnson, B. M., J. D. Stockwell, and D. G. Fontane. 1997. Modeling ecosystem responses to reservoir reoperation. American Society of Limnology and Oceanography, Sante Fe, NM. (Poster)

Johnson, B. M., J. D. Stockwell, and D. G. Fontane. 1997. Modeling ecosystem responses to reservoir reoperation. CO/WY American Fisheries Society, Cheyenne, WY. (Poster)

Stockwell, J. D. and B. M. Johnson. 1997. Forecasting changes in behavior and predation risk of a vertically migrating planktivore. American Fisheries Society National Meeting, Monterey, CA.

Stockwell, J. D. and B. M. Johnson. 1997. Modeling planktivorous fish responses to natural and human-induced alteration of thermal habitat. American Society of Limnology and Oceanography National Meeting, Sante Fe, NM.

Stockwell, J. D. and B. M. Johnson. 1997. Modeling kokanee responses to climate and dam reoperation in Blue Mesa Reservoir. CO/WY Chapter, American Fisheries Society, Cheyenne, WY.

Stockwell, J. D. and B. M. Johnson. 1997. A combined foraging and vertical migration model for kokanee salmon - how can it be applied to mysids? International Mysid Ecology Workshop, Cornell University, NY.

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Martinez, P. J. and B.M. Johnson. 1995. Trophic economics: Food for thought, Macs, Pike, etc. Colorado Wyoming Chapter of the American Fisheries Society, Casper, WY.

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Table 2. CSU accomplishments during Blue Mesa Reservoir Reoperation Study, July 1993- May 1998: Publications supported entirely or in part by the project, and scholarly awards.

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### **Publications**

Johnson, B. M. and P.J. Martinez. (In prep for NAJFM). Trophic economics and lake trout management across a productivity gradient in four montane reservoirs.

Faber, D. and B. M. Johnson. (In Prep for J. Freshwater Ecology). Patterns and Mechanisms of Kokanee Diel Vertical Migration in Blue Mesa Reservoir, Colorado.

Stockwell, J. D. and B. M. Johnson. (In review). Field evaluation of a bioenergetics -based foraging model for kokanee (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences.

Stockwell, J.D., K.L. Bonfantine, and B.M. Johnson. In Press. Kokanee salmon foraging: a Daphnia in the stomach is worth two in the lake. Transactions of the American Fisheries Society xx:0000-0000.

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 54:2659-2676.

Wise, M. J. 1997. Daphnia sampling efficiency, and the relative influence of kokanee predation on Daphnia population dynamics in Blue Mesa Reservoir, Colorado. M.Sc. Thesis, Colorado State University, Fort Collins, CO.

### **Awards**

Best Poster Award. Colorado/Wyoming Chapter of the American Fisheries Society, Cheyenne, WY, February, 1997.

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Table 3. Overview of sampling conducted by CSU on Blue Mesa Reservoir in 1997.

Parameter	Approach	Methods
Temperature	Profiles	Once a month, from June-August, at reference station in Sapinero Basin
Dissolved oxygen	Profiles	Once a month, from June-August, at reference station in Sapinero Basin
Secchi depth	Measurements	Once a month, from June-August, at reference station in Sapinero Basin
Chlorophyll	0-10 m Integrated	None
	Profiles	None
Zooplankton	Depth-stratified Samples	153 $\mu\text{m}$ mesh: 0-10 m in Sapinero Basin in June, July, and August
		500 $\mu\text{m}$ mesh: 0-5, 5-10, 10-15 m in Sapinero in May, June, July, and August
Fish (salmonids) size, spp, depths	Vertical Gill Nets (six meshes)	24 hr sets with frequent lifts in each of June, July, and August in Sapinero. One overnight set in Cebolla in May.
Diet	Vertical Gill Nets	Subset of fish collected on each date
Abundance	Hydroacoustics	Abbreviated Lakewide Survey, August
Diel Vertical Migration	Hydroacoustics	Three diel surveys in Sapinero in June, July, and August
Stream Temperatures	Logger	Maintained temperature logger in the Gunnison River above inlet to Blue Mesa (Cooper Ranch Picnic Area)

Table 4. Standardized transects used during hydroacoustics surveys at Blue Mesa Reservoir during 1994-1997.

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 5. Daphnia length and number of eggs in kokanee stomachs sampled from Blue Mesa Reservoir in July and August 1997.

Stomach sample no.	Kokanee Age	Kokanee Length (mm)	Kokanee Weight (g, wet)	Daphnia Mean length (mm)	Number of Daphnia measured	Mean number of eggs per Daphnia
BM070997037	1	182	55	2.02	15	0.00
BM070997049	1	208	85	1.71	14	0.00
BM070997006	1	216	95	1.73	25	.
BM070997005	1	235	125	1.74	25	.
BM070997013	2	330	415	1.95	15	0.13
BM070997024	2	294	280	1.85	15	0.00
BM070997009	3	382	625	1.88	25	.
BM070997010	3	374	535	1.83	25	.
BM080497066	1	212	130	1.92	20	0.00
BM080497058	2	295	275	1.85	20	0.00
BM080597005	2	348	435	1.82	18	0.00
BM080597007	1	270	205	1.96	20	0.15
BM080597033	1	230	120	1.82	20	0.00
BM080497056	2	336	425	1.75	20	0.00
BM080597021	2	335	285	1.81	20	0.00
BM080597036	1	225	115	1.81	20	0.00

Table 7. Mean length and weight at age (estimated from otoliths) of kokanees sampled from Blue Mesa Reservoir during May, July and August 1997.

Day of year	Age	N	Mean length (mm)	Standard error	Mean weight (g)
127	1	4	184	4.0	61
	2	3	287	11.5	241
	3	6	354	9.2	460
152	1	2	182	6.5	59
	2	36	288	4.4	243
	3	32	370	3.0	528
190	1	11	210	5.4	92
	2	17	314	5.6	318
	3	22	388	3.1	611
217	1	37	227	3.2	117
	2	12	318	5.1	331
	3	10	406	5.8	702

Table 6. Diet composition from rainbow trout stomachs sampled in 1995-1997 at Blue Mesa Reservoir. ZP=zooplankton, INV=macroinvertebrates, FISH=fish, CLA=Cladocera, COP=Copepoda, HYM=Hymenoptera, CHI=Chironomidae, COL=Coleoptera, EPH=Ephemeroptera, HEM=Hemiptera, TRI=Tricoptera, AMP=Amphipoda, CRA=crayfish.

Sample Date	Total Length (mm)	Percent Composition by Volume												
		ZP	INV	FISH	CLA	COP	HYM	CHI	COL	EPH	HEM	TRI	AMP	CRA
07-11-95	312	100	0	0	100	.	.	.	.	.	.	.	.	.
07-25-95	330	0	100	0	.	.	50	.	.	50	.	.	.	.
07-27-95	334	0	100	0	.	.	20	.	75	.	5	.	.	.
07-28-95	342	0	100	0	.	.	30	.	20	.	50	.	.	.
08-12-96	421	0	100	0	.	.	100	.	.	.	.	.	.	.
08-13-96	352	0	100	0	.	.	100	.	.	.	.	.	.	.
08-14-96	347	0	100	0	.	.	100	.	.	.	.	.	.	.
08-15-95	200	95	5	0	95	.	5	.	.	.	.	.	.	.
09-09-95	221	20	80	0	20	.	70	10	.	.	.	.	.	.
09-10-95	315	70	30	0	70	.	20	.	10	.	.	.	.	.
09-13-96	189	100	0	0	100	.	.	.	.	.	.	.	.	.
09-13-96	267	95	5	0	95	.	5	.	.	.	.	.	.	.
04-29-97	218	0	100	0	.	.	20	80	.	.	.	.	.	.
04-29-97	230	0	100	0	.	.	.	100	.	.	.	.	.	.
05-08-97	239	2	98	0	2	.	.	18	.	.	.	.	.	80
05-08-97	257	0	12	88	.	.	.	2	.	.	.	.	10	.
05-10-97	248	0	100	0	.	.	.	.	100	.	.	.	.	.
06-01-97	233	60	40	0	60	.	40	.	.	.	.	.	.	.
06-01-97	242	65	35	0	65	.	25	7	.	.	.	3	.	.
06-02-97	252	0	100	0	.	.	.	100	.	.	.	.	.	.
06-02-97	254	0	100	0	.	.	.	100	.	.	.	.	.	.
06-02-97	310	20	80	0	20	.	40	.	40	.	.	.	.	.
07-09-97	289	100	0	0	100	.	.	.	.	.	.	.	.	.
07-09-97	308	100	0	0	100	.	.	.	.	.	.	.	.	.
07-09-97	329	100	0	0	100	.	.	.	.	.	.	.	.	.
08-04-97	221	70	30	0	70	.	29	.	1	.	.	.	.	.
08-04-97	240	90	10	0	90	.	10	.	.	.	.	.	.	.
08-04-97	308	50	50	0	50	.	50	.	.	.	.	.	.	.
08-04-97	350	0	100	0	.	.	.	100	.	.	.	.	.	.
08-04-97	383	0	100	0	.	.	.	100	.	.	.	.	.	.
08-05-97	229	0	100	0	.	.	.	100	.	.	.	.	.	.
08-05-97	234	65	35	0	65	.	35	.	.	.	.	.	.	.
08-05-97	240	95	5	0	95	.	5	.	.	.	.	.	.	.
08-05-97	281	40	60	0	40	.	60	.	.	.	.	.	.	.
08-05-97	283	30	70	0	30	.	70	.	.	.	.	.	.	.
08-05-97	292	85	15	0	85	.	15	.	.	.	.	.	.	.
08-05-97	300	0	100	0	.	.	.	100	.	.	.	.	.	.
08-05-97	301	80	20	0	80	.	20	.	.	.	.	.	.	.
08-05-97	325	65	35	0	65	.	33	.	2	.	.	.	.	.
08-05-97	358	0	100	0	.	.	.	100	.	.	.	.	.	.



Table 7. Mean length and weight at age (estimated from otoliths) of kokanees sampled from Blue Mesa Reservoir during May, July and August 1997.

Day of year	Age	N	Mean length (mm)	Standard error	Mean weight (g)
127	1	4	184	4.0	61
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# Blue Mesa Reservoir

Gunnison County, CO

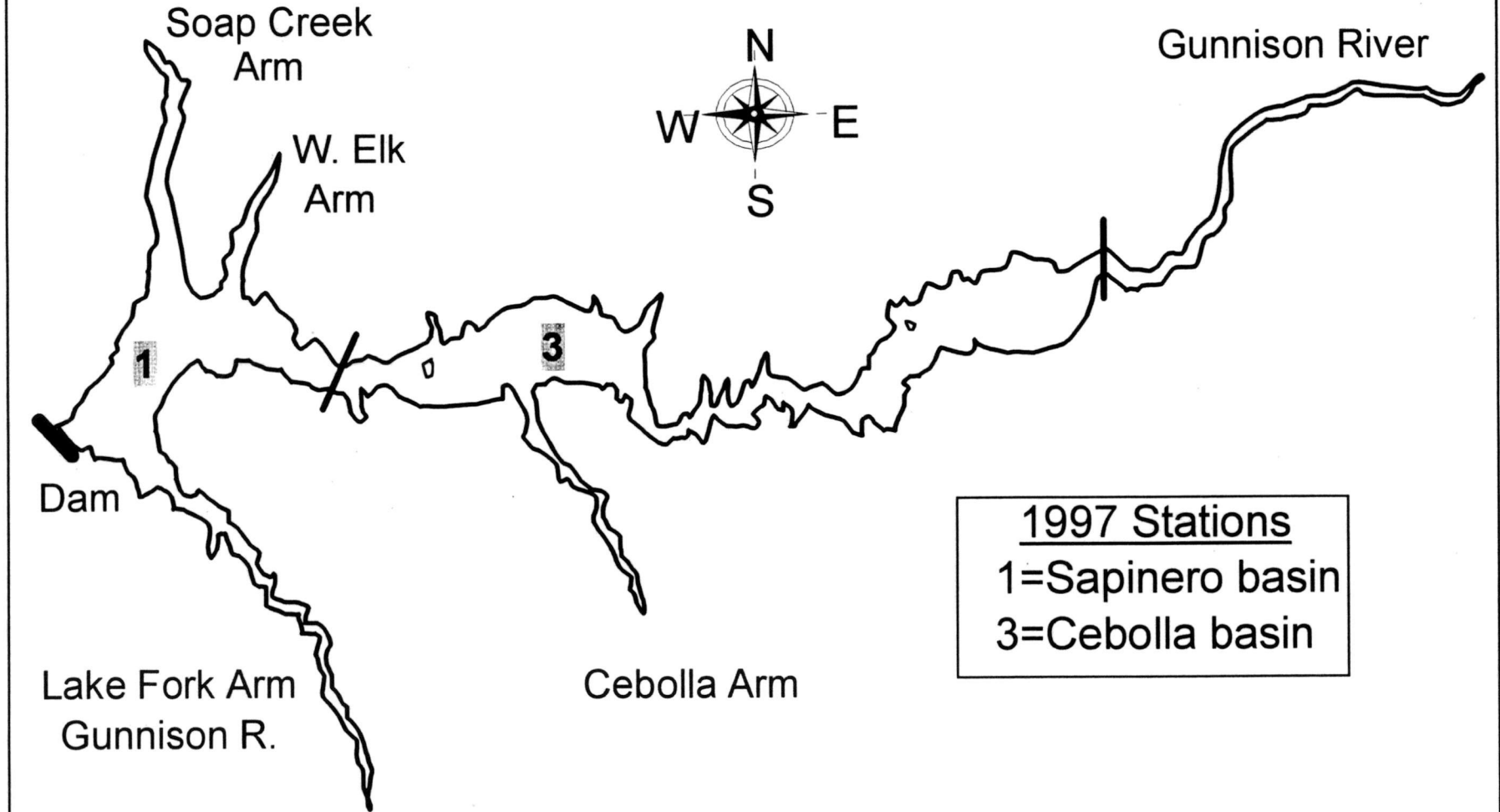


Figure 1.

# Inflow 1993-1997

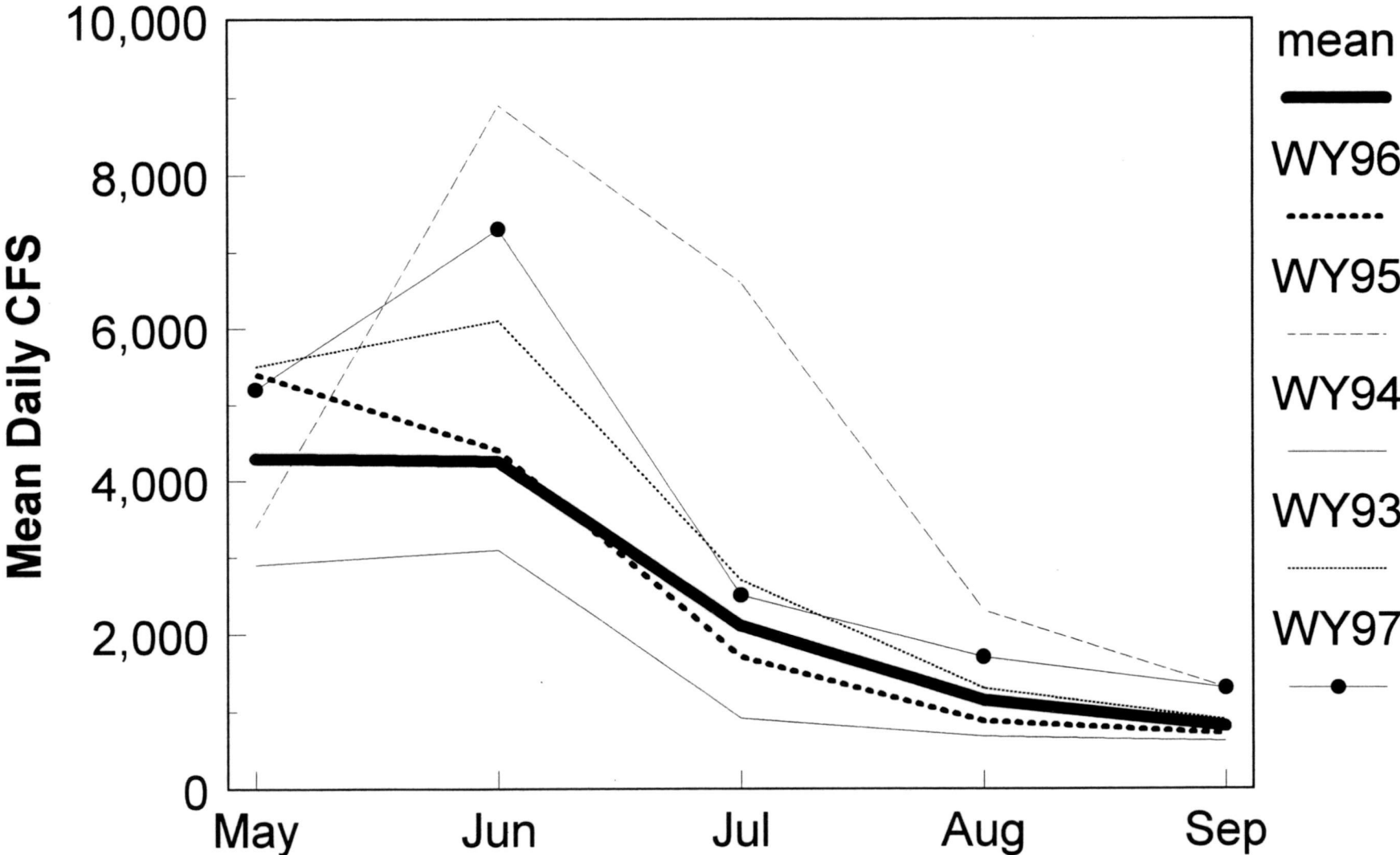


Figure 2.

# Blue Mesa Reservoir Surface Elevation

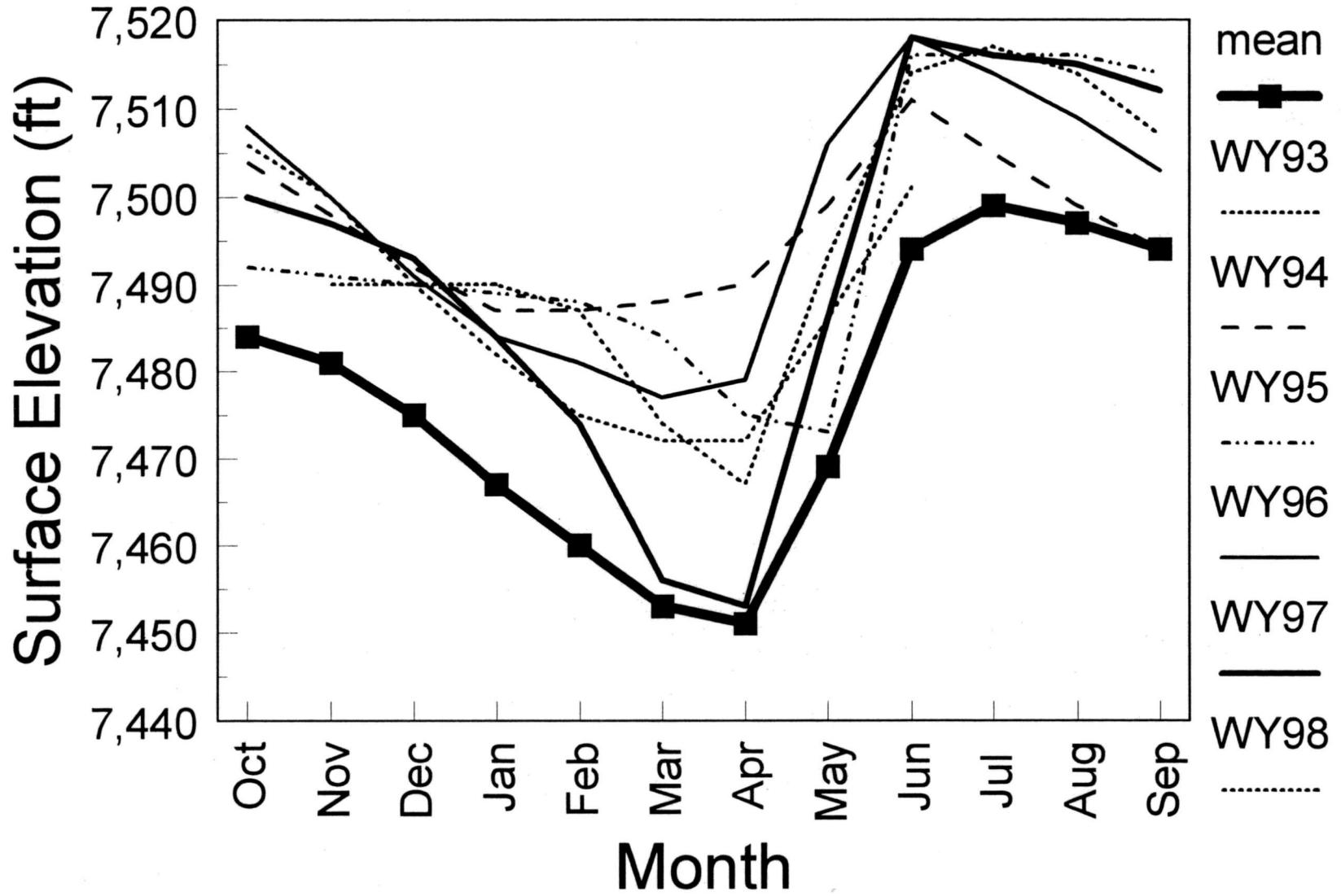
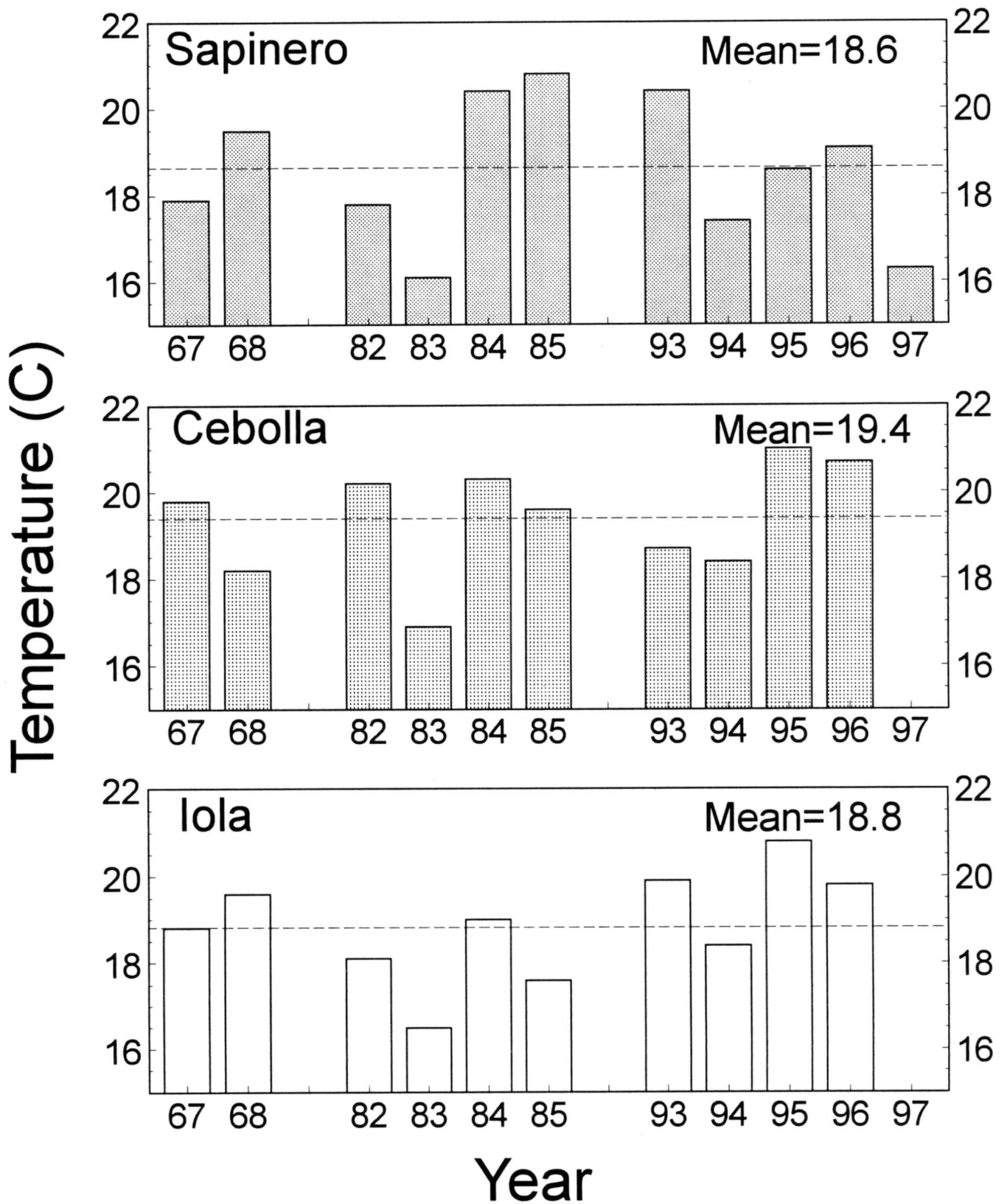
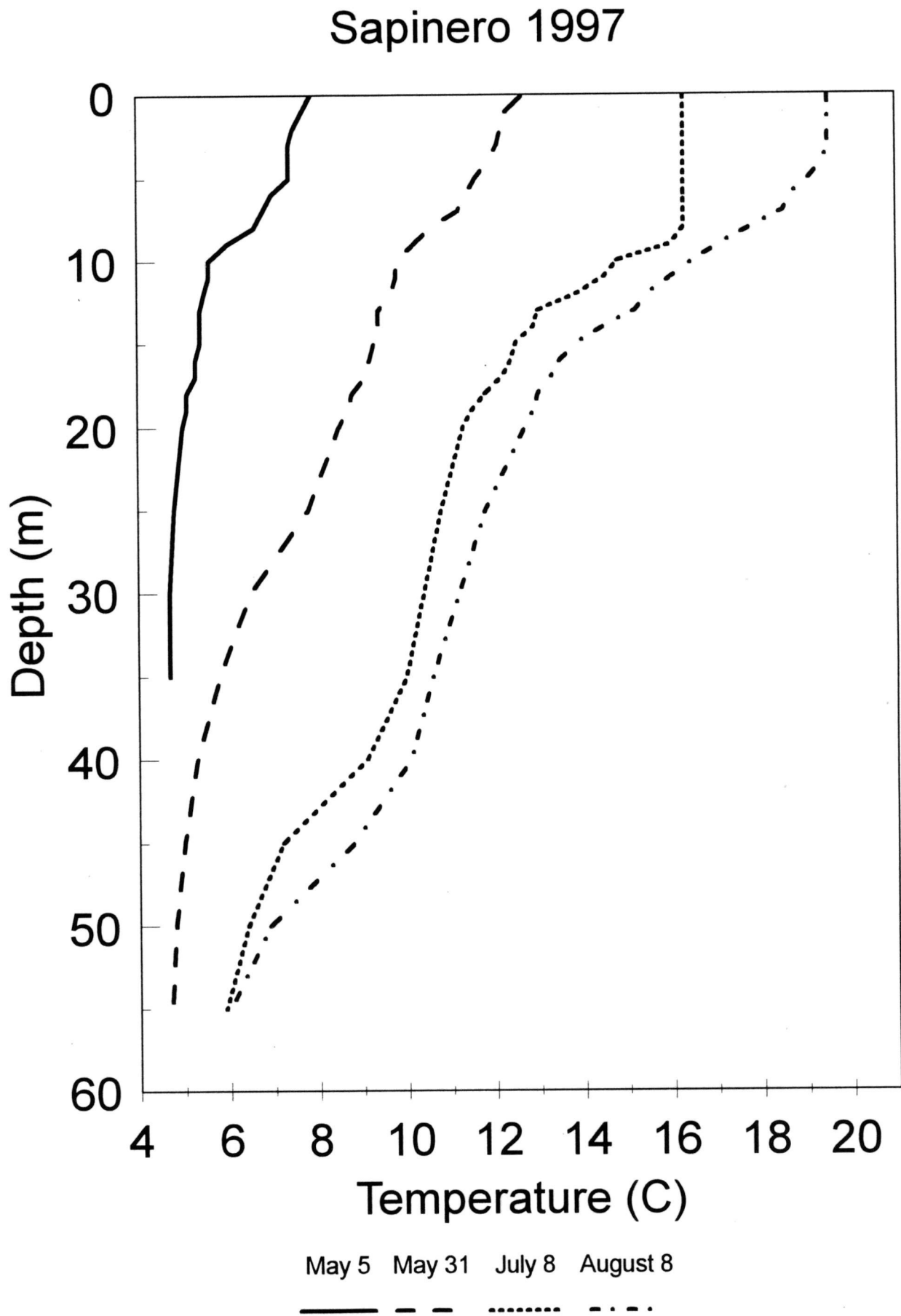


Figure 3.

Figure 4.







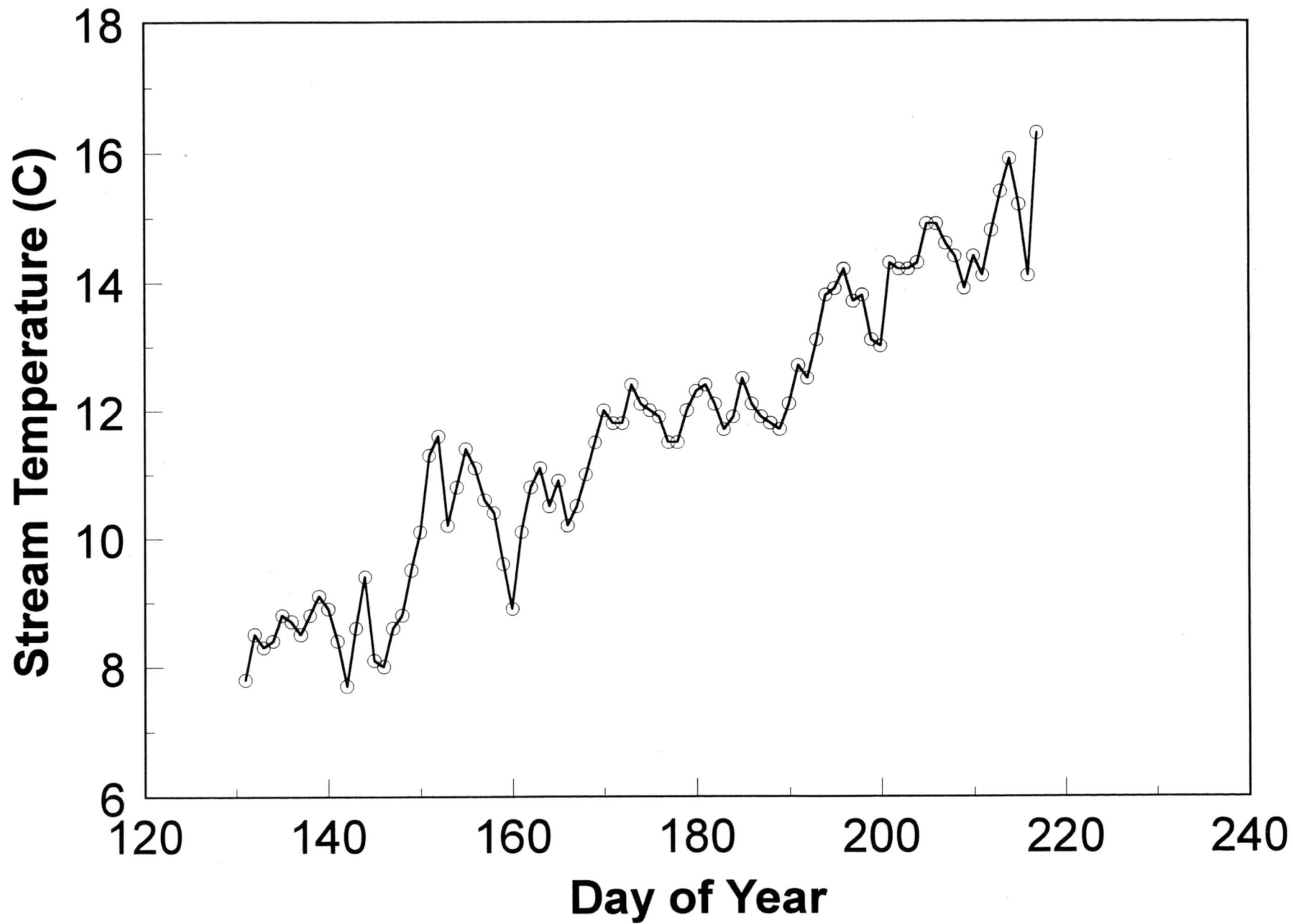
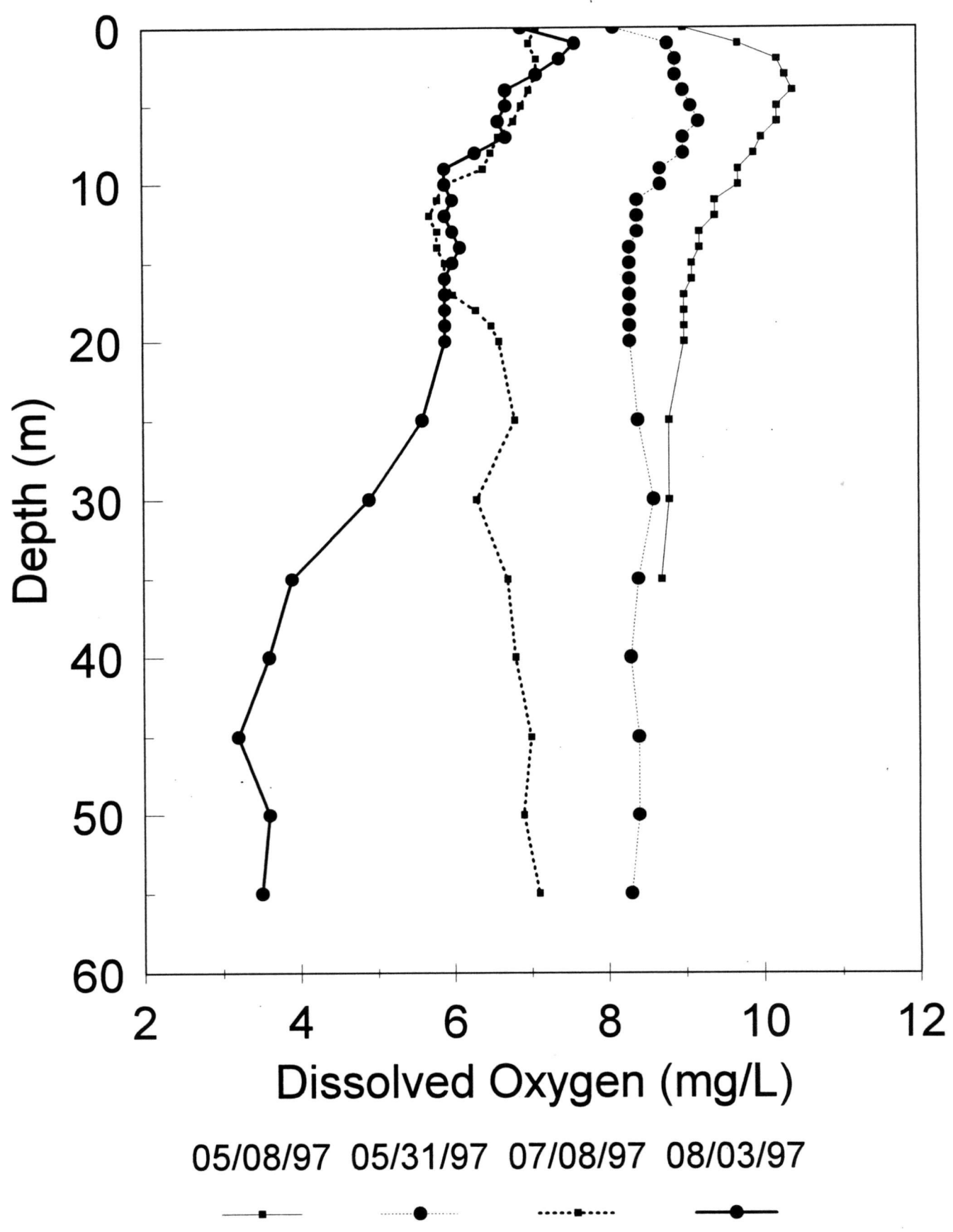


Figure 6.

### Sapinero 1997



# Secchi Depth (m)

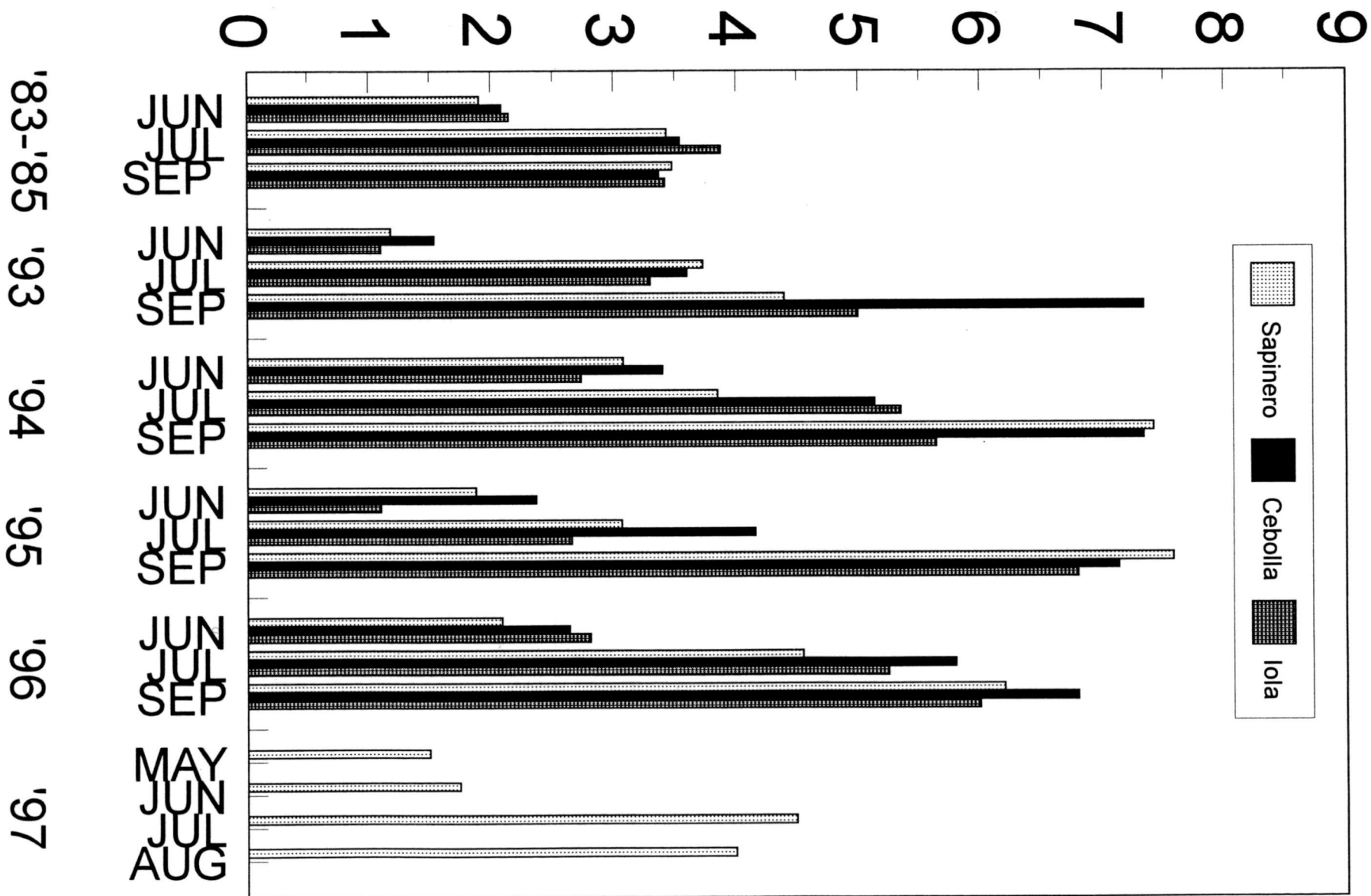


Figure 8.

Figure 9.

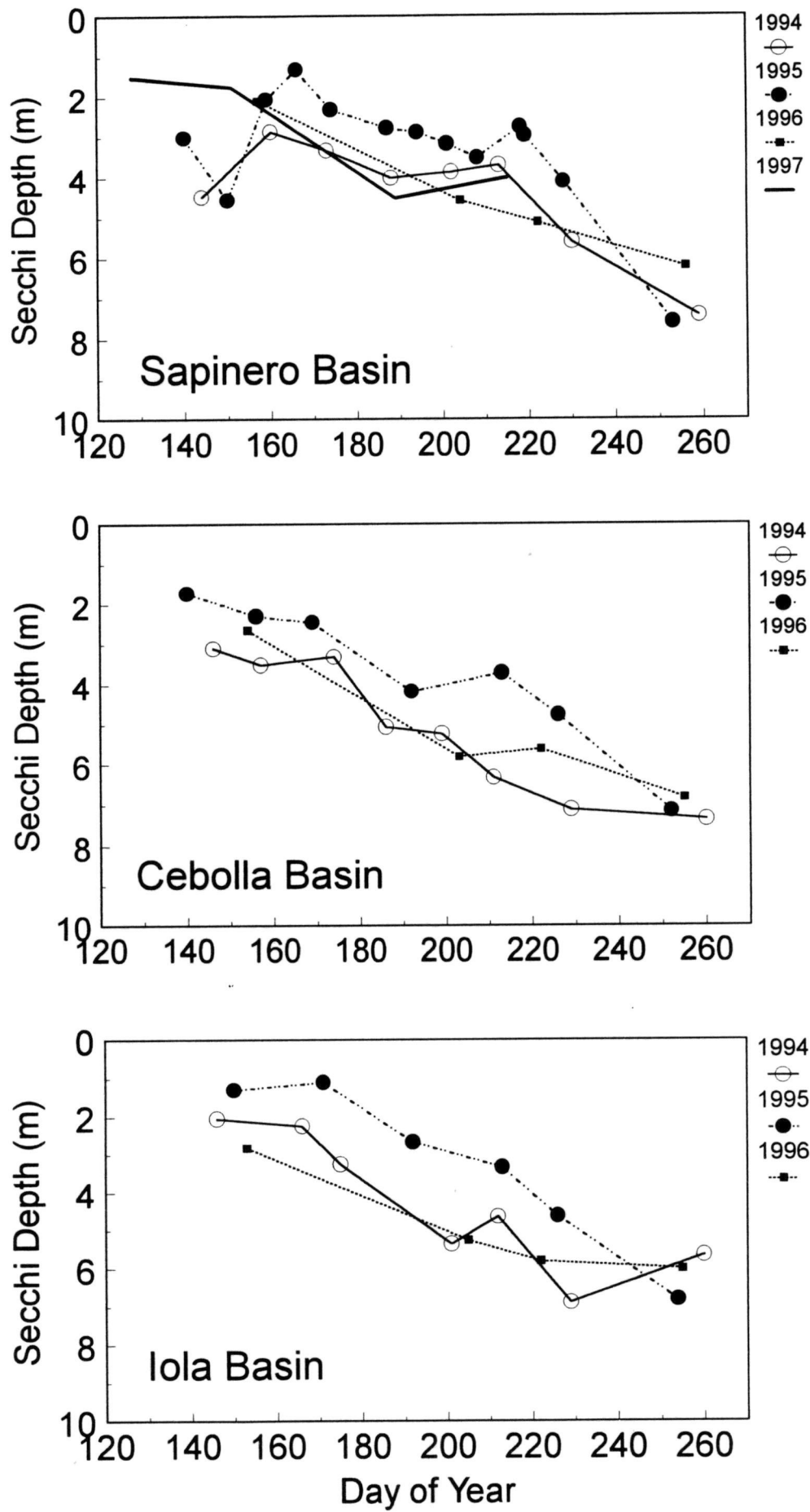


Figure 10.

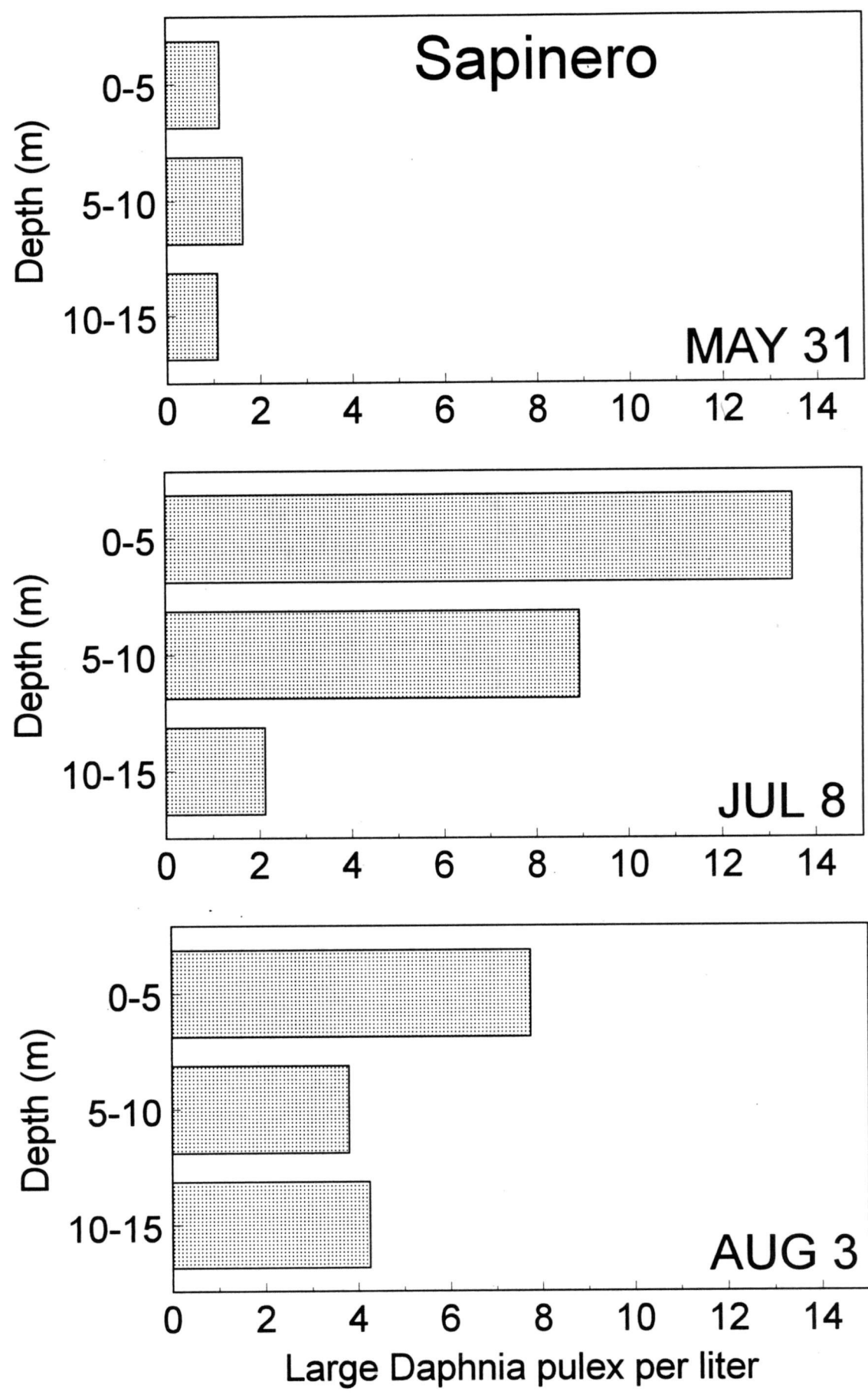
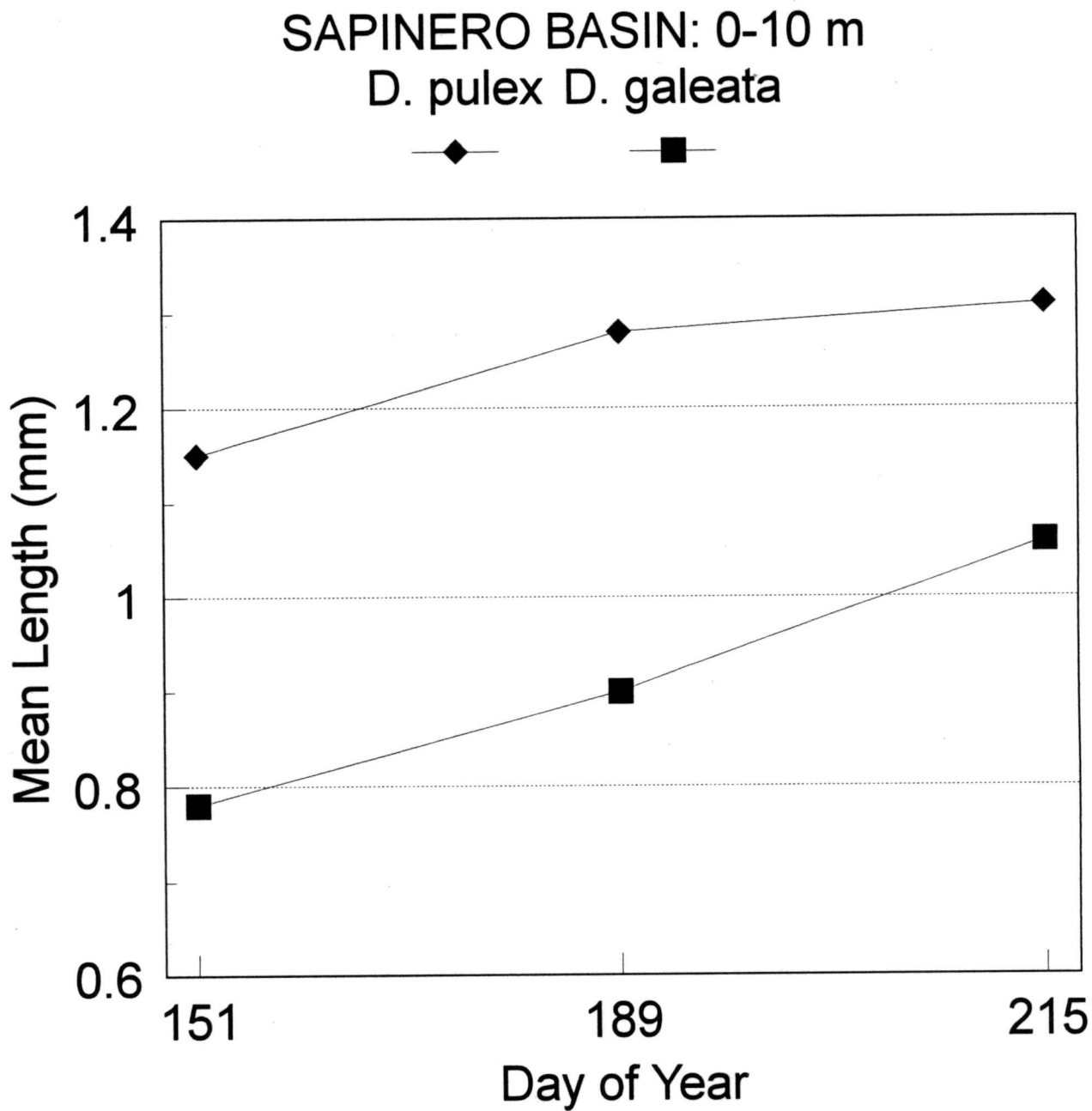
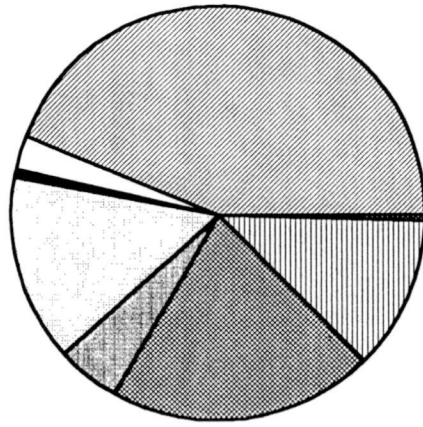


Figure 11.

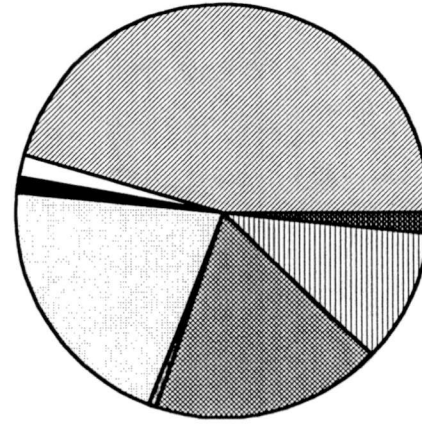


# Zooplankton Community Composition

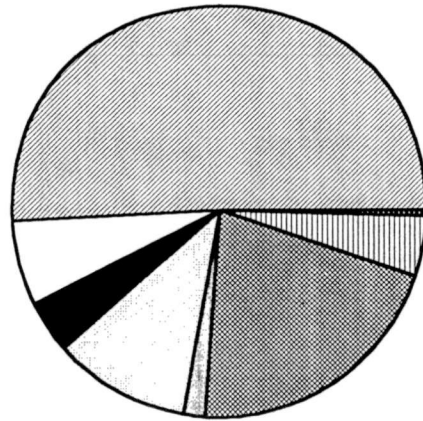
All dates, basins, for the 0-10m stratum



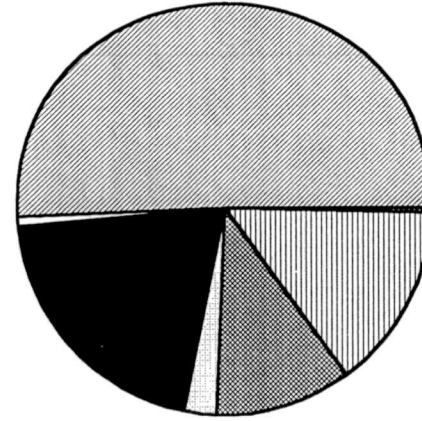
1994



1995



1996

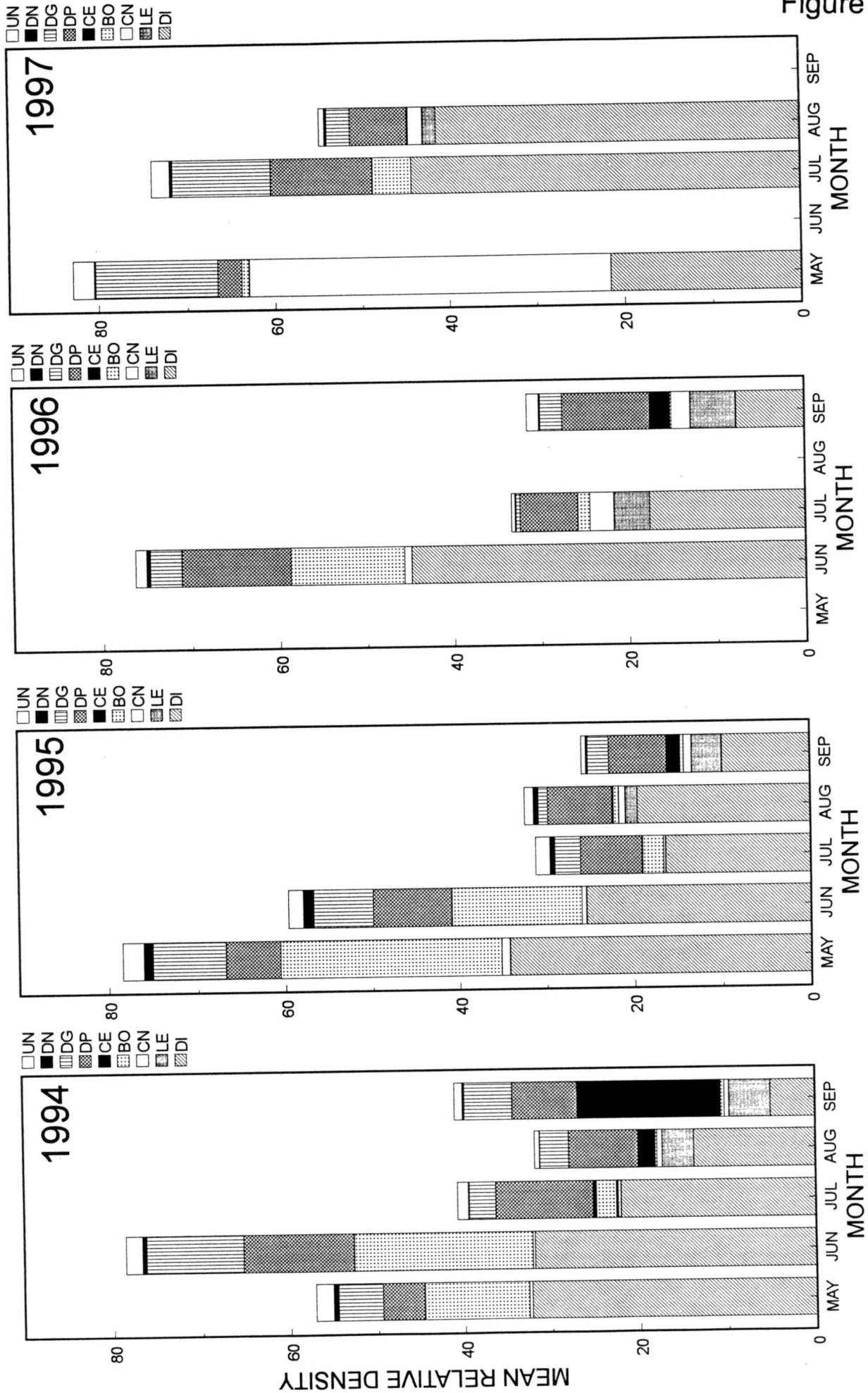


1997



Figure 12.

Figure 13.





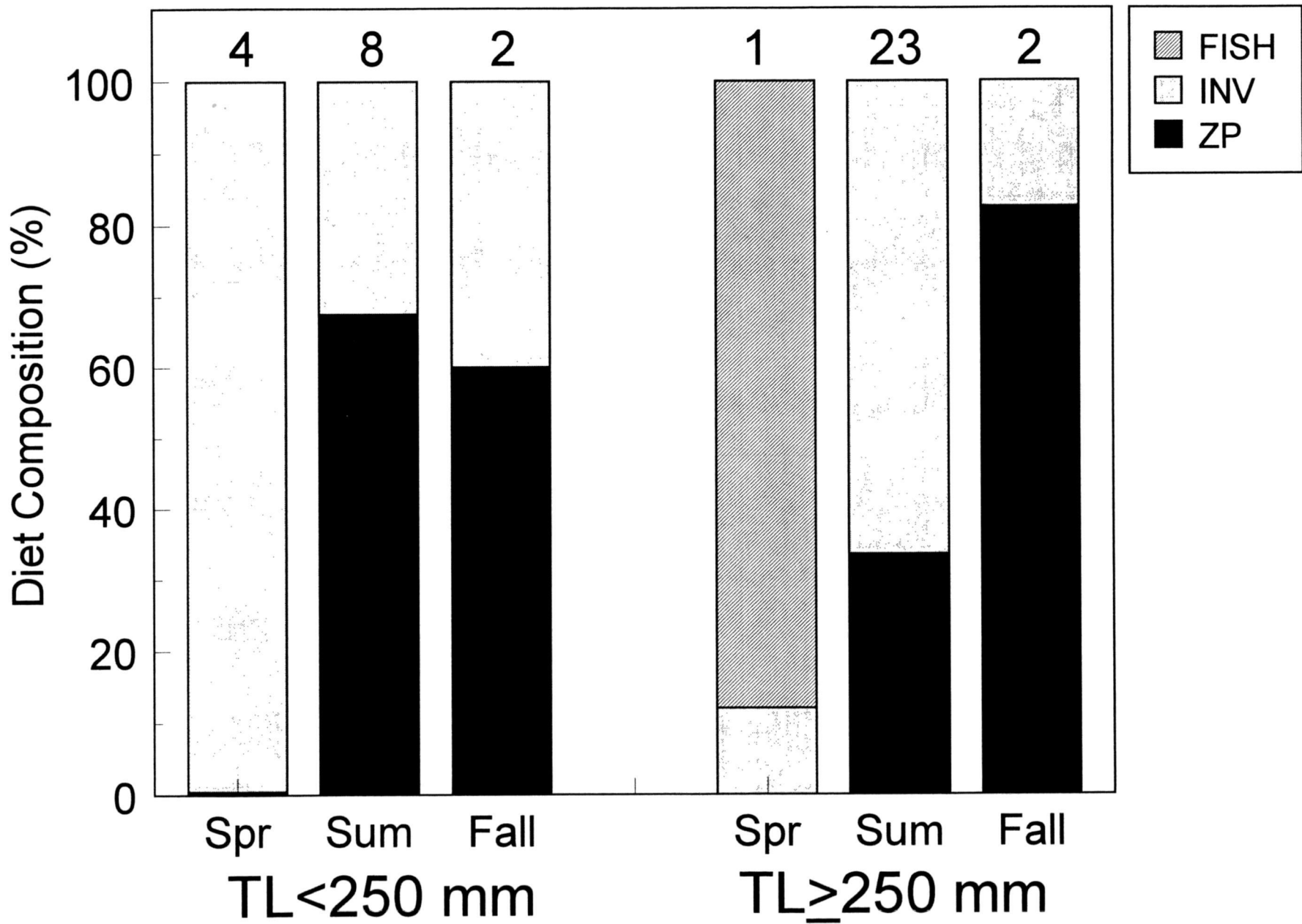
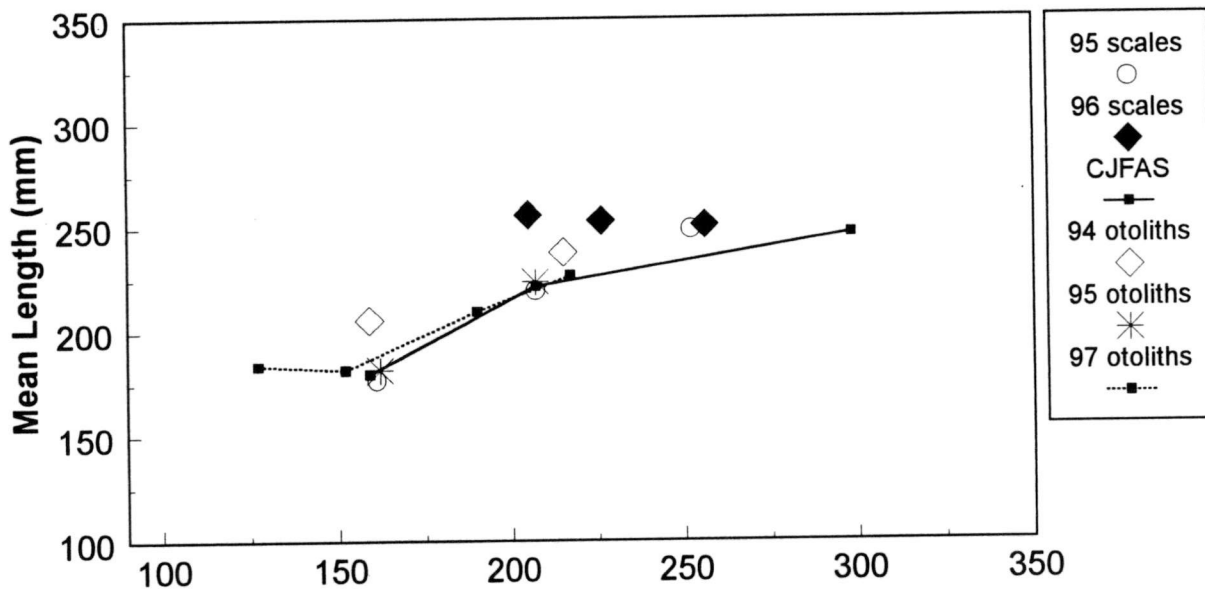
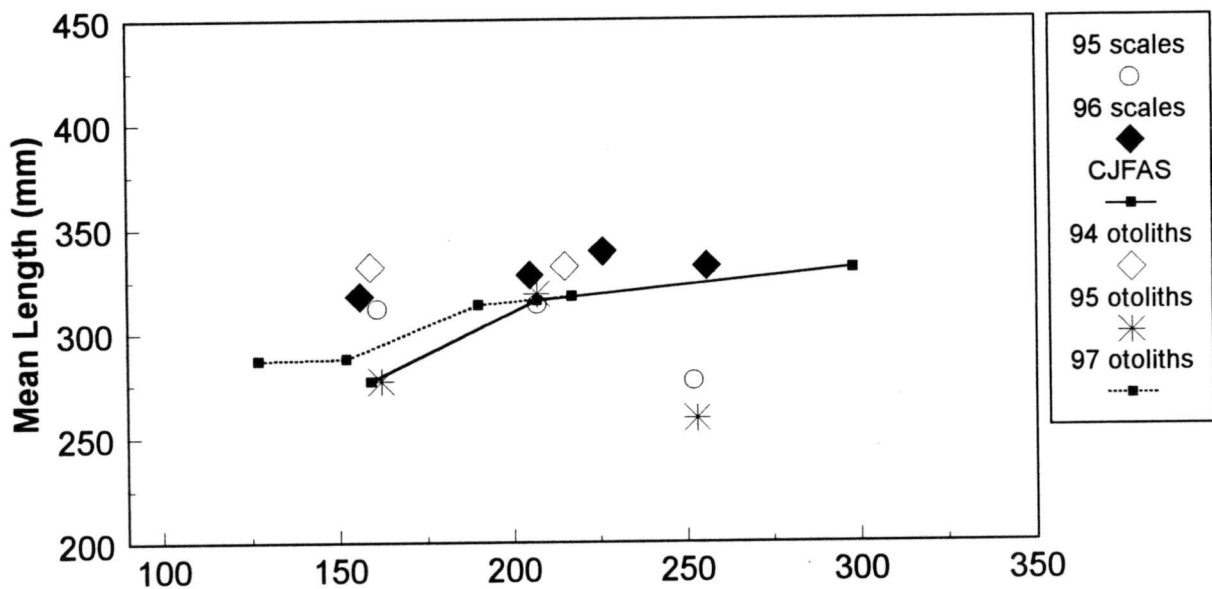


Figure 14.

Age-1 Kokanee - BMR



Age-2 Kokanee - BMR



Age-3 Kokanee - BMR

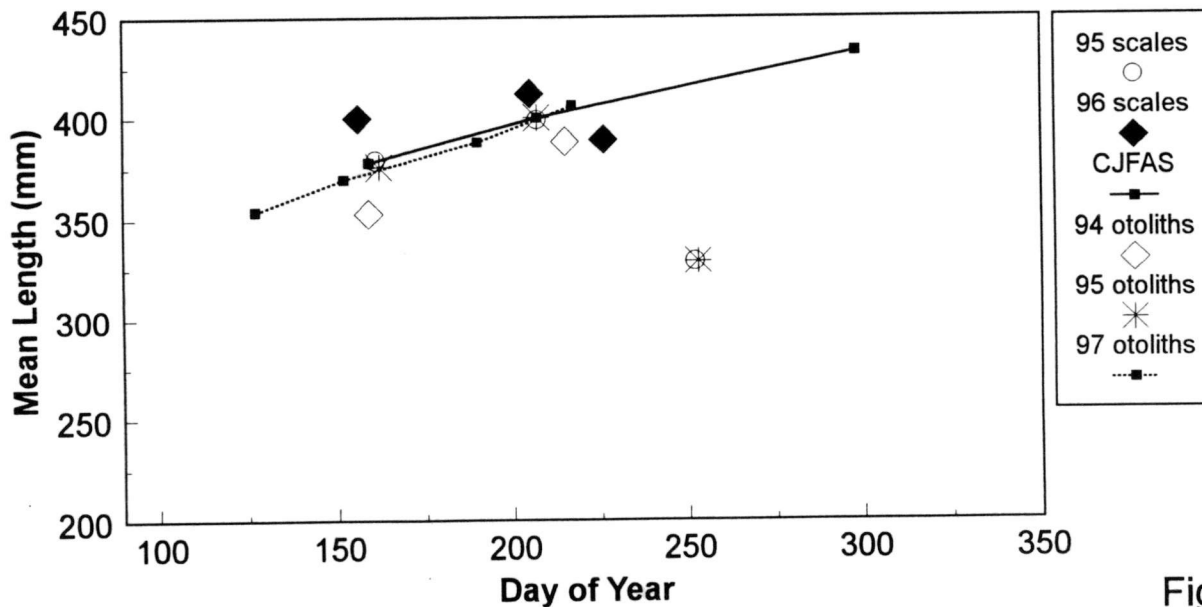
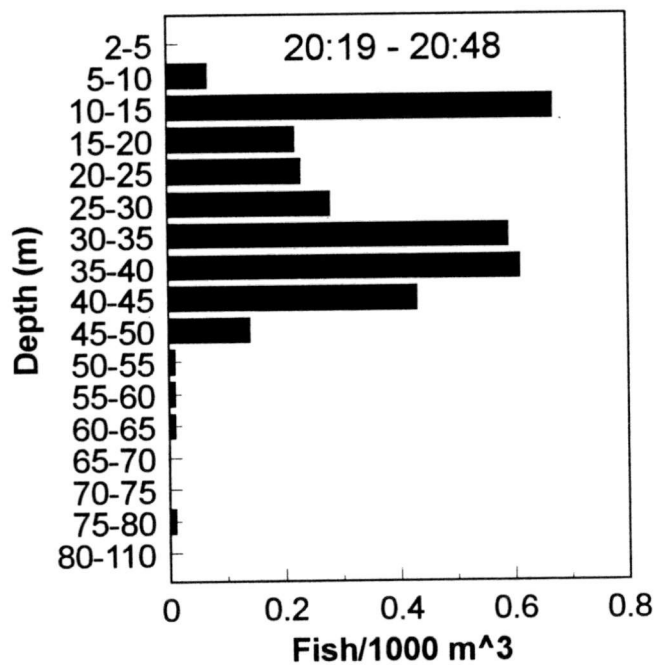
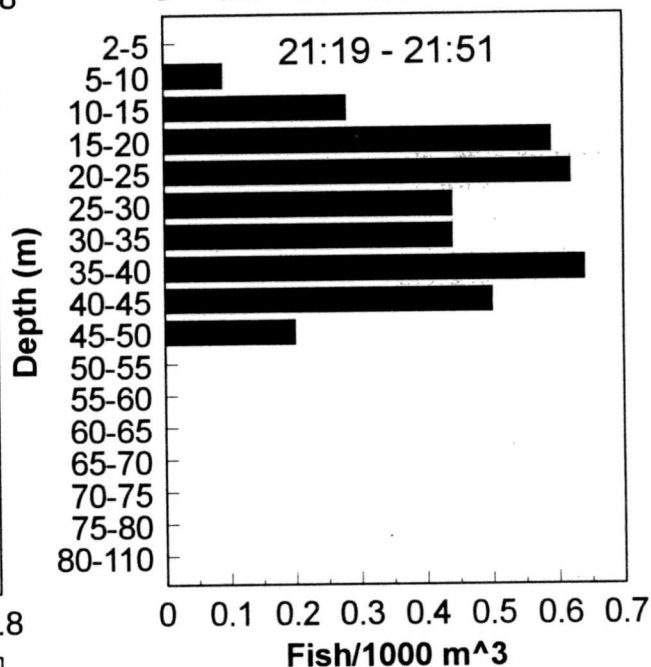
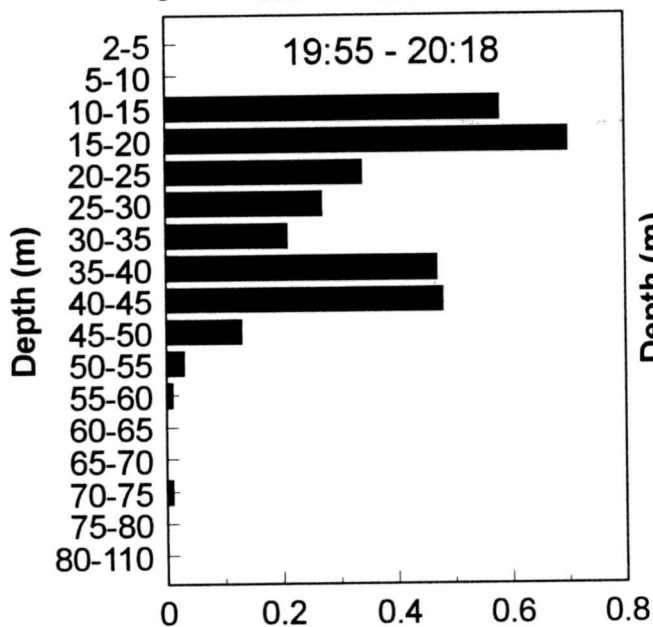
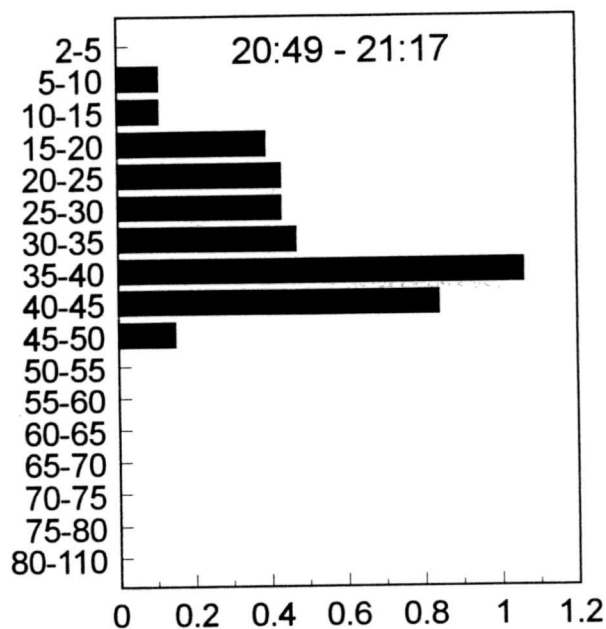
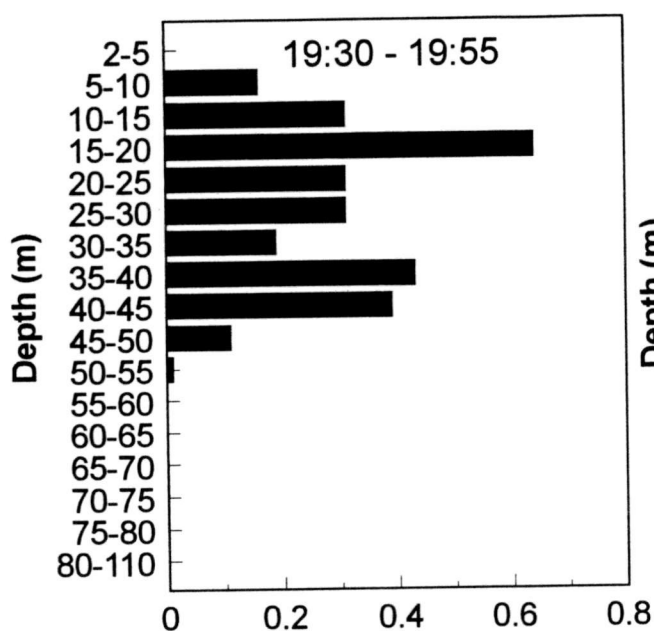


Figure 16.



Sapinero Sonar Results

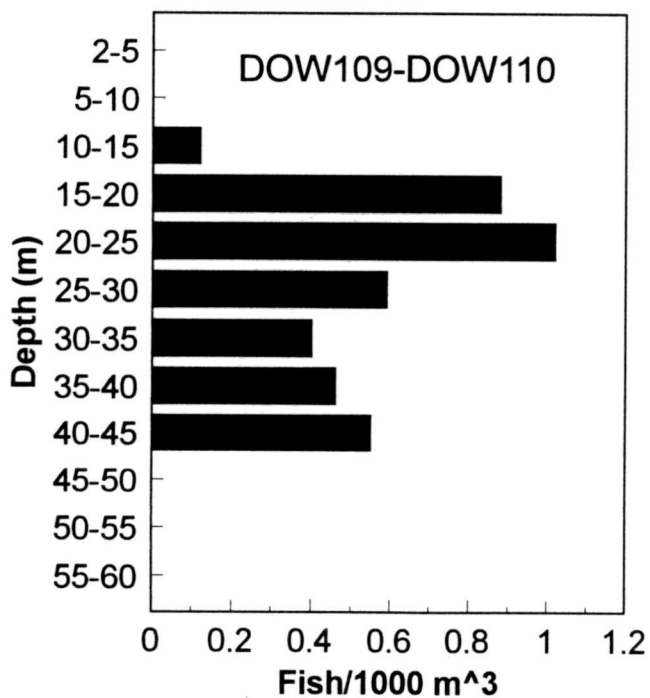
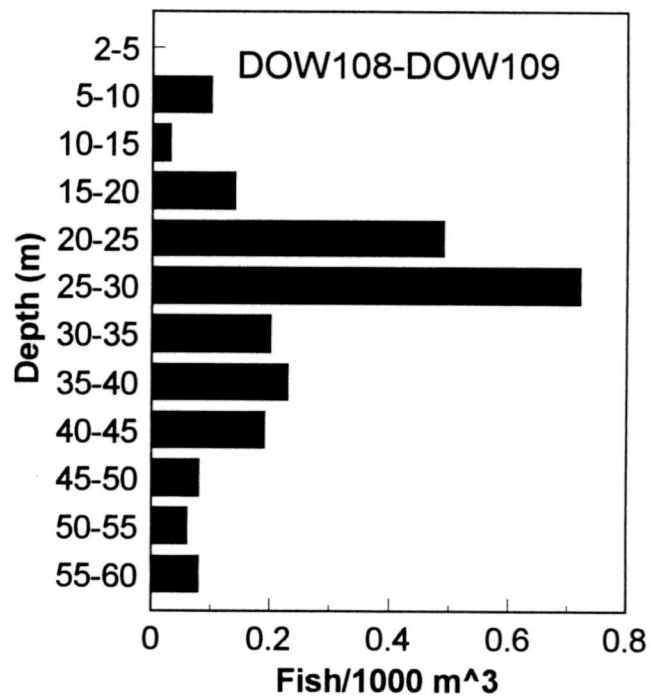
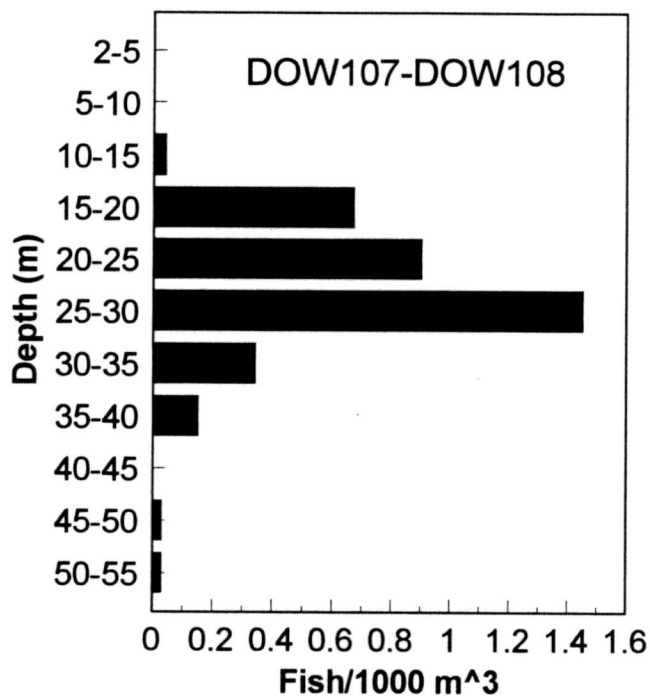
4 August 1997

Repeated Transect  
(SAPT1A to SAPT1B)

Targets from -55 to -33 db

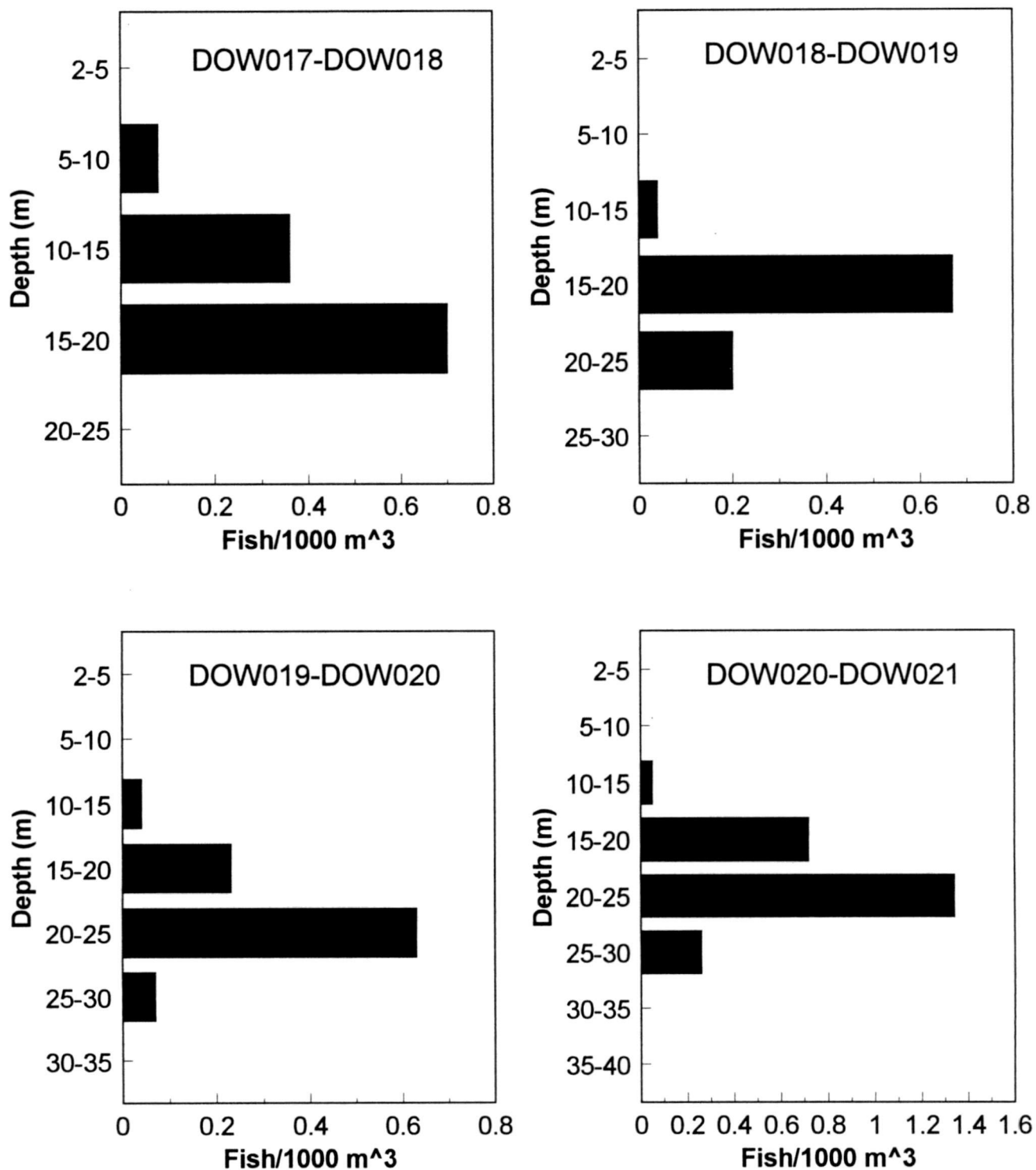
# Cebolla Sonar Survey - 7 August 1997

## Targets from -55 to -33 db



# Iola Sonar Survey - 6 August 1997

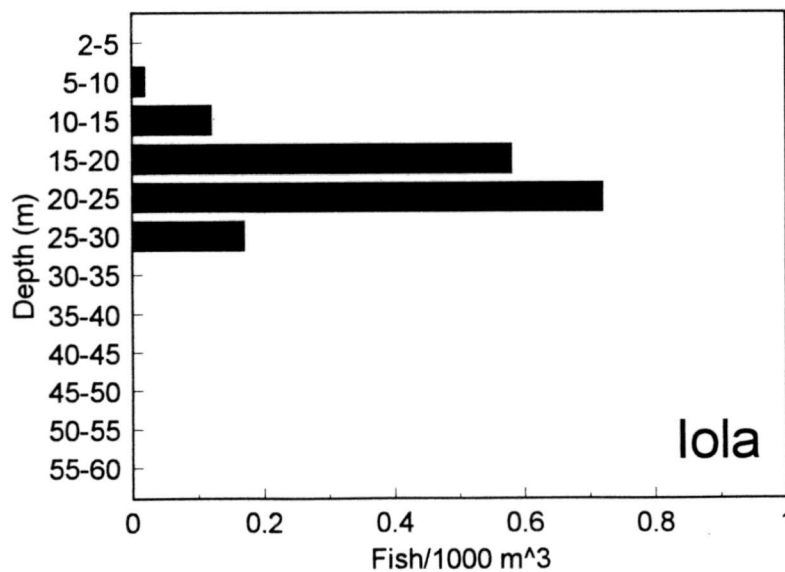
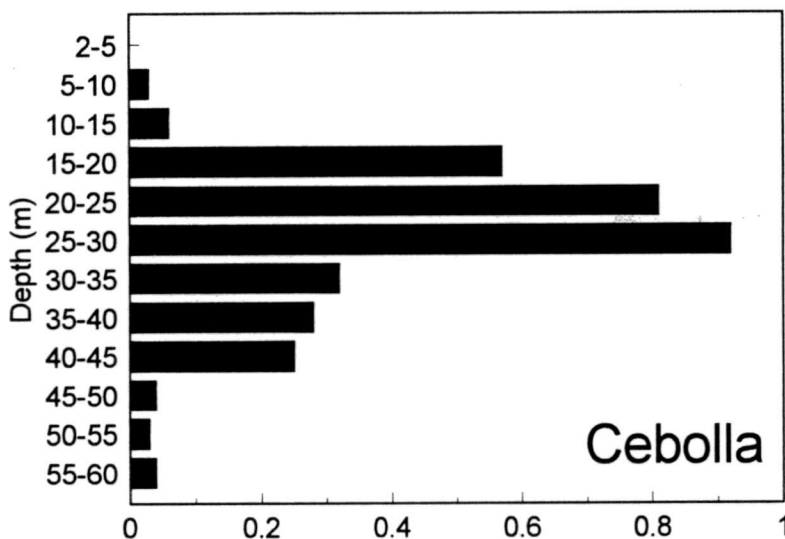
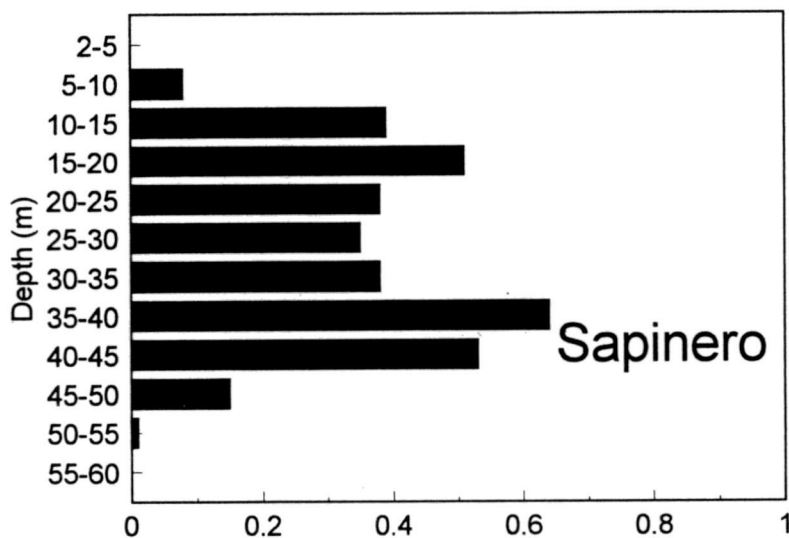
## Targets from -55 to -33 db



# Sonar Survey - 4-7 August 1997

## Mean of All Transects by Basin

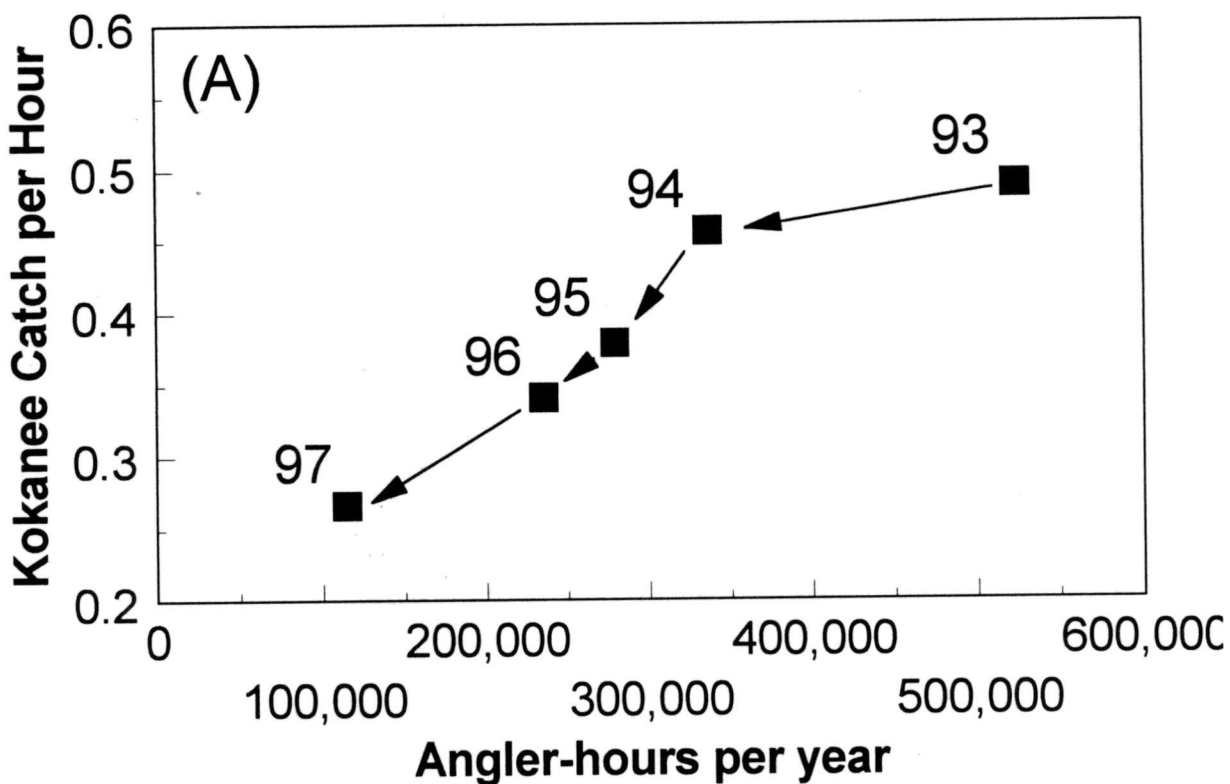
### Targets from -55 to -33 db



Fish/1000 m<sup>3</sup>

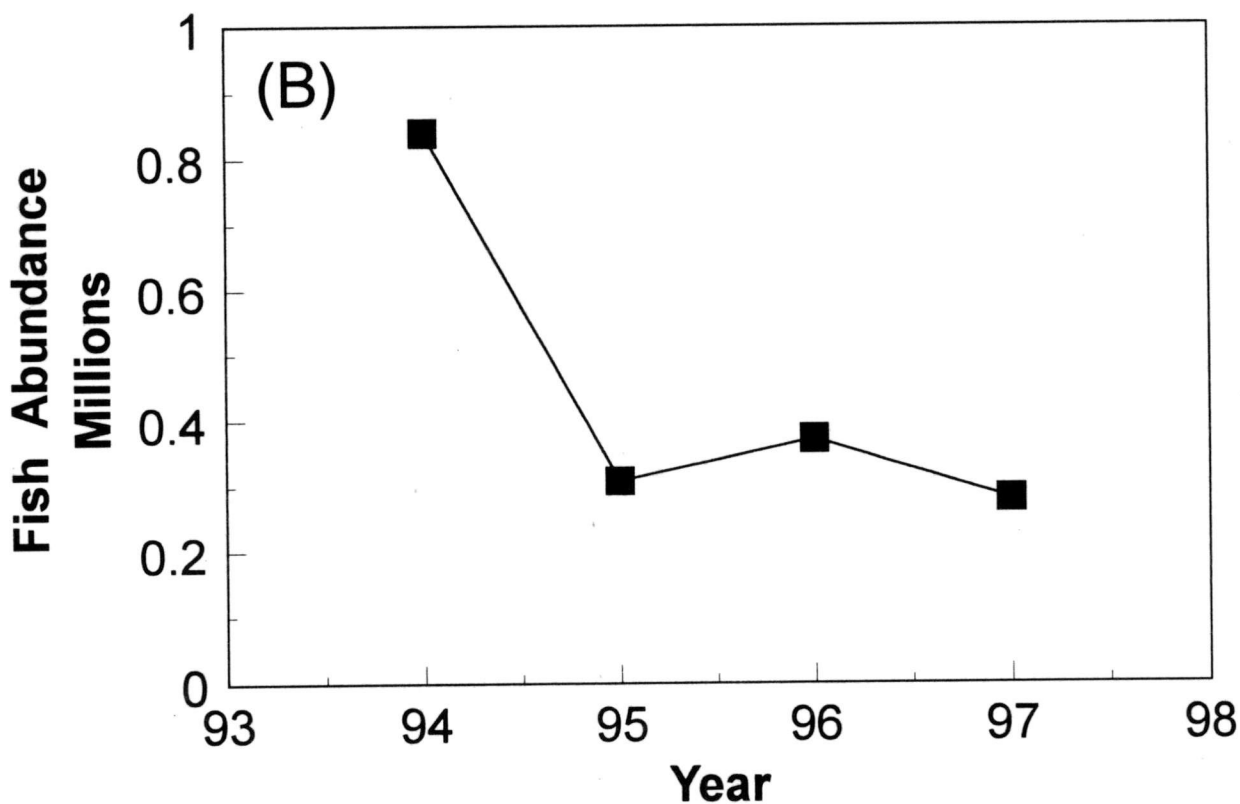
### Blue Mesa Kokanee Fishery

CDOW Creel Surveys



### Blue Mesa Kokanee

HTI Hydroacoustics Surveys



Appendix A.

Manuscript (In Review) for Canadian Journal of Fisheries and Aquatic Sciences, 1998.

**Field Evaluation of a Bioenergetics-based Foraging  
Model for Kokanee (*Oncorhynchus nerka*)**

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## Abstract

We used a bioenergetics-based foraging model to determine if bioenergetic and foraging constraints could explain kokanee (*Oncorhynchus nerka*) diel vertical migration (DVM) in Blue Mesa Reservoir, Colorado. We compared model predictions of daily growth and migration strategies with observed growth and diel vertical distributions on three dates during the summer. Results suggest that bioenergetic and foraging constraints were not sufficient to explain DVM early in the summer, when thermal stratification was weak. However, these constraints could explain observed patterns later in the summer, when optimal thermal habitat for kokanee was spatially segregated from food-rich surface waters. The onset of a strong thermocline, and its exclusion of piscivorous lake trout (*Salvelinus namaycush*) from surface waters, appeared to determine the relative importance of predation risk for kokanee DVM patterns. Our observations and modeling results suggest that the relative importance of various factors driving DVM changes seasonally. Furthermore, the relative importance of each factor likely varies from system to system, and may have caused the variety of single-factor hypotheses proposed to explain kokanee DVM. The model provides a framework for studying DVM across systems of differing thermal regimes, productivity, and predation pressures.

## Introduction

Vertical spatial structure is an important feature of many lentic systems. Depth gradients in light, temperature, and food are generally sharper and more heterogeneous than horizontal gradients (Legendre and Demers 1984). Many organisms exhibit daily vertical migrations (DVM), presumably to take advantage or cope with these vertical features. However, assuming predators also respond to vertical structure, then such daily migrations also likely affect the migrator's encounter rates with their predators. The fittest organisms will be those that optimize energetic and mortality tradeoffs. Understanding the factors driving DVM and their relative importance is an important step for developing more realistic models of predator-prey interactions, as well as developing predictive models that can be used to forecast impacts of environmental perturbations that alter the spatial structure of ecosystems.

Kokanee salmon (*Onchorynchus nerka*), and their anadromous form sockeye, exhibit strong DVM (e.g., Finnell and Reed 1969; Narver 1970; Levy 1987). Several hypotheses have been proposed to explain this behavior, including maximization of food consumption (Janssen and Brandt 1980; Wurtsbaugh and Neverman 1988), minimization of energetic costs (Brett 1971), and minimization of predation risk (Eggers 1978; Clark and Levy 1988). There appears to be no general consensus on which of these factors is most important for kokanee and sockeye. For example, Johnston (1990) rejected the bioenergetic efficiency hypothesis (Brett 1971, 1983) through field experiments, while Bevelhimer and Adams (1993) established the theoretical validity of the same hypothesis using a model and field observations. Levy (1990) suggested DVM in kokanee and sockeye might reflect an optimization of trade-offs among energy intake, physiological costs, and predation risk.

It is probable that the relative importance of each factor varies from system to system. For example, in the Pacific northwest, thermal stratification may not be as pronounced, and therefore less important, than at lower latitudes. Consequently, bioenergetic arguments may not be as important as predation in the northwest. Additionally, predation risk may vary greatly from system to system both within and among age classes.

The model of Bevelhimer and Adams (1993) is one approach that can be used to evaluate the relative importance of bioenergetic constraints. Their model is based on an energy budget and a

functional response, and therefore can directly evaluate the interplay between energy intake and physiological costs in relation to DVM (i.e., the growth maximization hypothesis; Bevelhimer and Adams 1993). If kokanee behave optimally with regard to thermal and resource gradients, then we would expect model predictions to be similar to field observations. If predictions deviate from observations, then other factors such as predation are probably more important than energetic constraints, and deserve further evaluation. An attraction of the modeling approach is that it could be readily applied to a range of systems exhibiting different thermal, resource, and predation conditions. Thus the model provides a framework for evaluating how kokanee respond to different spatial configurations of their environment.

In this study, we use the bioenergetics-based foraging model of Stockwell and Johnson (In press) to predict daily growth and vertical distribution of kokanee in Blue Mesa Reservoir (BMR), Colorado in June, July, and August 1997. The model is a modified version of the one developed by Bevelhimer and Adams (1993). It operates on a 30-min timestep, and uses inputs of temperature and prey density profiles, and fish mass, to evaluate kokanee growth as a function of migration strategies, feeding durations, and prey handling times. We used diel survey data to evaluate model predictions. Results from the comparison identified whether bioenergetic arguments are sufficient to explain kokanee growth and migration behavior in BMR.

## Methods

### *Model Inputs*

Field data on temperature, zooplankton densities, and fish size were collected from BMR for input to the model. All sampling occurred in early June, July, and August 1997 during the new moon. Blue Mesa is a 3,700-ha, mesotrophic reservoir located near Gunnison, Colorado. It is characterized by high abundances of large ( $\geq 1.0$  mm) *Daphnia* and some of the highest kokanee growth rates in North America (Stockwell and Johnson, In press). Blue Mesa supports a fish assemblage of kokanee, rainbow trout (*O. mykiss*), lake trout (*Salvelinus namaycush*), brown trout (*Salmo trutta*), cutthroat trout (*O. clarki*), white sucker (*Catostomus commersoni*), and longnose sucker (*C. catostomus*). Kokanee is the dominant pelagic fish species, comprising an average of 83% of all fish caught in experimental vertical gill nets from 1994-1996 (Johnson et al. 1995, 1996, 1997).

We used a YSI model 58 digital meter to measure temperature and dissolved oxygen during mid-morning from a reference station in BMR on 31 May, 8 July, and 4 August 1997. Measurements were taken at 1-m intervals from 0-20 m, and at 5-m intervals from 20-55 m. Temperature data were then averaged into seven depth strata (0-5, 5-10, 10-15, 15-20, 20-25, 25-30, and 30-50 m) for model input. Dissolved oxygen always exceeded  $3.2 \text{ mg}\cdot\text{L}^{-1}$  down to 60 m.

To determine prey densities to input to the model, we collected zooplankton samples at the same time as temperature measurements. We used a Wildco model 37-315 Clarke-Bumpus sampler with a 13-cm diameter opening and a 500- $\mu\text{m}$  mesh net to collect samples from each of the 0-5, 5-10, and 10-15-m depth strata. Samples were preserved in 4% sugared, buffered formalin. Samples were enumerated and identified as *Daphnia*, or copepods (the only two taxonomic groups sampled) under a compound microscope. Lengths of 50 *Daphnia* in each sample were measured to the nearest 0.01 mm using an ocular micrometer. Density of *Daphnia*  $\geq 1.0$  mm in each of the three depth strata were input to model simulations.

Kokanee were collected with vertical gill nets (mesh size range 1.25-5.1 cm) during each sampling trip. We measured length and mass, and extracted otoliths (subset of kokanee on each date) and stomachs (July and August). Ages were determined from otoliths and validated by length-frequency analysis. Kokanee growth for each age class was estimated by assuming exponential

growth (mean mass) between sampling dates (Stockwell and Johnson, In press).

#### *Model Digestion Function*

To evaluate the model's original digestion function (Brett and Higgs 1970), we extracted kokanee stomachs in July and August. Stomachs were immediately placed on dry ice, and were kept frozen until contents were removed from the frozen stomachs (Brett and Higgs 1970). Stomach contents were then weighed to the nearest 0.0001 g using an analytical balance. We found the original digestion function greatly underestimated the observed stomach evacuation rate. We therefore modified the temperature dependent function for the gastric evacuation rate,  $r$ , to fit observed decreases in stomach content mass for each age-class. This modification was then incorporated into the digestion function for model simulations.

#### *Single versus Multiple Migrations*

Observations from creel surveys from 1993-1996 indicated that kokanee had relatively full stomachs during late morning (BMJ, personal observation). Stomach samples from fish caught in gill nets in 1997 also indicated relatively full stomachs at dusk. Furthermore, gut evacuation data showed that kokanee must empty their stomachs between late morning and early evening. This suggests that kokanee had at least two foraging bouts (migrations) per day. We therefore allowed model kokanee to migrate twice per day in all simulations.

#### *Daphnia Energy Content*

Kokanee from BMR reduced the water content of their daphnid prey by 50%, compared to ambient prey, in July and August 1997 (Stockwell et al. In prep). We therefore reduced the mass of each individual *Daphnia* consumed by a factor of 0.5 on these simulation days. This effectively allowed kokanee to pack twice as many prey into the same stomach volume if feeding duration and handling time were not limiting. However, percent dry matter of stomach contents was similar in June (when *Daphnia* egg production was high), July, and August (mean 10.8%, range 10.0-11.8%; Stockwell et al. In prep). Using a mean dry-mass energy density of 22.4 kJ/g (based on 1.6 - 2.0 mm *D. pulicaria* from May to August, West Blue Lake, Manitoba; Snow 1972), we converted mass of *Daphnia* consumed to energy using a wet-mass energy density of 2.42 kJ/g (22.4 kJ/g multiplied by 10.8%) on all simulation days (Table 1).

#### *Model Simulations*

Simulations were run according to Stockwell and Johnson (In press), incorporating the modifications outlined above (Table 1). Briefly, model fish were allowed to locate at two depths (a feeding depth and a non-feeding depth) during each 24-h simulation. Depths were mid-points of the seven strata identified above (2.5, 7.5, 12.5, 17.5, 22.5, 27.5, and 40 m). All possible combinations of migration strategies were evaluated (e.g., fixed at 2.5 m, 2.5 to 7.5 m, 2.5 to 12.5 m, etc.). However, we did restrict feeding depths to the top three strata (2.5, 7.5, and 12.5 m) because kokanee diet in BMR consists almost entirely of large *Daphnia* (e.g., mean size of 1.84 mm in 1997; Stockwell et al. In prep), and most *Daphnia*  $\geq 1.0$  mm in are found in the 0-10-m stratum (Stockwell and Johnson In press). Simulations were referenced to daylength on each simulation day. Model kokanee remained at non-feeding depth during the night, feeding depth for half of the feeding duration during dawn and early morning, non-feeding depth for the middle portion of the day (24 h - night length - feeding duration), and then feeding depth for the remainder of the feeding duration (late afternoon and dusk). The start of dawn and end of dusk were based on local times for the beginning and ending of nautical twilight (when sun is 12° below the horizon). We used a range of prey handling times (1.2 - 0.16 s·*Daphnia*<sup>-1</sup>) and feeding durations (4-12 h) for each simulation.

#### *Model Evaluation*

We monitored kokanee vertical distribution over the diel cycle during each of the three

sampling trips using vertical gill nets and sonar. Vertical gill nets were set and lifted: 1-2 June between 11:30-19:00, 19:00-00:00, 00:00-08:00, and 08:00-13:00 hours; 8-9 July between 19:30-22:30, 22:30-02:00, 02:00-04:45, and 04:45-08:00 hours; and 4-5 August between 18:45-19:30, 21:30-01:00, 01:00-04:30, and 04:30-08:15 hours. Nets were set at the same reference station used for temperature measurements and zooplankton sampling. In addition to information taken from fish outlined above, we also recorded depth of capture.

Vertical distribution of fish was monitored acoustically using an HTI Model 240 split beam 200-kHz echo sounder. During each diel survey, we repeatedly traversed a 3.2-km transect for 3 to 4 h at sunrise (~03:30-07:00) and sunset (~19:00-22:00), 1 h during mid-day (~11:00-12:00), 1 h during mid-night in June (01:00-02:00), and 1 h during mid-morning in July and August (~09:00-10:00). Sonar data were processed using HTI software. Fish densities were calculated by echo counting. Volume sampled was determined by cone area and distance traveled. Analyses were limited to those parts of the transect  $\geq 60$ -m (June) or  $\geq 70$ -m depth (July and August) - typically from 1.5 to 2.8 km of the original transect. Due to weather and technical difficulties, we were not able to obtain a complete diel cycle of sonar data on any of the sampling dates.

Using Love's (1971) equation, we converted length-frequency distributions (mm) of all fish caught in the vertical gill nets to target strength (-dB) for each of the three sampling trips. We then used these distributions to parse target strengths from sonar into age 1, or age 2-3 size-classes. Vertical distributions of each age-class from sonar were used to infer feeding (within 0-15-m depth) and non-feeding depths.

We compared sonar observations with model predictions of depth distributions. Because several migration strategies in model simulations often resulted in model daily growth estimates close to the optimum growth estimate, we report the range in feeding and non-feeding depths that produced model growth rates within 10% of optimum. We also compared observed daily growth with optimum model daily growth.

## Results

### *Model Inputs*

On 31 May, water temperature decreased gradually from 12°C near the surface to <5°C at depth (Fig. A1). Surface waters warmed to >16 and >19°C in July and August, with the thermocline beginning at approximately 10 and 5-m depths, respectively (Fig. A1). Abundances of large *Daphnia* in the top 15 m of BMR were uniformly low (~ 1 L<sup>-1</sup>) early in the season (Fig. A1). In July and August, abundances peaked in 0-5-m stratum (~ 8 and 13 L<sup>-1</sup>, respectively) and decreased sharply in the 10-15-m stratum (2 and < 1 L<sup>-1</sup>, respectively; Fig. A1).

Mean masses of kokanee on the three sampling dates (1 June, 8-9 July, and 4-5 August) were as follows: age 1 - 58.4, 90.9, and 115.8 g; age 2 - 241.8, 315.7, and 330.1 g; age 3 - 525.5, 608.4, and 698.9 g. Assuming exponential growth between sampling dates (Stockwell and Johnson, In press), daily growth rates of each age class for each sampling date were as follows: age 1 - 0.68, 1.06, and 1.03 g·d<sup>-1</sup>; age 2 - 1.77, 2.22, and 0.48 g·d<sup>-1</sup>; age 3 - 2.03, 2.35, and 3.63 g·d<sup>-1</sup>.

### *Model Digestion Function*

The function used to model the amount (g) of food digested ( $D$ ) per unit time ( $t$ ) (Elliot and Persson 1978) is:

$$[1] \quad D = \left( C \cdot m - \frac{M_0}{r} \right) \cdot (1 - e^{-rt}) + C \cdot m \cdot t ,$$

where  $C$  = the number of *Daphnia* consumed in time  $t$ ,  $m$  = the mean mass of *Daphnia* (wet g),  $M_0$  = the initial stomach content mass (wet g), and  $r$  = the gastric evacuation rate. Gastric evacuation rate is a temperature-dependent function, and was originally taken from Brett and Higgs (1970):

$$[2] \quad r = 0.0140 \cdot T - 0.0154,$$

where  $T$  = temperature ( $^{\circ}\text{C}$ ).

Mass of kokanee stomach contents decreased through the night to near empty in early morning in July and August, indicating age 1-3 kokanee do not feed during the night (Fig. A2). We found Equation 1 to greatly underestimate the observed gastric evacuation (Fig. A2) when using Equation 2 to estimate  $r$ . We therefore iteratively adjusted the intercept of Equation 2, and found the function

$$[3] \quad r = 0.0140 \cdot T + 0.16$$

to provide reasonable estimates of the observed digestion for each age-class in July and August (Fig. A2). Consequently, we used Equation 3 for all simulations (Table 1).

#### *Model Predictions and Field Observations*

For all three simulation dates, model daily growth bounded or approached the observed growth for each age-class (Figs. 3-6). In June, a wide range of prey handling times and feeding durations could account for the observed growth. Model daily growth for an age 1 kokanee with 4 h of feeding and a prey handling time of  $1.2 \text{ s} \cdot \text{Daphnia}^{-1}$  was  $0.66 \text{ g} \cdot \text{d}^{-1}$ , compared to observed growth of  $0.68 \text{ g} \cdot \text{d}^{-1}$ . All other model growth estimates were  $\geq 1.27 \text{ g} \cdot \text{d}^{-1}$  (Fig. A3A). Model growth estimates for age 2 fish with prey handling times between  $0.16$  and  $0.33 \text{ s} \cdot \text{Daphnia}^{-1}$  for 4 h of feeding,  $0.67 \text{ s} \cdot \text{Daphnia}^{-1}$  for 8 h, and  $1.2 \text{ s} \cdot \text{Daphnia}^{-1}$  for 12 h approached the observed growth of  $1.77 \text{ g} \cdot \text{d}^{-1}$  (Fig. A3B). Observed growth for age 3 kokanee in June was  $2.03 \text{ g} \cdot \text{d}^{-1}$ , and was approximated by model predictions using prey handling times of  $0.16 \text{ s} \cdot \text{Daphnia}^{-1}$  for 4 h of feeding, between  $0.33$  and  $0.67 \text{ s} \cdot \text{Daphnia}^{-1}$  for 8 h, and  $0.67 \text{ s} \cdot \text{Daphnia}^{-1}$  for 12 h (Fig. A3C).

In July simulations, model growth estimates from a combination of prey handling times and feeding durations were close to the observed growth for age 1 and 2 fish (Fig. A4A,B). Model growth for age 1 kokanee approached their observed growth of  $1.06 \text{ g} \cdot \text{d}^{-1}$  using  $0.33$ ,  $0.67$ , or  $1.2 \text{ s} \cdot \text{Daphnia}^{-1}$  for 4, 8, or 12 h of feeding (Fig. A4A). Model predictions for age 2 fish approached their observed growth when allowed to feed at  $0.16 \text{ s} \cdot \text{Daphnia}^{-1}$  for 4 h, between  $0.16$  and  $0.33 \text{ s} \cdot \text{Daphnia}^{-1}$  for 8 h, or slightly  $>0.33 \text{ s} \cdot \text{Daphnia}^{-1}$  for 12 h (Fig. A4B). For age 3 kokanee, model simulations indicate they can approach their observed growth with a prey handling time slightly  $>0.16 \text{ s} \cdot \text{Daphnia}^{-1}$  for 8 h of feeding, or between  $0.16$  and  $0.33 \text{ s} \cdot \text{Daphnia}^{-1}$  for 12 h (Fig. A4C).

In August, model age 1 kokanee approached their observed growth using prey handling times of  $0.33$ ,  $0.67$ , or between  $0.67$  and  $1.20 \text{ s} \cdot \text{Daphnia}^{-1}$  while feeding for 4, 8, or 12 h, respectively (Fig. A5A). Age 2 kokanee required between  $0.16$  and  $0.33 \text{ s} \cdot \text{Daphnia}^{-1}$  with 4 h of feeding, and between  $0.33$  and  $0.67 \text{ s} \cdot \text{Daphnia}^{-1}$  with 8 or 12 h (Fig. A5B). Age 3 kokanee had to feed for 12 h with a prey handling time of  $0.16 \text{ s} \cdot \text{Daphnia}^{-1}$  to reach their observed growth of  $3.63 \text{ g} \cdot \text{d}^{-1}$  (Fig. A5C).

There was a wide range of patterns in kokanee vertical distribution over the course of the field season (Fig. A1). In June, age 1 fish were primarily concentrated between 15-25-m depth during daylight hours, although they were also present between 5-15 and 25-45-m strata (Fig. A1). Age 2-3 kokanee showed a bimodal distribution at this time, with peaks in the 0-5 and 15-25-m depth strata (Fig. A1). Kokanee from all three age-classes appeared to ascend at dusk, forming a thick layer

between 5-10 m during the night (Fig. A1).

The same general pattern occurred in July (Fig. A1). During darkness, kokanee were concentrated in a thick layer between 10 and 20-m depth. At dawn, kokanee were somewhat more dispersed but primarily located between 5 and 20-m depth (Fig. A1). During morning and midday, age 1 fish were concentrated between 5-10 and 15-25 m, while age 2-3 fish were scattered throughout the water column (Fig. A1).

In August, the migration patterns reversed (Fig. A1). Mid-morning distributions were located between 5 and 15 m for all ages. At dusk, kokanee occupied a much broader, and deeper range of depths (Fig. A1). At dark, vertical distributions were concentrated between 15 and 50 m for age 1 fish, and primarily between 15 and 30 m for age 2-3 fish (Fig. A1).

Comparisons between model predictions and observed vertical distributions show qualitative agreement, although discrepancies do exist. In June, the migration strategy for the only matching model growth estimate (at  $1.2 \text{ s} \cdot \text{Daphnia}^{-1}$  and 4 h) for age 1 fish was to migrate from 0-15 (feeding) to 15-50 m (non-feeding; Fig. A3A). This agrees with inferred feeding and non-feeding depths during daylight and dusk, but does not overlap with the nighttime (non-feeding period - see Fig. A2) distribution of 5-10 m (Figs. 1 and 3A). Similar results were found for age 2 and 3 fish (Figs. 1 and 3B,C).

Predicted and observed migration strategies overlap for age 1 kokanee in July for those feeding durations and handling times that generate model growth similar to observed growth (Fig. A4A). Comparisons between model and observed for July are slightly different for age 2 and 3 kokanee. For age 2 fish, model predictions of non-feeding depths differed from observed nighttime distributions for two of the three matching growth estimates (4 and 8 h of feeding; Fig. A4B). The predicted range for non-feeding depths for an age 2 kokanee feeding for 12 h ( $0.33 \text{ s} \cdot \text{Daphnia}^{-1}$ ) overlaps observed non-feeding depths (Fig. A4B). Non-feeding depths for age 3 fish overlap the observed depths for daytime distributions, but were also too deep for nighttime distributions (Fig. A4C).

The predicted vertical distributions in August were similar to the observed for all age-classes (Fig. A5), although we did not observe a midday descent (Fig. A1) because of incomplete sonar sampling.

## Discussion

Our diel observations show several interesting patterns in kokanee DVM behavior. First, it appears that in June and July, during the day, kokanee are distributed either bimodally or uniformly throughout the water column, indicating asynchronous migration behavior at this time. A portion of the population is near the surface, presumably feeding, while the remainder of the population is deeper where metabolic costs and/or predation risk are lower. During crepuscular periods most of the population moves shallower; they then form a relatively concentrated layer near surface waters at night. This same pattern was observed in BMR during June and July 1995 using vertical gill nets and a Lowrance X-16 fish finder (Johnson et al. 1996), indicating this "normal" diel cycle (*sensu* Levy 1990) may be consistent from year to year during these months. In August 1997, this pattern was reversed. Kokanee appeared highly concentrated in the 5-15-m depth stratum during daylight, and dispersed and descended during dusk and into the night. These results suggest a seasonal ontogeny in DVM behavior of kokanee.

The ranges in August feeding and non-feeding depths predicted by the model overlap the observed distributions, indicating the growth maximization hypothesis is sufficient to explain kokanee DVM at this time. The spatial segregation of maximum food densities and optimal thermal habitat in

BMR is greatest in August - environmental conditions under which DVM confers the greatest bioenergetic advantage (Bevelhimer and Adams 1993). For example, an age 1 kokanee would experience a 79% decrease in daily growth (from 0.84 to 0.18 g·d<sup>-1</sup>) if it did not migrate out of the 5-10-m depth stratum into colder water (based on simulations with 8 h of feeding and a prey handling time of 0.67 s·*Daphnia*<sup>-1</sup>). However, although daytime and twilight vertical distributions in June and July were predicted by the model for those model growth estimates that matched observed growth, nighttime vertical distributions were not (all age-classes in June, age 3 in July). Thus, the growth maximization hypothesis is not sufficient to explain kokanee DVM earlier in the summer.

We examined the hypothesis that kokanee may thermoregulate for digestion rate (Wurtsbaugh and Neverman 1988) in June - i.e., they may choose different day and night non-feeding temperatures to regulate digestion rate to ensure an empty gut by the time of next feeding. Several simulations using the observed vertical distributions from this time period (7.5 m for feeding and nighttime non-feeding depths and 22.5 m for daytime non-feeding depths) and model feeding durations and prey handling times that closely matched observed growth (age 1 - 4 h and 1.2 s·*Daphnia*<sup>-1</sup>; age 2 - 4 h and 0.33 s·*Daphnia*<sup>-1</sup>; age 3 - 8 h and 0.33 s·*Daphnia*<sup>-1</sup>) showed decreases of 12, 15, and 14% from maximum growth for each age-class, respectively. Therefore, thermoregulation of digestion rate does not appear to confer an advantage over constant non-feeding depths. It also demonstrates that a wide range of DVM strategies can generate model growth estimates within 15% of maximum growth when strong environmental gradients are not present, suggesting kokanee behavior in June is not constrained by temperature.

Predation risk is another factor that might explain the observed depth distributions of kokanee early in the summer. In BMR, lake trout is the primary predator. Because of relatively low water temperatures in June and July, these predators have access to the entire water column (e.g., 80% of all piscivorous lake trout-sized targets in June and July were <10-m depth; BMJ, unpublished data). We therefore might expect kokanee to disperse to deeper depths during the day, when not feeding, to avoid predators under decreased light levels. At night, kokanee could concentrate near surface waters with little risk of predation. Although predation risk explains these DVM patterns, it also assumes kokanee would prefer to locate exclusively in the 5-10-m stratum (over 80% of all kokanee were located in this stratum at night in June) when not feeding, but are restricted from this depth stratum during the day because of predation risk. Our modeling suggests there is no energetic advantage to this observed nighttime distribution. Based on the above simulations to evaluate thermoregulation of digestion rate, there also appears to be relatively little disadvantage to this behavior. Remaining in surface waters through the night may minimize migration costs, while allowing kokanee to be in close spatial proximity with prey to take advantage of the antipredation window at dusk and dawn (Clark and Levy 1988).

In July, model predictions for growth and corresponding depth distributions for age 1 kokanee match observations, suggesting bioenergetics is sufficient to explain their DVM at this time. Age 2 distributions are also explained by the model for feeding durations of 8 and 12 h. Model predictions for age 3 kokanee do not match observed nighttime distributions (for the model growth estimate that most closely matches observed growth). Using their observed depth distributions (7.5 m for feeding, 40 m for daytime non-feeding, and 17.5 m for nighttime) with a feeding duration of 8 h and a prey handling time of 0.16 s·*Daphnia*<sup>-1</sup>, growth was reduced by only 12% from the maximum (from 3.31 to 2.92 g·d<sup>-1</sup>). This suggests age 3 kokanee may be minimizing migration costs while taking advantage of the antipredation window in July. However, these results are counterintuitive - we would expect that the smaller age-classes should be more affected by predation risk than age 3 fish.

Measuring feeding durations in the field is difficult because gill nets offer only rather coarse

temporal resolution, and kokanee are nearly invulnerable to gill nets during daylight. Because of these challenges, feeding duration remains an uncertain parameter in our simulations. However, regardless of unknown feeding durations, the model does indicate that age 2 and 3 kokanee, at least in July and August, need to feed at a rate of 3-6 *Daphnia*·s<sup>-1</sup> to approach their observed growth. This estimate is higher than predicted by Stockwell and Johnson (In press), and is a result of reducing the mass of each *Daphnia* consumed by 50% (Stockwell et al. In prep). Modeling results from Stockwell and Johnson (In press) suggested kokanee might have the ability to gulp feed. Results from the present study further support the gulp feeding hypothesis. Laboratory feeding trials using densities of large *Daphnia* observed in this study are required to conclusively test this hypothesis.

Application of the model to other systems provides a framework for evaluating DVM with respect to the growth maximization hypothesis (Bevelhimer and Adams 1993). Deviations of model predictions from observations should point to other possible causal mechanisms. For example, Johnston (1990) evaluated the bioenergetics efficiency hypothesis (Brett 1971, 1983) for kokanee fry in Kootenay Lake, British Columbia. He showed that fry restricted to epilimnetic habitat grew better than ambient fry that performed DVM, thus negating the bioenergetics hypothesis as a causal mechanism for DVM of kokanee fry in this system. We ran simulations using August field conditions from BMR for a 3 g kokanee to evaluate the growth maximization hypothesis for the same sized fish used in Johnston's (1990) study. We used prey handling time (1.2 s·*Daphnia*<sup>-1</sup>) and feeding duration (4 h) that typically resulted in the most distinct migration strategies (e.g., see Figs. 3-5). The model predicted daily growth in the range of 0.17 (remaining in 0-5-m depth stratum) to 0.21 g·d<sup>-1</sup> (migrating from 20-50 m to 5-10 m). Our model has no built in cost for migration, other than that associated with changes in respiration rate as a function of temperature and swimming speed. Estimated energetic costs of migration, based on the work of Alexander (1972), range from 20% (Bevelhimer and Adams 1993) to 50% (Clark and Levy 1988) of daily growth. Given these estimates, it is likely more advantageous for kokanee fry to remain in surface waters than to migrate, consistent with findings from Johnston (1990). The presence of DVM for kokanee fry in Kootenay Lake suggests that another factor(s), such as predation risk, is driving their behavior (Johnston 1990). We have no field data for kokanee fry in BMR to compare with model results. Nevertheless, the simulations illustrate how the modeling framework can be used to examine the sufficiency of the growth maximization hypothesis to explain kokanee DVM in BMR, as well as other systems.

Results from the model also make predictions about kokanee DVM across latitudinal and productivity gradients. From the simulations, it appears that migration behavior becomes more flexible as acquisition of food becomes less limiting (increased time spent feeding or decreased prey handling time) and/or as thermoclines become less pronounced. From a bioenergetics perspective, we would therefore expect to see stronger DVM patterns in systems with low productivity and/or sharper thermoclines. Application of the model across a range of lakes of differing trophic status and/or latitudes would provide a baseline test of this hypothesis. Deviations of observations from model predictions would indicate that other processes might be driving DVM at a regional scale.

We propose that the seasonal variation of environmental conditions within lakes, as well as environmental variability among lakes, has led to the variety of single-factor hypotheses proposed to explain DVM. Results from this study, as well as other recent studies (e.g., Clark and Levy 1989; Levy 1990; Johnston 1990; Bevelhimer and Adams 1993) provide strong evidence that kokanee DVM is likely the product of several factors. In BMR, it appears that tradeoffs between bioenergetic constraints and predation risk can explain kokanee DVM. Moreover, our results suggest that the relative importance of each factor changes seasonally, as hypothesized by Bevelhimer and Adams (1993). The shift in DVM behavior in BMR appears to be directly related to abiotic conditions - the



strength of the thermocline determines the extent to which kokanee are susceptible to piscivorous lake trout in plankton-rich surface waters, and therefore the extent to which predation risk influences behavior. It is therefore likely that the relative importance of factors driving kokanee DVM in other systems will vary from lake to lake and through time. The modeling approach demonstrated in this study is relatively easy to apply, and can be used as a baseline reference given the environmental conditions of any lake. Supplementing model results with information on kokanee and predator depth distributions, or predator characteristics (e.g., thermal preference), can help evaluate the relative importance of the different hypotheses. In the future, explicit incorporation of other spatial variables like predation risk will be important to refine the model's ability to predict kokanee DVM.

### **Acknowledgments**

We thank Brady Allen, Kathleen Apakupakul, Krista Bonfantine, Dan Brauch, Tom Cady, Daren Carlisle, Daren Chacon, Gregg Chenu, Jason Garner, Sture Hansson, Steve Johnson, Shawndra Mawhorter, Ron Sutton, and Joe Zendt for their tireless help in the field. Pat Martinez, Dan Brauch, and the Colorado Division of Wildlife graciously provided the use of their boats and sonar equipment. Steve Johnson and Doran Mason provided valuable guidance with processing of sonar data. Krista Bonfantine processed zooplankton samples and aged fish. We also thank Rick Harris and the National Park Service for their logistical support. This study was supported by funds from the U.S. Department of the Interior, Bureau of Reclamation, Grand Junction Projects Office.

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Table 1. Modifications to the kokanee model from Stockwell and Johnson (In press). See text for justification of changes.

Parameter	Value	Source
$h$ , handling time ( $s \cdot Daphnia^{-1}$ )	1.2 - 0.16	
$m$ , Daphnia mass (wet mg)	$0.5 \cdot (0.052 \cdot L^{3.012})$ in July and August	Stockwell et al. (In prep)
$r$ , digestion coefficient	$0.014 \cdot T + 0.16$	This study
$E_{dap}$ , (kJ $\cdot$ wet $g^{-1}$ <i>Daphnia</i> )	2.42	Snow (1972); Stockwell et al. (In prep)

## Figures

Figure A1. (First column) Vertical profiles of prey densities (circles) and temperature (solid lines) from Blue Mesa Reservoir, Colorado used in model simulations. (Second - Fourth Columns) Vertical distributions of age 1, and age 2 and 3 kokanee in Blue Mesa Reservoir, Colorado as observed using sonar on 1 June (Top Row), 8-9 July (Middle Row), and 4-5 August 1997 (Bottom Row).

Figure A2. Mean mass ( $\pm 1$  SE) of observed stomach contents (solid squares) through the night for (A) age 1, (B) age 2, and (C) age 3 kokanee from Blue Mesa Reservoir on 4-5 August 1997. Solid line indicates simulated digestion (Eq. 1) based on the gastric evacuation rate of Brett and Higgs (1970) (Eq. 2), and used in the original application of the kokanee model (Bevelhimer and Adams 1993; Stockwell and Johnson, In press). Dashed line indicates simulated digestion based on the modified function for gastric evacuation rate (Eq. 3). Temperatures used in simulations were 10.3 °C for age 1 and 11.4 °C for age 2-3 kokanee, and were based on thermal profiles and observed nighttime distributions of kokanee using sonar (Fig. A1).

Figure A3. Maximum model daily growth and observed growth for (A) age 1, (B) age 2, and (C) age 3 kokanee in Blue Mesa Reservoir, Colorado. Model growth was estimated using vertical profiles of prey densities and temperature from 31 May 1997. Starting mass of each age-class for model simulations, as determined from field observations, was 58.4 g for age 1, 241.8 g for age 2, and 525.5 g for age 3. The horizontal dashed lines represent the observed growth, and facilitate comparisons with model results. The vertical bars indicate the ranges in feeding (solid) and non-feeding (dashed) migration depths producing model growth rates within 10% of maximum, and inferred from sonar observations. The observed upper non-feeding depth ranges indicate the nighttime vertical distributions of kokanee, while the bottom ranges indicate daytime and twilight non-feeding depths (see Fig. A1).

Figure A4. Same as Figure 3, but for 8 July 1997. Starting mass of each age-class for model simulations, as determined from field observations, was 90.9 g for age 1, 315.7 g for age 2, and 608.4 g for age 3.

Figure A5. Same as Figure 3, but for 4 August 1997. Starting mass of each age-class for model simulations, as determined from field observations, was 115.8 g for age 1, 330.1 g for age 2, and 698.9 g for age 3.

Figure A1.

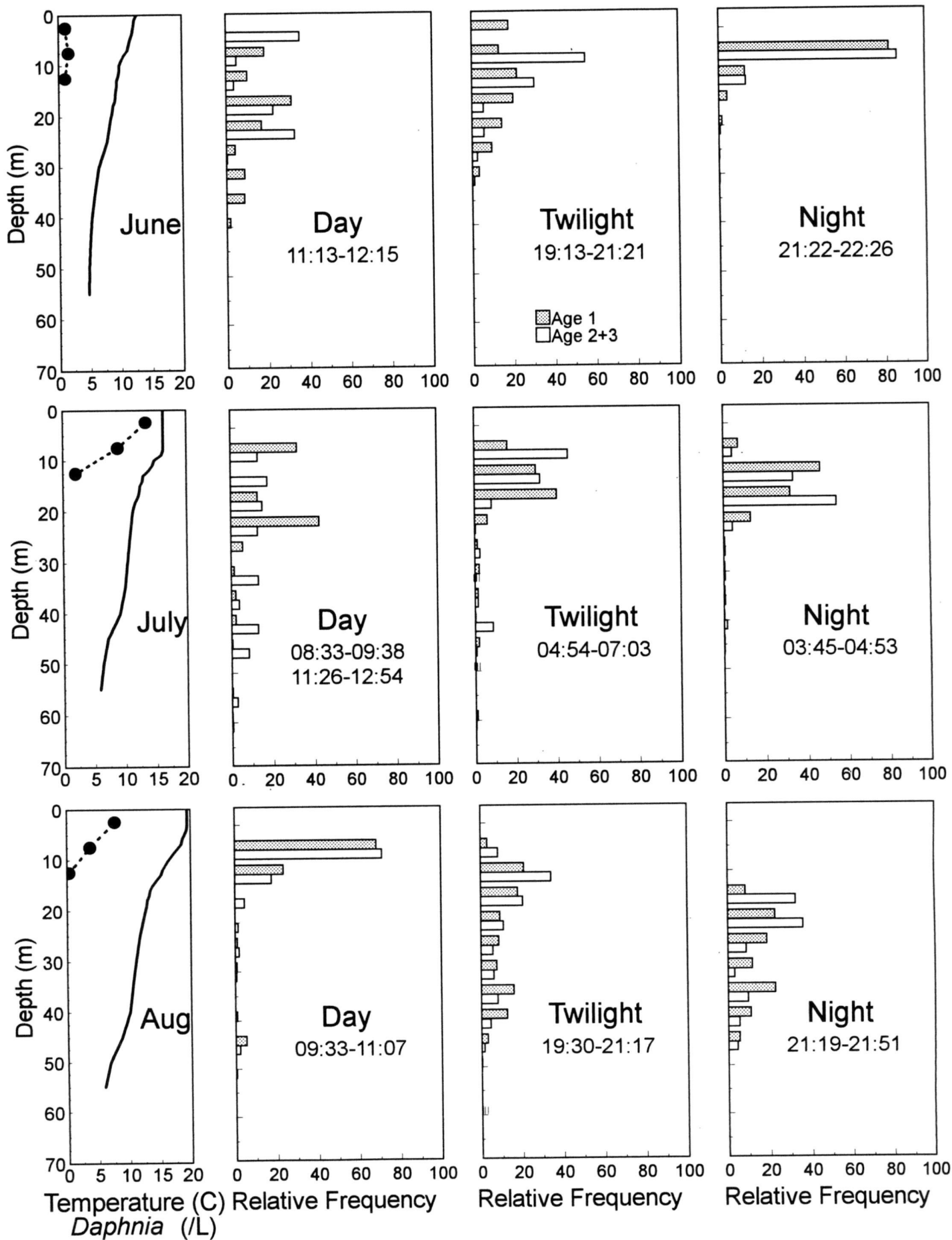


Figure A2.

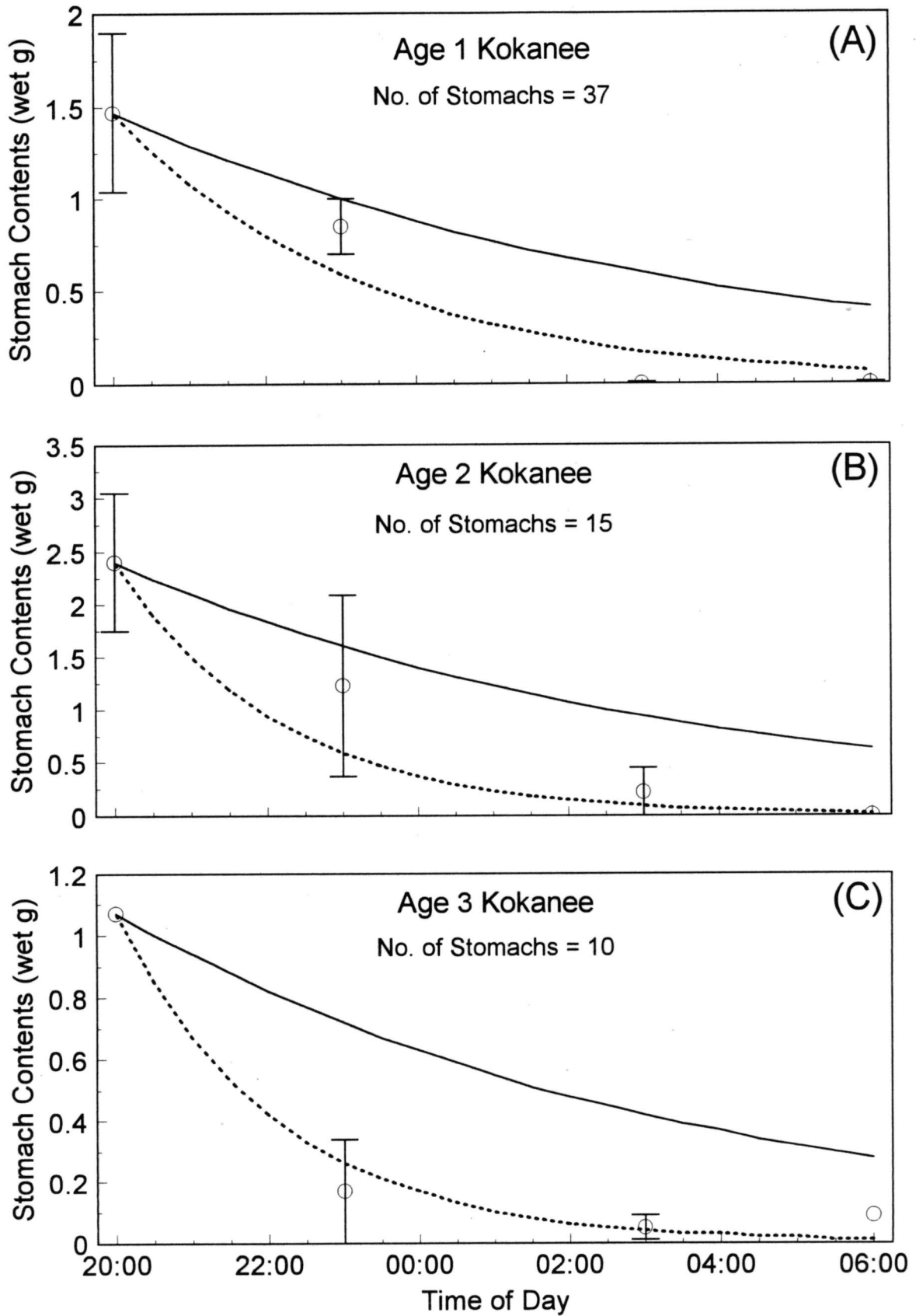
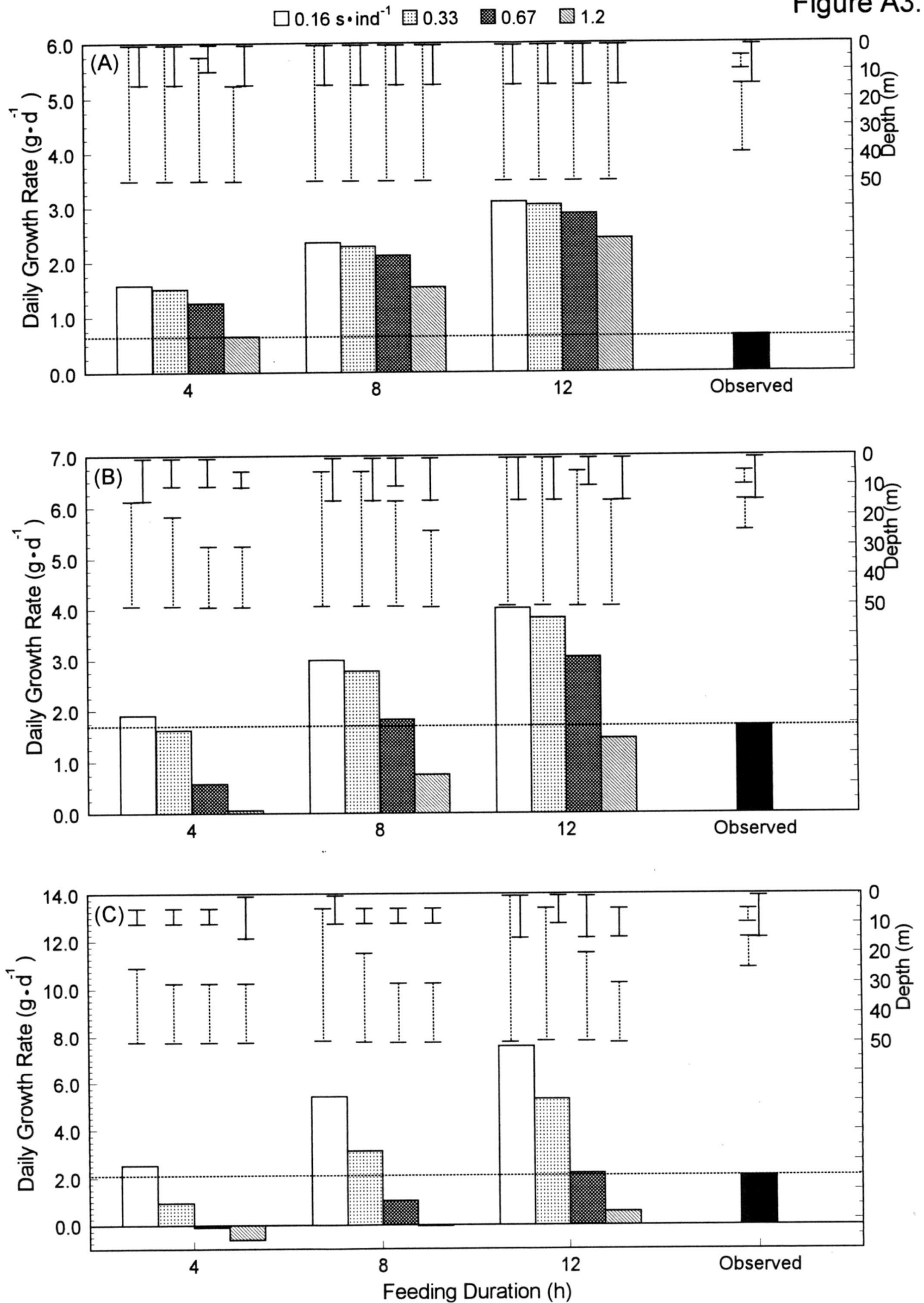
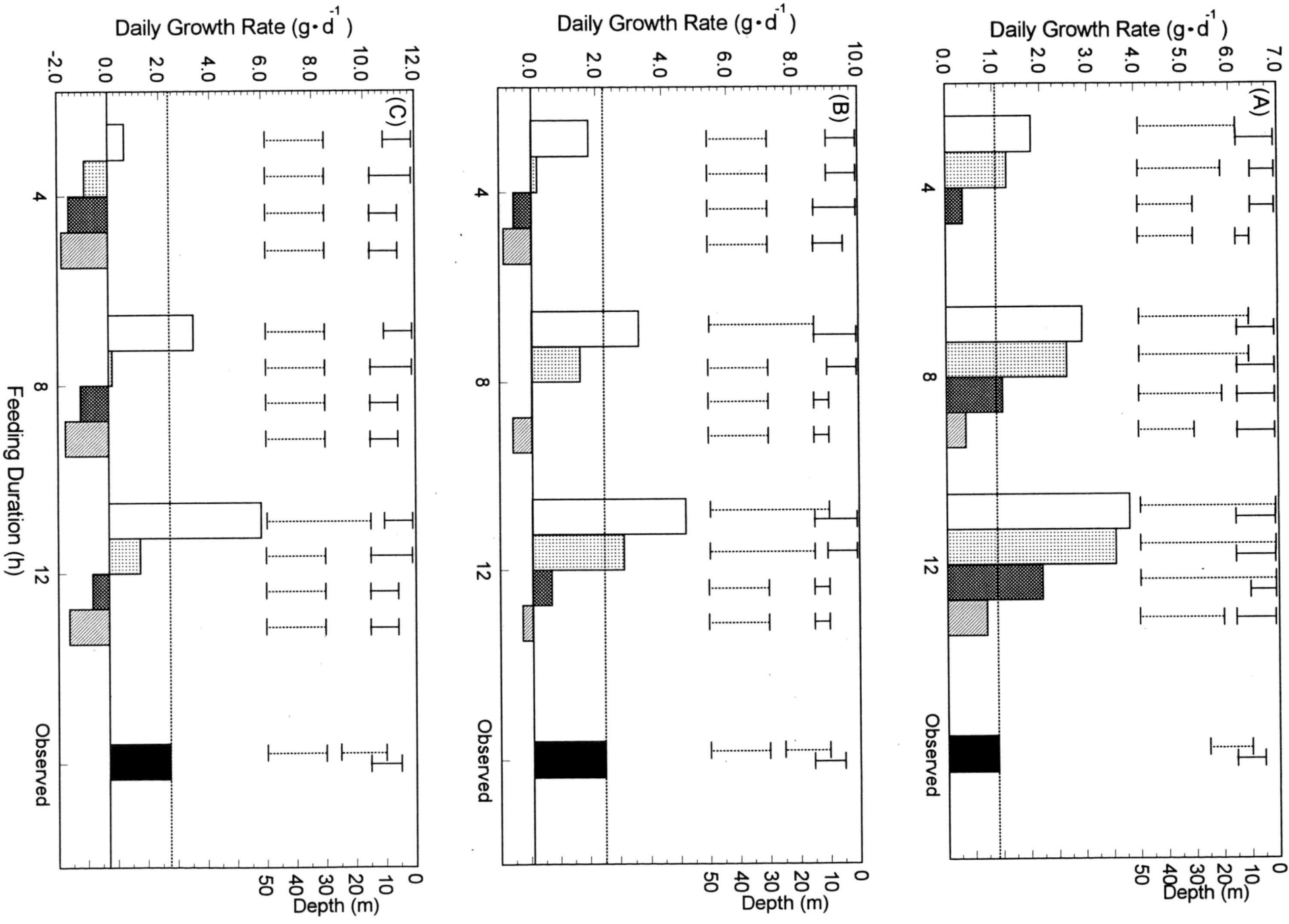


Figure A3.







□ 0.16  $s \cdot ind^{-1}$  ▤ 0.33 ■ 0.67 ▨ 1.2

Figure A4.

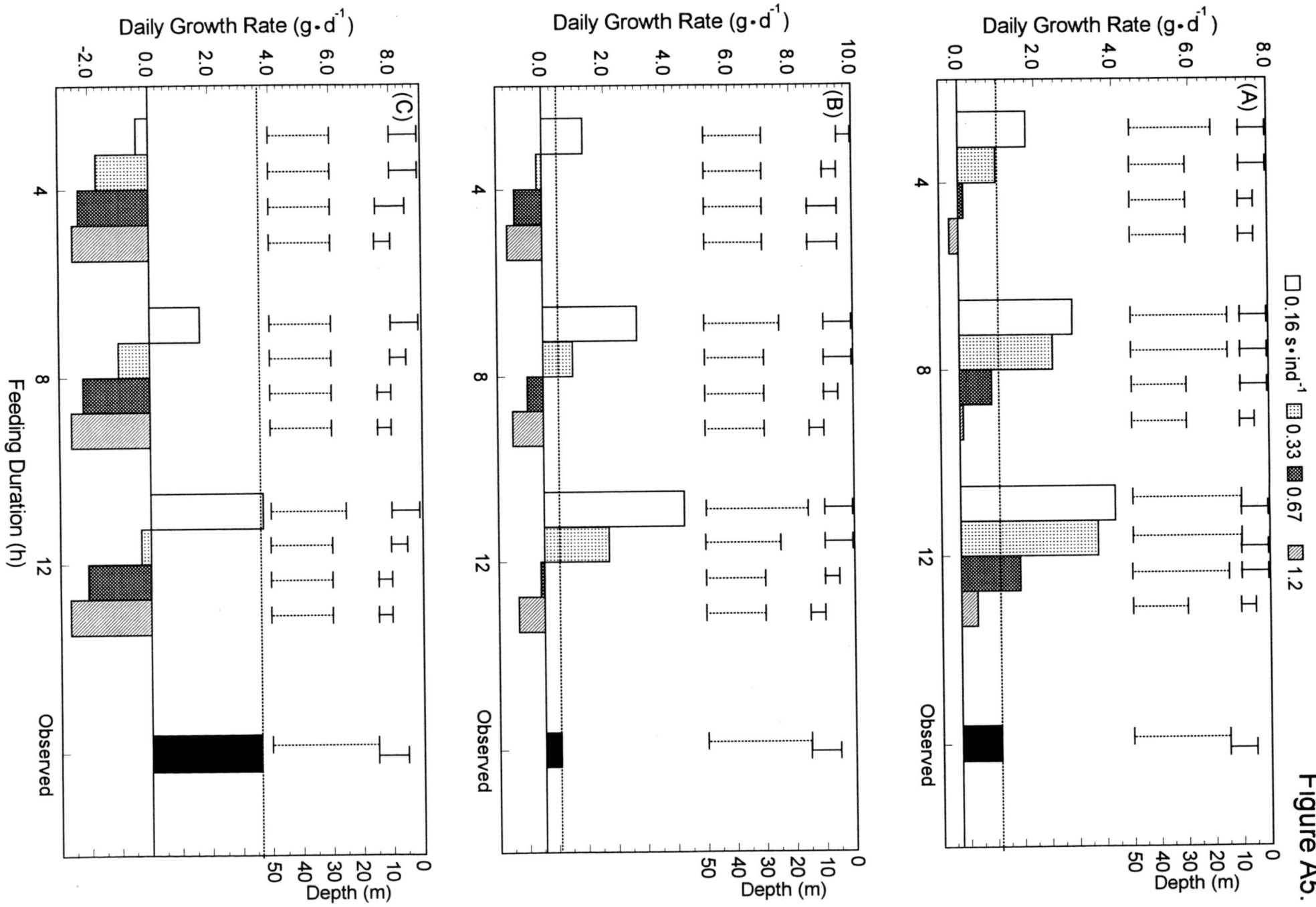


Figure A5.

