

**Rainbow Trout in the Lee's Ferry Recreational Fishery Below Glen Canyon  
Dam, Arizona, Following Establishment of Minimum Flow Requirements**

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Final report submitted to:  
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2255 N. Gemini Drive, Room 341  
Flagstaff, AZ 86001  
Cooperative Agreement No. 1425-97-FC-40-22690

September 1999

Grand Canyon Monitoring  
and Research Center

OCT 04 1999

Received  
Flagstaff, AZ



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## EXECUTIVE SUMMARY

This report presents results of quantitative analyses of data to describe spatial and temporal patterns of change in selected biotic and abiotic variables in the Lee's Ferry tailwater below Glen Canyon Dam (GCD) during 1991-1997 and to determine associations between rainbow trout, dam operations and other abiotic and biotic variables. Specifically, we sought to determine if releases from GCD, the aquatic food base and water quality variables (total nitrogen, total phosphorous, pH, temperature) influenced spatial and temporal differences in measurements of the rainbow trout population during 1991-1997. Operations of Glen Canyon Dam are the overriding variable influencing standing stocks of rainbow trout in the Lee's Ferry reach. Our results indicate that higher minimum and more stable releases from GCD provide conditions that support greater standing stocks of rainbow trout than do dam operations with lower minimum and more variable releases. Estimated population size of large rainbow trout more than doubled during enhanced flow regimes between 1991 and 1997. Densities of all size classes we examined increased after onset of enhanced flows in 1991, indicating greater success of spawning and recruitment to reproductive maturity. However, densities of fish  $>304$  mm declined until about 1993, after which densities of large fish 305-405 mm increased. Reproductive activity likely occurs throughout the year in the tailwater, but spawning peaks during winter. Gravel bars presently provide adequate substrate for spawning.

We found few variables other than dam operations that affected small rainbow trout. Our results indicate that abundance of small rainbow trout ( $<305$  mm) is more strongly influenced by physical factors (habitat, water temperature), whereas large fish ( $\geq 305$  mm) are more strongly affected by biotic factors. Consumption by small fish tended to meet maintenance energy requirements among years and seasons, and condition among years remained essentially stable. In comparison, condition of large fish increased between 1991 and 1994, then declined during 1994 to 1997, indicating generally a reduction in plumpness and physiological well-being, and this group in general seldom met maintenance energy requirements. Based on optimal combinations of relative density and condition, we estimate that carrying capacity of the tailwater for large fish is about 150,000 to 170,000 fish under the present operating regime (USDI 1996), corresponding tentatively with electrofishing densities of about 2.0 to 2.5 CPUE and 0.3 to 0.4 kg/min, and that carrying capacity was exceeded by 1994 to 1995. Variations in daily operation of GCD within the present operating regime (USDI 1996) may affect these estimations, since

carrying capacity will change as a function of mean and minimum releases from the dam and duration, frequency, magnitude and timing of flow variation.

We believe that rainbow trout 305-405 mm were food-limited as a result of interference and exploitative competition. This size fish failed to meet or exceed maintenance energy estimations all years and seasons, likely resulting in slow growth. Densities of the group correlated negatively with benthic densities of *Gammarus* and gastropods, suggesting degradation of the aquatic food base. Condition correlated negatively with standing stocks only for this size category, reflecting density-related competition and consumption of low nutritional quality.

Our findings enhance understanding of rainbow trout ecology by demonstrating spatial and temporal patterns indicating responses to enhanced flow regimes and associations between trout and dam operations and the aquatic food base. Results should contribute to future monitoring, research and management of the recreational fishery.

## INTRODUCTION

Closure of Glen Canyon Dam (GCD) in 1963 impounded the Colorado River near the Arizona-Utah border, formed a large, meromictic reservoir (Lake Powell) and significantly altered the hydrology, limnology and aquatic ecology of the downstream riverine environment. Numerous authors have compared pre- and post-dam hydrology (Dawdy 1991), sediment transport (Andrews 1991), limnology (Stanford and Ward 1991) and aquatic biology (Blinn and Cole 1991) of the Colorado River below GCD and discussed operations of the hydroelectric power facility (Hughes 1991, Ingram et al. 1991).

Daily, monthly and yearly flows below GCD since closure of the facility in 1963 have differed from pre-dam conditions (Andrews 1991, Hughes 1991, Patten 1991, Stanford and Ward 1991, United States Department of Interior [USDI] 1995). Although releases from the dam and flow regimes between 1963 to 1998 varied, mean daily flows have exceeded power plant capacity ( $852 \text{ m}^3 \text{ s}^{-1}$ ) only about three percent of the time (vs. 18% pre-dam) and have been less than  $142 \text{ m}^3 \text{ s}^{-1}$  about 10% of the time (vs. 16% pre-dam). Daily variations in flow have increased during much of the post-dam period (USDI 1995, 1996). More stable flow regimes were implemented in 1991, and higher mean and less variable flows generally were maintained during mid-1995 through 1997 (Figure 1; USDI 1995, 1996). Establishment of minimum flow regulations below hydroelectric power dams is frequently employed to benefit lotic biota, but effects of this management action are not well-established (Weisberg and Burton 1993, Travnicek et al. 1995).

Non-native rainbow trout (*Oncorhynchus mykiss*) were first introduced in 1964 (Stone 1964) into the Lee's Ferry reach, a 26 km tailwater immediately below GCD (Figure 2). Following introductions of benthic algae (*Cladophora glomerata*) and

macroinvertebrates (e.g., *Gammarus lacustris*, chironomids, gastropods) into the tailwater during 1966-1969 (Stone and Queenan 1967, Stone and Rathbun 1968, 1969, Maddux et al. 1987), the fishery achieved a "trophy" status by about 1977 (Reger et al. 1989). However, the fishery historically has undergone dramatic changes in angler use and catch rates, relative trout abundance and size, body condition, population structure and spawning success since 1984 (Persons et al. 1985, Maddux et al. 1987, McKinney and Persons 1998).

Operation of GCD is relevant to the ecology of non-native rainbow trout and the aquatic food base in the Lee's Ferry reach (Blinn et al. 1995, McKinney et al. 1996, 1997, McKinney and Persons 1998), but variables potentially influencing the trout fishery are poorly understood. This report presents results of quantitative analyses on the spatial and temporal patterns of change in biotic (fish, benthic macroinvertebrates, periphyton) and abiotic (dam operation, nutrients, pH temperature) variables in the tailwater. Specifically, we sought to determine if releases from GCD, the aquatic food base and water quality variables influenced spatial and temporal differences in measurements of the rainbow trout population during 1991-1997. Studies were conducted to meet the following objectives provided by Grand Canyon Monitoring and Research Center (GCMRC; Cooperative Agreement No. 1425-97-FC-40-22690):

**OBJECTIVE 1 (Research)**--Synthesize existing information (published and unpublished data) on the Glen Canyon/Lee's Ferry trout fishery and determine the fishery's likely response (growth, reproduction, recruitment, population structure, size and distribution) to dam operations. This objective was addressed in a previous report (McKinney and Persons 1998).

**OBJECTIVE 2 (Monitoring)**--Monitor the trout fishery in Lee's Ferry to determine population size, structure, distribution, reproductive success, growth and overall

recruitment to reproductive size in response to dam operations.

OBJECTIVE 3 (Research)--Develop methods for estimating the proportion of natural reproductive success in combination with stocking quantities and rates to determine desired levels of recruitment balanced against the carrying capacity for a range of dam operations.

OBJECTIVES 4, 5 (Research)--Develop evaluation criteria for and measure and assess the health and condition of the rainbow trout population and evaluate health and condition factors in relation to changes in the aquatic food base and nutrient levels and dam operations.

## STUDY AREA

Glen Canyon Dam impounds the Colorado River in north-central Arizona near the Arizona-Utah border and forms Lake Powell, a 653 km<sup>2</sup> meromictic, oligotrophic reservoir. Hypolimnetic releases from the reservoir into the Lee's Ferry tailwater are clear and cold (Stanford and Ward 1991, Stevens et al. 1997). The Lee's Ferry reach extends between the dam (river kilometer [RK] -25.5) and Lee's Ferry (RK 0), is confined within a narrow, deeply-incised canyon and has no perennially-flowing tributaries. Non-native rainbow trout are the predominant fish in the tailwater reach but coexist with native flannelmouth sucker (*Catostomus latipinnis*; McKinney et al. 1998b) and non-native common carp (*Cyprinus carpio*). Releases from GCD during investigations ranged from 142 to 1,278 m<sup>3</sup>s<sup>-1</sup>, but flows generally did not exceed about 625 m<sup>3</sup>s<sup>-1</sup>.

## METHODS

### Field Collections

#### Rainbow trout

We captured rainbow trout during all seasons between dusk and dawn 2-4 times per year (N = 22 trips) by single-pass electrofishing (EF) at fifteen (1991-1996) or nine (1997) standardized transects (ca. 33 min/transect; McKinney et al. 1996, 1997) using a stratified-random design for representative of cobble bars, pools and runs. We used a complex pattern of pulsed direct current, applying 215 volts and maintaining a 15 ampere average output to a 30 cm stainless steel anode system (Sharber et al. 1994). Fish were measured to the nearest mm total length (TL), weighed to the nearest gram (g) and released unless collected for analysis of food habits, health or growth. We categorized trout as ripe if gametes could be manually expressed.

#### *Health*

We examined and rated external and internal anatomical features for random samples of rainbow trout (N = 230; size range 157-593 mm) following established protocol (Goede and Barton 1990, Adams et al. 1993) between November 1995 and April 1997. We calculated a health assessment index (HAI) for each fish as per Adams et al. (1993); greater index values indicate poorer health.

#### *Population estimates*

**Mark-recapture.** Three standardized electrofishing transects were stratified by location in the reach (RK -16.4, RK -11.4 and RK -6.4) and sampled following the above procedures during July 9-12, 1998 to estimate population size following mark-recapture procedures. Trout  $\geq 150$  mm were implanted with passive integrated transponder (PIT) tags during the first three nights of EF, and presence/absence of PIT tags was recorded for fish caught on nights 2-4. All fish captured were released alive. Fish collected from the same sites as above during electrofishing trips in August 9-11, 1998 (no new tagging) were included in the final population estimate.

**Hydroacoustics.** We conducted preliminary testing of hydroacoustic technology during daylight (15:30 h - 18:00 h) on March 18, 1998 to determine potential applicability in assessing rainbow trout population size and structural indices in the Lee's Ferry reach. Conditions were cool, sunny and windy, and releases from GCD were about  $568 \text{ m}^3\text{s}^{-1}$ . Gordon Mueller (U. S. Geological Survey [USGS]) provided equipment and conducted the survey, which started at RK -25 and proceeded downstream following approximately mid-channel to RK 0. Acoustic data were collected continuously at an estimated speed between 4-6 mph on a BioSonics dual beam scientific echosounder (model DT-5000). The system operates on 430 kHz and uses a 6.5 and 15 degree transducer. Data were collected at a -60 dB threshold which under ideal conditions would allow detection of targets  $\geq 1.6 \text{ cm}$ .

#### *Snorkel surveys*

We conducted snorkel surveys for rainbow trout during daylight (start 10:30 h) at four of the standardized EF transects (RK -23.3, RK -18.8, RK -11.4, RK -4.8) on 26 August 1998 to develop and evaluate this method for potential use in monitoring. Results of the snorkel survey were compared to EF results obtained during August 9-11, 1998. Migration and emigration of trout between August 9-26 was assumed not to be a factor affecting results (AGFD unpublished data). We floated transects downstream, utilizing three divers positioned about 3-6 m apart and counting all fish observed between the mid-channel diver and the center diver, between the center diver and the nearshore diver, and toward shore by the nearshore diver. Observations were reported to and recorded by the boat driver at end of each transect.

#### *Spawning gravel surveys*

We sampled substrate particles (Wolman 1954) on two known rainbow trout spawning

bars (RK -6.4 and RK -13.2) to assess suitability of substrate particle composition for spawning. Discharge from the dam at time of sampling was approximately  $400 \text{ m}^3\text{s}^{-1}$ . We established a 50 m x 10 m grid on exposed substrata contiguous with the water line at RK -6.4. We collected spawning bed particles at 1 m intervals each of 10 transects spaced evenly along the long axis (downstream orientation) of the grid, which covered about 60% to 70% of the exposed bar. Most suitable spawning area at RK -13.2 was submerged but easily accessible, and we sampled a  $100 \text{ m}^2$  grid following procedures used at RK -6.4. We collected gravel (2-64 mm dia) and cobbles (64-256 mm dia) (Lane 1947) and estimated particle size by measuring to the nearest mm over long and intermediate axes and obtaining an average of these measurements.

#### Benthic macroinvertebrates, periphyton, macrophytes

We sampled benthic macroinvertebrates (Hess sampler  $0.09 \text{ m}^2$ ; 1 mm mesh), periphyton ( $0.415 \text{ cm}^2$  template; Angradi and Kubly 1993, Blinn et al. 1995) and submerged macrophytes (Hess sampler  $0.09 \text{ m}^2$ ; 1 mm mesh) at  $142 \text{ m}^3\text{s}^{-1}$  or higher discharge stages using a stratified-random design for transects associated with cobble bar and fine-sediment habitats in the nearshore wetted zone monthly (periphyton: 1991-1994) or quarterly (macrophytes and periphyton: 1995-1997). Periphyton and macrophyte samples for mass (ash free dry weight; AFDW) analyses were held on ice for transport to the laboratory. Zoobenthic samples were preserved at collection using 10% formalin.

#### Organic drift

Joe Shannon and Dean Blinn (Northern Arizona University [NAU]) provided Arizona Game and Fish Department (AGFD) with unpublished means from their drift studies conducted at Lee's Ferry during 1991-1997 following established procedures (Shannon et

al. 1996). We also collected drift samples monthly during May 1993 to July 1994 about 250 m above Lee's Ferry over 24 h periods coincident with low, rising, high and falling phases of the daily hydrograph. Depth was integrated by towing (minimal boat speed) and slowly raising and lowering a metered (flow meter attached centrally in net mouth) tow net (0.5 m diameter, 1 mm mesh) while traversing a standardized transect normal to direction of river flow. We attached a 6.8 kg depressor on a 1 m drop chain attached 0.6 m in front of the net. Sampling duration was generally 15 min, and a mean volume of  $87.08 \text{ m}^3$  ( $\pm 1.74 \text{ SE}$ ) of water passed through tow nets (Ayers and McKinney 1996, McKinney et al. 1998a).

#### Water quality

Susan Hueftle and William Vernieu provided AGFD with water quality and nutrient data (temperature [ $^{\circ}\text{C}$ ], total phosphorous and total nitrogen [ $\text{mg/L}$ ]) collected from dam penstocks approximately monthly between 1991 and 1997 (Hueftle and Vernieu, personal communication, 1998) to determine relationships between trout and these variables.

#### Dam operations

William Vernieu (GCMRC, personal communications) also provided hourly and daily discharge data from GCD (U. S. Bureau of Reclamation unpublished data). Flow data were acquired from the GCD computer system consisting of hardware and software called Supervisory Control and Data Acquisition (SCADA).

#### **Laboratory Procedures**

Stomach contents of trout were identified to the lowest practical taxonomic level and measured to the nearest mL using volumetric displacement. We calculated relative gut volume ( $\text{RGV} = \text{total volume of stomach contents (mL/TL [m])}$ ; Filbert and Hawkins 1995) for *Cladophora* and predominant

macroinvertebrates in trout stomachs and frequency of occurrence for predominant ingested items.

Benthic macroinvertebrate (numbers of each taxonomic group), periphyton and macrophyte densities were calculated per unit area of substrate sampled. Ash free dry masses (AFDW) of periphyton and macrophytes were determined by loss on ignition ( $100^{\circ}\text{C}$  24 h;  $550^{\circ}\text{C}$  2 h). We identified organic matter in the drift to the lowest practical taxonomic level. Macroinvertebrates collected in the drift were counted by taxon and further estimated using volumetric displacement, and plant material was quantified by volumetric displacement and AFDW.

#### **Analytical procedures**

All rainbow trout data were provided to Carl Walters, Josh Korman, Sean Cox and Robert Ahrens (University of British Columbia [UBC]) to develop conceptual ecosystem and rainbow trout stock assessment models. The trout model incorporates the von Bertalanffy growth model and Bayesian statistical analyses (Walters and Post 1993, Walters and Ludwig 1994). The stock assessment model will allow further estimation of population variables in relation to abiotic and biotic variables in the Lee's Ferry tailwater and contribute to formulation of fishery management options. We used this approach rather than Canonical Correspondence Analysis which we proposed in response to the GCMRC Request for Proposals for this project. Consultation with Carl Walters indicated the stock assessment model provides a more viable technique for management. We presently are working with the stock assessment model to learn, refine and expand its use with our data, and results are pending and not presented in this report.

We computed condition indices for trout  $\geq 100 \text{ mm}$  using relative condition factor [ $K_r = [W/10^{(-4.6 + 2.856\text{Log}_{10}(L))} \times 100]$ ], Fulton's condition factor [ $K = (W/L^3) \times 100,000]$  and

relative weight ( $W_r$ ; Simpkins and Hubert 1996). Ponderal indices for all fish were plotted against TL, and slopes were compared using an F test (Littel et al. 1991).

Mean trout catch rates (CPUE; catch per minute of electrofishing with current in the water), relative condition factor and size (length, weight) for years and seasons (winter = January-March; spring = April-June; summer = July-September; fall = October-December) were compared using analysis of variance (ANOVA). Years and seasons were treated as fixed effects, and sampling locations were treated as random effects. Selection of seasonal periods was based on seasonal patterns of change in standing stocks of the benthos. Data for CPUE and kg/min EF (mass) were kurtotic and were transformed, respectively, using  $\text{Log}_{10}$  and square root. Duncan's Multiple Range test was used for multiple comparisons where parametric statistical procedures indicated significant treatment effects in the absence of significant interaction effect.

Trout RGV data were highly skewed, and we used Kruskal-Wallis tests (K-W) to determine annual and seasonal differences for trout food habit variables with respect to length categories (small fish: <152 mm, 152-304 mm; large fish: 305-405 mm, 406-558 mm) and origin of fish (hatchery-reared, wild). Unfortunately, trout stomach samples collected during 1994 were lost and unavailable for analyses. Frequencies of empty stomachs among seasons were analyzed using a chi-square test of independence. Trends in frequencies of empty stomachs among years were tested using Spearman Rank Order correlations. Frequency of occurrence for stomach content data was computed only for fish with ingested food items, whereas frequency of empty stomachs were calculated as percent of all fish collected for food analysis. Fish health data were analyzed using ANOVA among months and using Pearson's product-moment correlations to determine relationships

between the health index, length, condition of fish, and relative abundance of nematodes in stomachs.

We calculated proportional stock density (PSD; Anderson and Neumann 1996) for trout captured by EF during all trips. Calculations were based on the number of fish within or exceeding a slot limit (406-558 mm) divided by the number of trout greater than or equal to minimal size "desired by fishermen" (305 mm; Reger et al. 1995).  $\text{Log}_{10}$ -transformed data were used to evaluate correlations of PSD against CPUE,  $K_n$  and mass for rainbow trout.

We used Spearman's Rank Order Correlations to explore relationships among variables for rainbow trout, dam operation, water quality and the aquatic food base. Due to temporal variability in sampling periods, benthic, drift and trout data were categorized by season and year for these analyses. We compared yearly, location and seasonal medians for periphyton and macrophytes (AFDW) and for benthic macroinvertebrate densities using K-W. We used linear regression and to compare number of fish captured by electrofishing and counted during snorkel surveys.

We developed an energy intake model for rainbow trout in the Lee's Ferry reach based on food consumption and gastric evacuation (Cummins and Wuychek 1971, Elliott 1975a, Boisclair and Leggett 1988, Storebakken and Austreng 1988, Angradi and Griffith 1990, Ensign et al. 1990, Rand et al. 1993, Bowen et al. 1995, Filbert and Hawkins 1995, Héroux and Magnan 1996, Weiland and Hayward 1997, Hayward and Weiland 1998). We selected macroinvertebrate prey taxa according to their frequencies of occurrence, percent stomach volume and relative nutritional value for modeling energy intake.

Diel energy ingested ( $E_{24}$ ) by rainbow trout was calculated first by estimating diel dry food weight ingestion ( $C_{24}$ ) using Eggers' (1977) model and assuming that feeding rates were constant over 24 h (Boisclair and

Leggett 1988, Storebakken and Austreng 1988, Angradi and Griffith 1990, Ensign et al. 1990, Angradi et al. 1992). Dry weights (DW) for *G. lacustris* were predicted from volume-dry weight regressions (AGFD unpublished data). We estimated total chironomid DW by multiplying volumes times the specific gravity constant (1.05; Filbert and Hawkins 1995) and assuming that DW was 10% of wet weight (Cummins and Wuychek 1971, Hewett and Kraft 1993).

Mean gastric evacuation rate (GER) for *Salmo trutta* fed *Gammarus* sp. over 5-15° C (Elliott 1972) was used for calculation of  $C_{24}$ . A separate  $C_{24}$  estimate for chironomids was made using GER for rainbow trout fed chironomid larvae (Hayward and Weiland 1998). Estimates of  $C_{24}$  for *Gammarus* and chironomids then were standardized by fish dry body weight (25% of wet weight; Hewett and Kraft 1993) and assigned energy density values (Joules/mg DW) derived for the Lee's Ferry tailwater by Blinn et al. (1995). Total  $E_{24}$  was estimated by summing individual estimates for *Gammarus* and chironomids. Diel maintenance energy (ME: J/mg fish body DW/day) was derived using Elliot's (1976) model for *S. trutta* in relation to body weight, water temperature and ration size. Water temperatures in the Lee's Ferry reach at time of stomach collections was incorporated into all metabolic calculations.

We compared median ME and  $E_{24}$  as stratified by fish size and among years and seasons using the Wilcoxon sign ranks test (Weiland and Hayward 1997). Data were also expressed as length-specific percentages of fish meeting or exceeding their maintenance ration within years and seasons. We also determined growth based on recaptures of hatchery-reared trout implanted with coded wire tags. Total lengths for each hatchery-reared cohort were plotted against elapsed time to recapture and fitted with logistic growth curves.

There are two methods of acoustically estimating fish densities, echo integration and

echo counting. The DT-5000 analysis program calculates fish densities using echo integration and examines total reflective energy measured from all targets (and noise) divided by energy received by an average size fish. This approach is best suited for environments containing large numbers of fish, and the procedure is inaccurate in noisy, shallow waters that have low fish densities.

The dual-beam system used measures the reflected energy returned by an underwater target by triangulation. Signal strength of a target return is directly proportionate to size and is indicative of its reflective characteristics (size and composition) and depth. Thus, we can estimate fish size by measuring echo strength. Echo counting greatly reduces biases associated with noise or large non-fish targets and measures fish density by dividing the number of fish detected by the total area or volume sampled. Echogram editing is best accomplished on small data files having high resolution, and the five files for this study were subdivided into 36 segments (1,000 pings) for analysis. Fish densities were calculated for each of the 36 segments by taking the number of targets detected (pings), estimating the detection area ( $m^2$ ) of the echosounder beam based on average depth of the river and converting values to numbers of fish detected per hectare for each of the 1,000 ping segments. Resulting values were corrected to 415 ha (estimated surface of the Lee's Ferry reach at discharges from the dam of ca.  $142 m^3 s^{-1}$ ; Persons et al. 1995).

While data were collected at a threshold of -60 dB, target recognition during the analysis phase was set at -40 dB to identify targets larger than 16 cm. We believe that this setting removed the majority of non-fish targets that were suspended in the water column but eliminated any fish < 16 cm.

We used a computer program (Program NOREMARK, online, G.C. White, Colorado State University, Ft. Collins) to estimate population size based on mark-recapture



studies of rainbow trout  $\geq 150$  mm. We determined density of fish for the area sampled and extrapolated this value to a total surface area of the Lee's Ferry tailwater (415 ha; Persons et al. 1985) and estimate population size.

## RESULTS

### Rainbow trout

We captured 22,853 rainbow trout between 31 and 637 mm TL during 1991-1997. Mean TL and weights for all fish differed among years ( $P < 0.001$ ) and declined from 1991-1993, then each increased about 7-8% by 1996-1997 (Figure 3). Mean TL and weights also differed seasonally ( $P < 0.001$ ) and were greatest in winter and lowest in summer (Figure 4). Based on assessments of ripe fish, most hatchery-reared and wild trout became sexually mature at about 300 mm (Figure 5). Breakdown of % ripe within size classes was:  $< 152$  mm = 0.06%; 152-304 mm = 1.6%; 305-405 mm = 10.6%; 406-558 mm = 18.7%. Numbers of ripe wild and hatchery-reared fish, respectively, within the 305-405 mm size class were about fourfold and twofold greater than for fish 152-304 mm. Numbers of ripe fish differed among seasons, and most were captured between October and April, with numbers peaking in February ( $P < 0.001$ ). However, presence of manually expressed gametes in other months (Figure 6) indicate that year-round spawning activities may have occurred. Percentages of ripe hatchery-reared fish were lower ( $P < 0.001$ ) after 1994, but percent of ripe wild fish showed no downward trend after that time (Figure 7). Monthly trends were similar for each source category (Figure 8). Numbers of ripe wild fish exceeded those of hatchery-reared trout by three to thirteen times for length categories examined (Figure 5). Sex ratios (male:female) for all fish and wild and hatchery-reared trout, respectively, were 3.3:1, 3.7:1 and 5.1:1

### Catch-per-minute of electrofishing

Catch-per-minute of electrofishing (CPUE) for all trout combined differed ( $P < 0.001$ ) among locations, years and seasons. No interactions were statistically significant, indicating that CPUE at all sites changed comparably over years and seasons. Mean CPUE among locations showed considerable overlap and no discernible patterns. Discharge from GCD did not significantly influence CPUE at time of sampling (ANCOVA). Catch rates for all trout declined from 1991-1993, stabilized at a higher level in 1994-1996, then increased in 1997 (Figure 9). Seasonally, CPUE for all fish was greatest in summer and fall and was minimal in winter and spring (Figure 10).

Length-specific catch rates also differed among years and seasons (Figures 9, 10). Effects of year, location and season were significant ( $P < 0.001$ ) for trout  $< 152$  mm, with no significant interactions. The CPUE for this length class was lowest during 1991-1993, increased through 1997 and was lowest in winter, intermediate in spring and highest in summer and fall. The CPUE for fish 152-304 mm was lowest during 1991-1993, increased during 1994-1997 and was lowest in winter, intermediate in spring and fall, and highest during summer ( $P < 0.001$ ). The CPUE for fish 305-405 mm differed by year and location ( $P < 0.001$ ), but not season, and interaction effects were not statistically significant. Catch rate for trout in this length category declined from 1991 to 1993, then increased from 1994 to 1997. Catch rates of trout 406-558 mm differed among seasons, years and locations ( $P < 0.001$ ), and interactions were not significant. The CPUE for this length group was highest in 1991, declined to a stable level between 1993 and 1996, then increased in 1997. Catch rate was greatest in winter and lowest during summer and fall for this length group.

Catch rates for hatchery-reared and wild trout differed ( $P < 0.05$ ) among years and location, but only hatchery-reared fish

differed ( $P < 0.05$ ) among seasons (Figures 11-14). There were no statistically significant interaction effects. The CPUEs for hatchery-reared and wild fish were lowest in 1992-1993. Catch rate for hatchery-reared fish increased ( $P < 0.001$ ) after 1993 to stable levels during 1994-1997, whereas CPUE of wild trout increased during that period (Figures 11, 13). Catch-per-minute of hatchery-reared trout was greatest ( $P < 0.03$ ) in summer (Figure 12). Length-specific catch rates for hatchery-reared and wild fish differed among years and seasons. The CPUE for hatchery-reared trout  $< 152$  mm differed among years ( $P < 0.02$ ) and seasons ( $P < 0.001$ ) but not among locations, and there were no significant interaction effects. The CPUE for fish of this origin and length category was highest during 1992-1994 and declined during 1995-1997 (Figure 11). The index was lowest in winter, intermediate in spring and fall and highest in summer (Figure 12). In contrast, the CPUE for wild fish  $< 152$  mm was stable and lowest during 1992-1994, then increased ( $P < 0.001$ ) to a maximum in 1997 (Figure 13). Seasonal effects were not statistically significant, but location effects were significant ( $P < 0.001$ ).

Hatchery-reared fish 152-304 mm differed in CPUE among years and location ( $P < 0.001$ ) but not among seasons, and interaction effects were not statistically significant. The CPUE for this size group increased from 1992-1993 to generally stable levels during 1994-1996 but declined in 1997 (Figure 11). Among wild trout 152-304 mm, CPUE differed among years and locations ( $P < 0.001$ ) and seasons ( $P < 0.005$ ), and interaction was not statistically significant. Catch-per-minute for wild fish in this length group was lowest in 1992-1993, gradually increased to a maximum in 1997 (Figure 13) and was highest in spring-summer (Figure 14).

Hatchery-reared fish 305-405 mm differed in CPUE among years ( $P < 0.001$ ) but not among locations or seasons, and interaction was not significant. The CPUE was lowest in 1993, intermediated in 1994 and stable and

highest during 1995-1997 (Figure 11). Catch-per-minute for wild trout 305-405 mm differed ( $P < 0.05$ ) among years and locations ( $P \leq 0.001$ ) and seasons, and interaction was not significant. The CPUE for this length group was lowest in 1992-1993 and increased from 1994 through 1997 (Figure 13). Catch rate was lowest in spring and winter, highest in summer and fall (Figure 14). In contrast, CPUE for hatchery-reared fish 406-558 mm did not differ among years or season, and there were no statistically significant interaction effects, but location effects within seasons differed significantly ( $P < 0.001$ ). Wild trout 406-558 mm differed ( $P < 0.002$ ) among years (Figure 13) and locations, but not among seasons, although location effect differed seasonally ( $P < 0.001$ ). The CPUE for this group was stable from 1992 to 1995 but increased slightly during 1996 and 1997.

#### Proportional composition

Trout in size classes  $< 152$  mm, 152-304 mm, 305-405 mm and 406-558 mm comprised 39%, 25%, 23% and 12%, respectively, of all trout captured by electrofishing. Analyses by 50 mm increments indicated stockpiling of smaller fish within the slot (slot limit: 406-558 mm; percentages of total catch all trout: 400-449 mm = 9.4%; 450-499 mm = 3.5%; 500-550 mm = 0.6%). Proportional composition of fish  $< 152$  mm increased almost fivefold between 1991 and 1993 then remained generally stable through 1997 but exhibited yearly variability (Figure 15). Proportion of trout 152-304 mm more than doubled during 1991 to 1994 and were stable in 1995-1996 but declined in 1997. Fish 305-405 mm declined about 50% in proportion from 1991 to 1993, then more than doubled by 1997, returning to 1991 levels (Figure 15). Trout 406-558 mm declined proportionally more than 70% between 1991 and 1994, when proportion stabilized through 1997 (Figure 15).

Percent composition of trout <152 mm tended to be highest in summer and fall, lowest in winter, but seasonal trends in composition differed from this for other size classes (Figure 15). Composition of fish 152-304 mm was highest in summer, and trout 305-405 mm did not differ in percent composition among seasons. Percent composition of trout 406-558 mm was greatest in winter, lowest in summer and fall.

#### Biomass/minute electrofishing

Mass of all fish  $\geq 100$  mm differed among years, location and seasons ( $P < 0.001$ ), and the interaction effects were not statistically significant. Mass was greatest in 1991, declined in 1992-1995, then increased through 1997 (Figure 9). Mass among years for all trout reflected primarily the pattern of change for trout 305-405 mm (Figure 9). Proportional mass (% of total mass/sample) generally was greatest for trout 305-405 mm and 406-558 mm between 1991 and 1997, and proportional mass of fish 406-558 mm exceeded that of fish 305-405 mm until mid-1993 and beyond, when the latter group comprised increasing proportional mass (Figure 16).

Masses for trout <152 mm and 152-304 mm were greatest ( $P < 0.001$ ) in summer, while mass of fish 305-405 mm did not vary significantly among seasons, and mass of fish 406-558 mm was greatest in winter ( $P < 0.001$ ; Figure 10). Masses of hatchery-reared and wild trout increased ( $P < 0.001$ ) during 1994 to 1997 but exhibited no seasonal differences (Figures 11-13). Mass of hatchery-reared fish <152 mm differed among years ( $P < 0.002$ ), location within years ( $P < 0.05$ ), and among seasons ( $P < 0.001$ ), but not among locations for seasons, and interaction effects were not statistically significant. Mass was stable and highest during 1992-1994 for this length class and origin but declined in 1995-1997 (Figure 11) and was greatest in summer, lowest in winter and spring (Figure 12). Mass of wild trout <152 mm differed among years and

location ( $P < 0.001$ ) and seasons ( $P < 0.02$ ). Mass was lowest in 1992-1993, then increased in 1994, was greatest in 1995-1997 (Figure 13), and was generally lowest in summer and greatest in spring (Figure 14).

Mass of hatchery-reared trout 152-304 mm differed among years and location for years ( $P < 0.001$ ), but effects of season and interaction were not statistically significant. Mass was lowest in 1992-1993, increased to higher, stable levels during 1994-1997 (Figure 11). Mass of wild fish of this length class differed among years and location ( $P < 0.001$ ) and season ( $P < 0.03$ ), and interaction effect was not statistically significant. Mass was lowest in 1992-1993, increased during 1994-1995 and again in each of 1996 and 1997 (Figure 13) and tended to be lowest in fall through spring (Figure 14).

Mass of all trout 305-405 mm differed among years and location ( $P < 0.001$ ), but seasonal and interaction effects were not statistically significant. Mass decreased from 1991 to 1993, increased in 1994 and 1995, then increased through 1997 and was greatest in summer (Figures 9, 10). Mass of hatchery-reared trout in this size category differed among years ( $P < 0.001$ ) but not among locations or seasons, and interaction effects were not statistically significant. Mass of hatchery-reared trout 305-405 mm was lowest in 1993, increased in 1994 and 1995 and remained stable through 1997 (Figure 11). Mass of wild fish 305-405 mm differed among years, location and season ( $P < 0.01$ ), and interaction effects were not statistically significant. Mass of this group increased steadily from 1992 to 1997 (Figure 13) and was highest in summer and fall (Figure 14).

Mass for all trout 406-558 mm differed among years, location and season ( $P < 0.001$ ), and interaction effects were not statistically significant. Mass of this group declined from 1991 to 1993, remained stable through 1996, then increased in 1997 (Figure 9). Mass of fish captured in this group was greatest in winter, lowest in fall and summer (Figure 10).

Mass of hatchery-reared trout 406-558 mm did not differ among years (1994-1997) or season, and location effect was significant ( $P < 0.02$ ) only within seasons. Mass of wild fish for this length class differed ( $P < 0.001$ ) among years and locations but not seasons, and interaction effects were not statistically significant. Mass was lower in 1992-1993 than during stable levels in 1994-1997 (Figure 13). Proportional mass of trout 305-405 mm increased dramatically between 1991 and 1997, whereas that of fish 152-304 increased between 1991 and 1994, then stabilized (Figure 16). In contrast, proportional mass of fish  $< 152$  mm varied little among years, and that of fish 406-558 mm declined.

#### Relative condition factor

Relative condition factor ( $K_n$ ) was selected for analyses, since slope of  $K_n$  on TL ( $\beta = -0.0158$ ) differed significantly ( $P < 0.001$ ) from and was less than slopes for Fulton's  $K$  ( $\beta = -0.0722$ ) and  $W_r$  ( $\beta = -0.0752$ ), indicating less length-related bias for  $K_n$ . Moreover,  $K_n$  is an appropriate index for population-specific assessments (Murphy et al. 1991). Relative condition factor for all trout captured differed ( $P < 0.001$ ) among years, locations and seasons, and interaction effects were not statistically significant. Condition was lowest in 1991, increased each year from 1992-1994 and declined in 1995-1996 and again in 1997 (Figure 17). Relative condition was lowest in winter, highest in summer (Figure 17).

Condition of all trout  $< 152$  mm did not differ significantly among years, location or season (Figure 17). Condition of fish 152-304 mm differed among years and location ( $P < 0.001$ ) and season ( $P < 0.02$ ). Condition for this length class was stable during 1992-1996 but declined about 8% in 1997, and the index was higher in summer and fall than in spring or winter (Figure 17). Condition of fish 305-405 mm differed among years, location and season ( $P < 0.001$ ), and interaction effects were not statistically significant. The index increased about 19% from 1991 to 1994, then

declined about 8% through 1997 (Figure 17). Condition of this size group was higher in summer than other seasons (Figure 17). Condition of all trout 406-558 mm differed among year and location ( $P < 0.001$ ) but not among seasons (Figure 17), and interaction effects were not statistically significant. Condition for this length class increased about 20% from 1992 to 1994, then declined about 10% by 1997 (Figure 17).

Condition of hatchery-reared fish declined ( $P < 0.001$ ) about 14% between 1991 and 1997 (Figure 18) but did not differ by location among years. The index for hatchery-reared fish also varied with location in seasonal comparisons ( $P < 0.05$ ) but did not differ among seasons, and interaction effects between location, year and season were not statistically significant. In comparison,  $K_n$  for wild fish increased from 1991 to 1994, then declined through 1997 ( $P < 0.001$ ; Figure 18) and was greatest ( $P < 0.02$ ) in summer and fall, lowest in winter and spring. Interaction effects were not statistically significant.

Length-specific  $K_n$  for hatchery-reared and wild fish differed among years with respect to each other (Figure 18), but seasonal differences were not significant for either category of origin. Condition for hatchery-reared trout  $< 152$  mm increased between 1994 and 1996 but declined to previous levels in 1997 ( $P < 0.001$ ; Figure 18). However, condition of wild fish for this size class did not differ significantly among years, location or season. Condition of hatchery-reared trout 152-304 mm declined ( $P < 0.002$ ) between 1991 and 1997 (Figure 18) but did not differ significantly among seasons or locations by year, although location effect was significant ( $P < 0.05$ ) for season. Condition of wild fish 152-304 mm (Figure 18) remained stable between 1992 and 1996 but declined ( $P < 0.001$ ) in 1997. Location effects differed ( $P < 0.003$ ) among years, but there were no significant seasonal or interaction effects.

Condition of hatchery-reared trout 305-405 mm was greatest ( $P < 0.001$ ) in 1991,

lowest in 1997 (Figure 18). Fish of this length category differed ( $P < 0.01$ ) among locations but not among seasons. Interaction effects were not statistically significant. Among wild fish in this group, condition differed ( $P < 0.001$ ) among years (Figure 18) and locations but not among seasons, and interaction effects were not statistically significant. The ponderal index for this length class was lowest in 1992, greatest in 1994 (Figure 18). Condition of hatchery-reared trout 406-558 mm differed ( $P < 0.001$ ) among years but not among locations or seasons. Relative condition factor was available for comparatively few hatchery-reared fish in this group but was greatest during 1994 and declined to stable levels 1995-1997 (Figure 18). Among wild trout 406-558 mm, sample size was larger, and condition differed ( $P < 0.01$ ) among years and locations but not among seasons, and year  $\times$  location interaction was statistically significant ( $P < 0.05$ ). Condition for this length class was lowest during 1992-1993, greatest in 1994 (Figure 18).

### Growth

Estimated growth of small trout ( $< 305$  mm) was about 140 mm to 191 mm per year, whereas growth of large fish ranged from about 10 mm to 76 mm per year (Figure 19). Exponent of the logistic growth equation for stocked cohorts was greatest for fish planted in 1995 (2.39), intermediate for those stocked in 1993 and 1994 (1.88 and 1.41, respectively), and lowest for those introduced in 1992 (0.78; Figure 18). Only 5% of recaptured hatchery-reared trout grew to lengths exceeding 405 mm.

### Health

We collected 230 rainbow trout 157-538 mm for health assessment. The HAI increased ( $P < 0.02$ ) between 1995 and 1997, indicating a decline in health of fish during that time and particularly following the 1996 flood. However, the HAI generally remained within

a range suggesting good health (Goede and Barton 1990, Adams et al. 1993, McKinney et al. 1996). The HAI correlated positively ( $R = 0.28$ ;  $P < 0.001$ ) with fish parasite (gut nematode) load, negatively with  $K_n$  ( $R = -0.18$ ;  $P < 0.01$ ) and positively with fish length ( $R = 0.19$ ;  $P < 0.001$ ). Ranked abundance of stomach nematodes ( $\pm$  SE) and HAI values ( $\pm$  SE; in parentheses) collected during 12/95, 4/96, 8/96, 11/96, and 4/97 were, respectively:  $2.5 \pm 0.1$  ( $23.2 \pm 3.4$ ),  $2.3 \pm 0.2$  ( $16.7 \pm 4.6$ ),  $2.0 \pm 0.3$  ( $22.8 \pm 4.6$ ),  $1.8 \pm 0.1$  ( $20.7 \pm 5.0$ ),  $1.6 \pm 0.2$  ( $34.7 \pm 5.4$ ), and  $2.2 \pm 0.2$  ( $41.2 \pm 6.1$ ). Ranked nematode abundances were: 0 = none; 1 = 1-100; 2 = 101-1,000; 3 =  $> 1,000$ .

### Population size estimates

#### *Mark-recapture*

Use of the NOREMARK model (Program NOREMARK, online, G.C. White, Colorado State University, Ft. Collins) provided a population estimate for the area sampled of 5,667 (95% confidence interval 4,031-8,409) rainbow trout  $\geq 150$  mm, which extrapolates to 783,935 trout  $\geq 150$  mm in the Lee's Ferry reach. Considering only trout  $\geq 305$  mm, we estimated 1,900 (95% confidence interval 1,217-3,286) fish in the area sampled, which equates to 262,000 trout of this size in the tailwater reach.

#### *Hydroacoustics*

The echosounder functioned normally during the March 18, 1998 sampling trip and showed a great deal of material within the water column. A large number of targets was detected which likely included air bubbles and suspended vegetation and debris. We observed fragments of *Cladophora*, *Potamogeton* sp. and other debris in the water column. Five data files were created for subsequent analysis and consisted of a total of 36,000 pings or samples. Data analysis detected 33 targets larger than 16 cm, out of 36,000 pings recorded. Reflective energy ranged from -20 to -38 dB, which

encompasses a size range between 160 mm and 1,500 mm. Eleven targets had an energy value of  $>-25$  dB. If these were fish, they would have to have been longer than 900 mm, indicating the targets were not fish. These reflective signatures must have resulted from reflective energy anomalies from large boulders or vegetation. These 11 targets were dropped from the data base, reducing the total number of targets believed to be fish to 22. Fish densities were highly variable, ranging from 0 to 154 fish/ha. Based on the average fish density of 16.8/h, the pelagic zone that we surveyed and analyzed contained an estimated 6,970 fish  $>16$  cm, representing fish found at depths  $>3$  m and a minimum of 0.3 m above substrata.

#### Snorkel surveys

Discharge from Glen Canyon Dam was generally stable at about  $653 \text{ m}^3\text{s}^{-1}$  during snorkel surveys. Underwater visibility ranged from  $<1$  m to 6 m, and low visibility resulted from higher turbidity along eroding cutbanks. We utilized two diver configurations, one where divers formed a line perpendicular to shore and one where divers formed a line about  $45^\circ$  to the shore, with the mid-channel (outside) diver farthest downstream. The  $45^\circ$  configuration proved more effective, since it minimized movements of spooked fish from nearshore into the observation zone of outside divers. We attempted using a 7 m section of PVC pipe to maintain diver separation at fixed (ca. 3 m) intervals, but this proved unsuccessful due to variability in current velocity between nearshore and deeper water toward mid-channel.

Coefficients of variation for fish counted between replicate drifts ranged from 9.4% to 78.7% for individual diver positions and from 4.1% to 23.2% for pooled counts of all divers (Figure 20); variation was lowest for the center dive position. The site-specific numbers of trout observed by the center diver correlated significantly ( $R^2 = 0.97$ ;  $P < 0.03$ ) with number of fish captured by electrofishing

the same sites about two weeks earlier (Figure 20). We completed eight dives in about 6 h and determined that five transects each could be surveyed twice in one day, assuming sites were characterized primarily by laminar flow.

#### Spawning gravel surveys

Median gravel diameter was 21.5 mm at RK -6.5 and 27.8 mm at RK -13.2. The Wolman (1954) method required about one hour to sample each spawning bar, and estimation of substrate particle diameters for both bars required about one hour.

#### Proportional stock densities

Proportional stock density differed ( $P < 0.001$ ) among years and seasons, and interaction between the two effects was not statistically significant. The structural index declined more from 1991-1992 through 1994 than during 1995-1997 (Figure 21). Seasonally, PSD was higher in winter than other seasons (Figure 21). Coefficients of determination for regressions of  $\text{Log}_{10}(\text{PSD})$  on  $\text{Log}_{10}(\text{CPUE})$  and  $\text{Log}_{10}(K_n)$ , respectively, were significant ( $R^2 = 0.54$ ,  $R^2 = 0.61$ ;  $P < 0.001$ ), but association was not significant for  $\text{Log}_{10}(\text{PSD})$  versus  $\text{Log}_{10}(\text{Kg/min})$ .  $\text{Log}_{10}(\text{PSD})$  varied as a negative parabolic function of  $\text{Log}_{10}(K_n)$ , whereas it varied as a negative linear function of  $\text{Log}_{10}\text{CPUE}$  (Figure 22).

#### Food habits

We collected 664 rainbow trout 110-550 mm over all years and seasons to obtain food habits data. *Cladophora*, *G. lacustris*, total chironomids and gastropods together accounted for more than 90% of trout stomach content volume, and *Gammarus* and chironomids generally comprised more than 90% of animal matter in trout stomachs. Frequency of occurrence of *Cladophora* ( $P \leq 0.001$ ), *Gammarus* ( $P = 0.005$ ) and gastropods ( $P = 0.004$ ) differed among years (Table 1). Frequencies of *Gammarus* and gastropods were lowest in 1991, whereas no

clear trends were apparent for frequencies of *Cladophora* and chironomids among years (Table 1). Frequencies of occurrence for all four ingested categories differed among seasons ( $P \leq 0.001$ ). *Cladophora* and chironomids were least frequent in the fall, whereas *Gammarus* were least frequent in winter and spring, and gastropods were least frequent in winter (Table 1).

Total RGV differed among years ( $P < 0.01$ ) and seasons ( $P < 0.001$ ), was lowest in 1993, greatest in 1997 (Figure 23). The pattern of change in total RGV between 1991-1997 reflected increases in *Gammarus* and *Cladophora* in diets (Figure 23). Total RGV was greater in summer than other seasons (Figure 22). Total RGV and RGVs for *Gammarus*, gastropods, *Cladophora* and total chironomids differed ( $P < 0.05$ ) among size classes of trout by years and seasons (Figures 24-28). Significant year-to-year trends were apparent primarily for trout 305-405 mm. Total RGV for this length group increased ( $P < 0.01$ ) between 1991 and 1997, as did RGVs for *Gammarus* ( $P < 0.001$ ) and *Cladophora* ( $P < 0.05$ ), but RGV for chironomids declined ( $P < 0.05$ ), and RGV for gastropods showed no clear trends. The RGVs for chironomid adults and pupae differed ( $P < 0.02$ ) among years for trout 152-304 mm, but no clear trend was evident. Also, RGV for chironomid pupae differed ( $P < 0.03$ ) among years for fish 406-558 mm and was greatest in 1993.

Total RGV was greatest ( $P < 0.03$ ) in summer for all length categories of fish (Figure 24). The RGV for *Cladophora* was greatest ( $P < 0.002$ ) in summer for trout  $\geq 305$  mm but was greater ( $P < 0.01$ ) during spring and summer for fish  $< 305$  mm (Figure 27). The RGV for *Gammarus* peaked ( $P < 0.01$ ) in summer for fish 305-405 mm but did not differ significantly among seasons for other size classes (Figure 25). Chironomid RGV peaked significantly ( $P < 0.05$ ) in spring only for fish  $< 406$  mm, while gastropod RGV

was greater ( $P < 0.02$ ) in summer and fall only for fish in this length group (Figures 26, 28).

Total RGV of wild trout increased ( $P < 0.01$ ) between 1993 and 1997, but annual differences in total RGV were not statistically significant among years for hatchery-reared fish (Figure 29). The RGVs for *Cladophora* (Figure 30) increased between 1993 and 1997 for both hatchery-reared ( $P < 0.01$ ) and wild trout ( $P < 0.05$ ), but RGVs for *Gammarus* (Figure 31), gastropods (Figure 32) and chironomids showed no significant trends for either hatchery-reared or wild trout.

Total RGV and the RGV for *Cladophora* were greatest for hatchery-reared fish ( $P < 0.05$ ) in summer and wild trout ( $P < 0.01$ ) in spring and summer (Figures 33, 34). The RGV for *Gammarus* also was greatest ( $P < 0.01$ ) in summer for wild fish, but seasonal differences were not statistically significant for hatchery-reared fish (Figure 35). Chironomid RGV was greater ( $P < 0.001$ ) in spring-summer for hatchery-reared fish ( $P < 0.02$ ) but did not differ significantly among seasons for wild trout (Figure 36). Gastropod RGV was greatest ( $P < 0.002$ ) for wild fish in summer-fall but did not differ significantly among seasons for hatchery-reared trout (Figure 37).

Length-specific total RGVs did not differ between hatchery-reared and wild trout. Hatchery-reared trout 152-304 mm consumed relatively greater ( $P < 0.05$ ) amounts of *Cladophora* than did wild fish, but consumption of the alga by other length classes did not differ significantly by origin of fish (Figure 38). The RGVs for *Gammarus* and chironomids did not differ significantly between hatchery-reared and wild fish, but hatchery-reared fish 152-304 mm and 406-558 mm consumed more gastropods than did wild fish of the same length categories (Figure 38). Total RGV increased significantly ( $P < 0.01$ ) between 1993 and 1997 only for wild fish 305-405 mm (Figure 29), and fish 305-405 mm increased ( $P < 0.02$ ) RGV for *Cladophora* between 1995 and 1997

(Figure 30). The RGV for *Gammarus* also increased ( $P < 0.01$ ) among years only for wild trout 305-405 mm (Figure 31). The RGV for gastropods declined only for hatchery-reared fish 152-304 mm (Figure 32), and no trends were apparent in consumption of chironomids for either origin of trout.

Total RGV was greatest ( $P < 0.02$ ) in summer than other seasons for all length categories of hatchery-reared trout, but total RGV was greatest ( $P < 0.01$ ) in summer only for wild fish 305-405 (Figure 33). Hatchery-reared and wild trout exhibited different length-related seasonal changes in the RGV for *Cladophora* (Figure 34). Hatchery-reared fish 152-304 mm and 305-405 mm consumed more of the alga in spring-summer than other seasons. Wild trout 305-40 mm and 406-558 mm also consumed more *Cladophora* in spring-summer (Figure 34). Neither hatchery-reared or wild trout of any length group examined differed significantly in seasonal consumption of *Gammarus* (Figure 35). Length-specific RGVs for chironomids were greatest ( $P < 0.05$ ) in summer and spring, respectively, for hatchery-reared fish 152-304 mm and 305-405 mm but did not differ among length classes of wild trout (Figure 36). In contrast, hatchery-reared fish did not differ seasonally for gastropod RGV, but wild fish  $< 406$  mm consumed more ( $P < 0.05$ ) gastropods in summer-fall (Figure 37).

Percent empty stomachs for all trout combined declined (Spearman  $R = -0.60$ ;  $P < 0.01$ ) during 1992-1997 (Figure 39). Percent empty stomachs (Figure 40) also differed ( $P < 0.001$ ) seasonally and tended to be lower in summer than other seasons. About 22% of stomachs (average) were empty over seasons and years for all trout combined. Frequency of empty stomachs among length classes (50 mm increments) ranged from 0 to 31% and tended to increase with length for trout  $\geq 300$  mm (Figure 41). Percent empty stomachs of fish 305-405 mm declined since 1991 (Spearman's  $R = -0.51$ ,  $P = 0.0312$ ; Figure 39) and were lowest ( $P < 0.001$ ) in

spring-summer, but no significant annual or seasonal trends were detected for other length classes (Figures 39, 40). We found no statistically significant differences between hatchery-reared or wild trout in percent empty stomachs on temporal scales, but when all samples were combined, percent of empty stomachs of hatchery-reared fish 305-405 mm (12%) was double ( $P < 0.03$ ) that for wild trout in the same size group.

### Angling and stocking

Stocking of trout declined to 20,000-25,000 per year in 1996-1997 but was about fourfold or more greater than these levels during 1991-1995 (McKinney and Persons 1998). Angler catch rates, however, increased twofold from 1991 to 1997, while hours per year of angler use declined fourfold from 1991 to 1993 and subsequently increased to about 73 % of 1991 levels in 1997 (McKinney and Persons 1998).

### Bioenergetics

Median daily energy intake by trout failed to meet ( $P < 0.001$ ) maintenance energy requirements (ME) during all years, but size class differences were apparent (Figure 42). Median daily energy intake ( $E_{24}$ ) by trout 152-304 mm met ME during 1991, 1992 and 1997, while  $E_{24}$  of trout 305-405 mm failed to meet ME during all years ( $P < 0.02$ ), and trout 406-558 mm failed ( $P < 0.05$ ) to meet ME during all years except 1991 and 1997 (Figure 42). Similarly,  $E_{24}$  of all fish combined and trout 305-405 mm failed to meet ME during all seasons ( $P < 0.0001$ ), but fish 152-304 mm and 406-558 mm met minimum energy requirements during summer (Figure 43). Percentage of trout in samples meeting maintenance energy levels in food intake, thereby likely obtaining energy for growth and other metabolic needs in excess of maintenance levels was greater in 1992 and 1997 (24.3% and 23.5%, respectively) than other years (9.5-14.5%) and was greatest during summer (24.4%), lowest in winter



(3.2%). Percentage of fish meeting maintenance energy levels in food intake was greater for fish 152-304 mm (23.1%) than other length classes.

### Benthos

Densities of *Gammarus* and chironomids differed ( $P < 0.001$ ) among years (Figure 45). Amphipod densities peaked in 1992, whereas chironomid densities peaked in 1994. Densities of *Gammarus* and gastropods were greatest ( $P < 0.001$ ) in the fall, but chironomid densities were greater ( $P < 0.001$ ) during spring than other seasons (Figure 45).

Periphyton mass differed ( $P < 0.001$ ) among years and seasons. Periphyton mass was lowest in 1993, greatest in 1997 (Figure 46). Periphyton mass was greater ( $P < 0.001$ ) in summer than other seasons (Figure 46). Mass of submerged macrophytes also differed ( $P < 0.001$ ) among years and seasons and was greater in 1995 than in other years and was greater during fall to winter than other seasons (Figure 47).

### Drift

Drift concentrations of total plant matter and total macroinvertebrates increased at Lee's Ferry between about 1994 and 1997, and concentrations of total macroinvertebrates and plant matter in the drift tended to be highest during spring-summer-fall (J.P. Shannon unpublished data). Our results during 1993-1994 generally support these seasonal differences in drift densities but are inadequate to assess long term trends.

### Water Quality

Mean temperatures of dam discharge into the Lee's Ferry tailwater differed ( $P < 0.001$ ) among years and seasons (Figure 48). Water temperatures differed ( $P < 0.001$ ) among years, was warmer during 1995 to 1997 than other years, and reached about 1993 levels in early 1998. Water temperatures among years ranged from about 8.7-9.9° C. Water temperatures were highest in fall, lowest in

spring, and differed about 20% between these seasons. Concentrations of total phosphorous differed ( $P < 0.001$ ) among years and were lowest in 1995 (Figure 49). There were no significant seasonal variations in total phosphorous concentrations. Total nitrogen concentrations and pH did not differ significantly among years or seasons.

### Correlations

Statistically significant correlations between variables are summarized in Tables 2-5. Catch-per-minute correlated positively with mean and mean minimum daily releases from GCD but correlated negatively with mean daily flow fluctuations, mean coefficient of daily flow variation (CV) and total hours  $\leq 227 \text{ m}^3\text{s}^{-1}$  during 1-2 seasons prior to EF (Table 2). Catch-per-minute of trout  $< 152 \text{ mm}$ , 152-304 mm and 305-405 mm correlated positively with mean and mean minimum daily flows during and 1-2 seasons prior to EF. In most cases, CPUE for the  $< 152 \text{ mm}$  and 152-304 mm size groups correlated negatively with total hours  $\leq 227 \text{ m}^3\text{s}^{-1}$ , mean daily flow fluctuations and mean CV during and/or in seasons prior to sampling. Catch-per-minute for the 305-405 mm size class usually was independent of indices of flow variability, while CPUE for fish 406-558 mm correlated positively with CV during seasons prior to sampling.

Mass of all fish captured by EF correlated positively with mean daily discharges from the dam 1-2 seasons prior to sampling but was independent of total hours per season  $\leq 227 \text{ m}^3\text{s}^{-1}$  (Table 2). Mass of fish  $< 152 \text{ mm}$  correlated positively with mean daily and mean daily minimum flows during and prior to sampling but correlated negatively with mean daily fluctuations in discharge, CV, and total hours  $\leq 227 \text{ m}^3\text{s}^{-1}$  during and 1-2 seasons prior to sampling. Mass of fish 152-304 mm also correlated positively with mean daily flows and mean daily minimum flows and correlated negatively with mean fluctuations in discharge, mean CV, and hours  $\leq 227 \text{ m}^3\text{s}^{-1}$

during and up to two seasons prior to sampling. Mass of trout 305-405 mm correlated positively with mean daily flow and mean minimum daily flow during the season prior to sampling but mass of fish 406-558 mm correlated positively with mean CV two seasons prior to sampling.

Catch-per-minute and mass of all trout combined correlated negatively with *Gammarus* benthic densities (Table 3). Trout mass correlated positively with periphyton mass. Condition of trout 152-304 mm correlated positively with benthic densities of *Gammarus*, gastropods and total invertebrates. Catch-per-minute and mass of trout 305-405 mm correlated inversely with benthic densities of *Gammarus* and gastropods. Catch-per-minute and mass of trout 406-558 mm correlated positively with periphyton standing stocks. Fish condition was inversely associated with CPUE and mass among and within size classes (Table 4). Catch-per-minute for all fish combined and for all length classes correlated positively with trout mass but negatively with  $K_n$ , especially for fish 305-405 mm. Trout mass also correlated negatively with  $K_n$  for all fish combined and for fish 305-405 mm. Also, CPUE and mass of fish <152 mm always correlated negatively with CPUE and mass of trout 406-558 mm.

Catch-per-minute correlated positively with mean daily and mean minimum releases from the dam for wild trout, and  $K_n$  correlated negatively with CPUE for both wild and hatchery-reared fish (Table 2). In contrast, CPUE correlated negatively with CV but positively with  $K_n$  for both wild and hatchery-reared fish. Only CPUE of wild trout correlated negatively with total hours  $\leq 227$  during the season prior to sampling.

Relative condition factor of both hatchery-reared and wild trout correlated negatively with mean daily discharge for small fish, and condition of large fish correlated negatively with fluctuating discharges (mean daily fluctuation, mean CV, total hours  $\leq 227$  m<sup>3</sup>s<sup>-1</sup>)

from GCD (Table 2). Negative correlations between condition of fish and dam releases were found during and 1-2 seasons prior to sampling. Proportional stock density correlated negatively with mean discharges from GCD and mean minimum flows (Table 2). In contrast, PSD correlated positively with mean daily fluctuations in flow, CV and total hours  $\leq 227$  m<sup>3</sup>s<sup>-1</sup> during or previous to sampling.

Condition of trout <305 mm correlated positively with densities of *Gammarus* in the drift (Table 3). Gastropod drift correlated negatively with mean daily fluctuations in flows, drift of *Cladophora* and chironomid larvae correlated positively with CV two seasons prior to sampling (Table 2), whereas drift of *Cladophora* and chironomid adults, respectively, also correlated positively with periphyton and chironomid benthic densities. Catch-per-minute of trout <152 mm correlated positively with invertebrate drift (Table 3). Total chironomid RGV correlated negatively with total invertebrate drift for trout 152-304 mm. In contrast, *Gammarus* RGV for trout 406-558 mm correlated positively with invertebrate drift.

Total RGV for all fish correlated positively with benthic densities of periphyton, chironomids and oligochaetes and negatively with densities of *Gammarus* (Table 3). The RGVs for *Cladophora* and macroinvertebrates other than *Gammarus* and oligochaetes correlated positively with mean daily discharge (Table 2). Conversely, total RGV and RGVs for *Cladophora*, *Gammarus* and gastropods correlated negatively with indices of daily flow variability (mean daily discharge fluctuation, CV), but RGVs of *Gammarus* correlated positively with total hours  $\leq 227$  m<sup>3</sup>s<sup>-1</sup> during or in seasons prior to sampling (Table 2). Feeding by trout (% empty stomachs) correlated negatively with mean discharges during and one season prior to sampling and with mean minimum daily flows during sampling.

Total invertebrate RGV for fish 152-304 mm correlated positively with mean daily flows but negatively with mean daily flow fluctuations during and prior to sampling (Table 2). The RGV for *Cladophora* correlated positively with mean and minimum daily flows but correlated negatively with mean daily flow fluctuations during the season of sampling. Gastropod RGV correlated negatively with CV during the season prior to sampling and with total hours  $\leq 227 \text{ m}^3 \text{ s}^{-1}$  during the sampling season.

Gastropod RGV for trout 305-405 mm correlated negatively with flow variability (mean daily fluctuation, CV, total hours  $\leq 227 \text{ m}^3 \text{ s}^{-1}$ ) recorded up to two seasons prior to sampling but correlated positively with mean daily flows during the season prior to sampling (Table 2). *Gammarus* RGV for this length class correlated negatively with mean daily fluctuations in flow. Percent empty stomachs correlated negatively with mean and mean minimum flows during sampling and with mean flows during the season prior to sampling.

*Gammarus* RGV for fish 406-558 mm correlated positively with total hours/season  $\leq 227 \text{ m}^3 \text{ s}^{-1}$  during and two seasons prior to sampling, while RGV for gastropods correlated positively with total hours/season  $\leq 227 \text{ m}^3 \text{ s}^{-1}$  during the season of sampling. *Cladophora* RGV correlated positively with mean daily flow during and two seasons prior to sampling (Table 2).

Catch-per-minute and mass for all fish combined correlated positively with RGV for *Cladophora* (Table 4). Relative condition factor correlated negatively with *Gammarus* RGV. Catch and condition indices were independent of RGVs for trout 152-304 mm. Catch-per-minute and mass correlated positively with *Cladophora* RGV only for trout 305-405 mm. No significant relationships existed between RGVs and CPUE,  $K_n$  or trout mass for fish 406-558 mm.

For all trout combined, RGVs for chironomid larvae, *Gammarus* and

*Cladophora* correlated positively with total RGV (Table 4), but only RGV for chironomid larvae correlated negatively with percent empty stomachs. Chironomid pupae RGV correlated inversely with RGVs for *Gammarus* and gastropods. The RGVs for chironomid pupae and larvae only for trout 152-304 mm correlated positively with *Cladophora* RGV. The RGVs for *Gammarus* and gastropods correlated positively, and RGVs for *Gammarus* and *Cladophora* correlated positively with total RGV for this size category. The RGVs for chironomid larvae and pupae correlated positively for fish 305-405 mm, but only RGV for larvae correlated positively with RGV for *Cladophora*. Total RGV for this size class correlated positively with RGVs for *Gammarus* and *Cladophora*. The RGVs of *Gammarus* and gastropods correlated positively for fish 406-558 mm, and RGV for *Cladophora* was positively correlated with total RGV.

Total RGVs for all fish combined correlated negatively with benthic densities of *Gammarus* (Table 3). The RGVs of chironomid larvae and *Cladophora* correlated negatively with benthic densities of *Gammarus* and gastropods. Benthic densities of chironomids correlated positively with RGVs for chironomid larvae and *Cladophora*, but not with chironomid adults or pupae. *Gammarus* densities correlated positively, while chironomid pupae standing stocks correlated negatively, with percent empty stomachs.

Total RGVs for trout 152-304 mm correlated negatively with *Gammarus* and total invertebrate benthic densities (Table 3). The RGV for *Cladophora* for this size class correlated negatively with benthic densities of *Gammarus* and gastropods, and RGVs for chironomid larvae and *Cladophora* correlated positively with chironomid benthic densities. The RGVs for *Gammarus* and gastropods also correlated positively with periphyton mass.

Total RGVs for trout 305-405 mm also correlated negatively with *Gammarus* benthic densities but positively with chironomid densities and periphyton mass (Table 3). The RGVs of chironomid larvae correlated negatively with *Gammarus* and gastropod benthic densities. The RGV for *Cladophora* also correlated negatively with *Gammarus* benthic densities. In general, chironomid RGVs correlated positively with benthic densities of their respective life stages. The RGV for *Cladophora* for this size group correlated positively with periphyton mass.

The RGVs for chironomid larvae and *Cladophora* correlated positively with chironomid densities for trout 406-558 mm, and gastropod densities correlated positively with RGV for *Gammarus* (Table 3). The RGV for *Cladophora* for this size group correlated negatively with *Gammarus* benthic density.

Mean total daily consumption and daily consumption of *Gammarus* correlated positively with total phosphorous concentrations in the water column for all trout combined (Table 2). Mean total daily consumption by trout 152-304 mm and 305-405 mm correlated negatively with mean flow fluctuation prior to or during season of sampling. Mean daily consumption of *Gammarus* by trout 152-304 mm and 305-405 mm also correlated negatively with mean flow fluctuations during or just prior to season of sampling. Consumption of the amphipod by trout 152-304 mm correlated positively with periphyton densities (Table 3). Mean daily consumption of chironomids by fish 305-405 mm correlated positively with total and larval chironomid benthic densities.

Condition of all fish combined correlated negatively with median daily consumption of *Gammarus* by trout 406-558 mm (Table 4), and median daily consumption of the amphipod by trout this size correlated positively with total invertebrate drift densities (Table 3). Mean daily total consumption by this size group also correlated

positively with total hours  $\leq 227 \text{ m}^3 \text{ s}^{-1}$  during and two seasons prior to sampling (Table 2) and with macroinvertebrate drift concentrations (Table 3).

Angler catch rates of rainbow trout correlated positively with CPUE of all fish, trout  $< 305 \text{ mm}$ , wild fish and mass of fish 152-304 mm (Table 5). Angler catch rate correlated negatively with PSD but did not correlate with  $K_n$  or stocking rates for trout. Mass, CPUE,  $K_n$  and PSD failed to correlate with stocking rates.

Densities of benthic macroinvertebrates correlated with dam operations, but results were taxon-specific (Table 2). *Gammarus* densities correlated negatively with mean flows and mean minimum daily flows during the season when samples were collected, and correlation was positive between amphipod densities and mean CV during the season prior to sampling. In contrast, chironomid densities exhibited no significant relationships with releases from GCD. Generally, gastropods were more affected than other taxa by discharges from the dam. Gastropod densities correlated negatively with mean and mean minimum daily flows during and one season prior to sampling. However, gastropod densities correlated positively with CV during 1-2 seasons prior to sampling and with total hours  $\leq 227 \text{ m}^3 \text{ s}^{-1}$  during the sampling season. Macrophyte densities were unrelated statistically to discharges from GCD, but periphyton correlated positively with mean maximum CV two seasons prior to season of sampling.

Within benthic assemblages, densities of gastropods and *Gammarus* correlated positively with each other, and both taxa correlated negatively with all chironomid life stages and periphyton standing stocks (Table 3). Densities of chironomid larvae correlated positively with pupae densities, and both groups correlated positively with periphyton.

Water temperature correlated positively with mean and mean minimum flows from the season prior to sampling and negatively with

flow variability (CV) and total hours  $\leq 227$   $\text{m}^3\text{s}^{-1}$  per month during 1-2 seasons prior to sampling (Table 2). Condition of or consumption by trout had no significant associations with mean water temperatures, but macroinvertebrate drift, CPUE for all trout combined, CPUE of wild fish, and CPUE and mass of trout  $< 305$  mm correlated positively with mean water temperatures. The RGV of gastropods also correlated positively with water temperature. Periphyton and macrophyte standing stocks failed to correlate significantly with total phosphorous concentrations in the water column.

## DISCUSSION

Our results support previous conclusions that alterations in flow regimes in regulated rivers profoundly influence fish populations (Bain et al. 1988, Weisberg and Burton 1993, Scheidegger and Bain 1995, Travnicek et al. 1995, Bowen et al. 1998). Overall, our results indicate that higher minimum and more stable releases from GCD provide conditions that support greater standing stocks of rainbow trout than do dam operations with lower minimum releases, more widely fluctuating flows, and frequent discharges  $\leq 227$   $\text{m}^3\text{s}^{-1}$ . However, single discharge events of moderate magnitude and brief duration during spring or summer have little influence on rainbow trout in the Lee's Ferry reach (McKinney et al. 1996, McKinney et al. 1997, 1999).

We infer that dam operation is a primary driving variable influencing the rainbow trout population in the 26 km Lee's Ferry tailwater below Glen Canyon Dam. Density-related interactions among large fish and dam operation was apparent about four years following inception of enhanced flow regimes and tended to override some positive effects of enhanced flow regimes.

Quality of the Lee's Ferry rainbow trout recreational fishery declined (reduced angler catch rates and mean sizes of fish creel)

between about 1980 to 1991 during periods of frequent very low minimum and widely fluctuating releases from Glen Canyon Dam (McKinney and Persons 1998). Higher minimum discharge stages and reduced flow variability were sustained after mid-1991 (Stevens et al. 1997), particularly between mid-1995 and 1997. The enhanced flow regimes during 1991-1995 provided conditions supporting greater rainbow trout standing stocks. Higher mean and less variable releases from GCD after mid-1995 provided conditions supporting further increases in trout standing stocks but were associated with declining condition of large fish.

Densities are a strong indicator of survival and growth of fish (Post et al. 1998). Recovery (increased CPUE and mass) of rainbow trout in the tailwater occurred for all size classes which we examined between 1993 and 1997 and suggested greater recruitment into reproductively mature size classes since about 1994. Although site-specific distribution within the Lee's Ferry reach influenced CPUE, mass and length, within-site changes in these variables were comparable among years and reflected similar trends, indicating insignificant effects of rainbow trout distribution. Since emigration and immigration of rainbow trout likely are not factors affecting fish densities in the tailwater (Angradi et al. 1992), increases in standing stocks of wild fish between 1993 and 1997 indicate increased natural reproduction and survival, corresponding with more extensive habitat and food base associated with greater, and less variable, permanently wetted perimeter (Blinn et al. 1995, Ayers and McKinney 1996, McKinney et al. 1996).

Although releases from the dam might influence electrofishing efficiency, we found no relationship between CPUE and discharge at the time of capture. Electrofishing procedures were standardized among locations, years and seasons, so that potential sampling bias cannot account for differences

in densities and population structure estimated for rainbow trout. Length-frequencies of rainbow trout were distributed bimodally during 1991 to 1997, with modes at about 150 mm and 350 mm between 1993 and 1997. Increased frequency distributions of small trout and fish 305-405 mm emerged within about a year following onset of more stable flows, but length frequencies for fish >405 mm was greatest in 1991. Dramatic increases in CPUE and mass (>30%) lagged inception of more stable and higher minimum releases from GCD by about three years, and increases in mean length and weight (7-8%) lagged onset of these conditions by about five years. Catch rates for rainbow trout 406-558 mm increased less than other length categories, and results suggest that increases in natural reproduction were associated with slow recruitment to larger and older fish.

Length frequency data derived by electrofishing may underestimate relative abundance of small fish, and results must be viewed with some caution (Reynolds 1996). Although catch/effort data may be suspect as a direct abundance index (Walters and Ludwig 1994), we electrofished on a spatially refined scale, and trends in CPUE and mass support the finding that the population of rainbow trout  $\geq 305$  mm in the Lee's Ferry tailwater reach more than doubled between 1991 (Morgensen 1991;  $98,000 \pm 29,000$  SE fish  $\geq 305$  mm) and 1997. Travnichek et al. (1995) also reported a fivefold increase in numbers of warmwater fishes in a dam tailwater following increased minimum water releases and reduced fluctuations in flows.

Percentages of ripe fish indicate that most rainbow trout reached reproductive maturity at about  $\geq 300$  mm in length, and densities of reproductively mature (ripe) size classes increased between 1991 and 1997; fish 305-405 mm especially increased between 1994 and 1997. Some reproductive activity may occur throughout the year in the Lee's Ferry reach, since ripe trout were found in most months. However, numbers of ripe fish

peaked in winter and was lowest during June to October, suggesting the primary spawning season is in winter. In comparison, spawning also peaked in winter (Persons et al. 1985, Maddux et al. 1987) during 1980 to 1985, but Angradi et al. (1992) reported peak spawning in March and early April during 1990-1991, suggesting that dam operation (i.e., high flow variability and low minimum releases from the dam) during that time (McKinney and Persons 1998) may have influenced reproductive behavior. Physicochemical variables (pH, dissolved oxygen, conductivity, salinity, temperature, turbidity) in the Lee's Ferry reach are within ranges suitable for reproduction, growth and survival of rainbow trout (Wiley and Dufek 1980, Persons et al. 1985, Maddux et al. 1987, Davis 1989, Griffith 1993, Davis 1994, Walters et al. 1996, Stevens et al. 1997), although cold water temperatures likely impair growth rates (Austreng et al. 1987).

Howard and Dolan (1981) reported erosion of gravels and finer sediments in the tailwater, and Kondolf et al. (1989) suggested that rainbow trout spawning may be threatened by transport of gravel downstream in absence of replenishment from upstream. Progressive armoring of the river bed and reduction of suitable spawning gravels has been reported below other large dams (Buer et al. 1981, Walburg et al. 1981). Median gravel diameters in our study were about twofold greater than reported by Kondolf et al. (1989), who measured fines, for the same river locations we sampled, and geometric standard deviations were about fourfold less. Similarly, Angradi et al. (1992) used a sampling method comparable to ours at RK - 6.5 and found that mean substrate particle size was about half of our values. Results of our study and those of Kondolf et al. (1988) and Angradi et al. (1992) suggest slight armoring of the spawning bars since 1984.

Use of Wolman's (1954) technique has recently increased among fisheries biologists (McMahon et al. 1996), and we believe the

method is cost effective, representative of spawning substrate composition and suitable for monitoring long-term trends in armoring. Substrate particle sizes from our study fall within the range of those reported by Kondolf et al. (1989) for unspawned gravels in the Lee's Ferry tailwater and are comparable to those from other field studies of known salmonid spawning areas (Crisp and Carling 1989, Grost et al. 1991), indicating adequate substrate particle composition on spawning bars in the Lee's Ferry reach. Further, observed particle composition of gravel bars in the tailwater should provide adequate survival of salmonid embryos (Tappel and Bjorn 1983, Sowden and Power 1985), consistent with changes and trends we observed among years in densities and frequencies of small wild trout and enhanced success of natural reproduction. We suggest that periodic (e.g., 5 yr intervals) monitoring of coarse substrate particles (i.e.,  $\geq 2$  mm) is of primary importance in evaluating progressive armoring in the tailwater.

In contrast to trends observed for CPUE, mass, weights and lengths, condition of rainbow trout in the Lee's Ferry reach was more than 20% greater in 1994 than in 1991, and was about 10% lower in 1997 than in 1994. This decline indicates a reduction in plumpness and physiological well-being of fish (Murphy et al. 1991, Liao et al. 1995), but target ranges for condition of the species are uncertain and should be defined based on management objectives (Murphy et al. 1991). We weighed fish as total weight, including stomach contents, possibly biasing our measure of condition but not affecting inferences about long-term or seasonal trends. Condition of all trout combined failed to correlate with mean and mean minimum daily discharges from the dam but correlated negatively with measures of flow variability, supporting positive influences of more stable releases from GCD.

We calculated the health index to provide baseline data (Goede and Barton

1990, Adams et al. 1993, Robinson et al. 1998) for the reach but believe that its use generally provides little information about status of the Lee's Ferry fishery that is not more readily obtained through assessment of food habits and energetics, endoparasite load, length frequency distributions, densities, relative condition factor and proportional stock densities. Landye et al. (1993) identified the parasitic nematode *Bulbodacnitis ampullastoma* in gastrointestinal tracts of rainbow trout in the Lee's Ferry reach. In our studies, higher nematode parasite load was associated with poorer health of fish, and uninfected trout were in better health than infected fish. Moreover, health was poorer with increasing length of fish. The trend toward poorer health following the 1996 experimental flood (Rubin et al. 1998) suggests slight negative impacts of the high flow event on health of fish. Hiscox and Brocksen (1973) found in laboratory investigations that rainbow trout inoculated with *B. ampullastoma* exhibited increased food consumption and decreased growth rates with increasing parasite load. Health and condition of salmonids may vary seasonally (Goede and Barton 1990, Denton and Yousef 1975, Lane 1979), and mesenteric lipids reflect the intensity of feeding and energy deposition (Goede and Barton 1990). Lowest mesenteric fat indices for trout in the Lee's Ferry reach occurred during summer (McKinney et al. 1996), conforming to an expected seasonal trend, but increased feeding in spring-summer is a general pattern for salmonids (Goede and Barton 1990, Cunjak and Power 1986, Denton and Yousef 1975) in both regulated (Weiland and Hayward 1997, Filbert and Hawkins 1995) and unregulated (Elwood and Waters 1969, Cada et al. 1987, Ensign et al. 1990) systems.

The proportion of large trout ( $\geq 305$  mm) in the Lee's Ferry reach (35%) approximated that (ca. 40%) in a catch-and-release area of the South Platte River in Colorado (Griffith 1993), suggesting that the Lee's Ferry

tailwater produces a reasonably expected proportion of large fish. However, managers may need to consider a trade-off between producing large numbers or large sizes of rainbow trout in the tailwater (Walters and Post 1993, Bohlin et al. 1994). High densities of fish often correspond with declines in survival, growth, size and condition (Medland and Beamish 1985, Elliott 1987, Walters and Post 1993), which may be density-related and mediated through negative impacts on the available food base (Weiland and Hayward 1997). Above some level of fishing pressure, "quality" aspects of a fishery may be sacrificed, because larger and older fish exist in greatly reduced numbers (Anderson and Nehring 1984).

Proportional stock densities declined between 1991 and 1997, reflecting stockpiling of fish 305-405 mm without concurrent proportional recruitment to slot lengths. Growth of hatchery-reared trout slowed considerably during this period for fish 305-405 mm, and relatively few grew to slot lengths. Understanding of the theoretical basis of the PSD structural index is incomplete, applications to coldwater lotic systems are rare, and desired target ranges of the index for rainbow trout are lacking (Willis and Scalet 1989, Murphy et al. 1991, Anderson and Neumann 1996). Angler catch rates correlated negatively with PSD, suggesting influences of fishing on fish >405 mm. Angler catch rate is positively related to densities of rainbow trout less than 406 mm in the Lee's Ferry tailwater, and negative associations between angler catch rates and PSD may be an artifact of statistical analyses. However, angler use is highest in the Lee's Ferry reach in spring to fall (Reger et al. 1995), when PSD tended to decline, and lowest in winter, when PSD tended to increase, suggesting that angling-related injuries and mortalities, particularly of large fish, may be significant, even in a catch-and-release fishery (Ferguson and Tufts 1992, Muoneke and Childress 1994, Dotson 1982,

Mitton and McDonald 1994, Schill et al. 1986). Proportional stock densities may typically vary seasonally (Willis and Scalet 1989), and higher values we found in winter than other seasons might reflect shifts in habitat use which result in greater vulnerability of fish >405 mm to electrofishing (Carline et al. 1984).

Stocking rates (20,000 to 103,000 per year) had no clear consequences for rainbow trout during enhanced flow regimes in the tailwater and did not significantly associate with CPUE, mass, condition, PSD, angler catch rate or angler use (McKinney and Persons 1998). Interestingly, however, a 41% increase in number of fish stocked in 1994 (McKinney and Persons 1998) was followed over the next three years by declining condition, primarily of large trout, suggesting adverse influences of overstocking in that year (Weiland and Hayward 1997). Moreover, positive correspondences of angler catch rates and use (McKinney and Persons 1998) with our estimates of fish standing stocks indicate that fishing pressure failed to regulate densities of rainbow trout.

Dam operation since 1991 improved habitat and food base for benthic macroinvertebrates by altering and stabilizing wetted perimeter of the reach and enhancing area of substrate supporting primary and secondary production (Angradi and Kubly 1993, Blinn et al. 1995, Ayers and McKinney 1996, McKinney et al. 1996, Stevens et al. 1997). Conversely, negative consequences of fluctuating discharges on the benthos below GCD are well-documented (Angradi and Kubly 1993, Blinn et al. 1995, Ayers and McKinney 1996). Benthic densities of macroinvertebrates are closely linked to densities of *Cladophora glomerata*, epiphyton and other periphyton (Shannon et al. 1994, Blinn et al. 1995), and densities of periphyton and chironomids increased after 1993. Although nutrient limitation of *Cladophora* is likely in the tailwater (Gloss et al. 1980, Angradi et al. 1992, Ayers and McKinney



1996), periphyton densities failed to correlate with total nitrogen and phosphorous concentrations in the water column. However, lack of response of periphyton mass to nutritional variations in the water column does not necessarily mean that production of *Cladophora* in the reach is not nutrient-limited (deAngelis et al. 1990). In contrast, benthic densities of *Gammarus* declined between 1991 and 1997. Increases in periphyton mass may result from declines in macroinvertebrate grazer densities (Feminella and Hawkins 1995). Mass and CPUE of trout correlated negatively with *Gammarus* benthic densities, and consumption of *Cladophora* correlated negatively with benthic densities of *Gammarus* and gastropods, indicating that high densities of large fish were associated with degradation of the aquatic food base, which in turn influenced food habits of rainbow trout and resulted in consumption of a lower quality diet.

More than 90% of trout stomach contents consisted of *Gammarus*, chironomids, gastropods and *Cladophora*. Total ingested matter declined between 1991 and 1993, then increased through 1997, but frequencies of occurrence of items in trout diets generally were stable between 1992 and 1997. In contrast, percent empty stomachs declined during this period, suggesting that more trout ate more *Cladophora* and *Gammarus*. Rainbow trout are primarily drift feeders (Elliott 1973, Cada et al. 1987, Bres 1986, Angradi and Griffith 1990). Drift concentrations of plant material and total invertebrates increased between 1994 and 1997 and were lower in winter than other seasons, corresponding with increased total consumption among years and in summer. Invertebrate drift concentrations correlated positively with mean water temperatures, but drift concentrations and water temperatures failed statistically to correlate with consumption by rainbow trout, likely due to the narrow range of water temperatures in the tailwater which are well below the optimum

for growth (Griffith 1993, Filbert and Hawkins 1995). Consumption of *Cladophora*, chironomids and gastropods corresponded with seasonal benthic production and drift of these groups (Ayers and McKinney 1996, Shannon et al. 1996). However, *Gammarus* benthic standing stock is greatest in summer to fall (Leibfried and Blinn 1987, Blinn et al. 1994, Ayers and McKinney 1996). Drift of the amphipod is highest in early summer and in winter (McKinney et al. 1998a), and consumption of the amphipod is greatest during summer, suggesting that trout may feed less on the amphipod than its availability in drift during winter, possibly due to spawning activities during that period. In contrast to our results (McKinney et al. 1998a), Shannon et al. (1996) found no seasonal variation in *Gammarus* drift from Lee's Ferry downstream. Our results suggest that factors other than water temperature in the Lee's Ferry reach influenced seasonal differences in feeding, e.g., life cycles of stenothermic prey taxa, inherent annual rhythms or post- or pre-spawning nutritional requirements.

We also found that trends in standing stocks, consumption and condition of rainbow trout and relationships among variables differed with regard to origin (hatchery-reared versus wild) and length classes (large =  $\geq 305$  mm; small =  $< 305$  mm) of fish. The CPUE of wild fish about doubled during 1994-1997, while catch rates for hatchery-reared fish increased slightly in 1994 but stabilized after that when stocking was reduced from about 100,000 to 20,000 fish per year (McKinney and Persons 1998). There were some differences in food habits of hatchery-reared and wild fish, but few length-related differences occurred. Total RGV increased only for wild trout between 1993 and 1997, but increased consumption of *Cladophora* was independent of fish origin. Only wild trout 305-405 mm consumed more *Gammarus* during this period, and hatchery-reared fish consumed more gastropods and *Cladophora*

than wild trout, indicating that, in general, hatchery-reared trout consumed a diet of lower nutritional quality (Cho and Kaushik 1990, Angradi 1994, Bowen et al. 1995, Weiland and Hayward 1997) and likely fed epibenthically more than wild fish (Tippets and Moyle 1978, Bachman 1984, Angradi and Griffith 1990).

Although condition of hatchery-reared trout exceeded that of wild fish throughout the study, condition declined from 1992-1997 more for hatchery-reared than for wild trout. Reimers (1963) and Ersbak and Haase (1983) also observed declining condition of hatchery-reared trout following stocking. Hatchery-reared trout have poor ability to compete with wild fish and may be unable to obtain necessary energy intake to meet requirements for basal metabolism and survival (Reimers 1963, Ersbak and Haase 1983, Bachman 1984, Mesa 1991). Recapture of hatchery-reared trout indicates that they tend to survive about five years or less. However, growth of hatchery-reared and wild fish may differ (Cooper 1961), and we caught few stocked fish within the slot. We anticipate that recapture of wild fish marked with PIT tags during our studies to estimate population size will provide information about growth and survival of this group.

Several lines of evidence also indicate that consequences of dam operations and density-related competition differ among length classes of fish. Our results indicate that small fish are more responsive to physical habitat conditions, while large fish are more responsive to exploitative competition. Schlosser (1985) also suggested that abundance of younger age classes of fish is more strongly influenced by physical factors such as temperature and water level, whereas abundance of older age classes is more strongly regulated by biotic interactions. We found that few factors other than releases from the dam influenced variables for small trout. Mass and catch of small fish were positively associated with mean and mean

minimum daily releases from the dam but negatively with indices of flow variability and hours per month for flows at minimum levels.

We found no evidence of exploitative competition among small rainbow trout, since no food-related differences were found for this group among years or seasons. Also, relative condition was generally greater for small than large fish, growth rates of small fish generally improved since 1992, and small fish met or surpassed maintenance energy requirements more often than did large fish. It may be that negative associations between condition of small fish and mean daily discharge and between condition of large fish and indices of flow variability are related to increased interference competition (Li and Brocksen 1977). Interference competition infers agonistic behavior which exacts a cost in lost growth opportunity. Exploitative competition infers indirect interactions among individuals which are mediated through food availability. Resource scarcity likely would negatively influence small trout due to greater mass-specific metabolic rates and lower energy storage (Shuter and Post 1990). In comparison to our studies, consumption by rainbow trout <260 mm in a cold dam tailwater exceeded maintenance rations only in summer (Weiland and Hayward 1997). Elwood and Waters (1969) also found that small brook trout (<63 g) met a greater percentage of maintenance requirements than large fish (>63 g), except in the fall. Filbert and Hawkins (1995) also reported that condition of small rainbow trout (ca. 200 mm) in a regulated river was affected little by changes in the food-temperature gradient. Interference competition likely is related to differential habitat utilization by small or large fish (Griffith 1993, Walters and Post 1993, Scheidegger and Bain 1995, Post et al. 1998). Lack of significant correlation between fish densities and condition and between fish densities and volume of stomach contents also supports absence of food limitation for small fish (Cada et al. 1987,

Ensign et al. 1990, Filbert and Hawkins 1995).

Consumption data further indicate that small trout, as compared to large fish, had a greater scope for growth (Elliott 1975a, Weiland and Hayward 1997, Post et al. 1998). Small hatchery-reared fish in the thermally constant tailwater generally were growing about 100-160 mm per year, well below growth rates in a tailwater of the Green River, where water temperatures are elevated to near-optimal levels during summer (Wiley and Dufek 1980, Filbert and Hawkins 1995). If relative condition provides an index of growth (Varley et al. 1971, Gabelhouse 1991, Filbert and Hawkins 1995), growth rates of wild-spawned and hatchery-reared trout may differ. Growth rates are delimited by cold water temperatures in the Lee's Ferry tailwater (Hokanson et al. 1977, Jobling 1981) but compare favorably with those reported for rainbow trout in cool-water streams in the West (Carlander 1969). Near-optimal water temperatures (to about 20° C) have been recorded in nearshore and backwater nursery areas during high, steady releases from Glen Canyon Dam and when mainchannel temperatures were about 9°-10° C (Arizona Game and Fish Department unpublished data). Annual mainchannel water temperatures differed <10% among years, and observed annual and seasonal temperature variations between about 8.2° C to 10.0° C likely have comparatively little effect on trout consumption (Elliott 1975b, Storebakken and Austreng 1988), growth (Edwards et al. 1979, Austreng et al. 1987) or efficiency of food utilization (Cho and Kaushik 1990).

Suitable habitat is a key variable influencing fishes in coldwater streams (Binns and Eiserman 1979, Orth and Maughan 1982, Griffith 1993). Our results indicate that less suitable habitat is available for small trout in the Lee's Ferry reach during fluctuating and minimum releases from Glen Canyon Dam and support the conclusion (Bain et al. 1988) that frequent and large fluctuations in

discharge from hydroelectric power dams impairs the function of shallow, nearshore habitats. Water temperatures were associated positively with mean and mean minimum daily flows but negatively with indices of flow variability, suggesting that warmer nearshore habitats necessary for refuge and nurseries develop during more stable flows but are impaired by fluctuations in flow. Increased standing stocks of rainbow trout also associated positively with water temperature, particularly for wild fish, suggesting beneficial effects of warmer water (Cho and Kauschik 1990, Filbert and Hawkins 1995, Childs et al. 1998), especially for juvenile trout (Hokanson et al. 1997). Small fish tend to inhabit shallow, nearshore zones and not move into deeper water toward mid-channel until they increase in size (Griffith 1993, Walters and Post 1993, Scheidegger and Bain 1995). As stream size increases, large concentrations of small fish may become increasingly restricted to stream margins, while deeper areas are inhabited primarily by larger, older fish (Bain et al. 1988). If unstable shallow-water habitats provide less effective refuge areas for small fish, reductions in their densities would occur (Bain et al. 1988).

When population levels are high, mortality of salmonids during the first few months of life is an important population regulating process (Griffith 1993). We suggest that variation in releases from Glen Canyon Dam within legally required limits while maintaining flow minimum to not less than 227 m<sup>3</sup>s<sup>-1</sup>, particularly during late spring through summer (after emerge of larvae from spawning gravels), may reduce abundance of small trout but tend to maintain carrying capacity for large fish in the Lee's Ferry reach, which we estimate may be about 150,000 to 170,000 trout ≥305 mm. This estimate is surely minimal and most useful as an index, since we are unable to determine fish densities in deep water habitats. Results from the hydroacoustic survey suggest that

trout densities in these habitats are lower than in nearshore areas susceptible to electrofishing. Both daily flow variability and total hours  $\leq 227 \text{ m}^3 \text{ s}^{-1}$  correlated negatively with densities only for small fish in our studies. Management activities might improve growth rates through changes in regulations favoring greater harvest of large rainbow trout 305-405 mm, as well as density manipulations via fluctuating discharges (Walters and Post 1993) and structural modifications to Glen Canyon Dam to increase water temperatures and sediment load (Schmidt et al. 1998).

Responses of standing stocks of large rainbow trout were strongly density-dependent and driven mainly by exploitative competition within the group, supporting the conclusion (Schlosser 1985) that abundance of older age classes may be more strongly regulated by biotic interactions. Our results further support the prediction (Walters and Post 1993) that if small and large fish have different habitat preferences, increases in densities will affect large fish more than small ones. Among large fish, electrofishing catch and mass only of fish 305-405 mm increased dramatically with higher mean and mean minimum daily flows, but they were independent of diel variability in releases from the dam. In comparison, mass and catch of slot length fish occasionally correlated positively with indices of flow variability, suggesting displacement of fish from deeper to shallower, nearshore habitats under conditions of fluctuating releases from the dam. Negative association of PSD with mean and mean minimum daily releases from the dam support the notion that dam operations since 1991 associated with increased standing stocks of rainbow trout 305-405 mm more than those of slot-length fish. Conversely, positive association between PSD and indices of flow variability indicate that fluctuating discharges tend to favor slot-length fish.

Liao et al. (1995) also suggested that condition might vary inversely with fish

densities due to interference competition. Positive associations of standing stocks of fish 406-558 mm with flow variability further may reflect interference competition favoring the group and result in direct energy costs to large fish (305-405 mm) just below slot length (Li and Brocksen 1977, Medland and Beamish 1985, Marchand and Boisclair 1998). Benefits of social dominance may be less at high than at low population densities, consistent with declining condition for large fish.

Older and larger individuals tend to have advantage in exploitative competition (Li and Brocksen 1977, Koebele 1985, Griffith 1993, Post et al. 1998). Exploitative competition typically differs in relation to size structure or resource abundance (Elwood and Waters 1969, Cada et al. 1987, Filbert and Hawkins 1995, Post et al. 1998). We believe that declining condition of large fish, particularly those 305-405 mm, between 1994 and 1997 reflects exploitative competition, depletion of energy reserves (Goede and Barton 1990) and slower growth (Filbert and Hawkins 1995). Total consumption and consumption of *Cladophora*, *Gammarus* and gastropods increased over time primarily for fish 305-405 mm, suggesting compensatory increases in feeding and lower nutritional quality of the diet, due to increased consumption of the alga (Lee and Putnam 1973, Grove et al. 1978, Bowen et al. 1995, Weiland and Hayward 1997), as trout standing stocks increased and condition declined. Mass, CPUE and total consumption correlated negatively with benthic densities of *Gammarus* and gastropods primarily for this size category, suggesting that these fish degraded relative availability of benthic prey (Bolger and Connolly 1989, Liao et al. 1995, Filbert and Hawkins 1995, Marwitz and Hubert 1997). Given the energy content (Blinn et al. 1995) of an average size *Gammarus*, estimated minimum daily energy requirements for trout (Elliott 1976, Cho 1992), and assuming that *Gammarus* comprise about 60% of available

energy from animal components of diet, a 350 mm trout in the Lee's Ferry reach might consume about 125 amphipods per day. *Gammarus lacustris* provides good nutritional quality for rainbow trout (Mathias et al. 1982), and abundance of the amphipod likely is critical in affecting well-being of a rainbow trout fishery in a cold tailwater with a depauperate food base (Weiland and Hayward 1997).

Percent empty stomachs tended to decrease among years only for fish 305-405 mm, and highest percent empty stomachs in winter, lowest in summer were apparent only for this length group. Percent empty stomachs for fish 305-405 mm correlated negatively with mean and mean minimum daily flows, suggesting that more fish this length, as compared to other length classes, were feeding and consuming more. These differences in consumption and feeding likely reflect adjustments to lower nutritional quality of the diet (Grove et al. 1978, Weiland and Hayward 1997, Bowen et al. 1995). Also, rainbow trout that consume large amounts of food may grow less efficiently than fish that consume less (Gregory and Wood 1998). Invertebrate drift correlated positively with consumption of *Gammarus* only for trout 406-558 mm, indicating that slot-length fish are effective drift feeders and as a group likely maintain competitive advantages regarding territories and feeding loci in the reach (Fausch 1984, McCarthy et al. 1992, Post et al. 1998).

Our estimates of ingested energy incorporated only *Gammarus* and chironomids and therefore are biased conservatively. Due to minimal energetic value to trout, *C. glomerata* and its epiphytes were eliminated from consumption estimates and the energy intake model; the algae provide little or no nutritional value for rainbow trout (Cho and Kaushik 1990, Cho 1992, Angradi 1994, Weiland and Hayward 1997). We excluded gastropods from the energy intake model due to their generally

low frequencies of occurrence and proportional composition in trout diets and to uncertain mass/energy data. Conversely, *G. lacustris* and chironomids are the predominant macroinvertebrate prey of rainbow trout in the Lee's Ferry tailwater and provide nutritional value to trout (Mathias et al. 1982, Angradi 1994, Weiland and Hayward 1995), although food quality of chironomids may be lower than that of *Gammarus* (Hayward and Weiland 1998). However, chironomids have high energy content (Blinn et al. 1995). If our estimates of consumption and growth approximate actual levels in the population, comparatively few large fish met or surpassed maintenance energy levels. Their growth ranged generally from 10 mm to 76 mm per year, but large fish may allocate more energy to reproduction than somatic growth. Only rainbow trout 305-405 mm failed to meet maintenance energy requirements in all years and seasons, while fish 405-558 mm failed to do so most years but met ME during summer. Although our data demonstrate recruitment to reproductive maturity in the Lee's Ferry reach, energy deficiencies might contribute to slower maturation and reduced fecundity (Scott 1962, Bagenal 1969).

Stabilization of PSD and decline in condition after about 1993 suggest that growth was reduced, especially for fish 305-405 mm. Correspondingly, we observed stockpiling of trout 305-405 mm and found few fish within slot length or a preferred-memorable-trophy size range (501-650 mm; Gabelhouse 1984, Anderson and Neumann 1996). Weiland and Hayward (1997) concluded that the food base is degraded by high rainbow trout densities and that growth potential is poorer for larger fish because they have higher energy demands.

Thus, we believe that rainbow trout 305-405 mm were food-limited coincident with degradation of the food base and with exploitative and interference competition and that slow growth or mortality were primary

factors reducing recruitment to >405 mm TL. This interpretation is consistent with tendencies we observed for larger fish to be in poorer condition and health and to consume diets of poorer nutritional quality. Further supporting our conclusion of food limitation in the Lee's Ferry tailwater, total consumption by seasons for all fish was less than or equal to that reported for rainbow trout in the food-limited tailwater fishery in Green River (Filbert and Hawkins 1995). Filbert and Hawkins (1995) also reported that rainbow trout 300-350 mm showed the strongest response to food-temperature gradients in the regulated Green River and concluded that stream trout often may be food-limited due to high fish densities. Elliott and Persson (1978) suggested that larger fish are rarely able to feed to satiation in the field, and Weiland and Hayward (1997) observed food limitation for rainbow trout >260 mm in a cold tailwater. Cada et al. (1987) also reported food limitation of age-1 and older rainbow trout in unregulated Appalachian streams.

## CONCLUSIONS AND RECOMMENDATIONS

Operation of Glen Canyon Dam is the overriding variable influencing standing stocks of rainbow trout in the Lee's Ferry reach. Overall, our results indicate that higher mean ( $\geq 300 \text{ m}^3 \text{ s}^{-1}$ ), higher minimum ( $> 227 \text{ m}^3 \text{ s}^{-1}$ ), and more stable releases from GCD provide conditions that support greater standing stocks of rainbow trout than do dam operations with lower minimum and more variable releases. Estimated population size of large rainbow trout more than doubled between 1991 and 1997, during enhanced flow regimes. Densities of all length classes we examined increased following onset of enhanced flows, indicating greater success of spawning and recruitment to reproductive maturity. Reproductive activity likely occurs throughout the year, but spawning peaks

during winter, and gravel bars in the tailwater presently provide adequate substrate for spawning.

Our results indicate that abundance of small rainbow trout (<305 mm) is more strongly influenced by physical factors (habitat, water temperature), whereas large fish (>304 mm) are more strongly affected by biotic factors. We found few variables other than dam operations that affected small rainbow trout. Consumption by this group tended to meet maintenance energy requirements among years and seasons, and condition remained essentially stable among years. In comparison, condition of large fish declined between about 1994 and 1997, indicating generally a reduction in plumpness and physiological well-being, and this group in general seldom met maintenance energy requirements. We estimate that carrying capacity (based on condition, densities and size of fish) of the tailwater for large fish was exceeded by 1994 to 1995 and likely is presently about 150,000 to 170,000 fish under the present operating regime (USDI 1996), corresponding tentatively with electrofishing densities of about 2.0 to 2.5 CPUE and 0.3 to 0.4 kg/min. However, we presently are unable effectively to sample fish in deep water habitats, and estimates of population size and carrying capacity therefore suspect and more useful as indices rather than absolute values for the entire reach. Variations in daily operation of GCD within the present operating regime (USDI 1996) and assessment of relative trout abundance in deep water areas may affect these estimations, since carrying capacity will change as a function of suitable habitat, mean and minimum releases from the dam, and duration, frequency, magnitude and timing of flow variation, as well as structural modifications to provide greater sediment transport rates and thermal variability downstream from Glen Canyon Dam (Schmidt et al. 1998).

However, we believe that rainbow trout 305-405 mm were food-limited as a result of interference and exploitative competition. This size fish failed to meet median maintenance energy estimations all years and seasons, likely resulting in slow growth. Densities of the group also were negatively associated with benthic densities of *Gammarus* and gastropods, suggesting degradation of the aquatic food base. Also, condition was negatively associated with standing stocks only for this size category, reflecting density-related competition and consumption of low nutritional quality.

Our findings enhance understanding of rainbow trout ecology by demonstrating spatial and temporal patterns indicating responses to enhanced flow regimes and associations between trout, dam operation and the aquatic food base. Results should contribute to stock assessment models (Hilborn and Walters 1992), future monitoring, research and management of the recreational fishery. We recommend that the following should be considered by resource managers responsible for operations of Glen Canyon Dam and the recreational rainbow trout fishery in the Lee's Ferry reach:

- 1) Consider the necessity of trade-off between producing large numbers or large sizes of rainbow trout. Enhancement of the large fish component of the fishery might exacerbate degradation of the food supply. Sport fisheries in large rivers often are under-exploited, and increased harvest by angling of fish 305-405 mm over the short term might adjust abundance of this group toward a balance with carrying capacity and allow more fish to grow to slot-length. However, influences of harvest on long-term stability of a population are rarely obvious and are determined by the extent to which replacement by reproduction is altered. Angler harvest should be evaluated in association with densities of large fish and effects of flow variability suggested above on small fish to determine and meet management

objectives and goals (Reger et al. 1997). Maintain higher mean and minimum and more stable releases from GCD to provide conditions that support greater standing stocks of rainbow trout than operations with lower minimum releases, greater ramping rates, more widely fluctuating flows and frequent discharges  $\leq 227 \text{ m}^3 \text{ s}^{-1}$ . Abundance of younger age classes is more strongly influenced by physical factors (habitat, water temperature), whereas large fish are more strongly affected by biotic factors. We found few variables other than dam operations that affected small rainbow trout, but our bioenergetics models, relative condition and top-down effects on prey abundance support a hypothesis that biotic factors also may influence younger fish.

- 2) The Lee's Ferry rainbow trout fishery is presently self-sustaining, and comparatively few hatchery-reared fish spawn in the tailwater. Assessment of fish densities and structural indices should provide reliable indications of natural reproductive success. Stocking should be terminated or maintained at present low levels only to allow assessment of trout growth in the reach based on coded wire tags. Low recaptures of wild trout implanted with PIT tags emphasize the difficulty in evaluating growth of wild fish in the cold tailwater. Any proposed changes in stocking should be coordinated with monitoring and research studies and done in concert with specific management objectives.

- 3) Continue mark-recapture studies of wild fish at intervals of about five years or more. This procedure for estimating population size is suspect (i.e., wide confidence intervals) unless a high percentage of the population are marked and recaptured and fish are sampled in deep water habitats. Such studies may provide indices of abundance and support use of population size estimates and monitoring data in stock assessment models, but frequent estimations do not appear to be cost effective in the Lee's Ferry reach. Acoustic methods to estimate

fish densities and derive population size provided poor results in the tailwater. In contrast, electrofishing investigations provide information about growth, length, weight and associated structural indices, and relative population abundance that better serve needs of resource managers. We suggest that electrofishing densities of about 2.0-2.5 CPUE and 0.3-0.4 kg/min are tentative target values to achieve a population of large rainbow trout in balance with carrying capacity. Our findings support other results indicating viability of using snorkel surveys of salmonids (Hill and Platts 1998), and the method appear to hold promise as a monitoring procedure in the Lee's Ferry reach. Further investigations in this area are needed to develop the procedure, determine applicability during all seasons, and evaluate use of the technique to estimate relative trout densities in deep water habitats. However, electrofishing provides more information needed by resource managers than do snorkel surveys and is a viable monitoring and research tool.

4) Knowledge of fish health provides limited information needed for effectively managing a trout fishery. We suggest that the labor-intensive and time consuming acquisition of HAI data contributes little information regarding fish condition and health that is not more readily obtained from analyses of food habits, bioenergetic models, enumeration of parasitic gut nematodes and calculation of relative condition factor and other structural indices.

## ACKNOWLEDGMENTS

Grand Canyon Monitoring and Research Center funded the present analyses under Cooperative Agreement No. 1425-97-FC-40-22690 and provided logistical support. Collection of data was funded by Glen Canyon Environmental Studies. We are grateful to W. Vernieu, S. Hueftle (GCMRC),

J. Shannon and D. Blinn (NAU) for assistance in compiling unpublished data. We also thank G. Mueller (USGS) for conducting the hydroacoustic survey. We thank C. Walters, J. Korman, S. Cox and R. Ahrens (UBC) for developing a rainbow trout stock assessment model, providing this to us and training us in its use and application. We are grateful to J. Korman (UBC) and Colorado River fishing guide D. Foster for their assistance in conducting snorkel surveys and thank T. Robinson and S. Bryan (AGFD) for reviewing earlier drafts of this report and providing insightful suggestions.



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Table 1. Annual and seasonal frequencies of occurrence for predominant items in stomachs of rainbow trout captured by electrofishing, Lee's Ferry reach, 1991-1997. CG = *Cladophora glomerata*; GL = *Gammarus lacustris*; CH = total chironomids; GT = Gastropods.

	YEARS						SEASON			
	1991	1992	1993	1995	1996	1997	Summer	Fall	Winter	Spring
CG	47.6	21.6	42.3	22.3	46.4	45.8	52.6	12.1	55.1	50.3
GL	52.4	75.7	63.5	71.8	80.7	71.9	82.1	75.8	66.7	62.1
CH	59.5	32.4	55.8	45.9	48.2	46.4	46.8	31.9	59.4	60.1
GT	11.9	24.3	7.7	34.1	24.1	19.6	22.4	31.9	7.3	17.7

Table 2. Spearman's R correlations between flow and water quality variables and RBT, benthos, drift and water quality variables, Lee's Ferry reach. Flow variable season codes are as follows: 0=during EF sampling season, 1=season prior to EF, 2=two seasons prior to EF. Size class codes: 1=<152 mm (CPUE) or <152 mm (Kg/minute EF,  $K_n$ ); 2=152-304 mm; 3=305-405 mm; 4=406-558 mm; All=all size classes combined.

Variable 1	Season	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
Mean daily discharge	0	CPUE (1)	0.5109	0.0127	23
	0	CPUE (2)	0.5237	0.0103	
	0	CPUE (3)	0.5316	0.0090	
	0	CPUE (All)	0.6265	0.0014	
	1	CPUE (1)	0.5988	0.0025	
	1	CPUE (2)	0.6670	0.0005	
	1	CPUE (3)	0.5326	0.0089	
	1	CPUE (All)	0.6611	0.0006	
	2	CPUE (3)	0.5138	0.0121	
	2	CPUE (All)	0.5267	0.0098	
	0	Kg/minute EF (1)	0.5563	0.0058	23
	0	Kg/minute EF (2)	0.5751	0.0041	
	0	Kg/minute EF (3)	0.5148	0.0119	
	1	Kg/minute EF (1)	0.5583	0.0056	
	1	Kg/minute EF (2)	0.7460	<0.0001	
	1	Kg/minute EF (3)	0.5435	0.0074	
	2	Kg/minute EF (2)	0.5375	0.0082	
	2	Kg/minute EF (3)	0.5514	0.0064	
	2	Kg/minute EF (All)	0.4753	0.0219	
	0	$K_n$ (2)	-0.4891	0.0179	23
	2	$K_n$ (1)	-0.4219	0.0449	
	2	$K_n$ (2)	-0.4625	0.0263	
	0	% empty stomachs (All)	-0.5521	0.0175	18
	0	% empty stomachs (3)	-0.5375	0.0214	
	1	% empty stomachs (All)	-0.5088	0.0311	
	1	% empty stomachs (3)	-0.4734	0.0472	
	0	RGV <i>Cladophora</i> (All)	0.5356	0.0220	18
	2	RGV chironomid pupae (All)	-0.5026	0.0335	
	0	RGV <i>Cladophora</i> (2)	0.5137	0.0349	
	0	RGV total invertebrates (2)	0.5000	0.0410	
Mean daily discharge	1	RGV gastropoda (3)	0.4870	0.0404	18
	0	RGV <i>Cladophora</i> (4)	0.5368	0.0263	
	2	RGV <i>Cladophora</i> (4)	0.4975	0.0421	

Table 2. (continued)

Variable 1	Season	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
Mean daily minimum discharge	0	PSD	-0.5998	0.0025	23
	1	PSD	-0.7945	<0.0001	
	0	CPUE wild fish (All)	0.7049	0.0011	18
	0	K <sub>n</sub> stocked fish (All)	-0.7523	0.0003	
	0	K <sub>n</sub> wild fish (All)	-0.6202	0.0060	
	1	CPUE wild fish (All)	0.8142	<0.0001	
	1	K <sub>n</sub> stocked fish (All)	-0.7255	0.0007	
	1	K <sub>n</sub> wild fish (All)	-0.6112	0.0070	
	2	CPUE wild fish (All)	0.6367	0.0045	
	2	K <sub>n</sub> stocked fish (All)	-0.6017	0.0083	
	2	K <sub>n</sub> wild fish (All)	-0.6677	0.0025	
	0	<i>Gammarus</i> m <sup>2</sup>	-0.7110	0.0009	18
	0	Gastropoda m <sup>2</sup>	-0.6835	0.0018	
	0	Total invertebrates m <sup>2</sup>	-0.5624	0.0151	
	1	Gastropoda m <sup>2</sup>	-0.5431	0.0198	
	2	Total invertebrates m <sup>2</sup>	-0.5769	0.0122	
	1	Mean water temperature	0.6804	0.0001	28
	0	CPUE (1)	0.6314	0.0012	23
	0	CPUE (2)	0.6354	0.0011	
	0	CPUE (All)	0.5593	0.0055	
	1	CPUE (1)	0.6690	0.0005	
	1	CPUE (2)	0.7312	<0.0001	
	1	CPUE (3)	0.4417	0.0349	
	1	CPUE (All)	0.6571	0.0007	
	2	CPUE (1)	0.5870	0.0032	
	2	CPUE (2)	0.5613	0.0053	
	2	CPUE (All)	0.4763	0.0216	
Mean daily minimum discharge	0	Kg/minute EF (1)	0.6887	0.0007	23
	0	Kg/minute EF (2)	0.6828	0.0003	
	1	Kg/minute EF (1)	0.6333	0.0012	
	1	Kg/minute EF (2)	0.7945	<0.0001	
	1	Kg/minute EF (3)	0.4664	0.0249	
	2	Kg/minute EF (1)	0.5672	0.0048	23
	2	Kg/minute EF (2)	0.6779	0.0004	
	2	K <sub>n</sub> (4)	0.4990	0.0153	
	0	PSD	-0.6897	0.0003	

Table 2. (continued)

Variable 1	Season	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
	1	PSD	-0.8350	<0.0001	23
	2	PSD	-0.6047	0.0022	
	0	% empty stomachs (All)	-0.5005	0.0344	18
	0	% empty stomachs (3)	-0.5251	0.0253	
	0	RGV <i>Cladophora</i> (2)	0.5534	0.02120	17
	0	CPUE wild fish (All)	0.7152	0.0008	18
	0	K <sub>n</sub> stocked fish (All)	-0.7503	0.0003	
	0	K <sub>n</sub> wild fish (All)	-0.6409	0.0042	
	1	CPUE wild fish (All)	0.8266	<0.0001	
	1	K <sub>n</sub> stocked fish (All)	-0.7276	0.0006	
	1	K <sub>n</sub> wild fish (All)	-0.6120	0.0070	
	2	CPUE wild fish (All)	0.6367	0.0045	
	2	K <sub>n</sub> stocked fish (All)	-0.6017	0.0083	
	2	K <sub>n</sub> wild fish (All)	-0.6677	0.0025	
	0	<i>Gammarus</i> m <sup>2</sup>	-0.7007	0.0012	18
	0	Gastropoda m <sup>2</sup>	-0.6970	0.0013	
	0	Total invertebrates m <sup>2</sup>	-0.5501	0.0180	
	1	Gastropoda m <sup>2</sup>	-0.5607	0.0155	
	2	Total invertebrates m <sup>2</sup>	-0.5562	0.0165	
	1	Mean temperature	0.6492	0.0002	28
	1	CPUE (1)	-0.4832	0.0195	23
	2	CPUE (1)	-0.7569	<0.0001	
	2	CPUE (2)	-0.5682	0.0047	
	2	CPUE (All)	-0.4368	0.0372	
	1	Kg/minute EF (1)	-0.4862	0.0187	
	2	Kg/minute EF (1)	-0.7273	0.0001	
	2	Kg/minute EF (2)	-0.5583	0.0056	
	2	K <sub>n</sub> (4)	-0.4625	0.0263	23
Mean daily discharge fluctuation	1	PSD	0.4358	0.0377	23
	2	PSD	0.6245	0.0014	
	0	RGV <i>Cladophora</i> (2)	-0.5236	0.0310	17
	1	Total RGV (2)	-0.4902	0.0458	
	0	RGV <i>Gammarus</i> (3)	-0.5523	0.0175	18
	2	RGV gastropoda (3)	-0.4724	0.0478	



Table 2. (continued)

Variable 1	Season	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
Mean daily coefficient of variation of discharge	1	Total invertebrates/m <sup>2</sup>	0.5604	0.0156	18
	2		-0.4881	0.0399	
	0	C <sub>24</sub> of <i>Gammarus</i> (3)	-0.5191	0.0273	18
	0	Total C <sub>24</sub> (3)	-0.5232	0.0259	17
	1	C <sub>24</sub> of <i>Gammarus</i> (2)	-0.5074	0.0376	17
	1	Total C <sub>24</sub> (2)	-0.5172	0.0335	17
	0	Gastropoda/m <sup>3</sup>	-0.7610	0.0283	8
	2	Total invertebrates/m <sup>3</sup>	0.7143	0.0465	
	0	CPUE (1)	-0.6667	0.0018	19
	0	CPUE (2)	-0.7649	0.0001	
	0	CPUE (All)	-0.5386	0.0174	
	1	CPUE (1)	-0.7414	0.0002	20
	1	CPUE (2)	-0.7263	0.0003	
	1	CPUE (All)	-0.5880	0.0064	
	2	CPUE (1)	-0.7474	0.0002	
	2	CPUE (2)	-0.7549	0.0001	
	2	CPUE (4)	0.5203	0.0187	
	2	CPUE (All)	-0.5865	0.0066	
	0	Kg/minute EF (1)	-0.6947	0.0010	19
	0	Kg/minute EF (2)	-0.8088	<0.0001	
Mean daily coefficient of variation of discharge	1	Kg/minute EF (1)	-0.7940	<0.0001	20
	1	Kg/minute EF (2)	-0.7444	0.0002	
	2	Kg/minute EF (1)	-0.7699	0.0001	
	2	Kg/minute EF (2)	-0.7940	<0.0001	
	2	Kg/minute EF (4)	0.4947	0.0266	
	0	K <sub>n</sub> (4)	-0.5018	0.0286	19
	1	K <sub>n</sub> (4)	-0.5459	0.0128	20
	2	K <sub>n</sub> (3)	-0.4526	0.0451	
	2	K <sub>n</sub> (4)	-0.5985	0.0053	20
	0	PSD	0.7333	0.0004	19
	0	CPUE stocked fish (All)	-0.5912	0.0260	14
	0	CPUE wild fish (All)	-0.8330	0.0002	

Table 2. (continued)

Variable 1	Season	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
	0	K <sub>n</sub> stocked fish (All)	0.6835	0.0070	14
	0	K <sub>n</sub> wild fish (All)	0.5473	0.0428	
	1	CPUE stocked fish (All)	-0.5214	0.0462	15
	1	CPUE wild fish (All)	-0.7786	0.0006	15
	1	K <sub>n</sub> stocked fish (All)	0.5964	0.0189	
	1	K <sub>n</sub> wild fish (All)	0.5964	0.0189	
	2	CPUE stocked fish (All)	-0.6107	0.0156	
	2	CPUE wild fish (All)	-0.7500	0.0013	
	2	K <sub>n</sub> stocked fish (All)	0.6286	0.0121	
	2	K <sub>n</sub> wild fish (All)	0.5607	0.0300	
	1	RGV gastropoda (All)	-0.6643	0.0069	15
	1	RGV gastropoda (2)	-0.6542	0.0111	14
	1	RGV gastropoda (3)	-0.6728	0.0480	15
	1	RGV <i>Gammarus</i> (3)	-0.5179	0.0060	
	2	RGV gastropoda (3)	-0.5383	0.0385	
	0	RGV oligochaeta (4)	0.7097	0.0066	13
	1	RGV oligochaeta (4)	0.7003	0.0053	14
	0	Oligochaeta/m <sup>2</sup>	-0.8107	0.0002	15
	1	<i>Gammarus</i> /m <sup>2</sup>	0.6206	0.0103	16
	1	Oligochaeta/m <sup>2</sup>	-0.5088	0.0441	
	1	Gastropoda/m <sup>2</sup>	0.7741	0.0004	
	2	Gastropoda/m <sup>2</sup>	0.7535	0.0008	
	0	Mean temperature	-0.4229	0.0444	23
	2		-0.4715	0.0173	25
	0	Chironomid larvae/m <sup>3</sup>	0.7857	0.0208	8
	0	<i>Cladophora</i> AFDW/m <sup>3</sup>	0.8286	0.0416	6
Total hours ≤ 227 m <sup>3</sup> s <sup>-1</sup>	0	CPUE (1)	-0.5561	0.0134	19
	1	CPUE (1)	-0.7063	0.0005	20
	1	CPUE (2)	-0.6506	0.0019	
	1	CPUE (All)	-0.4693	0.0368	
	0	Kg/minute EF (1)	-0.5772	0.0097	19
	1	Kg/minute EF (1)	-0.6235	0.0033	20
	1	Kg/minute EF (2)	-0.6461	0.0021	20
	2	Kg/minute EF (2)	-0.5197	0.0188	

Table 2. (continued)

Variable 1	Season	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
Mean water temperature (°C)	2	K <sub>n</sub> (4)	-0.4475	0.04786	20
	1	PSD	0.7093	0.0005	20
	1	CPUE of wild fish (All)	-0.5987	0.0184	15
	0	RGV gastropoda (2)	-0.7404	0.0040	13
	0	RGV gastropoda (4)	0.6011	0.0298	
	0	RGV <i>Gammarus</i> (4)	0.7510	0.0030	
	0	RGV gastropoda (All)	-0.5736	0.0320	
	1	RGV gastropoda (3)	-0.5770	0.0243	14
	1	RGV oligochaeta (4)	0.6950	0.0058	15
	2	RGV <i>Gammarus</i> (4)	0.5716	0.0327	14
	0	Gastropoda/m <sup>2</sup>	0.5612	0.0295	15
	2	Total invertebrates/m <sup>2</sup>	0.7035	0.0024	16
	0	C <sub>24</sub> of <i>Gammarus</i> (4)	0.6135	0.0258	13
	0	Total C <sub>24</sub> (4)	0.7473	0.0033	
	2	C <sub>24</sub> of <i>Gammarus</i> (4)	0.6156	0.0191	14
	2	Total C <sub>24</sub> (4)	0.6689	0.0089	
	1	Mean temperature	-0.6541	0.0005	24
	2	Total phosphorus	-0.4525	0.0452	20
	0	CPUE (All)	0.4585	0.0278	23
	0	CPUE (1)	0.6206	0.0016	
	0	CPUE (2)	0.5632	0.0051	
	0	Kg/minute EF (1)	0.5148	0.0119	
	0	Kg/minute EF (2)	0.5494	0.0067	
	0	CPUE wild fish (All)	0.5129	0.0295	18
Total phosphorous (mg/L)	0	RGV gastropoda (All)	0.4923	0.0380	18
	0	AFDW/m <sup>3</sup> invertebrate drift	0.6444	0.0443	10
	0	K <sub>n</sub> (2)	-0.4916	0.0325	19
	0	K <sub>n</sub> (3)	-0.5640	0.0119	
	0	K <sub>n</sub> (All)	-0.5446	0.0159	
	0	<i>Gammarus</i> /m <sup>3</sup>	-0.9429	0.0048	6
	0	C <sub>24</sub> <i>Gammarus</i> (All)	0.6805	0.0037	16
	0	C <sub>24</sub> Total (All)	0.5000	0.0486	16

Table 3. Spearman's R correlations among food base (benthos, drift) independent variables and RBT catch, condition and food habit dependent variables. 1= <152 mm (CPUE) or <152 mm (Kg/minute EF,  $K_n$ ), 2=152-304 mm, 3=305-405 mm, 4=405-558 mm; All=all sizes combined.

Variable 1	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
<i>Gammarus</i> /m <sup>2</sup>	CPUE (3)	-0.6824	0.0036	16
	CPUE(All)	-0.5471	0.0283	
	Kg/minute EF (3)	-0.6176	0.0108	16
	Kg/minute EF (All)	-0.6029	0.0134	
	$K_n$ (2)	0.7118	0.0020	16
	RGV <i>Cladophora</i> (2)	-0.7459	0.0034	13
	Total RGV (2)	-0.5879	0.0346	
	RGV chironomid larvae (3)	-0.7017	0.0075	
	RGV <i>Cladophora</i> (3)	-0.7098	0.0066	
	Total RGV (3)	-0.6978	0.0080	12
	RGV <i>Cladophora</i> (4)	-0.7413	0.0058	
	RGV chironomid larvae (All)	-0.6978	0.0080	13
	RGV <i>Cladophora</i> (All)	-0.8571	0.0002	
	Total RGV (All)	-0.6429	0.0178	
	% empty stomachs (All)	0.5714	0.0413	
	Chironomid larvae/m <sup>2</sup>	-0.5955	0.0091	18
	Chironomid pupae/m <sup>2</sup>	-0.6512	0.0034	
	Total chironomids/m <sup>2</sup>	-0.5872	0.0104	
	Gastropoda/m <sup>2</sup>	0.6495	0.0035	
	Total invertebrates/m <sup>2</sup>	0.6594	0.0029	
	Periphyton AFDW/m <sup>2</sup>	-0.5604	0.0156	
Chironomid larvae/m <sup>2</sup>	RGV chironomid larvae (2)	0.5967	0.0313	13
	RGV <i>Cladophora</i> (2)	0.7238	0.0052	
	RGV chironomid larvae (3)	0.7845	0.0015	
	RGV chironomid pupae (3)	0.5659	0.0438	
	RGV <i>Cladophora</i> (3)	0.7978	0.0011	
	RGV total chironomids (3)	0.6209	0.0235	
	Total RGV (3)	0.6429	0.0178	
	RGV chironomid larvae (4)	0.6381	0.0256	
	RGV <i>Cladophora</i> (4)	0.7343	0.0065	
	RGV chironomid larvae (All)	0.8187	0.0006	
	RGV <i>Cladophora</i> (All)	0.7527	0.0030	

Table 3. (continued)

Variable 1	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
Chironomid larvae/m <sup>2</sup>	Chironomid pupae/m <sup>2</sup>	0.7874	0.0001	18
	Total chironomid/m <sup>2</sup>	0.9959	<0.0001	
	Gastropoda/m <sup>2</sup>	-0.4739	0.0469	
	Periphyton AFDW/m <sup>2</sup>	0.8163	0.0004	
	C <sub>24</sub> chironomids (3)	0.6374	0.0191	13
	Chironomid adults/m <sup>3</sup>	0.7178	0.0194	10
Chironomid pupae/m <sup>2</sup>	RGV chironomid larvae (2)	0.6961	0.0082	13
	RGV <i>Cladophora</i> (2)	0.7845	0.0015	
	RGV chironomid larvae (3)	0.7182	0.0057	
	RGV chironomid pupae (3)	0.6044	0.0287	
	RGV <i>Cladophora</i> (3)	0.7785	0.0017	
	Total RGV (3)	0.6758	0.0112	
	RGV <i>Cladophora</i> (4)	0.6713	0.0168	12
	RGV chironomid larvae (All)	0.8516	0.0002	13
	RGV <i>Cladophora</i> (All)	0.7527	0.0030	
	Total RGV (All)	0.5604	0.0463	
	% empty stomachs (All)	-0.6044	0.0287	
	Total chironomids/m <sup>2</sup>	0.8142	<0.0001	18
	Gastropoda/m <sup>2</sup>	-0.5452	0.0193	
	Periphyton AFDW/m <sup>2</sup>	0.7523	0.0003	
Total chironomids/m <sup>2</sup>	RGV chironomid larvae (2)	0.5691	0.0424	13
	RGV <i>Cladophora</i> (2)	0.7072	0.0087	
	RGV chironomid larvae (3)	0.7901	0.0013	
	RGV chironomid pupae (3)	0.5824	0.0367	
	RGV <i>Cladophora</i> (3)	0.8088	0.0008	
	RGV total chironomids (3)	0.6319	0.0205	
	Total RGV (3)	0.6538	0.0153	
	RGV chironomid larvae (4)	0.6599	0.0196	12
	RGV <i>Cladophora</i> (4)	0.7133	0.0092	
	RGV chironomid larvae (All)	0.8242	0.0005	13
	RGV <i>Cladophora</i> (All)	0.7363	0.0041	
	Gastropoda/m <sup>2</sup>	-0.4801	0.0437	18
	Periphyton AFDW/m <sup>2</sup>	0.8328	>0.0001	
	C <sub>24</sub> chironomids (3)	0.6484	0.0165	13
Total chironomids/m <sup>2</sup>	Chironomid adults/m <sup>3</sup>	0.7178	0.0194	10

Table 3. (continued)

Variable 1	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
Oligochaeta/m <sup>2</sup>	CPUE (2)	0.5118	0.0427	16
	CPUE (All)	0.5059	0.0456	
	RGV chironomid adults (4)	-0.6504	0.0220	12
Gastropoda/m <sup>2</sup>	CPUE (3)	-0.6166	0.0110	16
	Kg/minute EF (3)	-0.5578	0.0248	16
	K <sub>n</sub> (2)	0.5283	0.0354	16
	K <sub>n</sub> (3)	0.5180	0.0398	
	RGV chironomid larvae (2)	-0.5643	0.0445	13
	RGV <i>Cladophora</i> (2)	-0.5837	0.0362	
	RGV chironomid larvae (3)	-0.6889	0.0092	
	RGV chironomid adults (3)	-0.6041	0.0288	
	RGV <i>Cladophora</i> (4)	-0.7110	0.0095	12
	RGV <i>Gammarus</i> (4)	0.6053	0.0370	
	RGV <i>Cladophora</i> (All)	-0.6933	0.0322	13
	RGV chironomid larvae (All)	-0.5942	0.0086	
	Periphyton AFDW/m <sup>2</sup>	-0.4760	0.0459	18
Total invertebrates/m <sup>2</sup>	K <sub>n</sub> (2)	0.6912	0.0030	16
	CPUE (3)	-0.5059	0.0456	16
	RGV <i>Cladophora</i> (2)	-0.6133	0.0258	13
	Total RGV (2)	-0.5604	0.0463	
	RGV <i>Cladophora</i> (All)	-0.7308	0.0045	
Periphyton AFDW/m <sup>2</sup>	Kg/minute EF (All)	0.4812	0.0317	20
	Kg/minute EF (4)	0.4586	0.0443	
	CPUE (4)	0.4541	0.0443	
	RGV <i>Gammarus</i> (2)	0.5912	0.0260	13
	RGV Gastropoda (2)	0.6271	0.0164	
	RGV <i>Cladophora</i> (3)	0.6738	0.0059	
	Total RGV (3)	0.6607	0.0073	
	RGV <i>Cladophora</i> (All)	0.6964	0.0039	
Periphyton AFDW/m <sup>2</sup>	Total RGV (All)	0.5214	0.0462	13
	C <sub>24</sub> <i>Gammarus</i> (2)	0.5824	0.0289	14

Table 3. (continued)

Variable 1	Variable 2 (+ RBT size class where applicable)	Spear- man's R	P	N
mg AFDW invertebrate drift/m <sup>3</sup>	Chironomid adults/m <sup>3</sup> (CPOM)	0.6163	0.0328	12
	ml <i>Cladophora</i> /m <sup>3</sup> (CPOM)	0.7343	0.0065	
	CPUE (1)	0.7186	0.0446	8
	RGV total chironomids (2)	-0.7928	0.0334	7
	RGV <i>Gammarus</i> (4)	0.8829	0.0085	
	C <sub>24</sub> <i>Gammarus</i> (4)	0.8829	0.0085	7
	Total C <sub>24</sub> (4)	0.8289	0.0212	
<i>Gammarus</i> /m <sup>3</sup> (AGFD)	K <sub>n</sub> (1)	0.8857	0.0188	6
	K <sub>n</sub> (2)	0.8857	0.0188	

Table 4. Spearman's R correlations among rainbow trout catch, condition and food habit variables. Trout size classes are defined as: 1= <152 mm (CPUE) or <152 mm (Kg/minute EF,  $K_n$ ), 2=152-304 mm, 3=305-405 mm, 4=405-558 mm; All=all sizes combined.

Variable 1 (+ RBT size class where applicable)	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
CPUE (All)	Kg/minute EF (All)	0.5415	0.0076	23
	Kg/minute EF (1)	0.6887	0.0003	
	Kg/minute EF (2)	0.8182	<0.0001	
	Kg/minute EF (3)	0.7441	<0.0001	
	$K_n$ (2)	-0.4140	0.0495	23
	PSD	-0.7085	0.0002	23
	RGV <i>Cladophora</i> (All)	0.5046	0.0327	18
	CPUE (2)	0.8320	<0.0001	23
	CPUE (4)	-0.4852	0.0189	
	Kg/minute EF (1)	0.9190	<0.0001	23
CPUE (1)	Kg/minute EF (2)	0.7569	<0.0001	
	Kg/minute EF (4)	-0.4862	0.0187	
	$K_n$ (All)	0.4773	0.0213	23
	$K_n$ (4)	0.4822	0.0198	
	PSD	-0.8192	<0.0001	23
	Kg/minute (1)	0.7885	<0.0001	23
	Kg/minute (2)	0.9526	<0.0001	
	$K_n$ (4)	0.5415	0.0076	23
	PSD	-0.8281	<0.0001	23
	CPUE (4)	0.5445	0.0072	23
CPUE (2)	Kg/minute EF (All)	0.9130	<0.0001	23
	Kg/minute EF (2)	0.5020	0.0147	
	Kg/minute EF (3)	0.9921	<0.0001	
	Kg/minute EF (4)	0.5000	0.0151	
	$K_n$ (All)	-0.5020	0.0147	23
	$K_n$ (2)	-0.6966	0.0002	
	$K_n$ (3)	-0.4644	0.0256	
	CPUE (3)	0.5617	0.0153	18
	RGV <i>Cladophora</i> (3)	0.5617	0.0153	18
	CPUE (3)	0.5617	0.0153	18



Table 4. (continued)

Variable 1 (+ RBT size class where applicable)	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
CPUE (4)	Kg/minute EF (All)	0.8024	<0.0001	23
	Kg/minute EF (1)	-0.4427	0.0344	
	Kg/minute EF (3)	0.5504	0.0065	
	Kg/minute EF (4)	0.9763	<0.0001	
	K <sub>n</sub> (All)	-0.7411	0.0001	23
	K <sub>n</sub> (3)	-0.7579	<0.0001	
	PSD	0.4397	0.0358	23
	Kg/minute EF (All)	0.9170	<0.0001	23
	Kg/minute EF (4)	0.7816	<0.0001	
	K <sub>n</sub> (All)	-0.6561	0.0007	23
Kg/minute EF (1)	K <sub>n</sub> (2)	-0.5810	0.0036	
	K <sub>n</sub> (3)	-0.6294	0.0013	
	RGV <i>Cladophora</i> (All)	0.6017	0.0083	18
	Kg/minute EF (2)	0.7372	0.0001	23
	Kg/minute EF (4)	-0.4585	0.0278	
	K <sub>n</sub> (All)	0.4585	0.0278	
	K <sub>n</sub> (4)	0.4951	0.0163	
	PSD	-0.7589	<0.0001	
	K <sub>n</sub> (All)	0.4585	0.0278	23
	K <sub>n</sub> (4)	0.4951	0.0163	
Kg/minute EF (2)	PSD	-0.7589	<0.0001	23
	Kg/minute EF (3)	0.5217	0.0107	23
	K <sub>n</sub> (4)	0.5978	0.0026	23
	PSD	-0.8370	<0.0001	23
Kg/minute EF (3)	Kg/minute EF (4)	0.5099	0.0129	23
	K <sub>n</sub> (All)	-0.4713	0.0232	23
	K <sub>n</sub> (1)	-0.4289	0.0412	
	K <sub>n</sub> (2)	-0.6690	0.0005	
	K <sub>n</sub> (3)	-0.4437	0.0340	
Kg/minute EF (3)	RGV <i>Cladophora</i> (3)	0.5679	0.0140	18
Kg/minute EF (4)	K <sub>n</sub> (All)	-0.6522	0.0007	23
	K <sub>n</sub> (3)	-0.6522	0.0007	

Table 4. (continued)

Variable 1 (+ RBT size class where applicable)	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
	PSD	0.4743	0.0222	23
$K_n$ (All)	$C_{24}$ <i>Gammarus</i> (4)	-0.5984	0.0111	17
	$C_{24}$ total (4)	-0.5833	0.0140	
	RGV <i>Gammarus</i> (All)	-0.5851	0.0107	18
RGV chironomid larvae (All)	RGV chironomid pupae (All)	0.6216	0.0059	18
	RGV <i>Cladophora</i> (All)	0.5410	0.0204	
	RGV total chironomid (All)	0.6804	0.0019	
	Total RGV (All)	0.5142	0.0290	
	% empty stomachs (All)	-0.5896	0.0100	
RGV chironomid pupae (All)	RGV <i>Gammarus</i> (All)	-0.4778	0.0449	18
	RGV gastropoda (All)	-0.5212	0.0266	
	RGV total chironomids (All)	0.8390	<0.0001	
RGV <i>Cladophora</i> (All)	Total RGV (All)	0.8142	<0.0001	18
RGV <i>Gammarus</i> (All)	RGV total chironomids (All)	-0.4716	0.0482	18
	Total RGV (All)	0.5253	0.0252	
RGV chironomid adult (All)	RGV oligochaeta (All)	0.5112	0.0301	18
	RGV total chironomids (All)	0.4689	0.0497	
RGV chironomid larvae (2)	RGV chironomid pupae (2)	0.8484	<0.0001	17
	RGV <i>Cladophora</i> (2)	0.7457	0.0006	
	RGV total chironomids (2)	0.8325	<0.0001	
RGV chironomid pupae (2)	RGV <i>Cladophora</i> (2)	0.6230	0.0076	17
	RGV total chironomids (2)	0.9110	<0.0001	
RGV chironomid adults (2)	RGV total chironomids (2)	0.5474	0.0229	17
RGV <i>Cladophora</i> (2)	RGV total chironomids (2)	0.6791	0.0027	17
	Total RGV (2)	0.7991	0.0001	
RGV <i>Gammarus</i> (2)	RGV gastropoda (2)	0.5308	0.0284	17
	Total RGV (2)	0.6201	0.0079	
RGV chironomid larvae (3)	RGV chironomid pupae (3)	0.4886	0.0396	18
	RGV <i>Cladophora</i> (3)	0.7540	0.0003	
	RGV total chironomids (3)	0.5571	0.0163	
	Total RGV (3)	0.7033	0.0011	

Table 4. (continued)

Variable 1 (+ RBT size class where applicable)	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
RGV chironomid pupae (3)	RGV total chironomids (3)	0.8617	<0.0001	18
RGV chironomid adult (3)	RGV oligochaeta (3)	0.5874	0.0104	18
RGV <i>Cladophora</i> (3)	Total RGV (3)	0.8725	<0.0001	18
RGV <i>Gammarus</i> (3)	Total RGV (3)	0.7049	0.0011	18
RGV chironomid larvae (4)	Total RGV (4)	0.6095	0.0094	17
RGV chironomid pupae (4)	RGV total chironomid (4)	0.9269	<0.0001	17
RGV <i>Cladophora</i> (4)	Total RGV (4)	0.6544	0.0044	17
RGV <i>Gammarus</i> (4)	RGV gastropoda (4)	0.5691	0.0171	17

Table 5. Spearman's R correlations between angler catch rates and experimental catch rates. Trout size classes are defined as: 1= <152 mm (CPUE) or <152 mm (Kg/minute EF), 2=152-304 mm, All=all sizes combined.

Variable 1	Variable 2 (+ RBT size class where applicable)	Spearman's R	P	N
Angler catch rate (fish/hr)	CPUE (All)	0.9643	0.0005	7
	CPUE (1)	0.7857	0.0362	
	CPUE (2)	0.8214	0.0234	
	Kg/minute EF (2)	0.8214	0.0234	7
	CPUE wild-spawned fish (All)	0.9429	0.0048	6
	PSD	-0.8571	0.0137	7

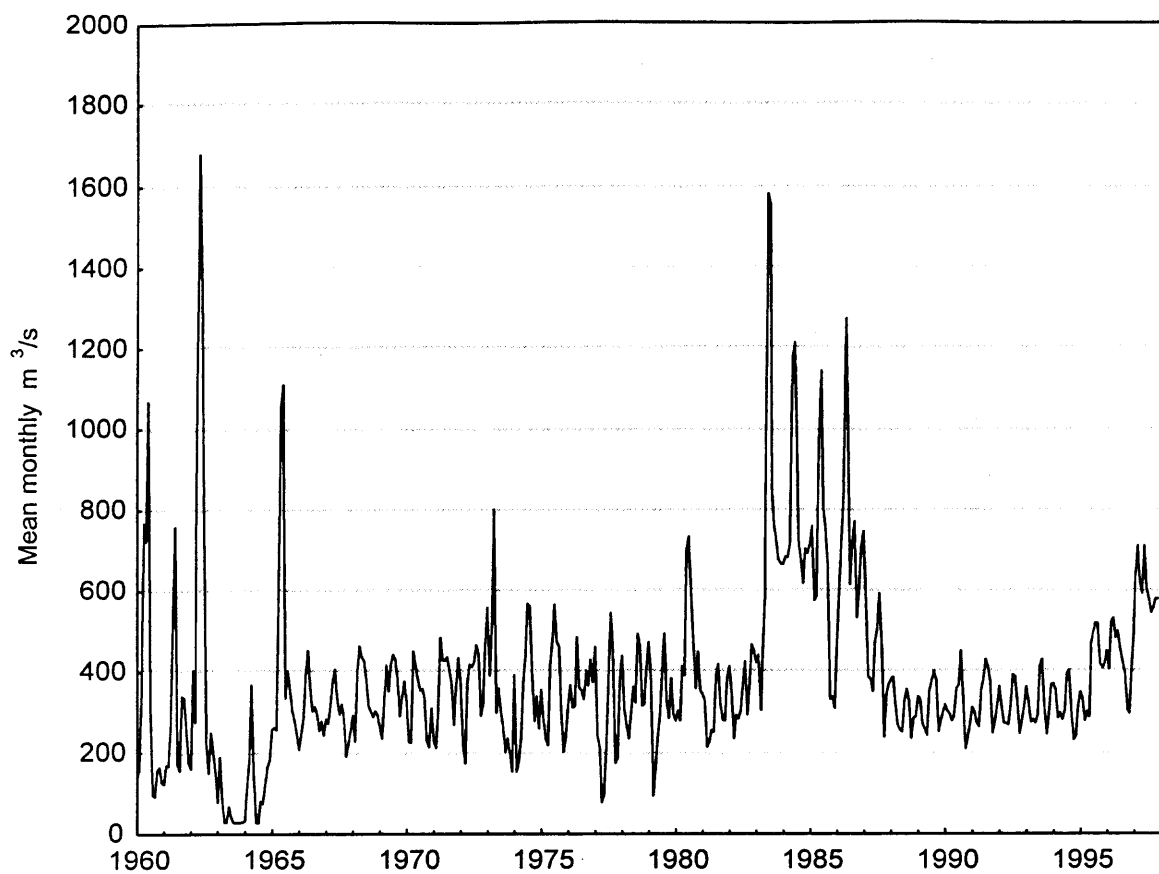


Figure 1. Mean monthly releases from Glen Canyon Dam, Colorado River, 1960-1997.

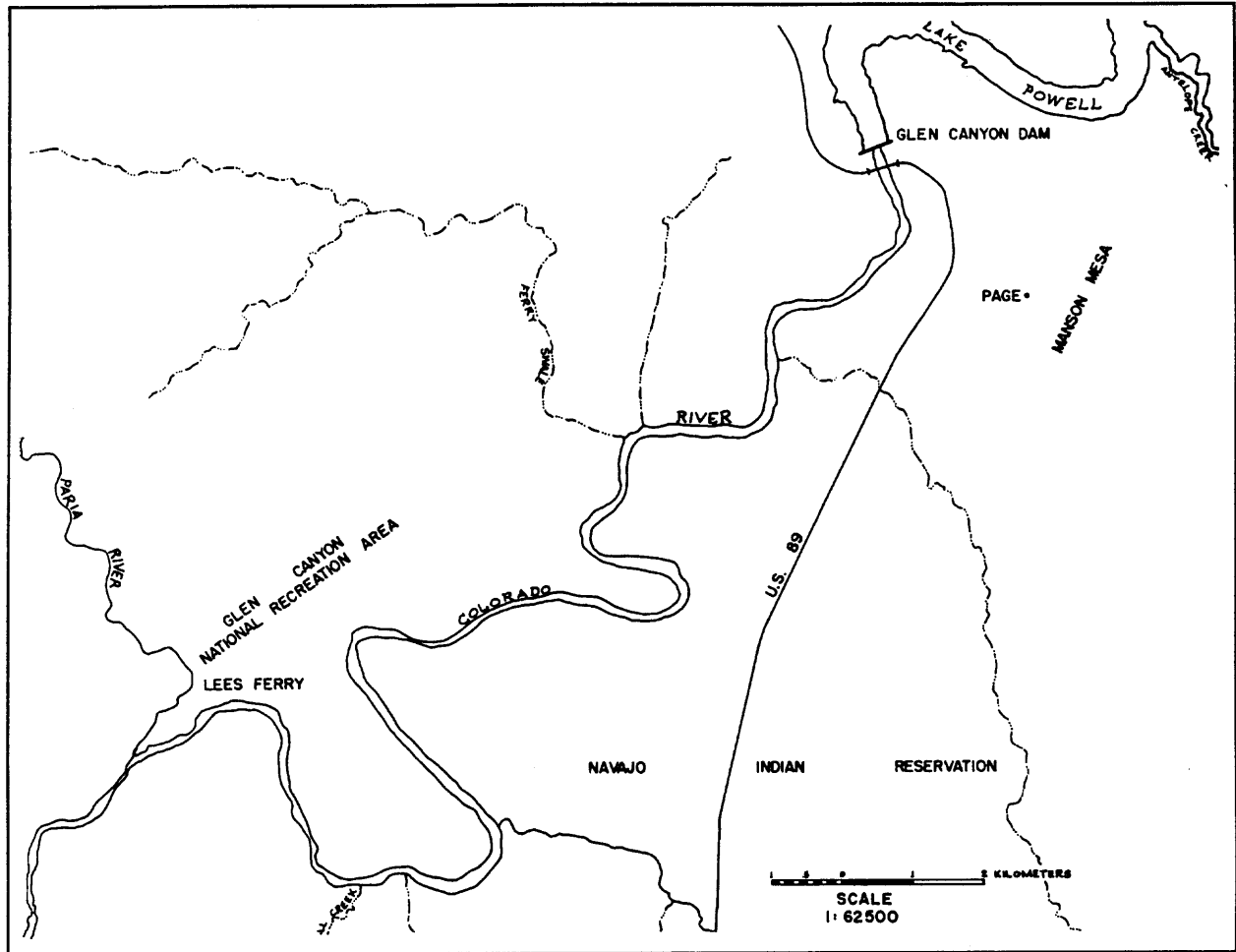


Figure 2. Map of the Colorado River in Arizona/Utah.

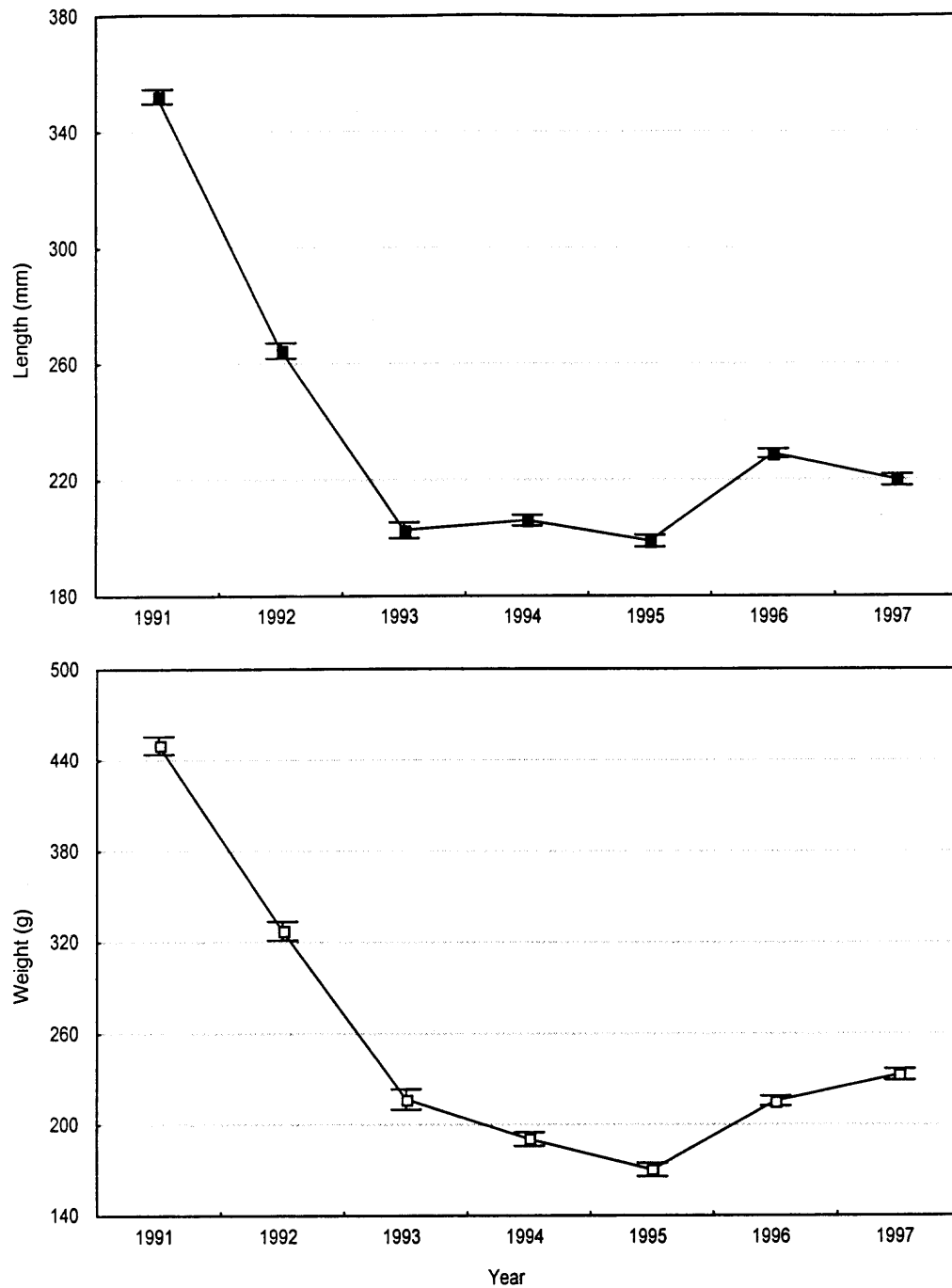


Figure 3. Yearly mean length (mm, top, closed boxes) and weight (g wet, bottom, open boxes) of rainbow trout ( $\pm 1$  SE) in the Lee's Ferry reach, Colorado River, 1991-1997.

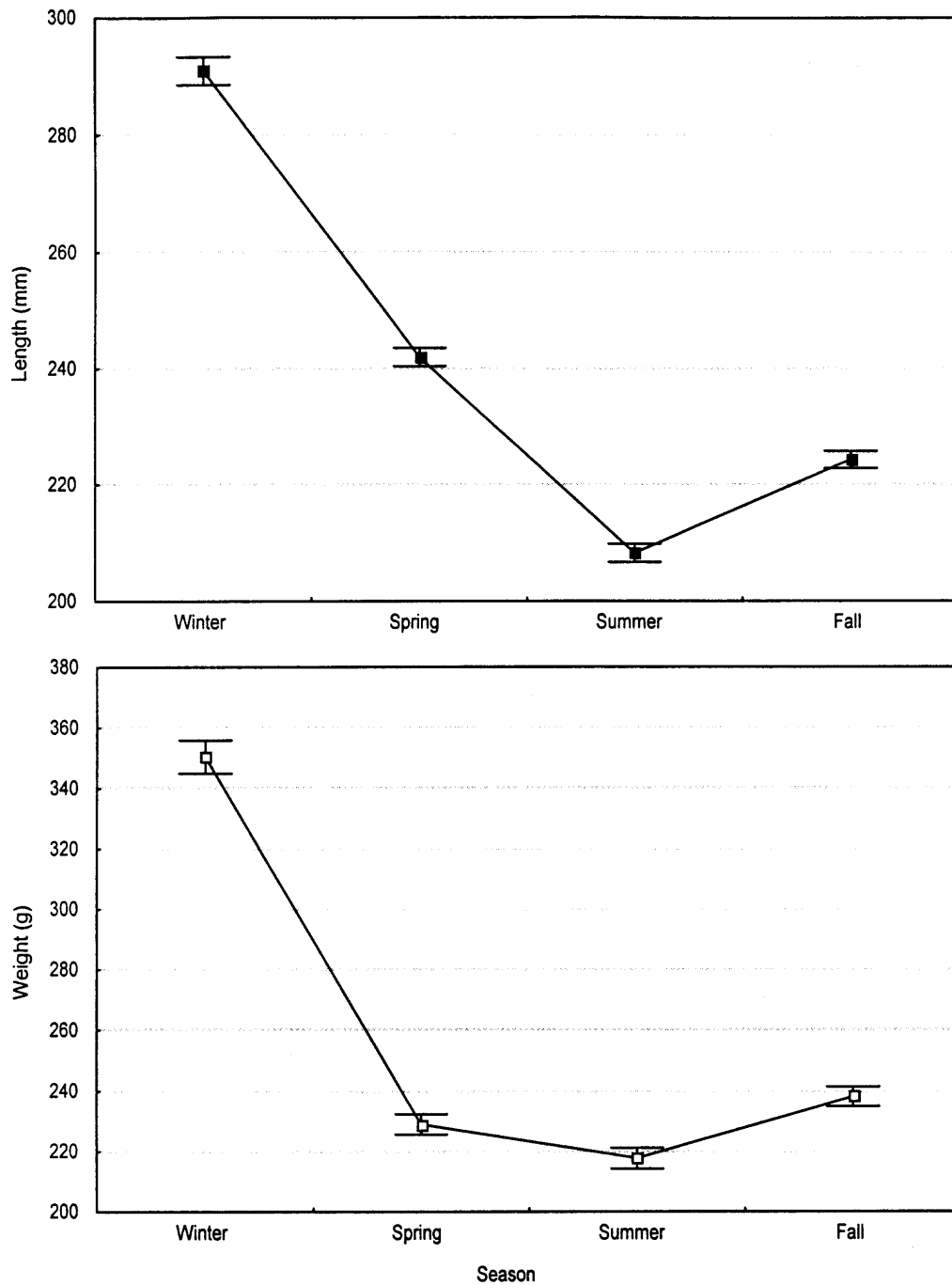


Figure 4. Seasonal mean length (mm, top, closed boxes) and weight (g wet, bottom, open boxes) of rainbow trout ( $\pm 1$  SE) in the Lee's Ferry reach, Colorado River, 1991-1997.



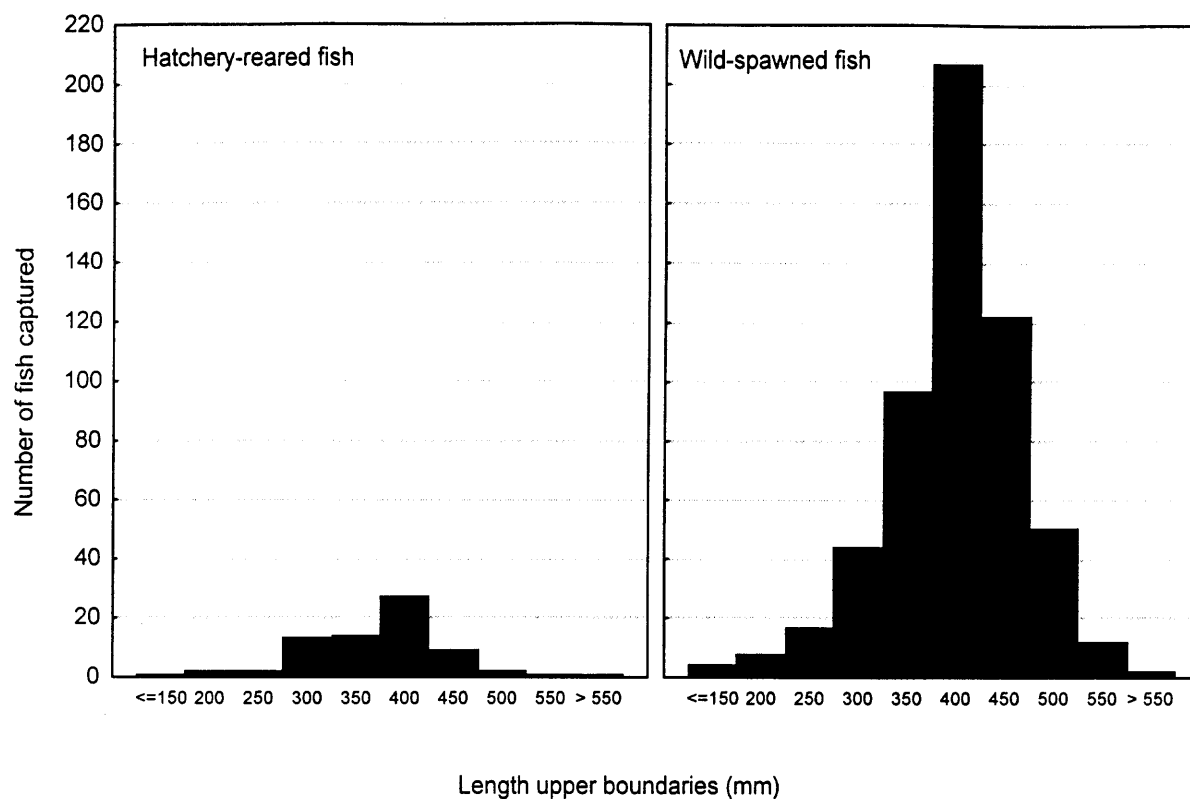


Figure 5. Length frequency distribution of ripe (gametes manually extruded) hatchery-reared and wild-spawned rainbow trout in the Lee's Ferry reach, Colorado River, 1993-1997.

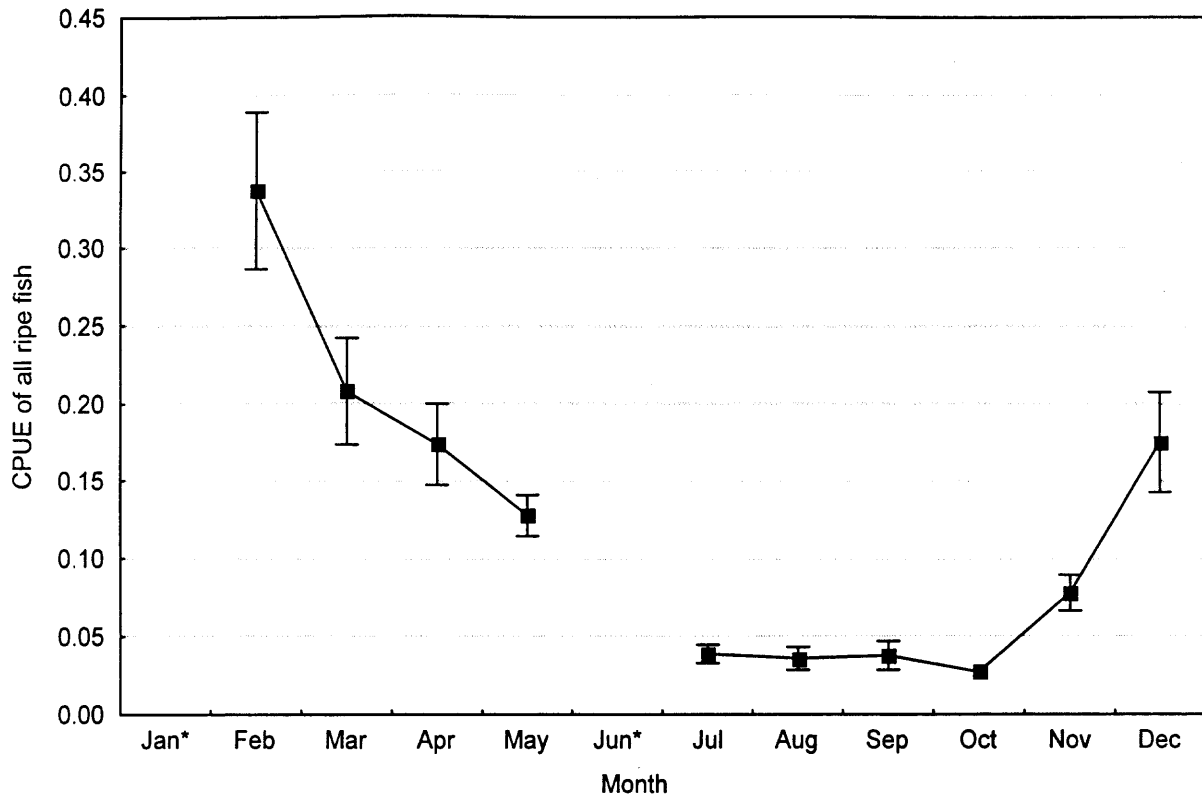


Figure 6. Monthly CPUE ( $\pm 1$  SE) of ripe rainbow trout in the Lee's Ferry Reach, Colorado River, 1993-1997. Asterisk (\*) indicates no sampling conducted during that month.

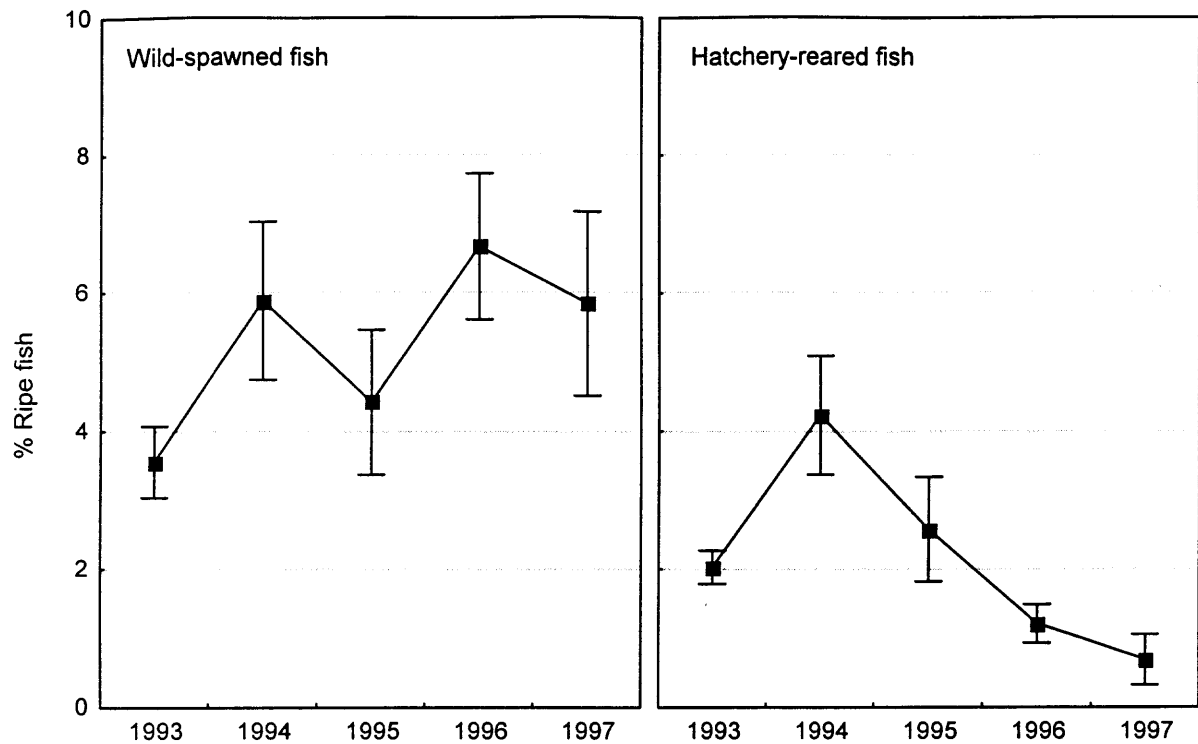


Figure 7. Yearly percentage ( $\pm 1$  SE) of ripe rainbow trout in the Lee's Ferry reach, Colorado River, 1993-1997.

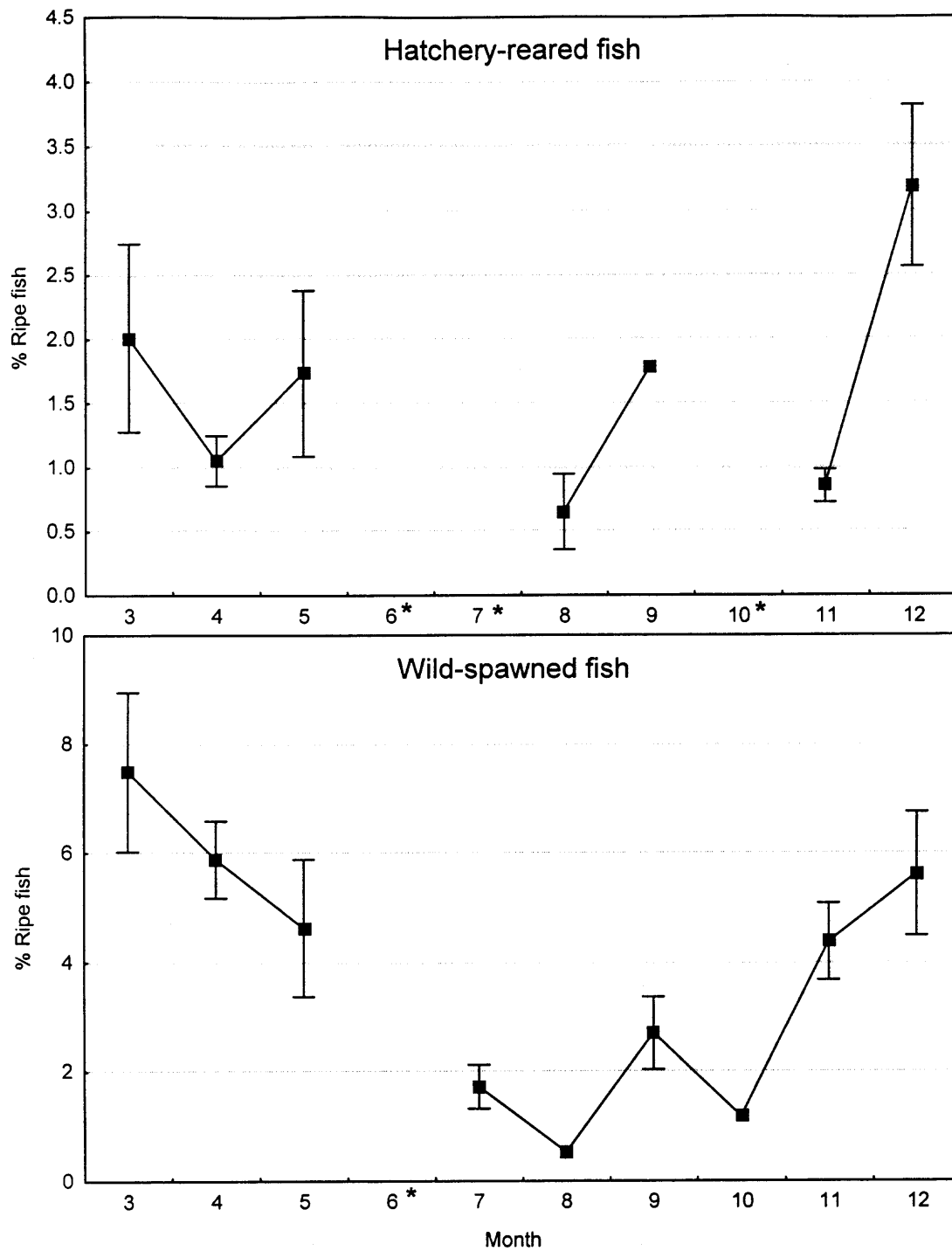


Figure 8. Monthly percentages ( $\pm 1$  SE) of ripe rainbow trout for hatchery-reared (top) and wild-spawned (bottom) fish. Asterisk (\*) indicates no sampling conducted during that month.

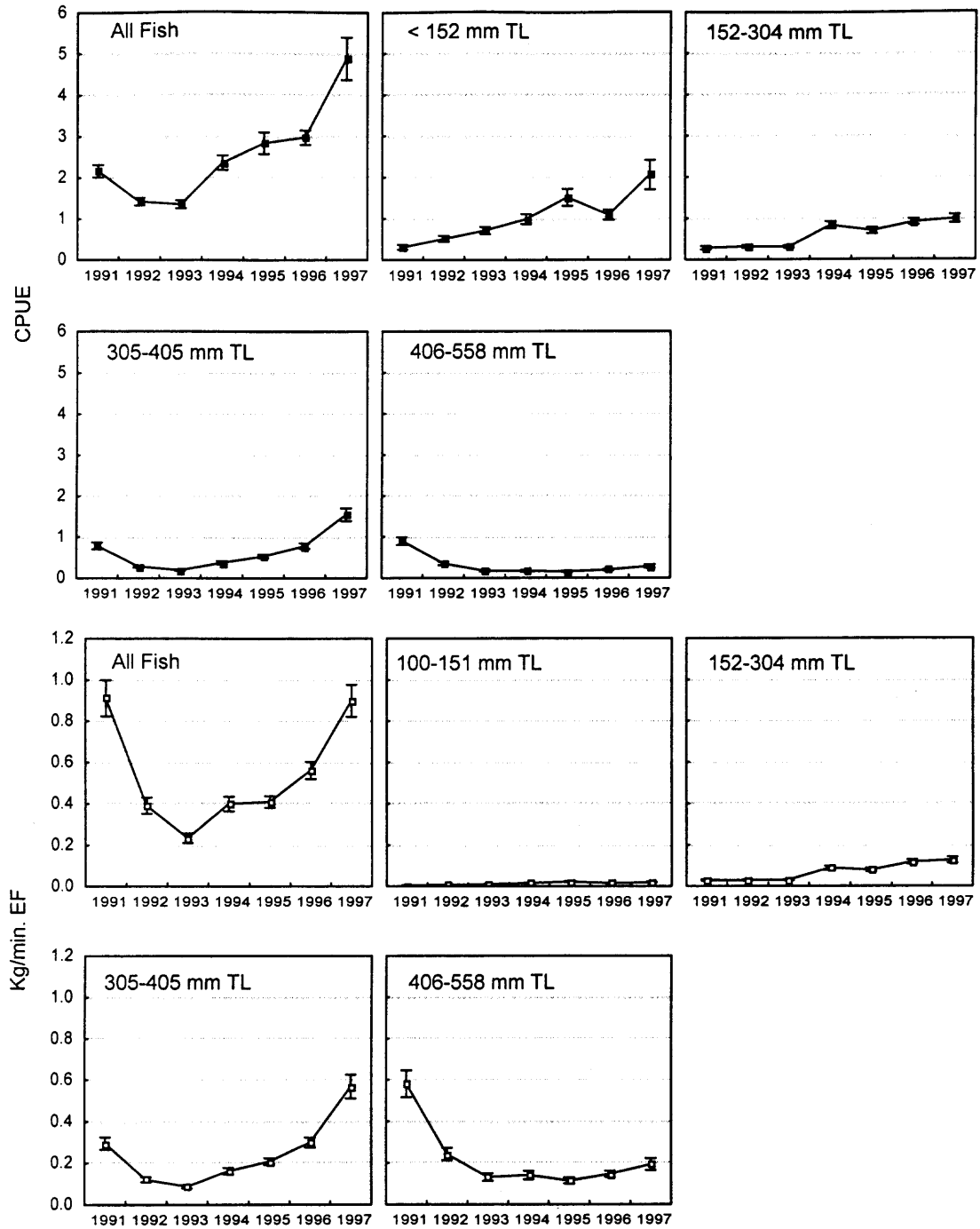


Figure 9. Yearly CPUE (top, closed boxes) and kg-per-minute electrofishing (bottom, open boxes) of rainbow trout ( $\pm 1$  SE) in the Lee's Ferry Reach, Colorado River, 1991-1997

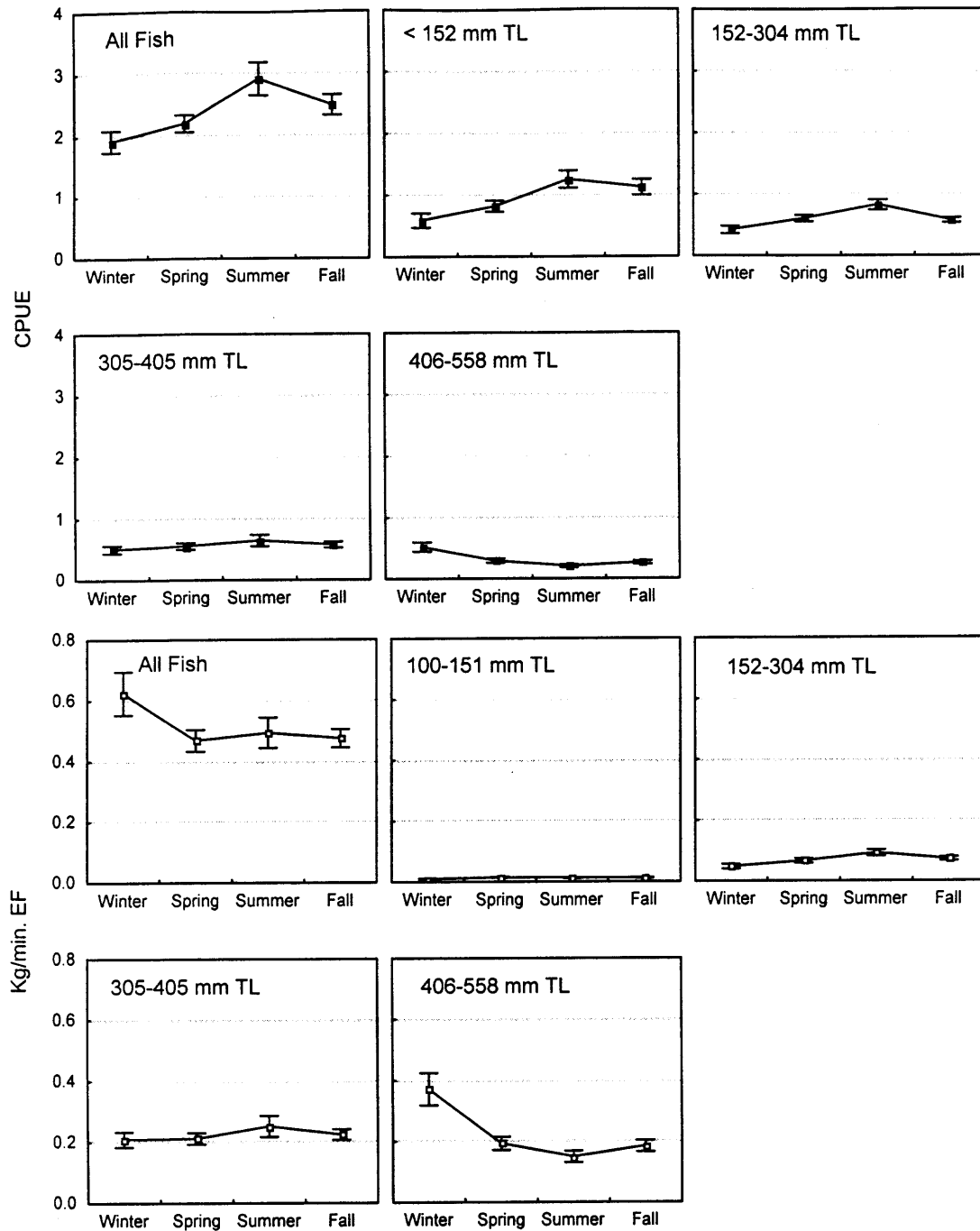


Figure 10. Seasonal CPUE (top, closed boxes) and kg-per-minute electrofishing (bottom, open boxes) of rainbow trout ( $\pm 1$  SE) in the Lee's Ferry Reach, Colorado River, 1991-1997

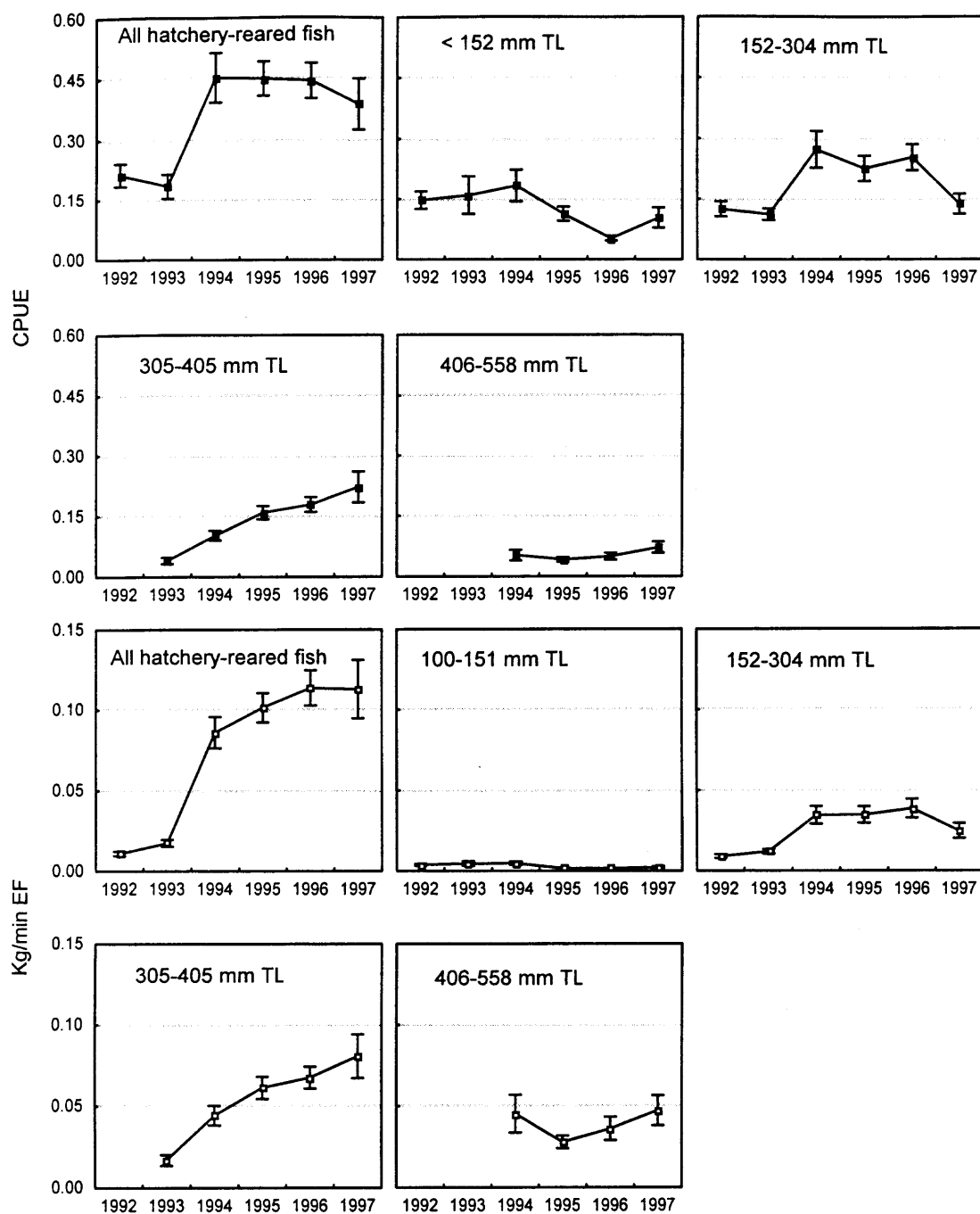


Figure 11. Yearly CPUE (top, closed boxes) and kg-per-minute electrofishing (bottom, open boxes) of hatchery-reared rainbow trout ( $\pm 1$  SE) in the Lee's Ferry Reach, Colorado River, 1992-1997

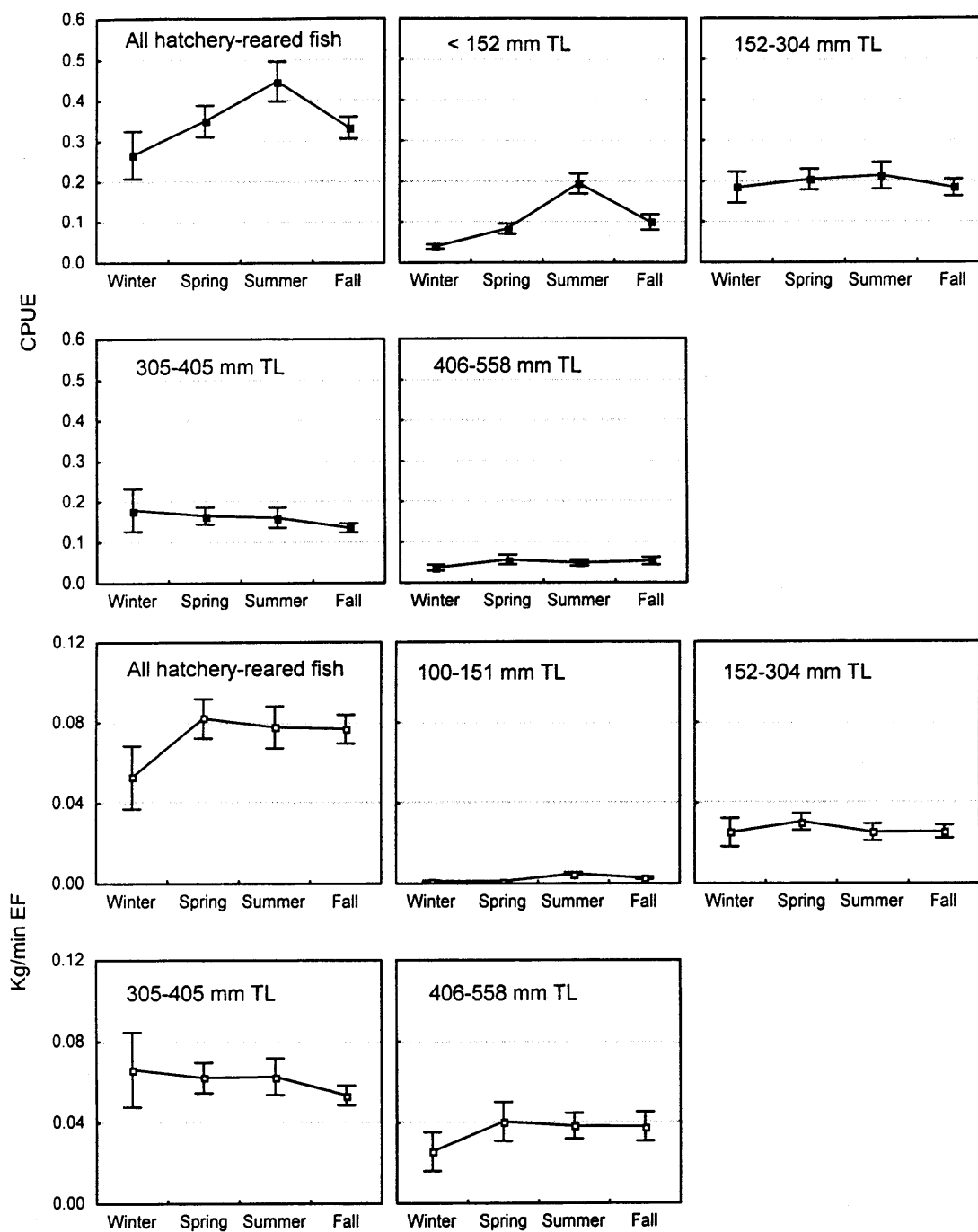


Figure 12. Seasonal CPUE (closed boxes) and kg-per-minute electrofishing (open boxes) of hatchery-reared rainbow trout ( $\pm 1$  SE) in the Lee's Ferry Reach, Colorado River, 1991-1997.



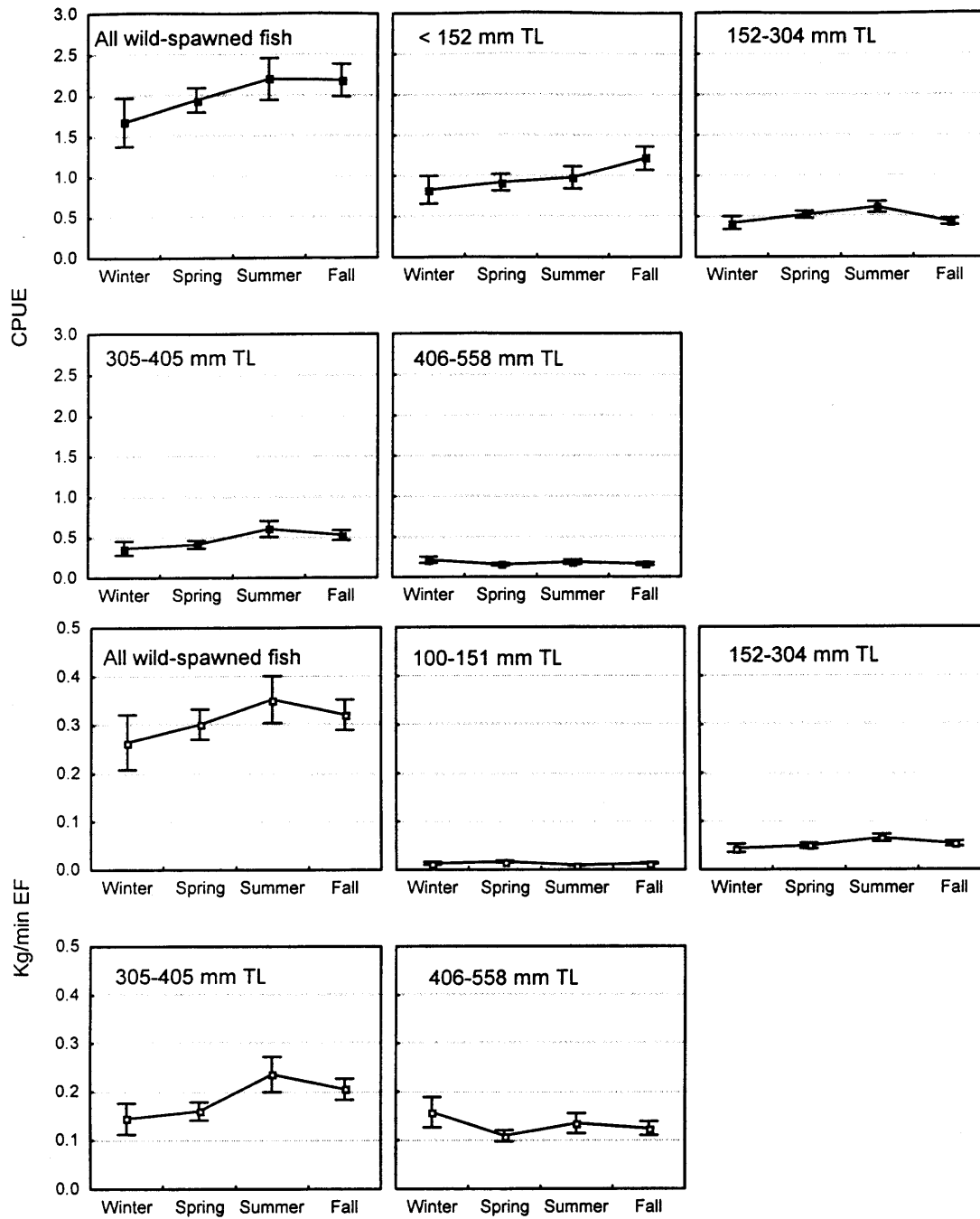


Figure 13. Yearly CPUE (top, closed boxes) and kg-per-minute electrofishing (bottom, open boxes) of wild-spawned rainbow trout ( $\pm 1$  SE) in the Lee's Ferry Reach, Colorado River, 1992-1997

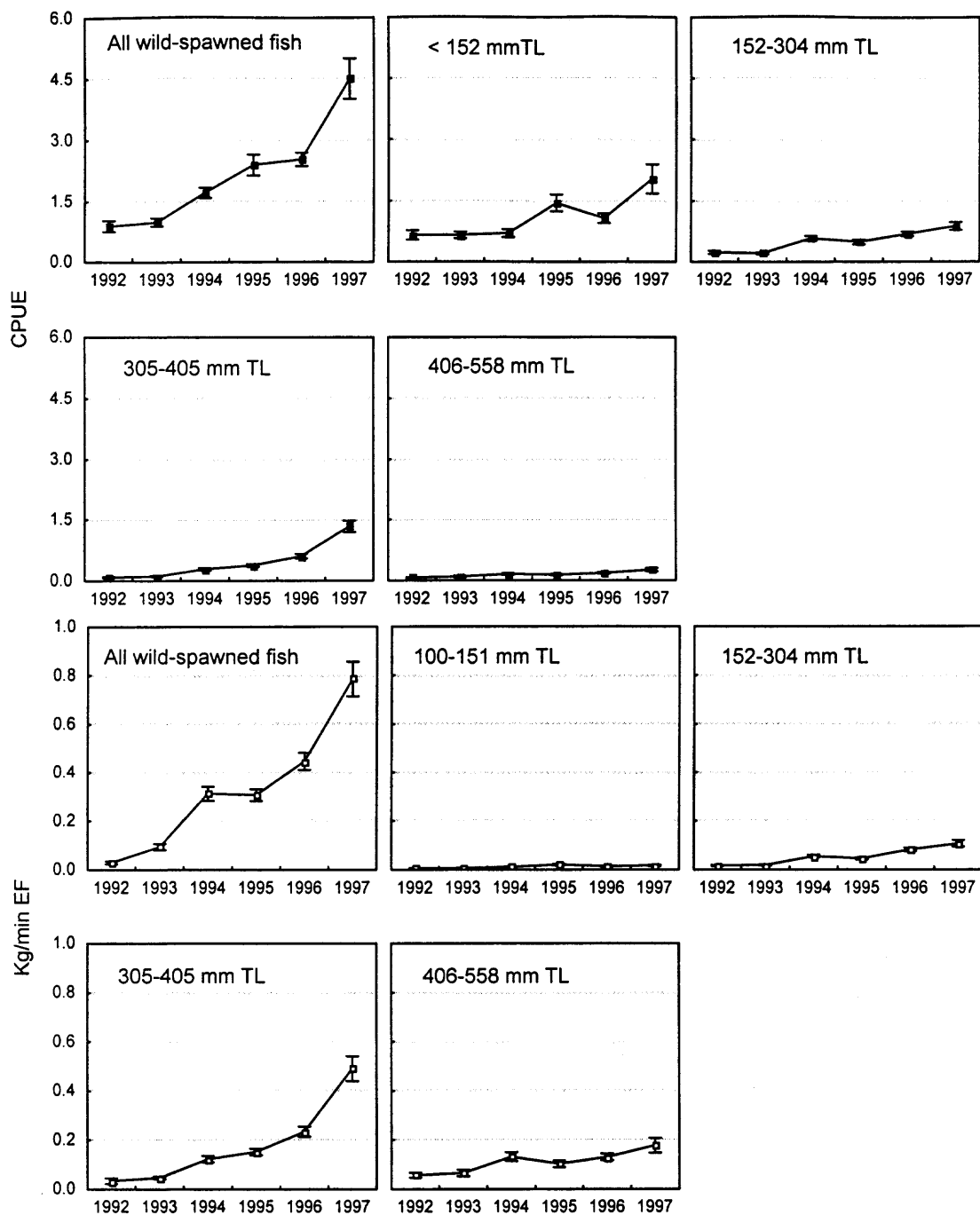


Figure 14. Seasonal CPUE (top, closed boxes) and kg-per-minute electrofishing (bottom, open boxes) of wild-spawned rainbow trout ( $\pm 1$  SE) in the Lee's Ferry Reach, Colorado River, 1991-1997

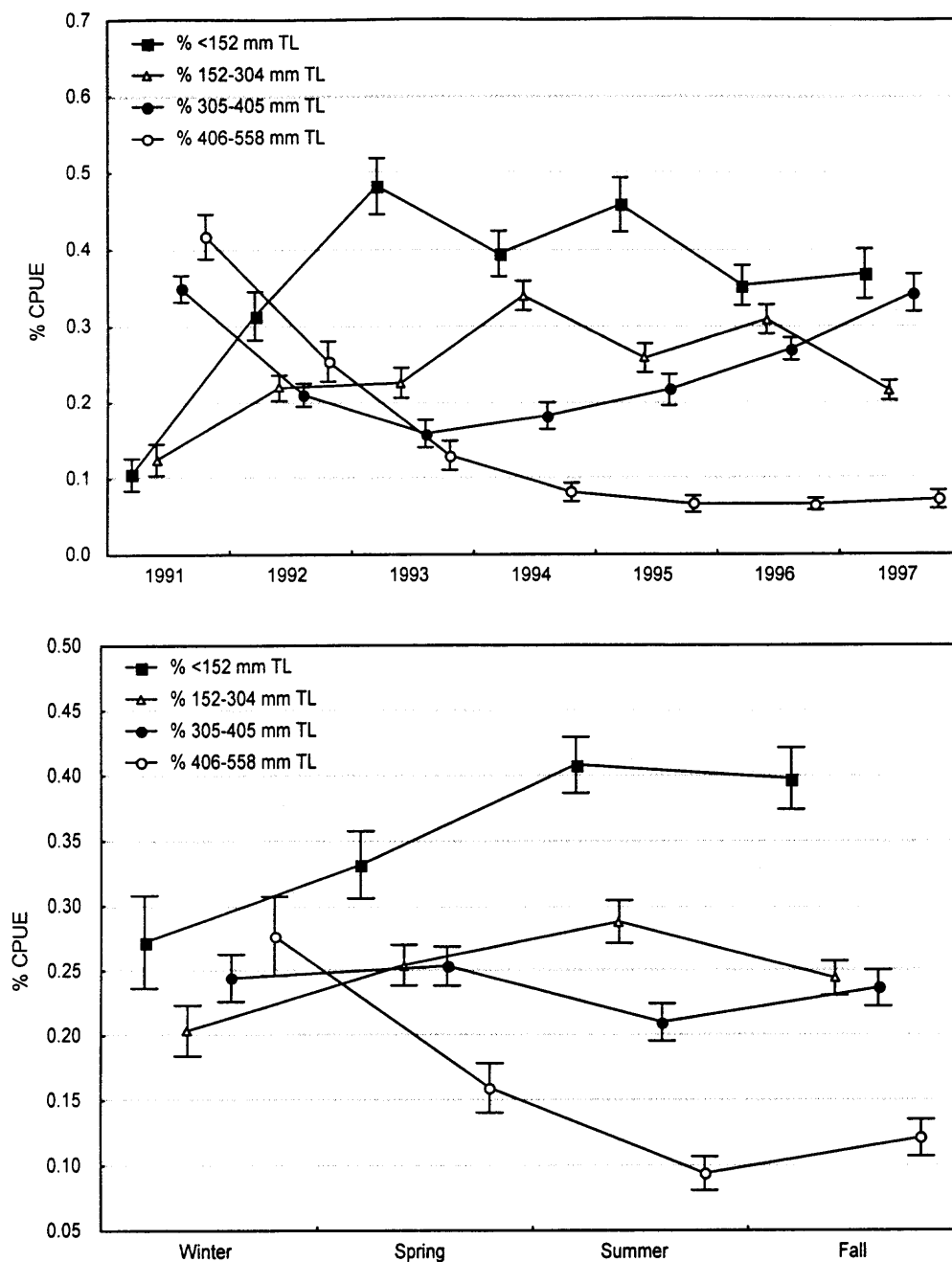


Figure 15. Size-specific percent composition of rainbow trout CPUE ( $\pm 1$  SE) by year (top) and seasons (bottom) in the Lee's Ferry reach, Colorado River, 1991-1997.

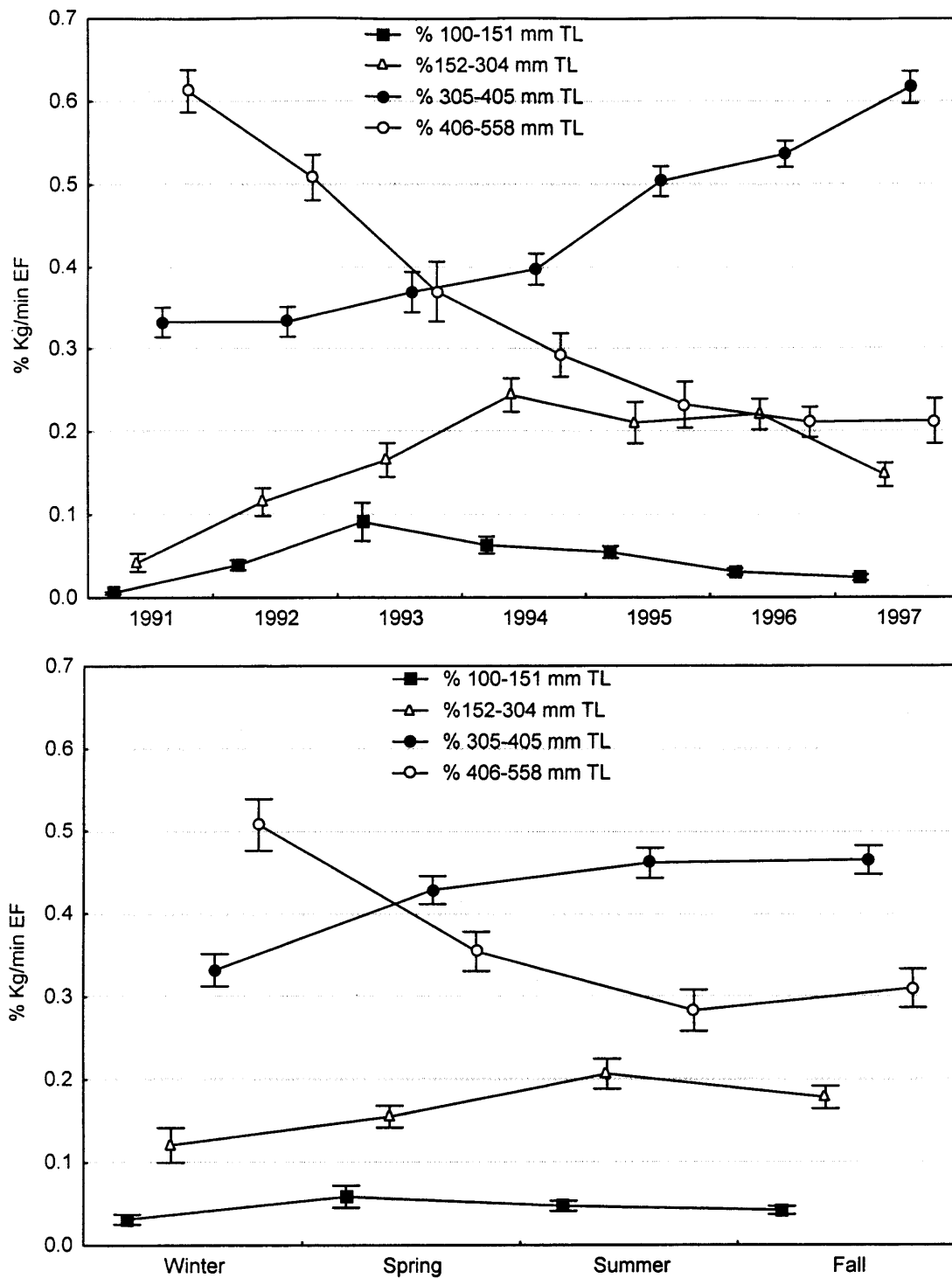


Figure 16. Size-specific percent composition of rainbow trout kg/minute EF ( $\pm 1$  SE) by year (top) and seasons (bottom) in the Lee's Ferry reach, Colorado River, 1991-1997.

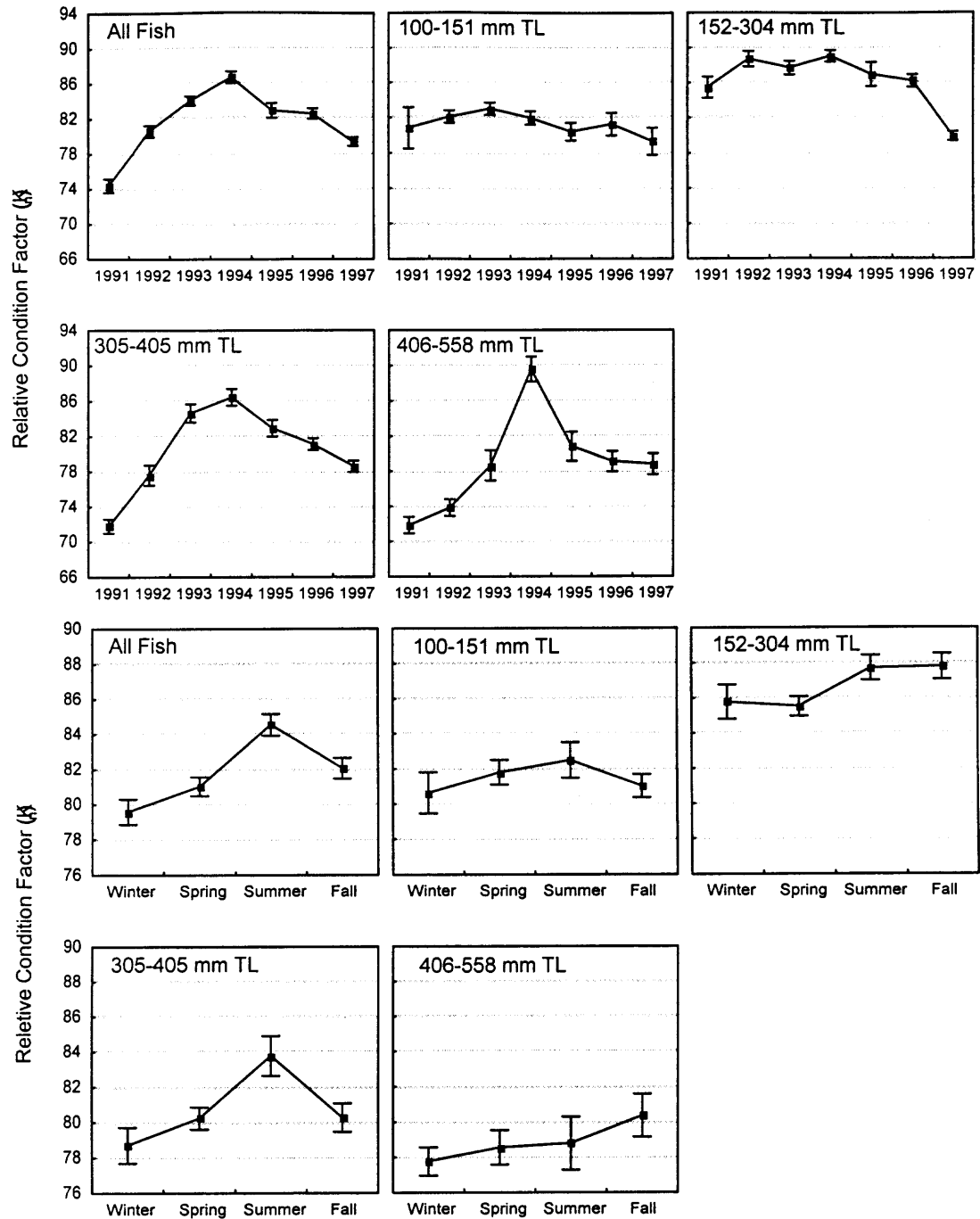


Figure 17. Relative condition factor of rainbow trout ( $\pm 1$  SE) by year (top) and season (bottom) in the Lee's Ferry reach, Colorado River, 1991-1997.

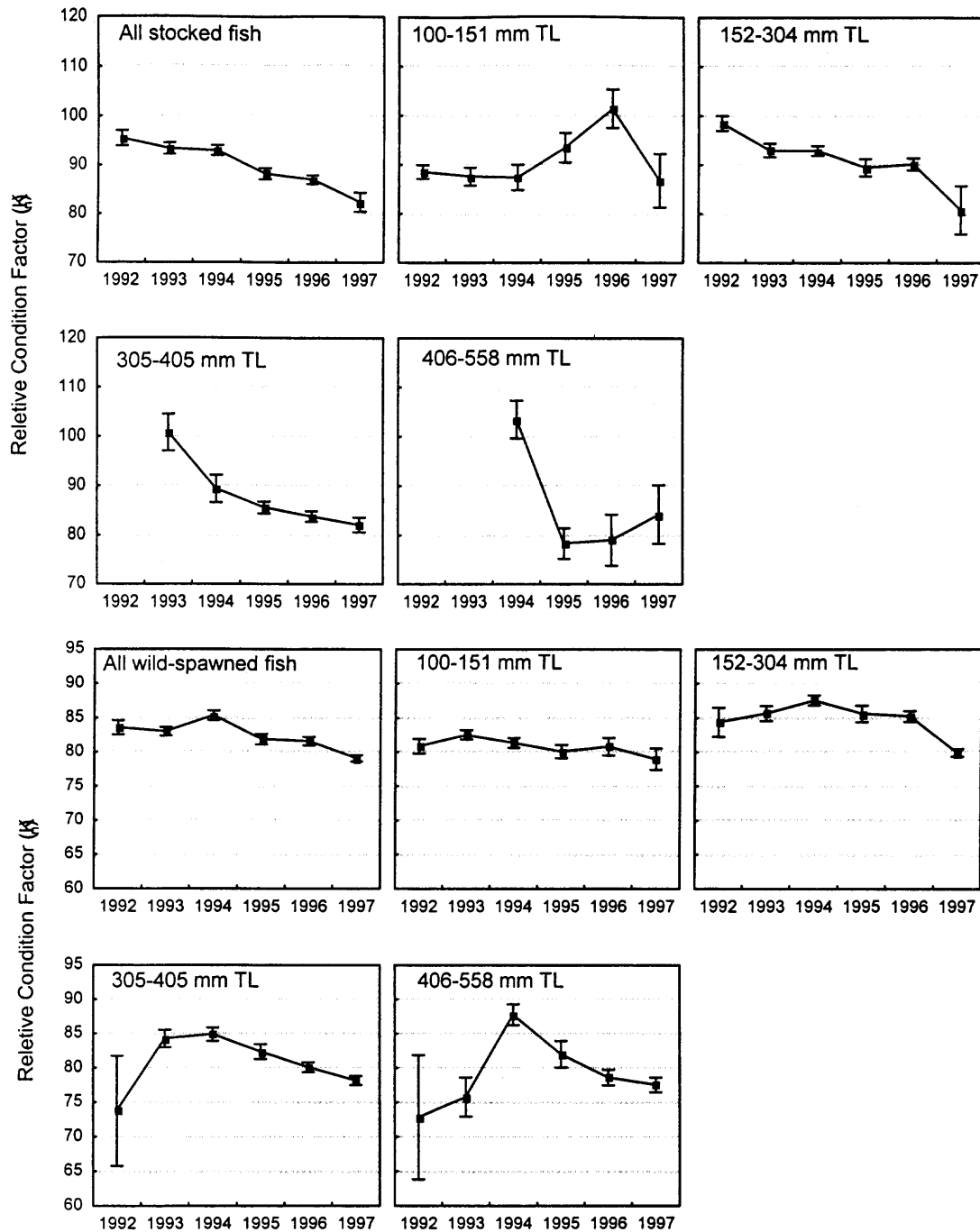


Figure 18. Yearly relative condition factor of hatchery-reared (top) and wild (bottom) rainbow trout ( $\pm 1$  SE) in the Lee's Ferry reach, Colorado River, 1992-1997.

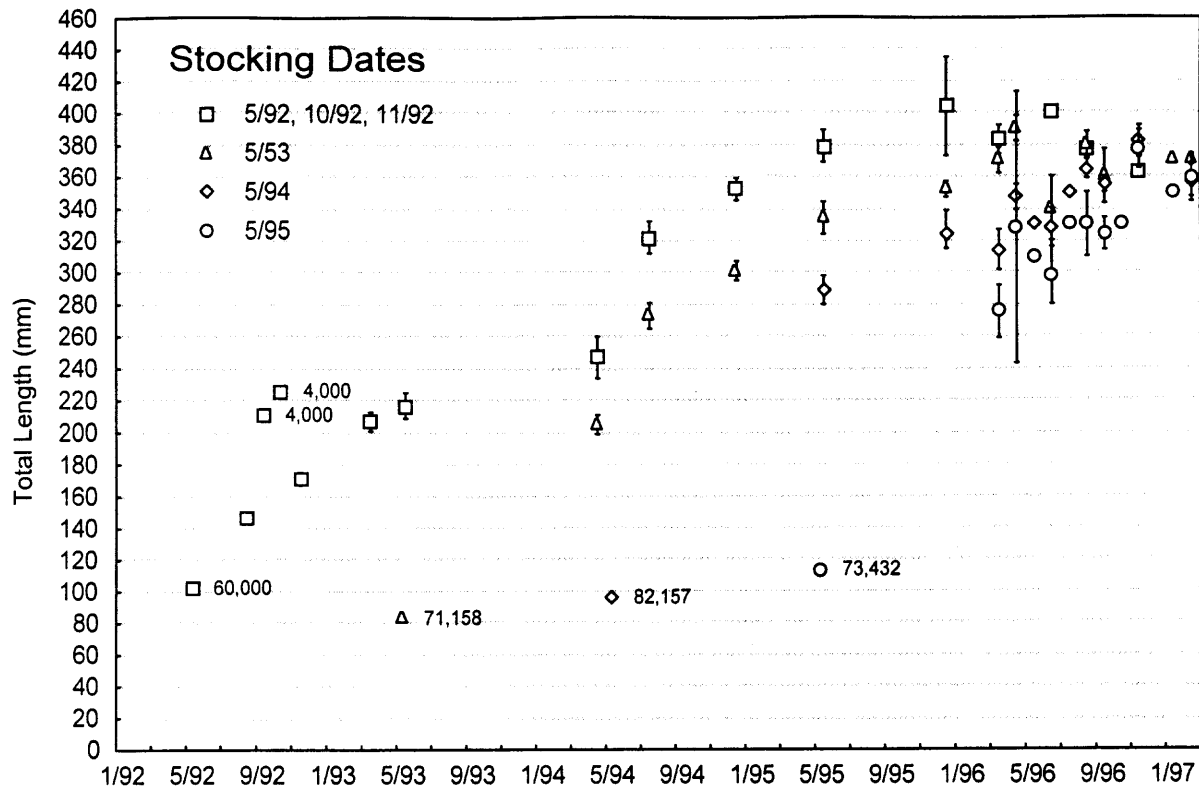


Figure 19. Mean lengths of coded-wire tagged rainbow trout ( $\pm 1$  SE) in the Lee's Ferry reach, Colorado River, 1992-1997. Number of fish per stocking is indicated following initial mean length at stocking.

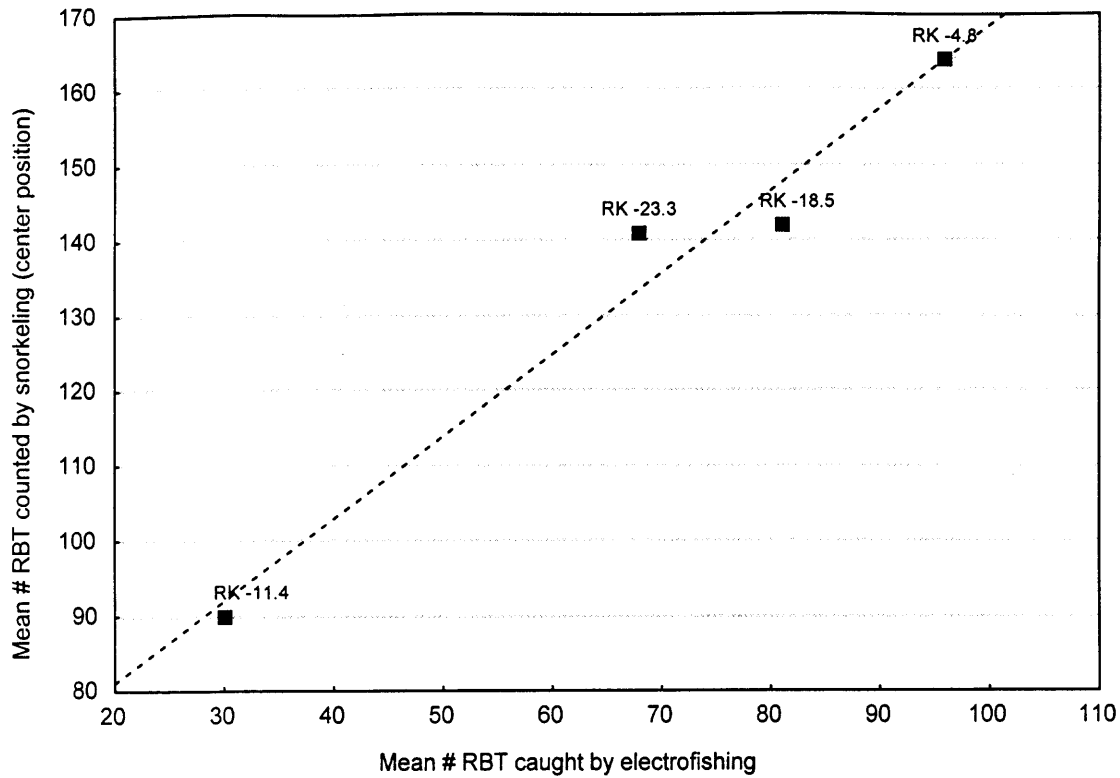


Figure 20. Mean number of rainbow trout counted by center diver in snorkel survey on August 26, 1998 in relation to number of fish caught by electrofishing at the same sites on August 7-9 1998, Lee's Ferry reach, Colorado River ( $Y=59.2 + 1.09X$ ).



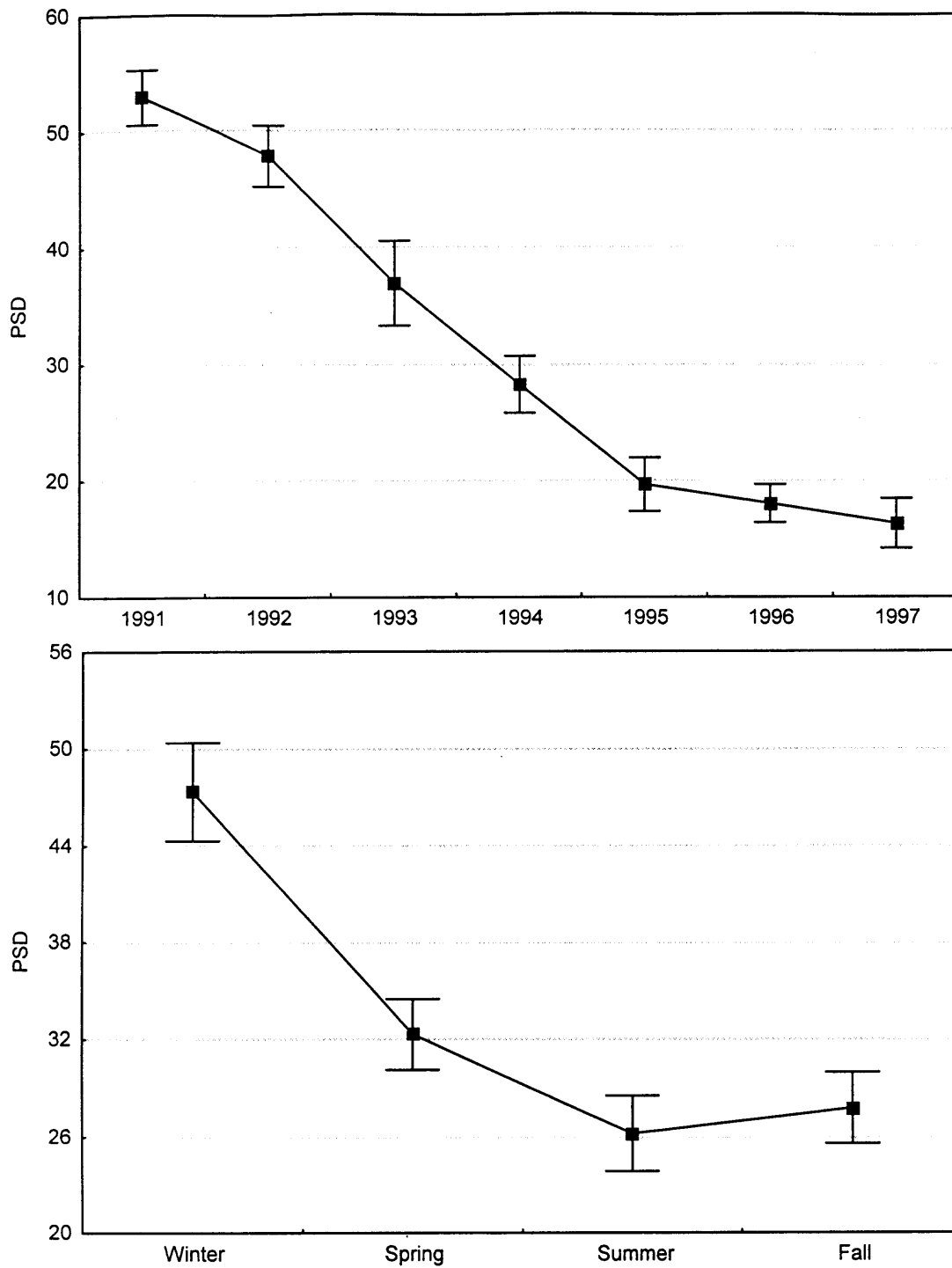


Figure 21. Yearly (top) and seasonal (bottom) proportional stock densities ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1991-1997.

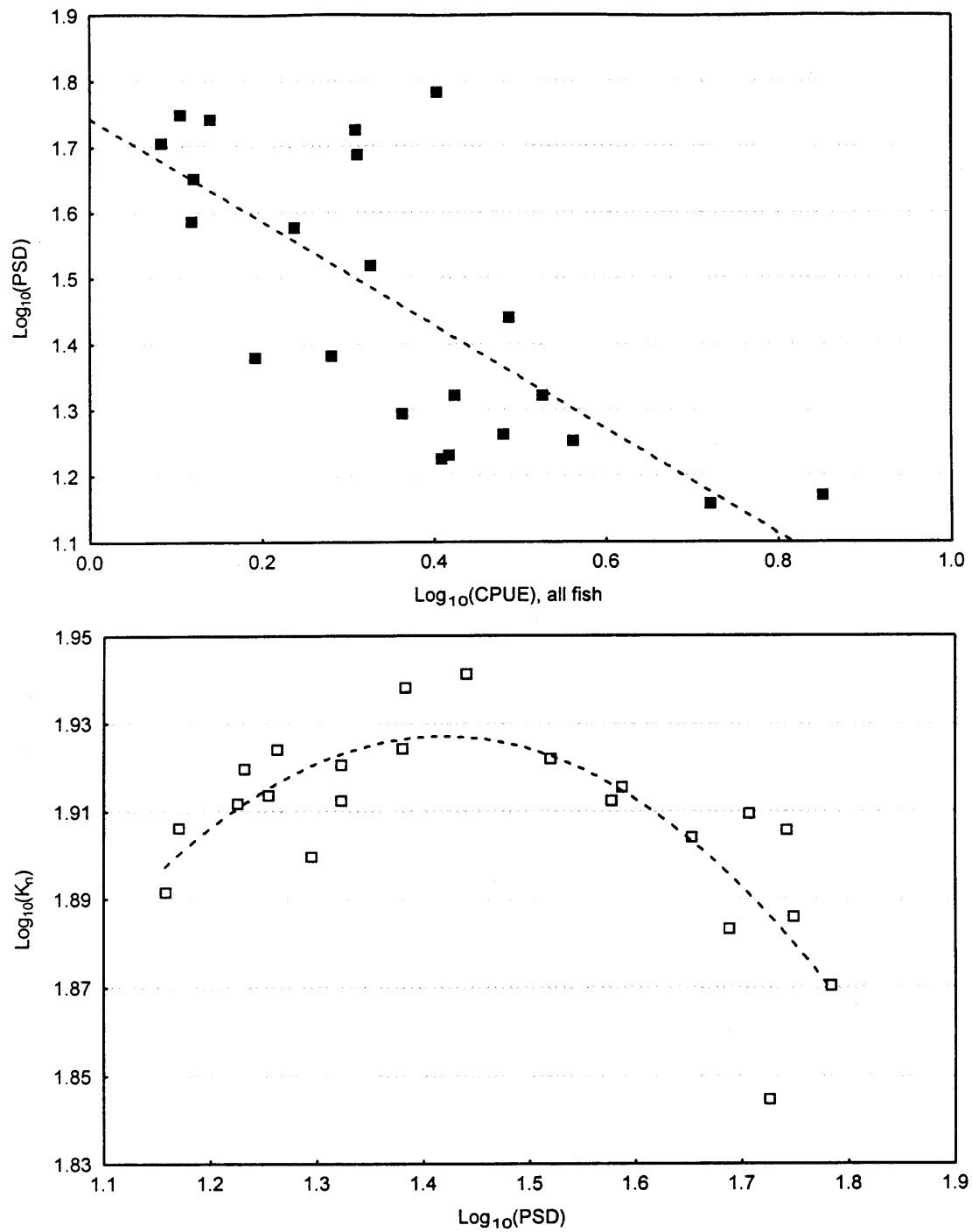


Figure 22. Relationships between proportional stock density and CPUE ( $Y=1.74 - 0.79X$ , top, closed boxes) and relative condition factor ( $Y=1.05 + 1.23X - 0.43X^2$ , bottom, open boxes) in the Lee's Ferry reach, 1991-1997.

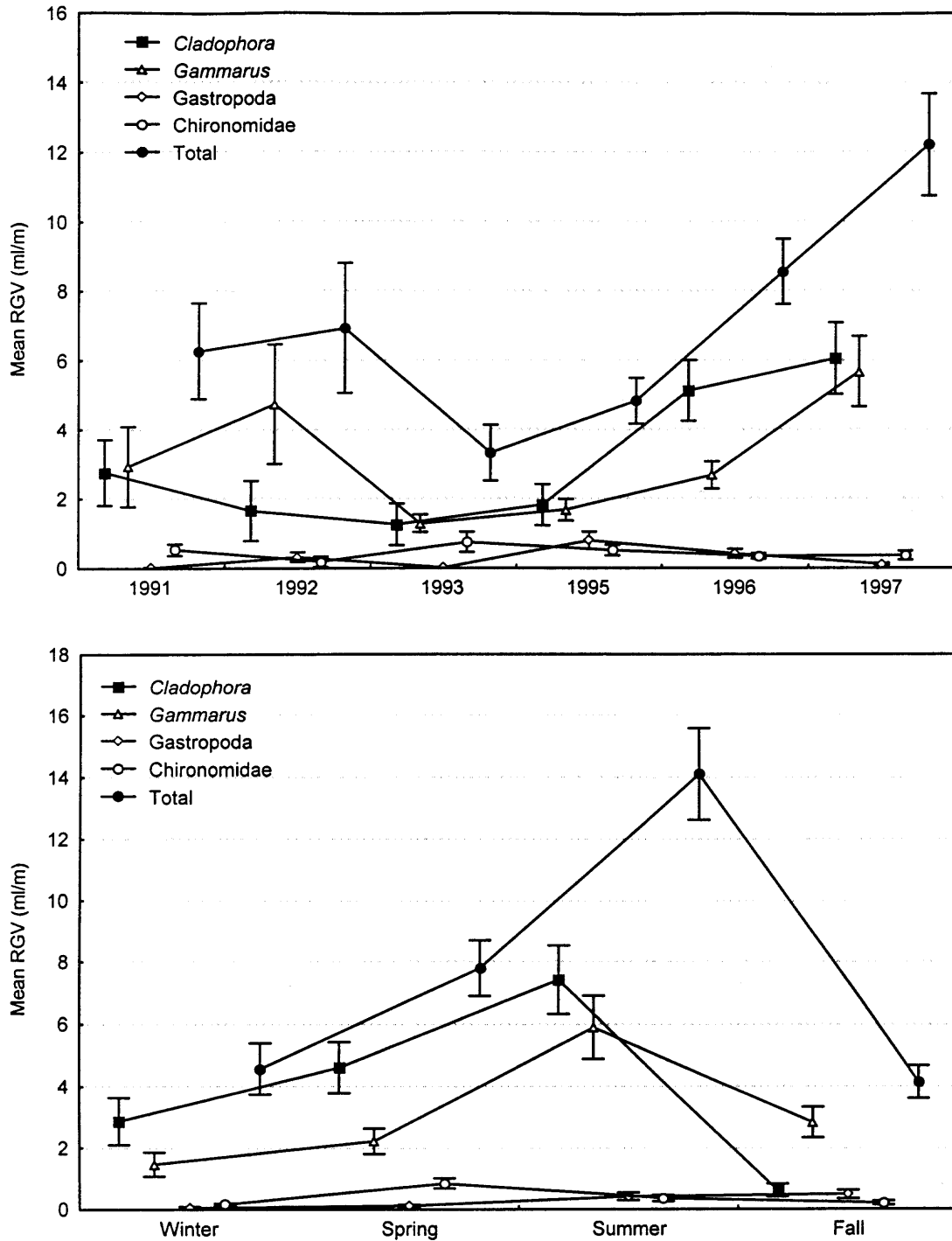


Figure 23. Yearly (top) and seasonal (bottom) mean relative gut volume (ml prey/m fish total length,  $\pm 1$  SE) of all rainbow trout for major prey taxa in the Lee's Ferry Reach, Colorado River, 1991-1997.

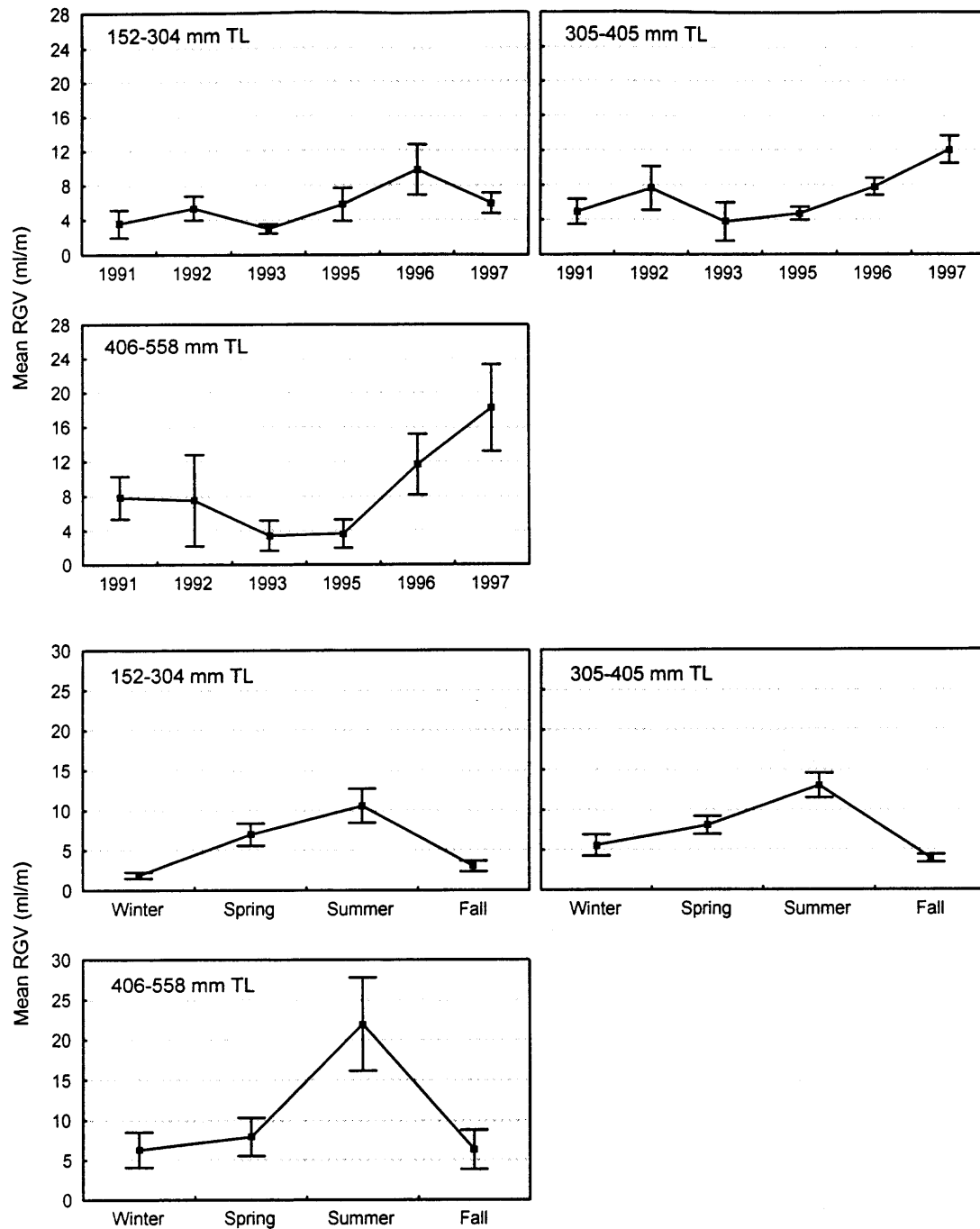


Figure 24. Yearly (top) and seasonal (bottom) size-specific total RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1991-1997.

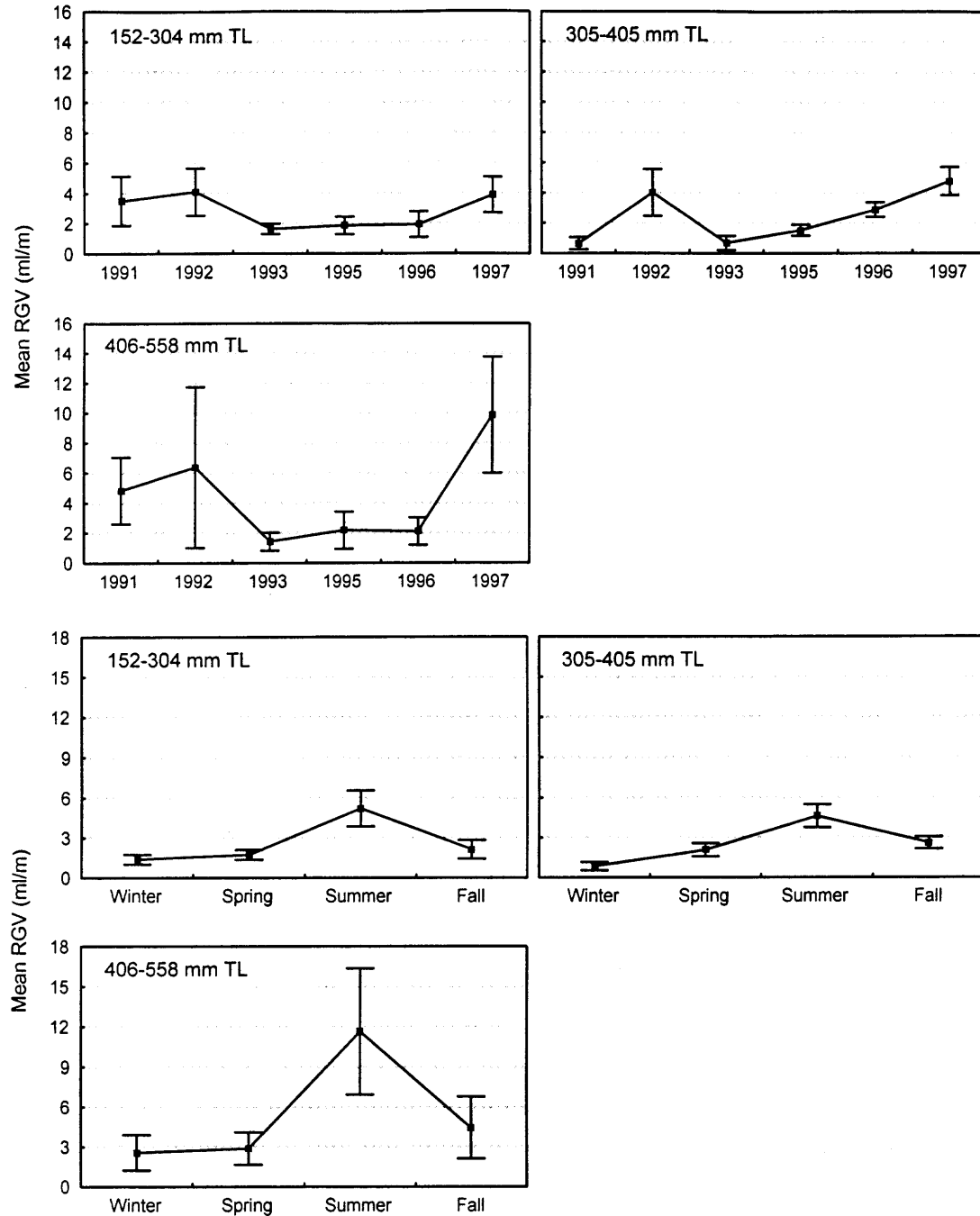


Figure 25. Yearly (top) and seasonal (bottom) size-specific *Gammarus* RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1991-1997.

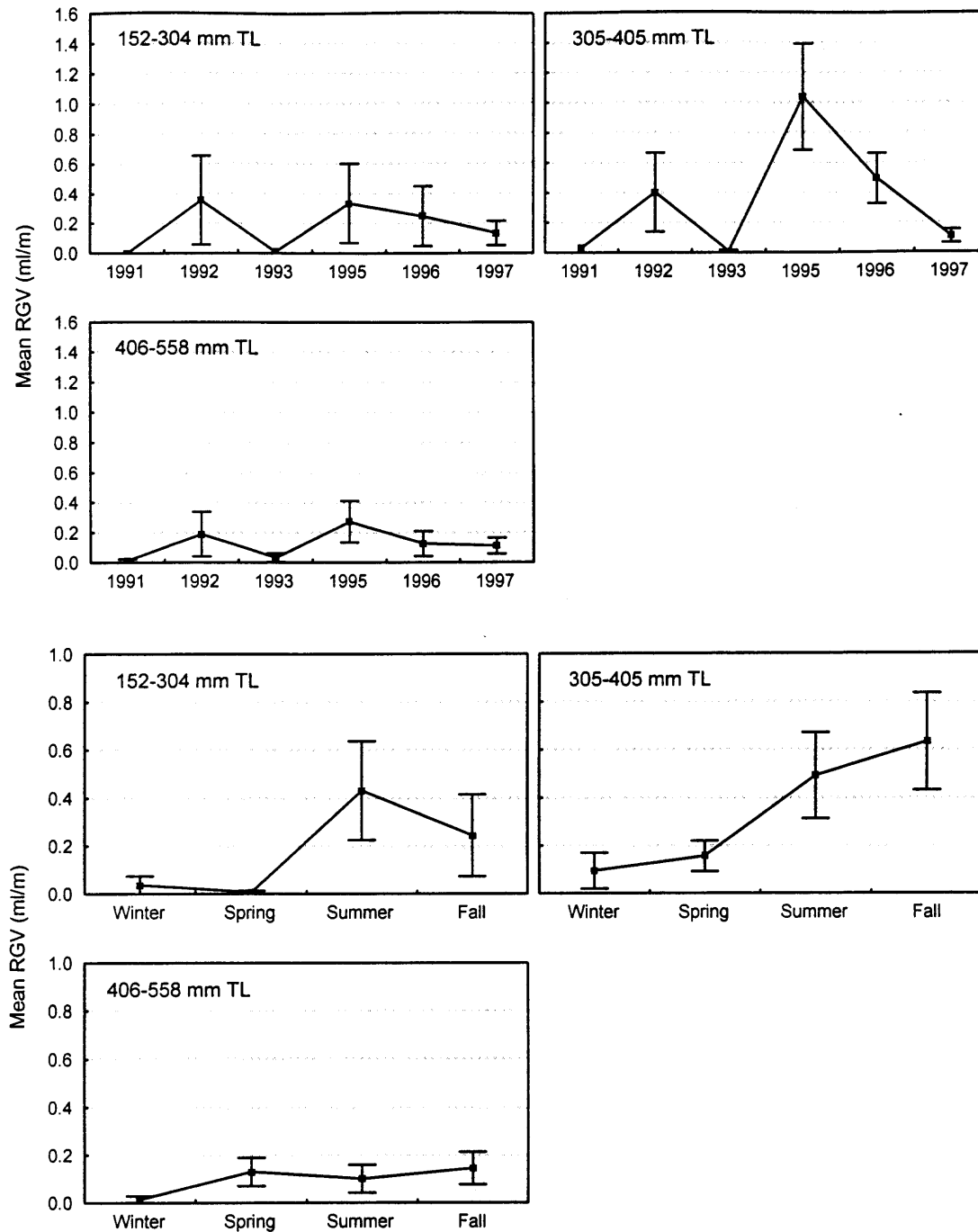


Figure 26. Yearly (top) and seasonal (bottom) size-specific gastropod RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1991-1997.

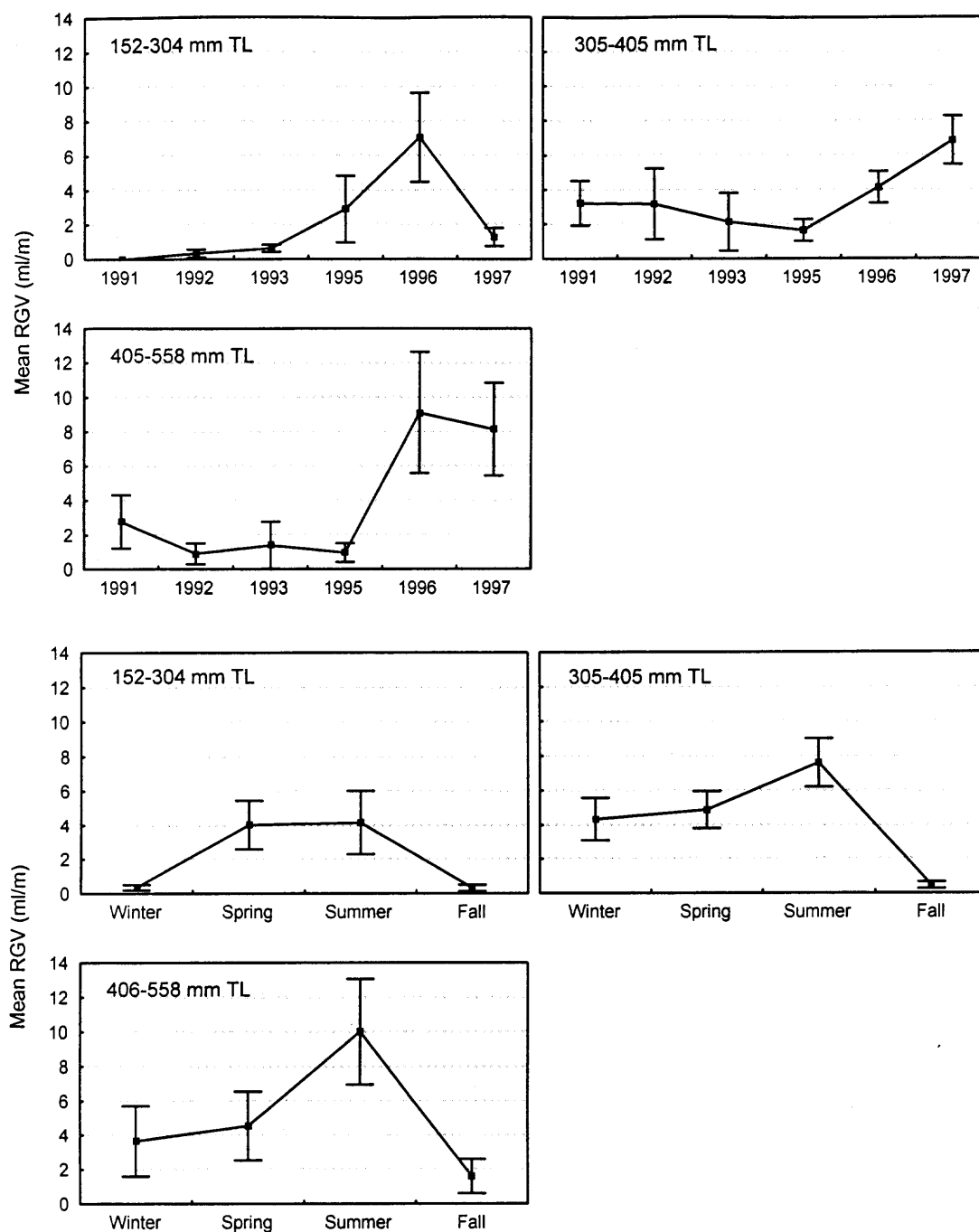


Figure 27. Yearly (top) and seasonal (bottom) size-specific *Cladophora* RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1991-1997.

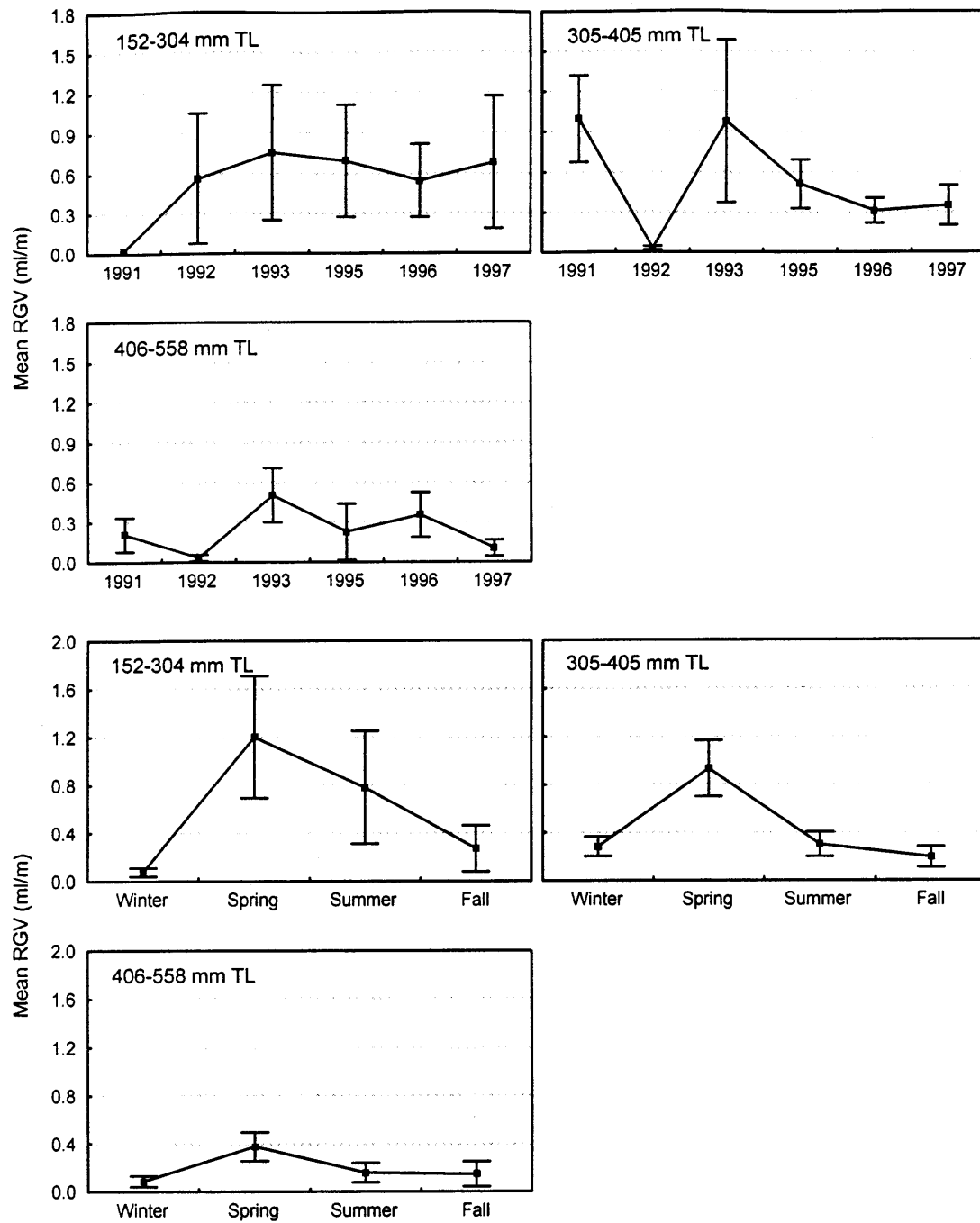


Figure 28. Yearly (top) and seasonal (bottom) size-specific chironomid RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1991-1997.



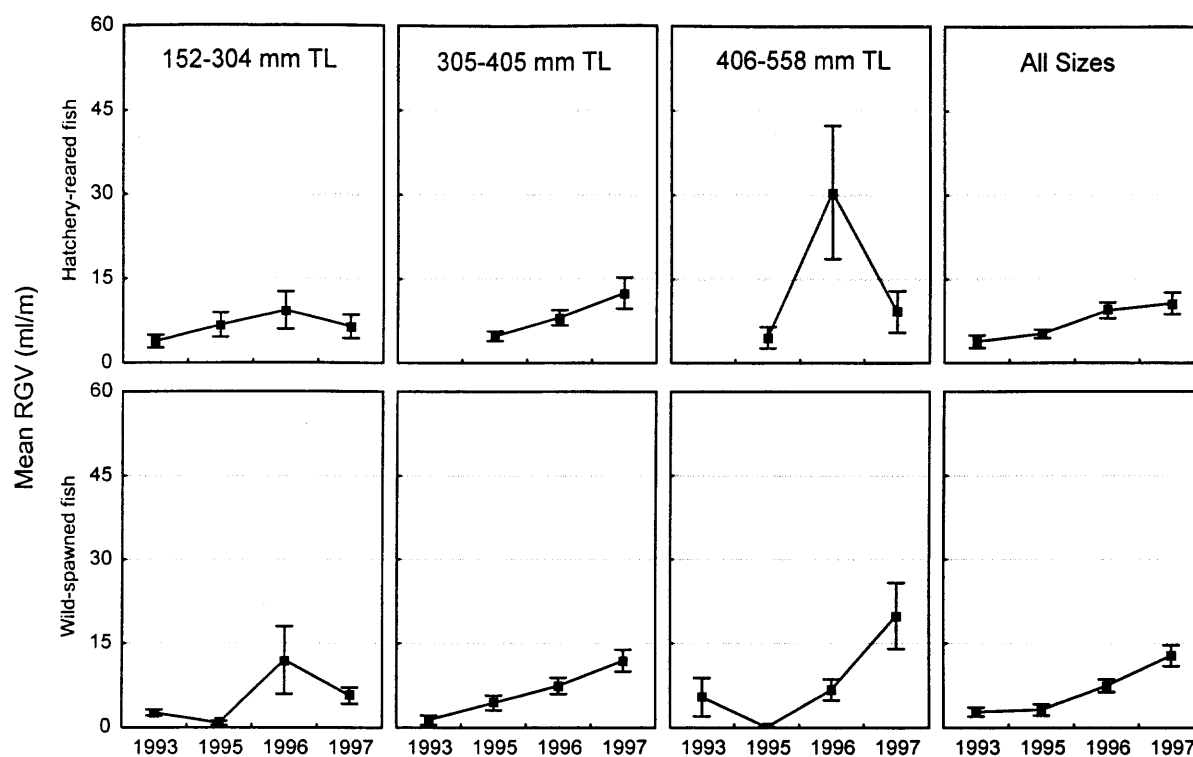


Figure 29. Yearly size- and origin-specific mean total RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1993-1997.

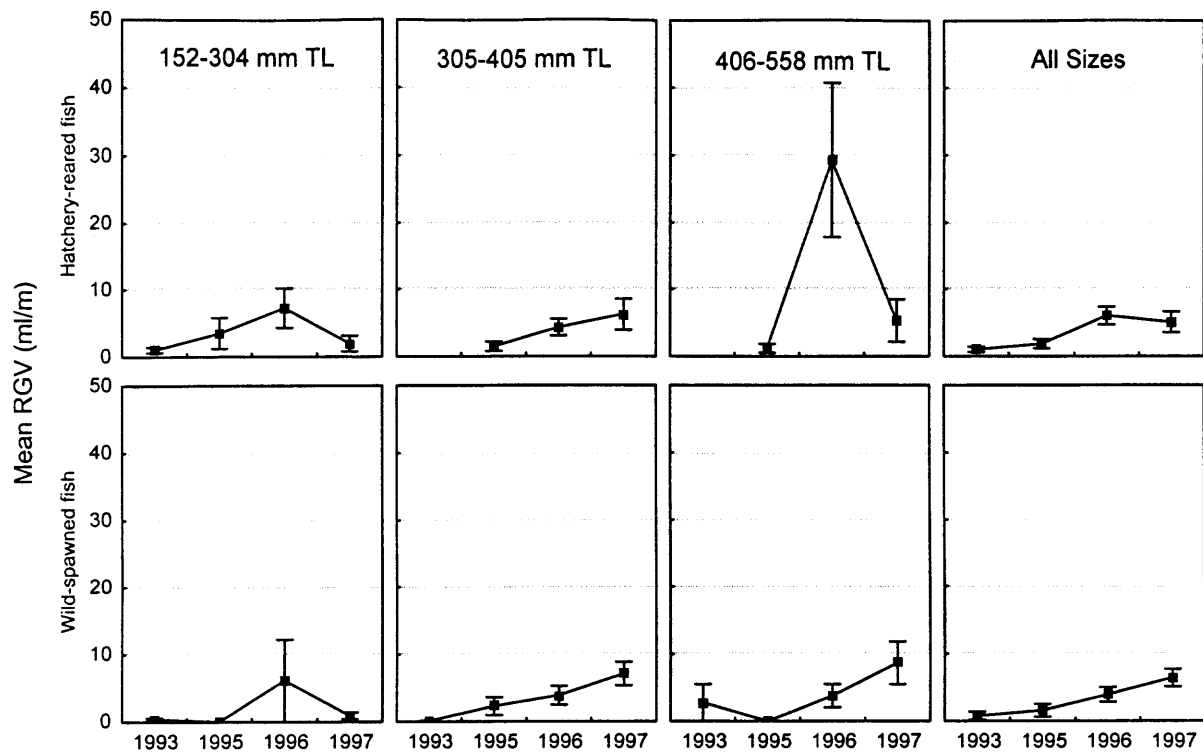


Figure 30. Yearly size- and origin-specific mean *Cladophora* RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1993-1997.

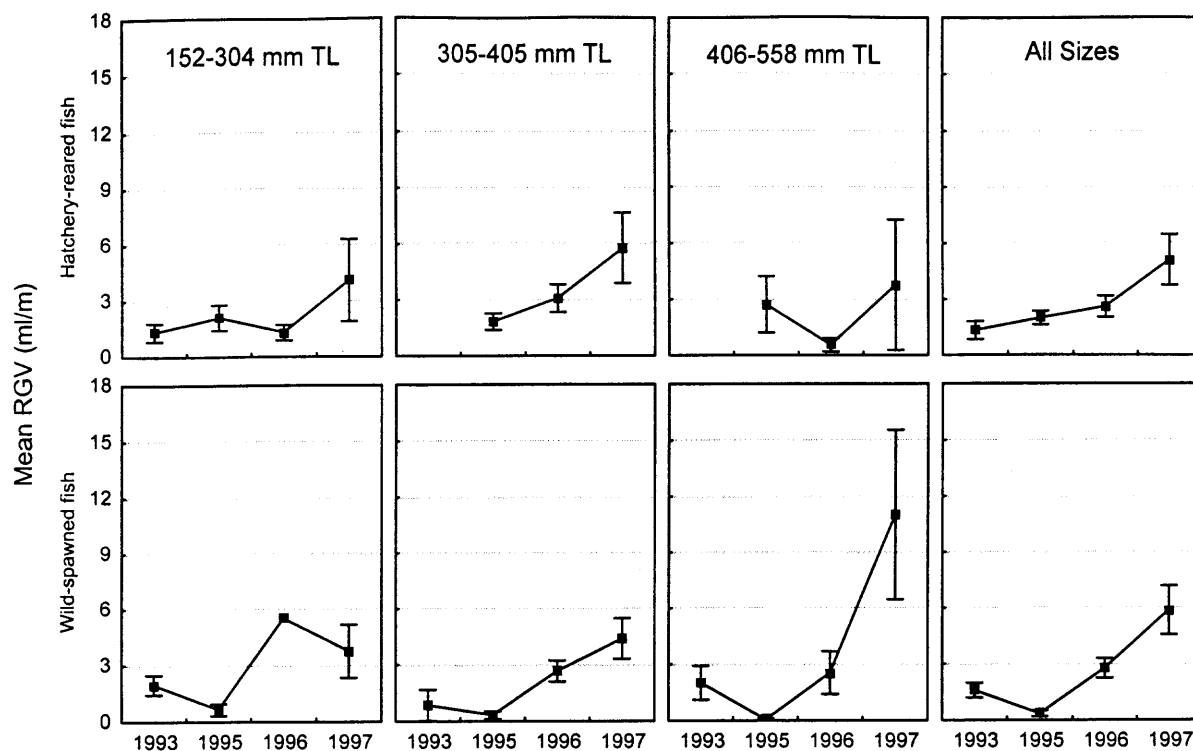


Figure 31. Yearly size- and origin-specific mean *Gammarus* RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1993-1997.

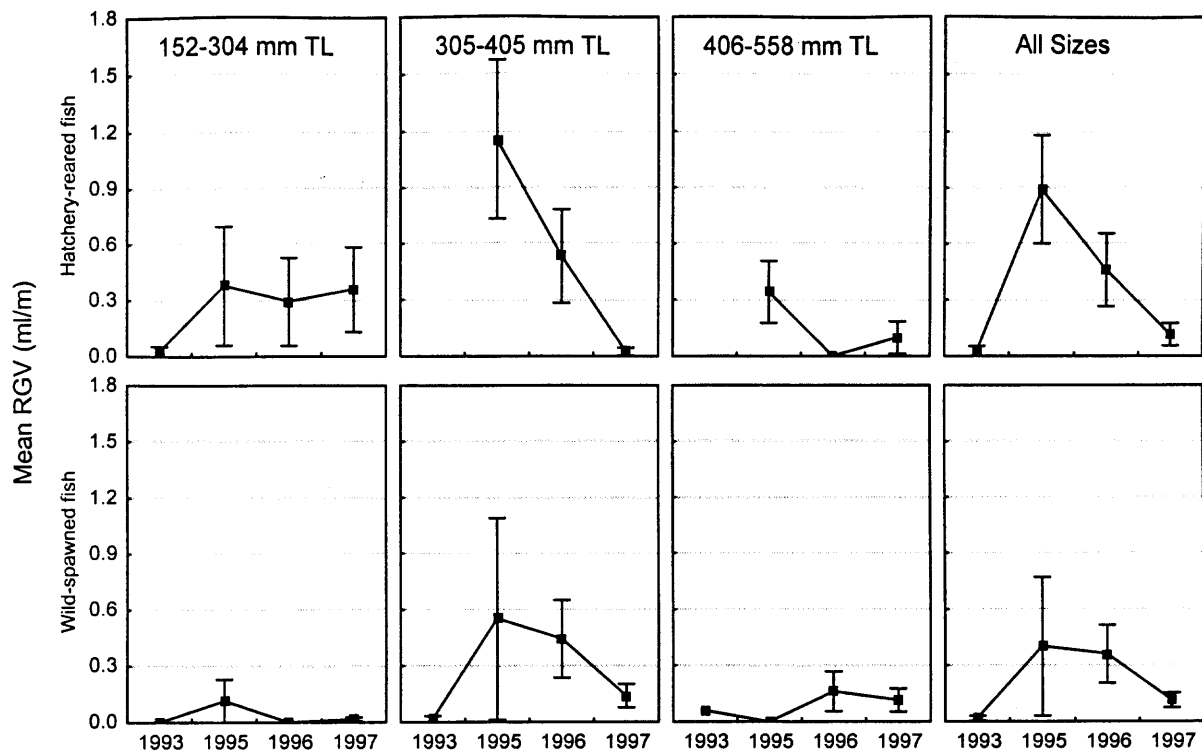


Figure 32. Yearly size- and origin-specific mean gastropod RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1993-1997.

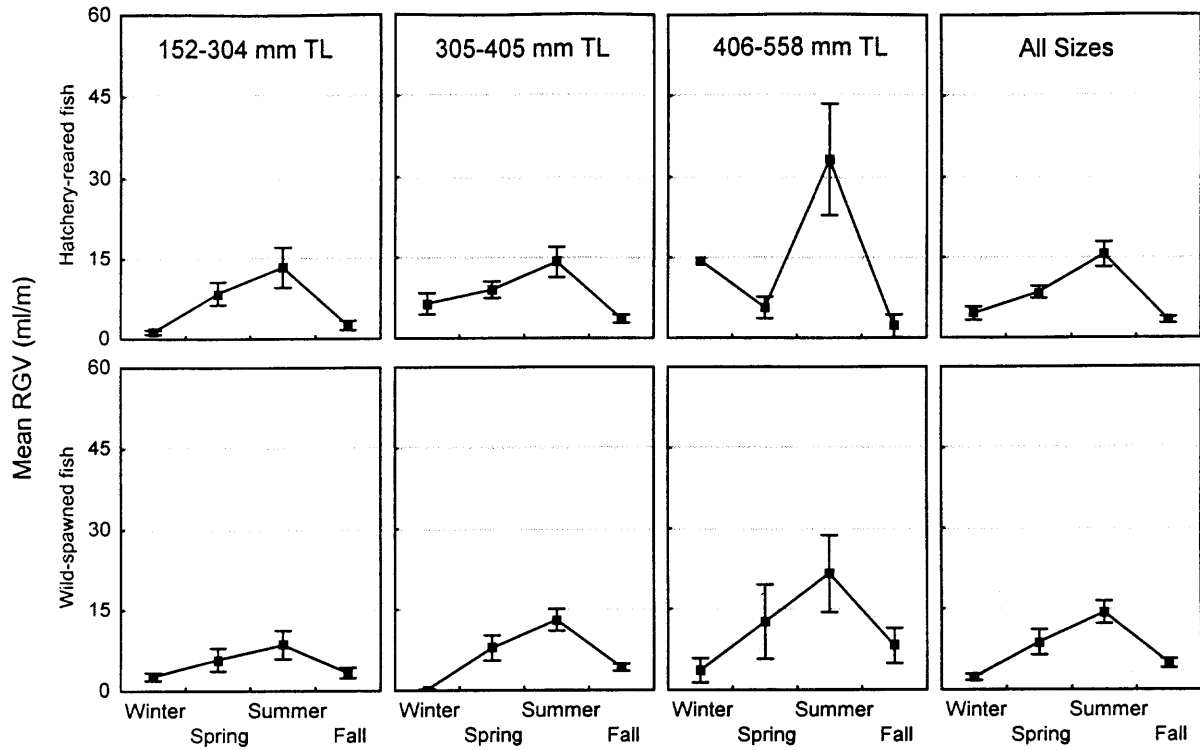


Figure 33. Seasonal size- and origin-specific mean total RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1992-1997.

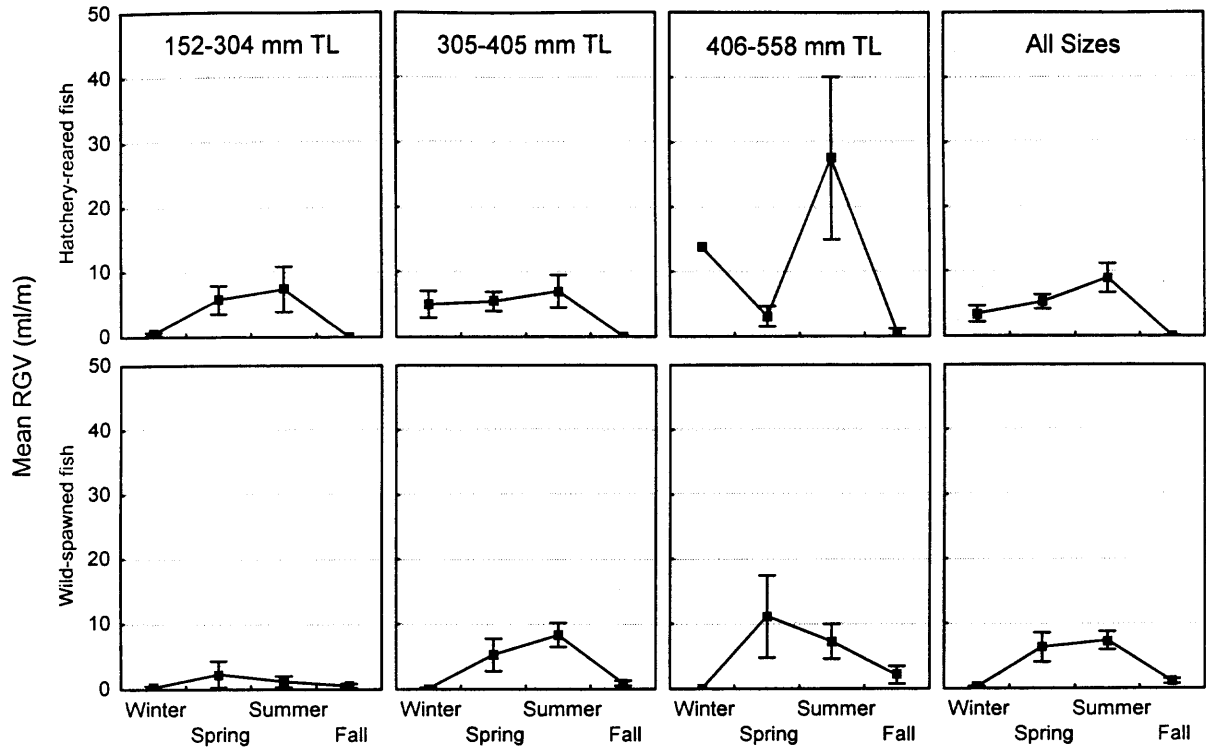


Figure 34. Seasonal size- and origin-specific mean *Cladophora* RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1992-1997.

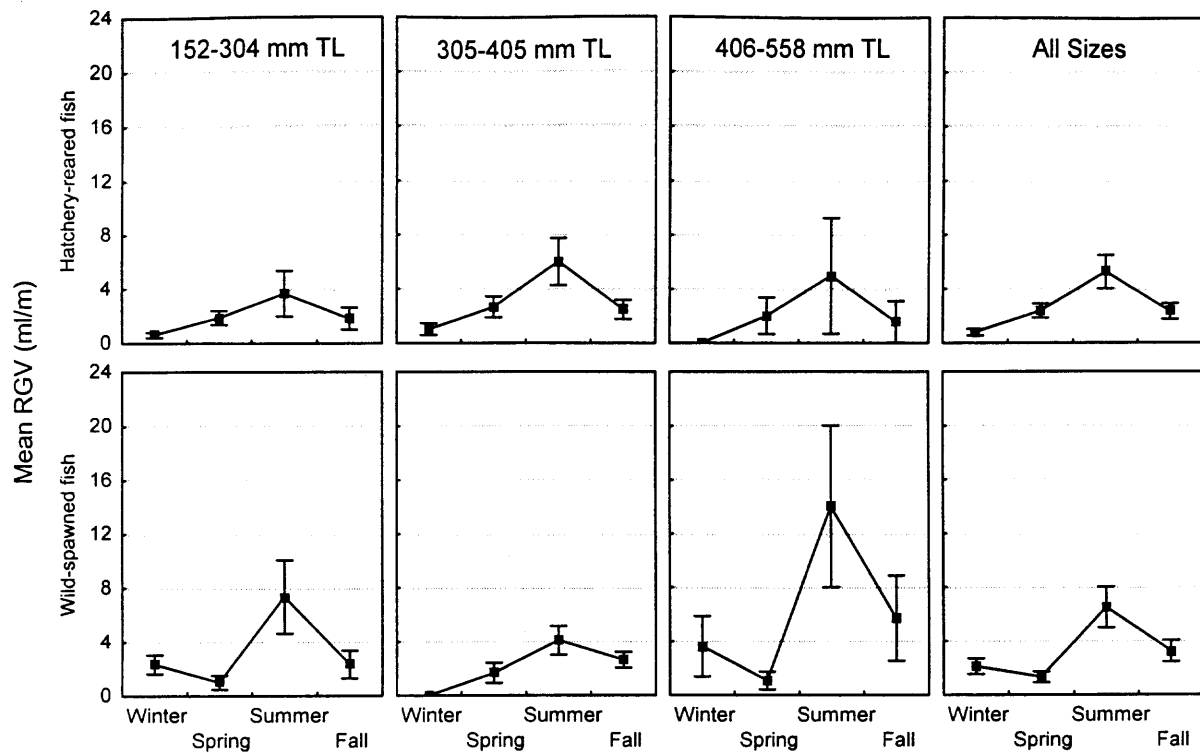


Figure 35. Seasonal size- and origin-specific mean *Gammarus* RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1992-1997.

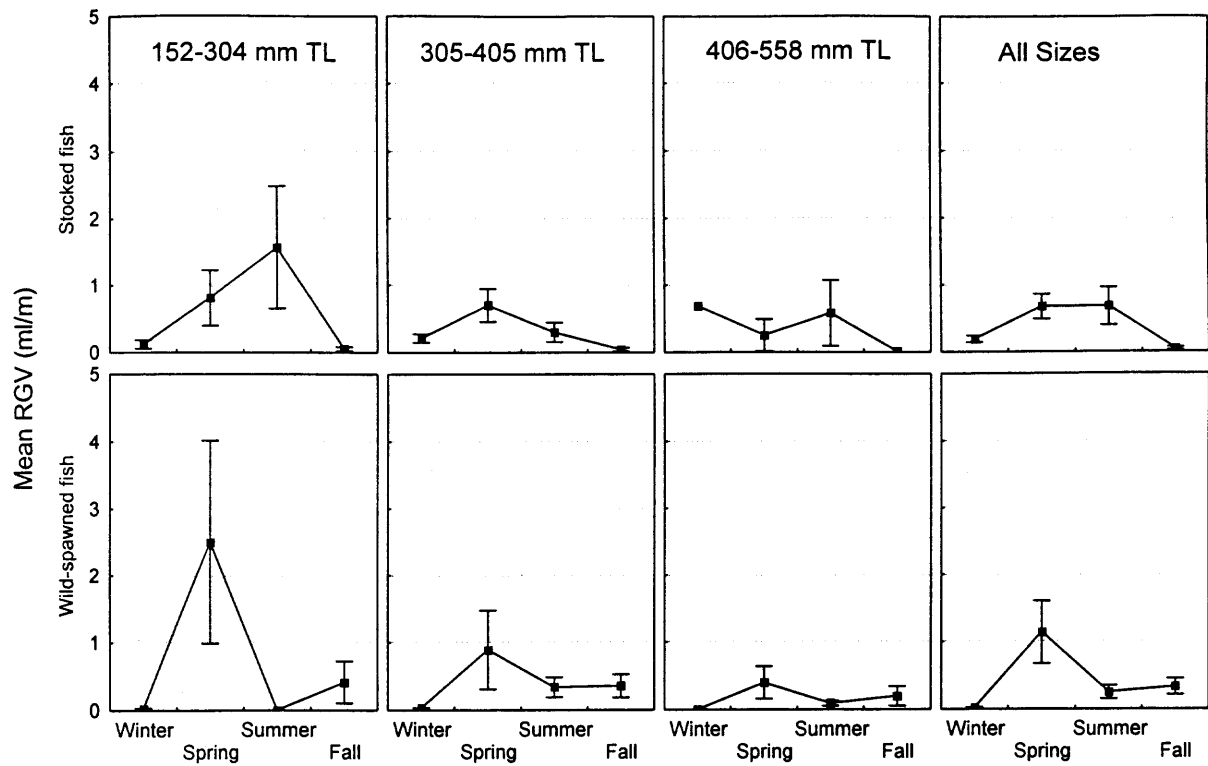


Figure 36. Seasonal size- and origin-specific mean chironomid RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1992-1997.



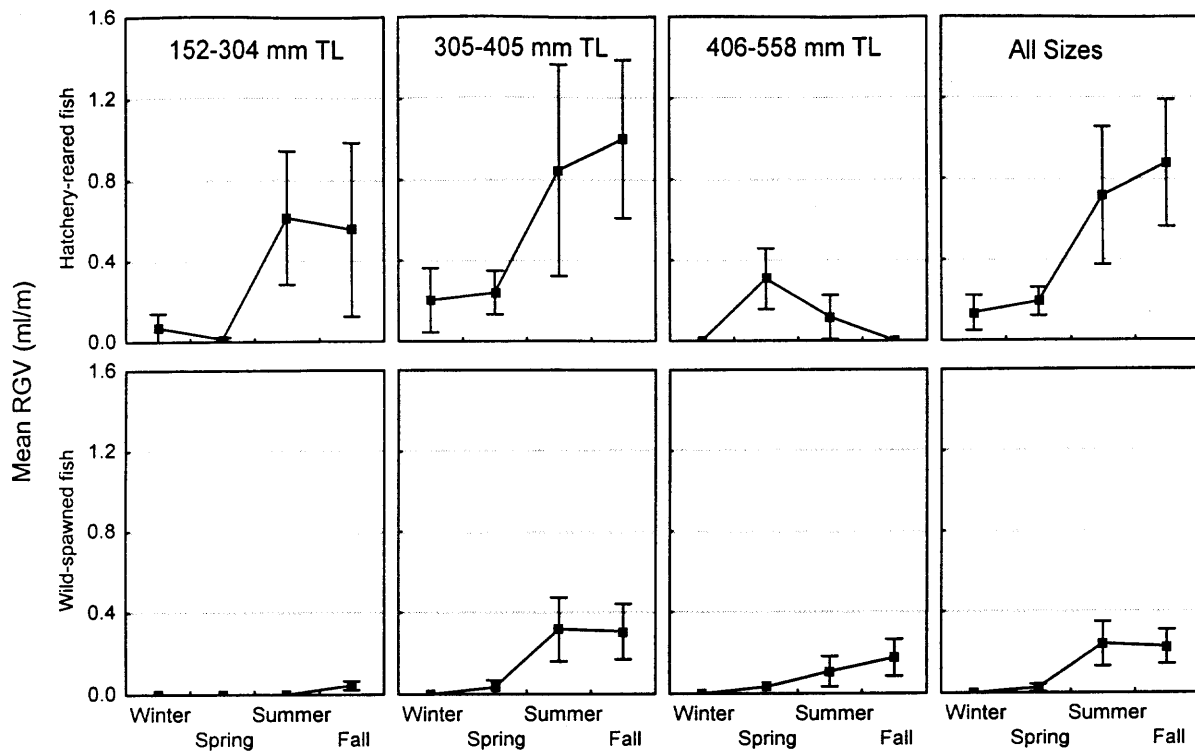


Figure 37. Seasonal size- and origin-specific mean gastropod RGV ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1992-1997.

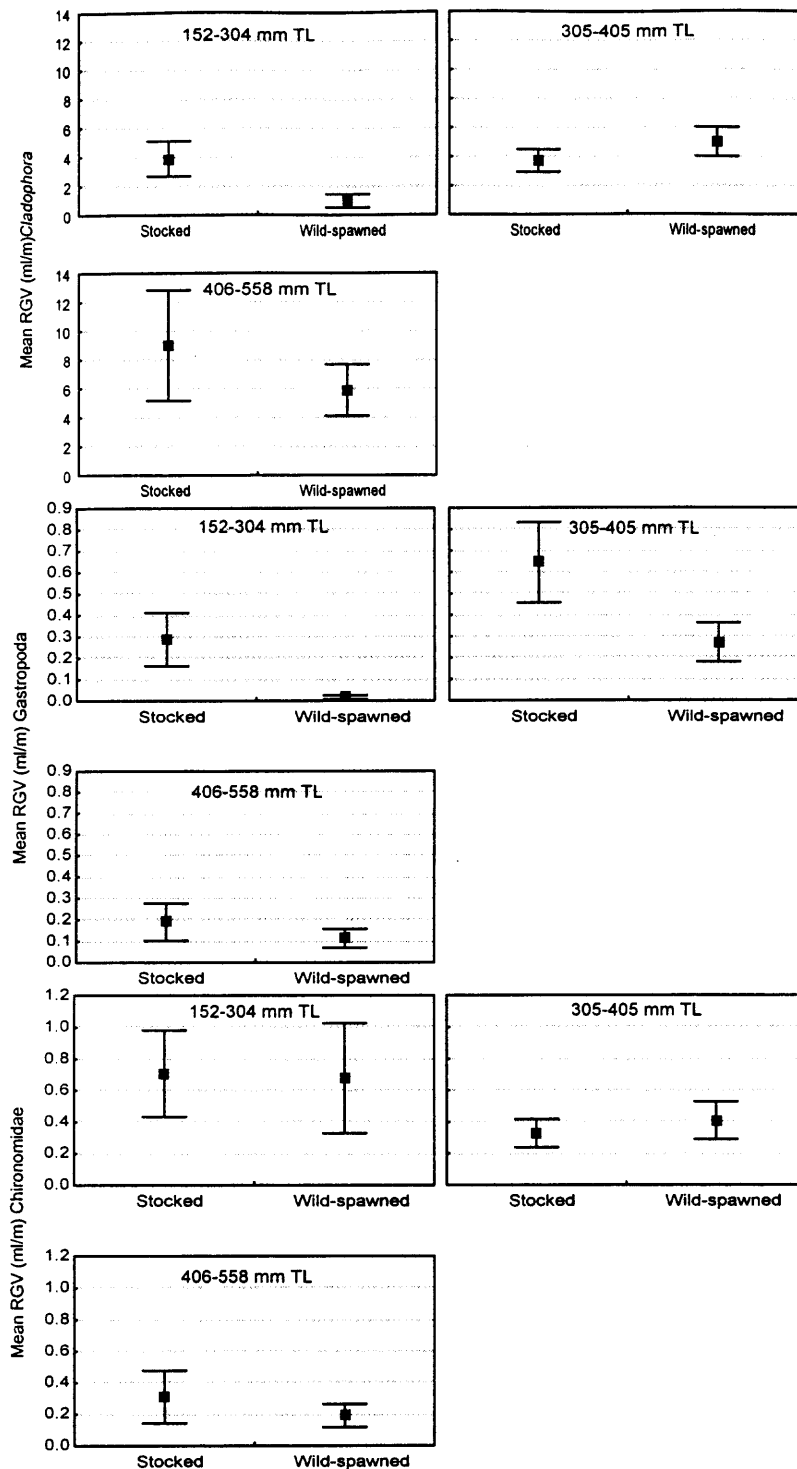


Figure 38. Mean *Cladophora* (top), gastropoda (middle) and chironomid (bottom) RGV ( $\pm 1$  SE) of hatchery- and wild-spawned rainbow in the Lee's Ferry reach, Colorado River, 1992-1997.

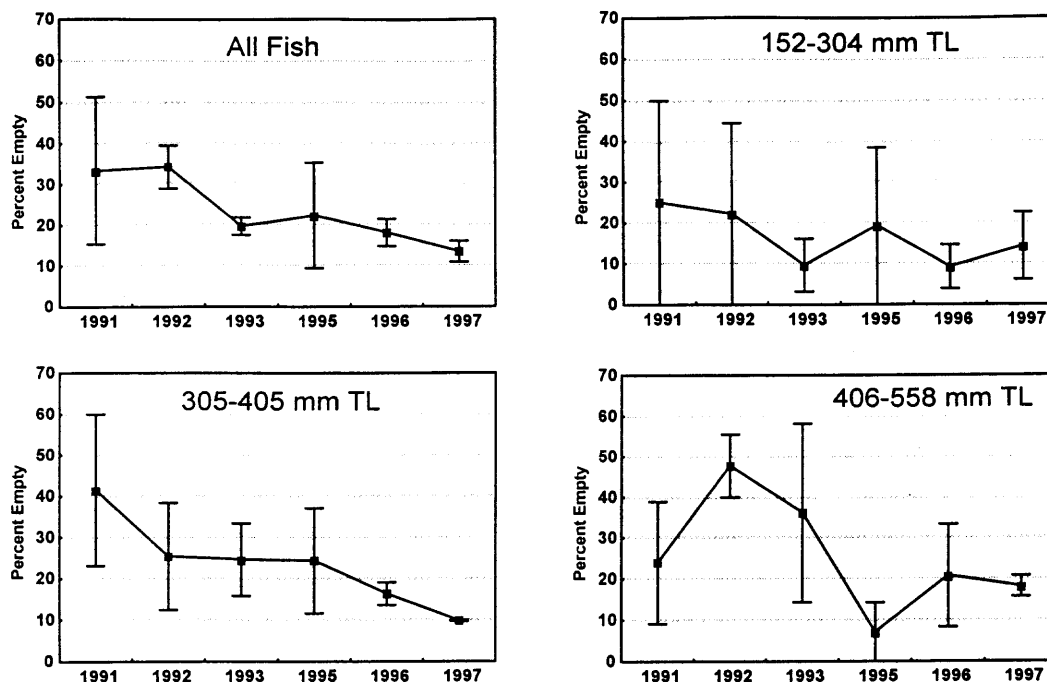


Figure 39. Length-specific yearly percentages of empty stomachs ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1991-1997.

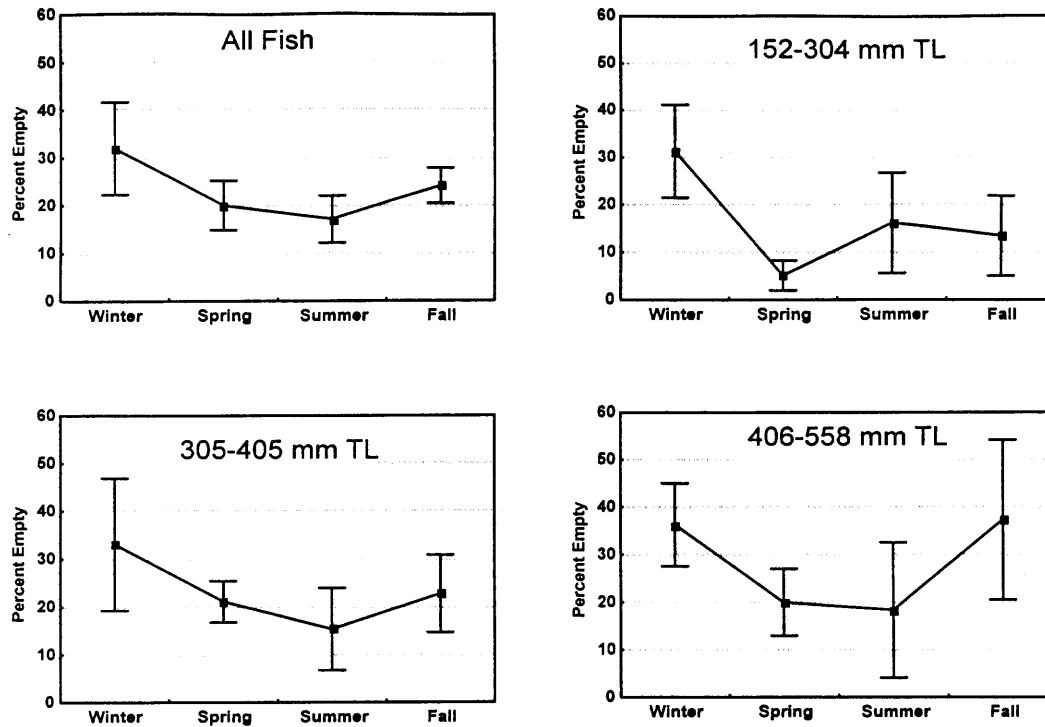


Figure 40. Length-specific seasonal percentages of empty stomachs ( $\pm 1$  SE) of rainbow trout in the Lee's Ferry reach, Colorado River 1991-1997.

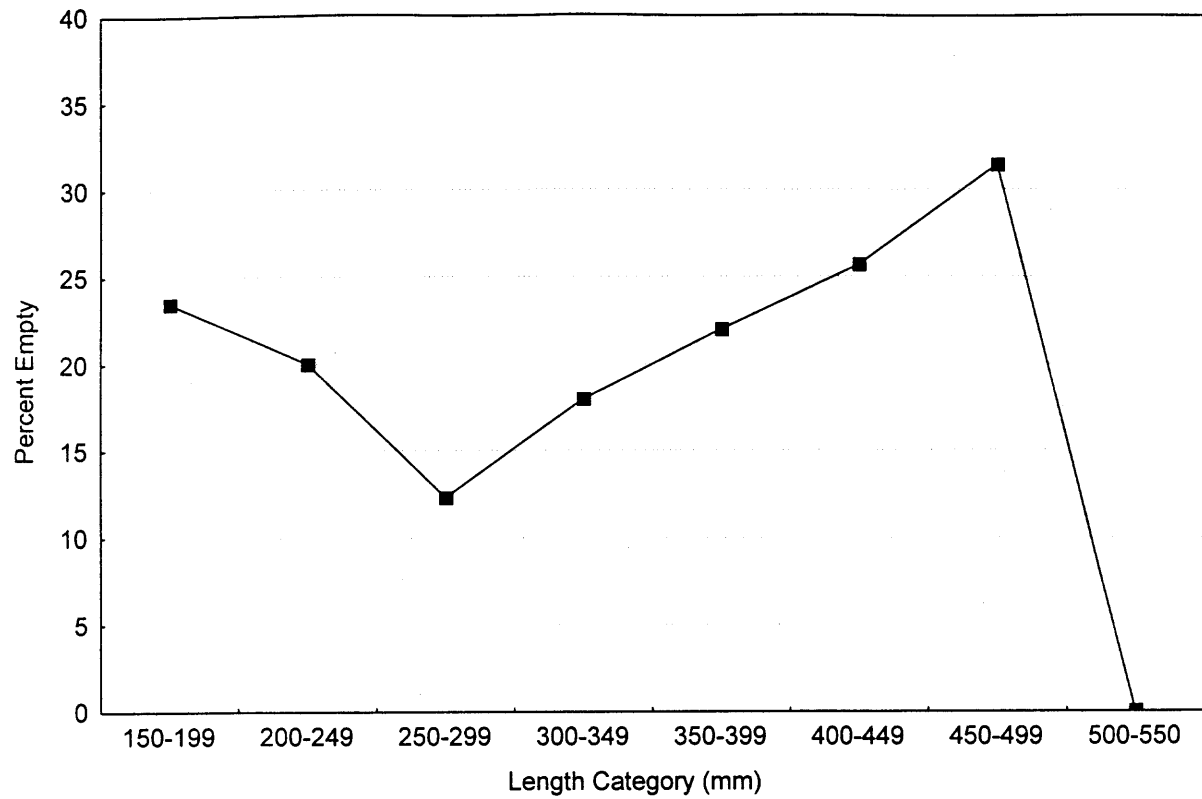


Figure 41. Percent empty stomachs of rainbow trout by 50 mm increments, Lee's Ferry reach, Colorado River, 1991-1997.

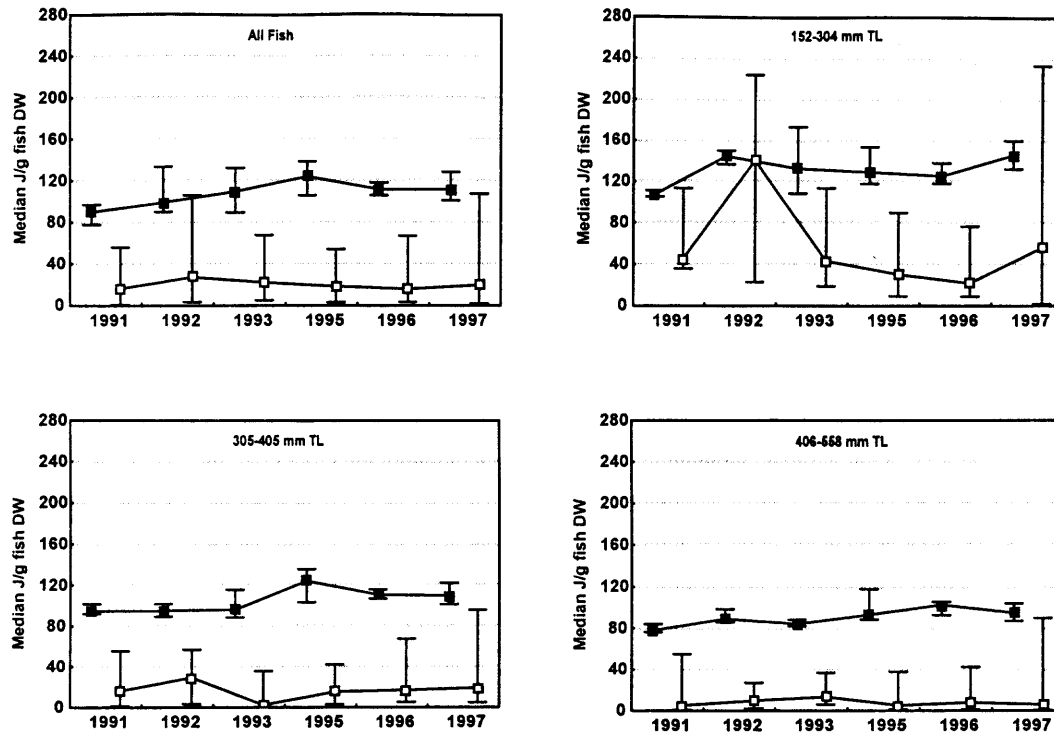


Figure 42. Yearly median (and 25% and 75% percentiles) maintenance energy requirement (J/g fish DW; closed boxes) and observed daily energy intake (open boxes) of rainbow trout in the Lee's Ferry reach, Colorado River, 1991-1997.

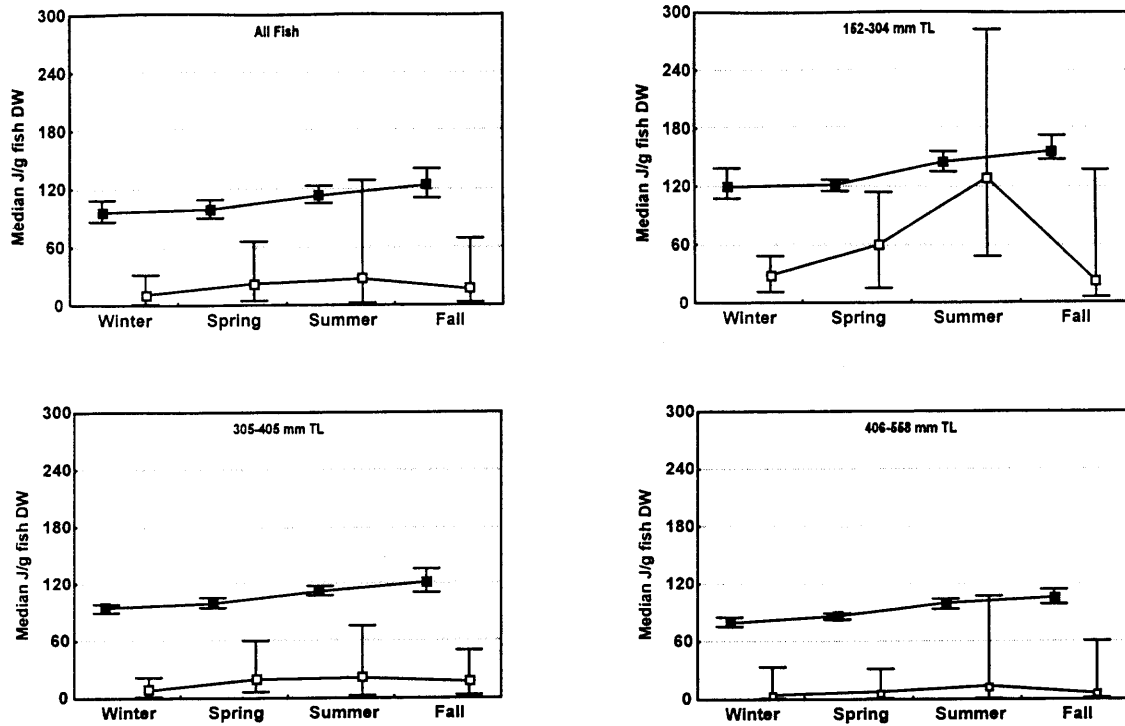


Figure 43. Seasonal median (and 25% and 75% percentiles) maintenance energy requirement (J/g fish DW; closed boxes) and observed daily energy intake (open boxes) of rainbow trout in the Lee's Ferry reach, Colorado River, 1991-1997.

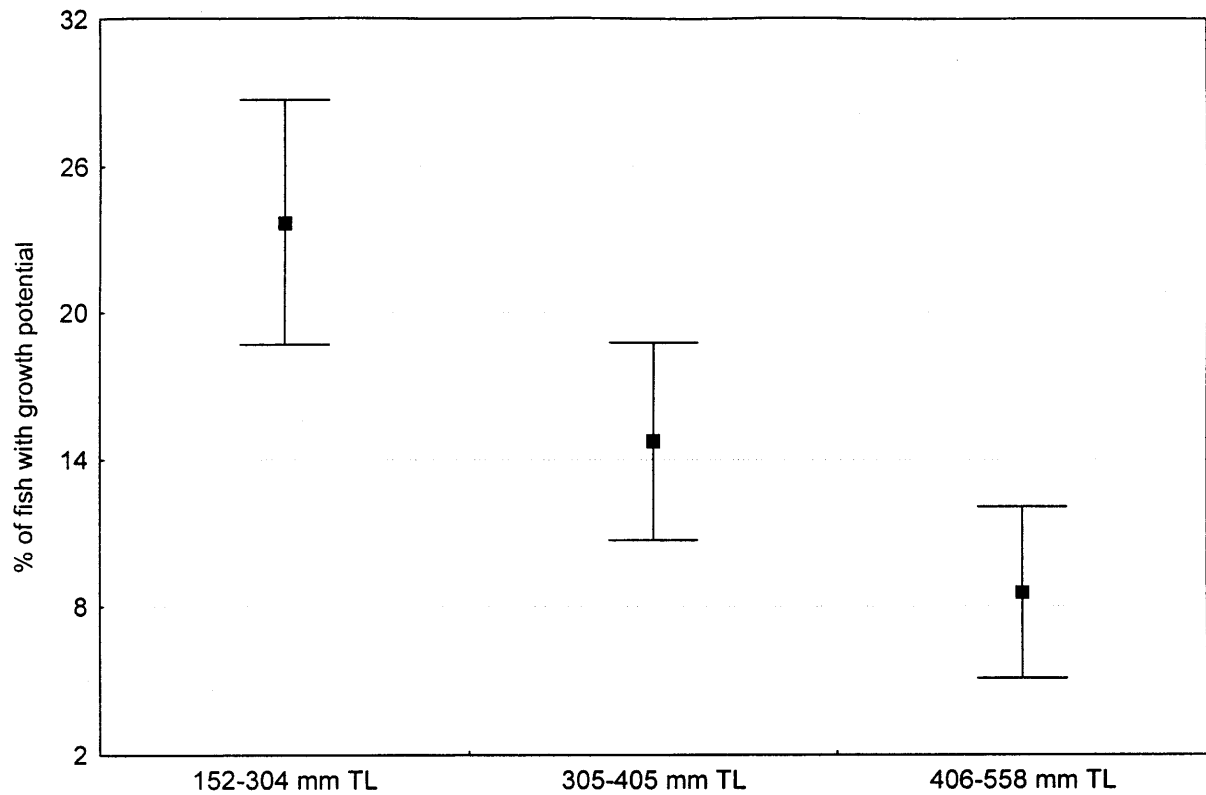


Figure 44. Length-specific percentages ( $\pm 1$  SE) of rainbow trout meeting or exceeding maintenance energy requirements in the Lee's Ferry reach, Colorado River, 1991-1997.



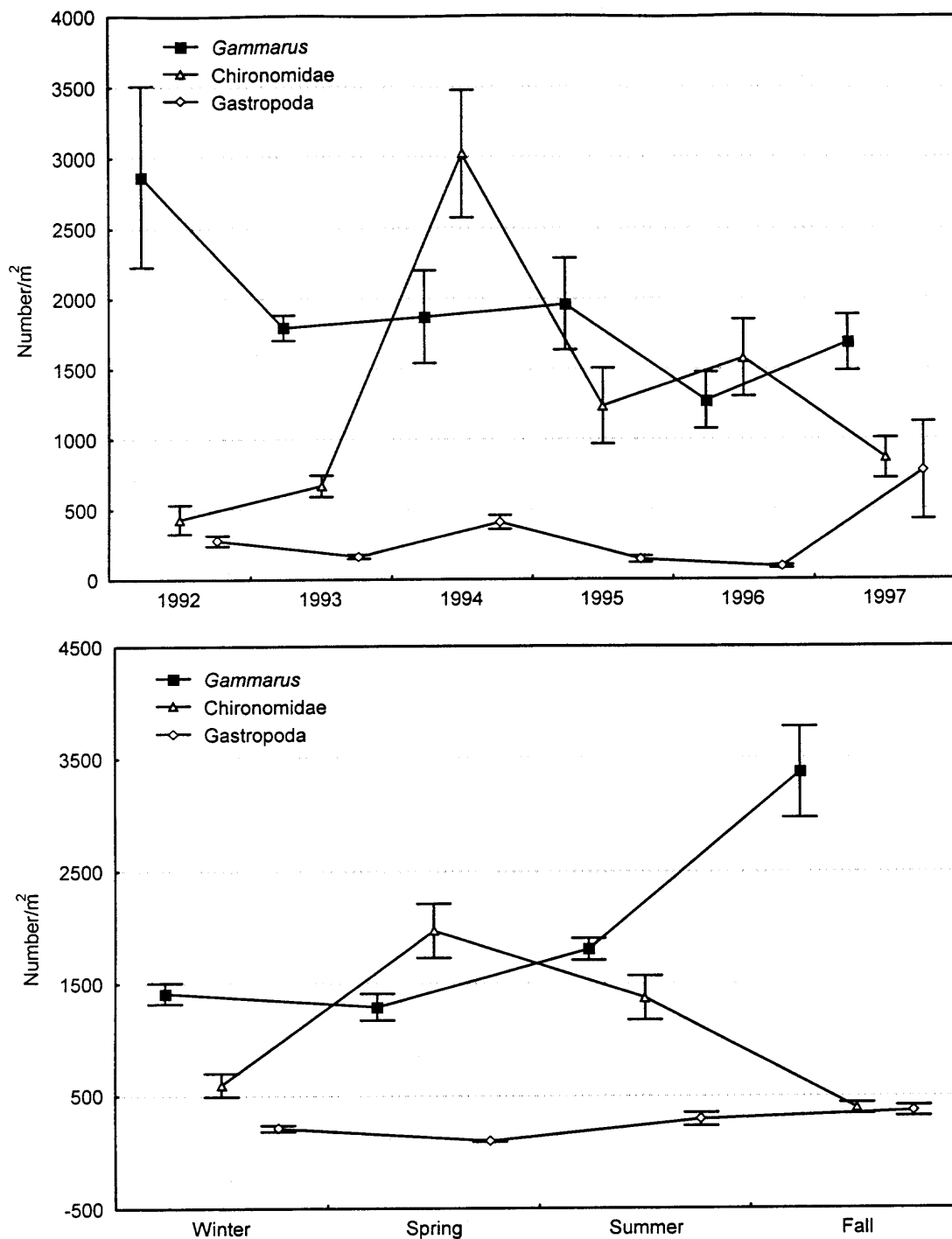


Figure 45. Yearly (top) and seasonal (bottom) mean density ( $\pm 1$  SE) of benthic macroinvertebrates collected from the permanently inundated portion of the Lee's Ferry reach, Colorado River, 1992-1997.

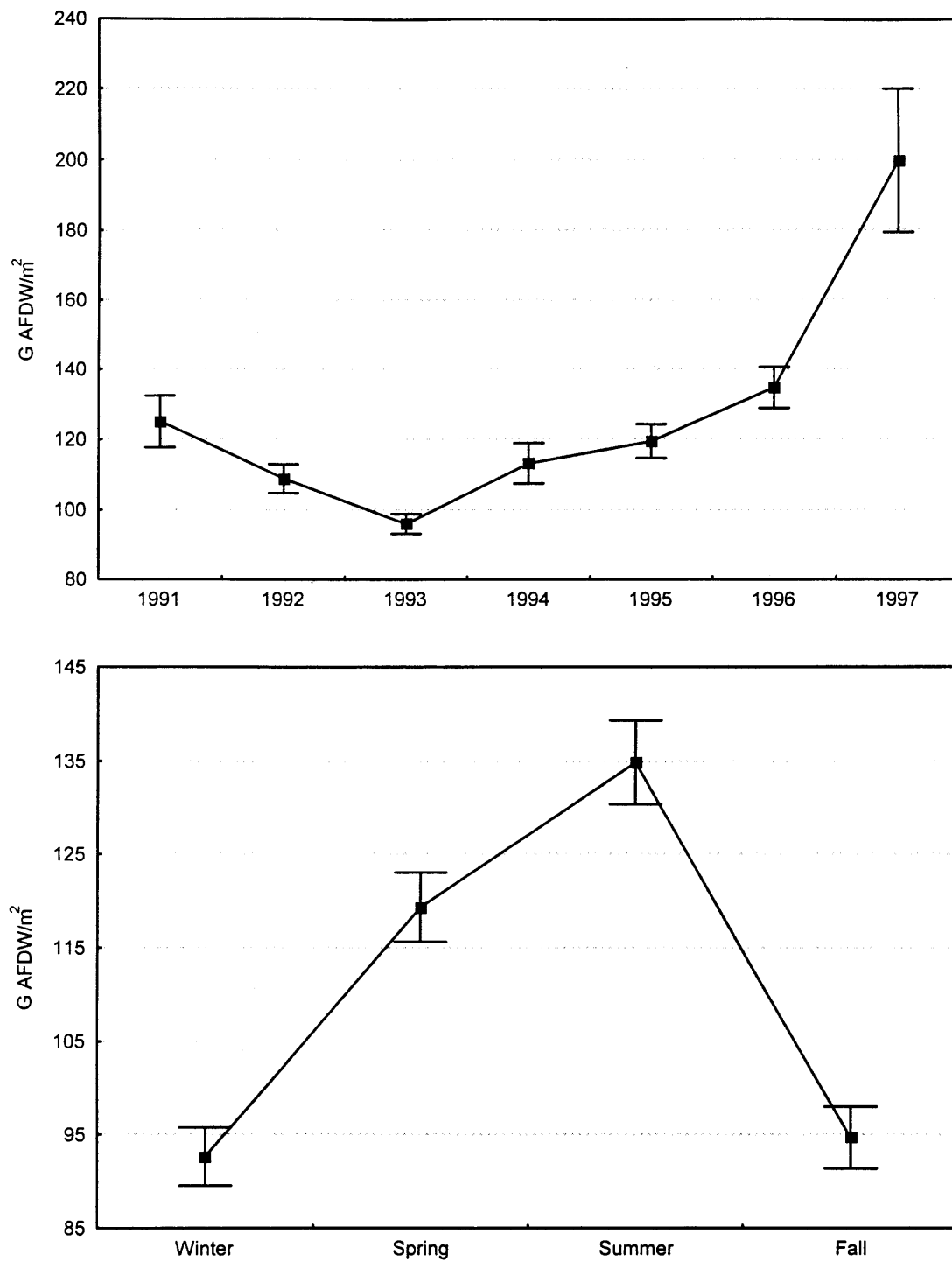


Figure 46. Yearly (top) and seasonal (bottom) mean biomass ( $\pm 1$  SE) of periphyton collected from the permanently inundated portion of the Lee's Ferry reach, Colorado River, 1991-1997.

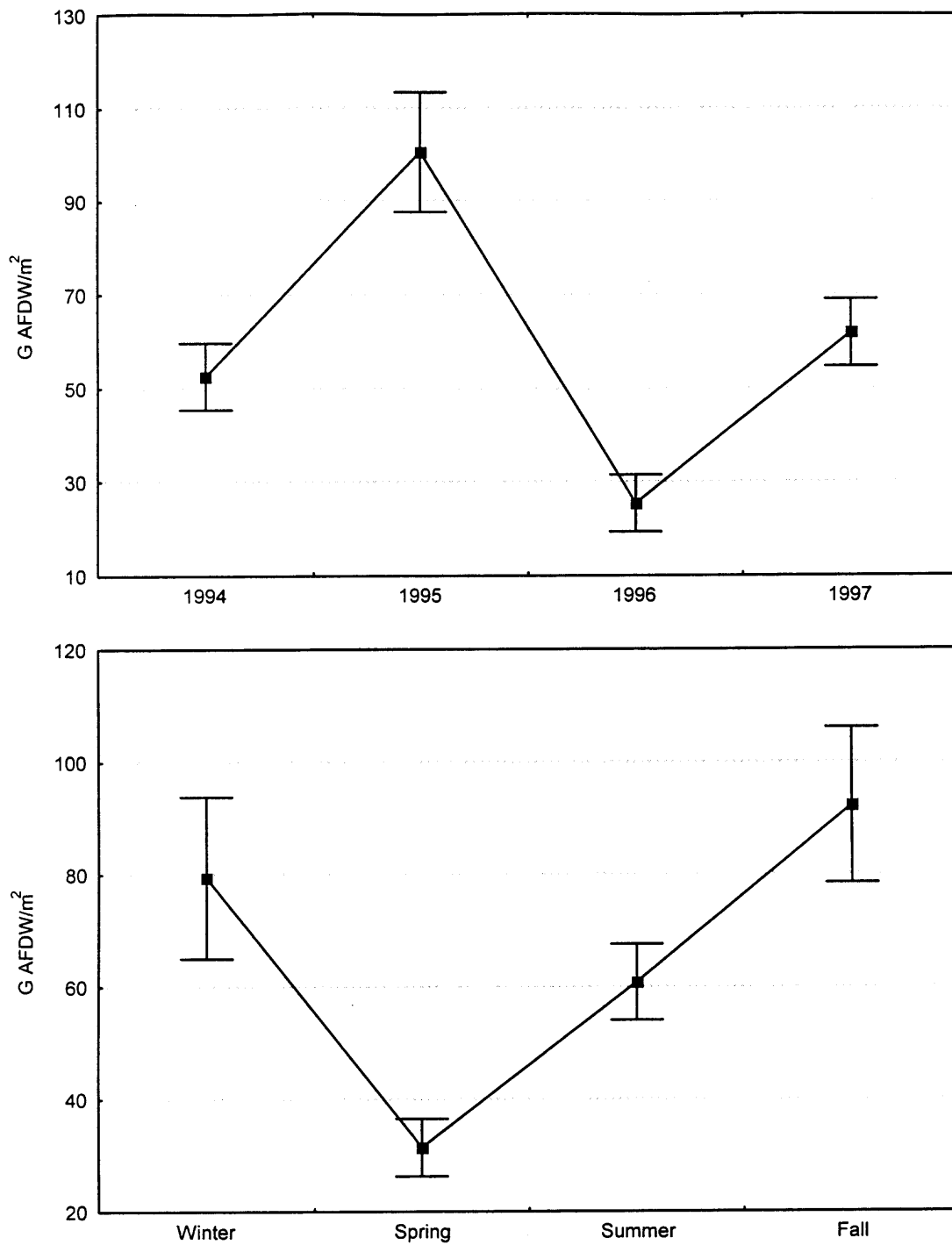


Figure 47. Yearly (top) and seasonal (bottom) mean biomass ( $\pm 1$  SE) of aquatic macrophytes collected from the Lee's Ferry reach, Colorado River 1994-1997.

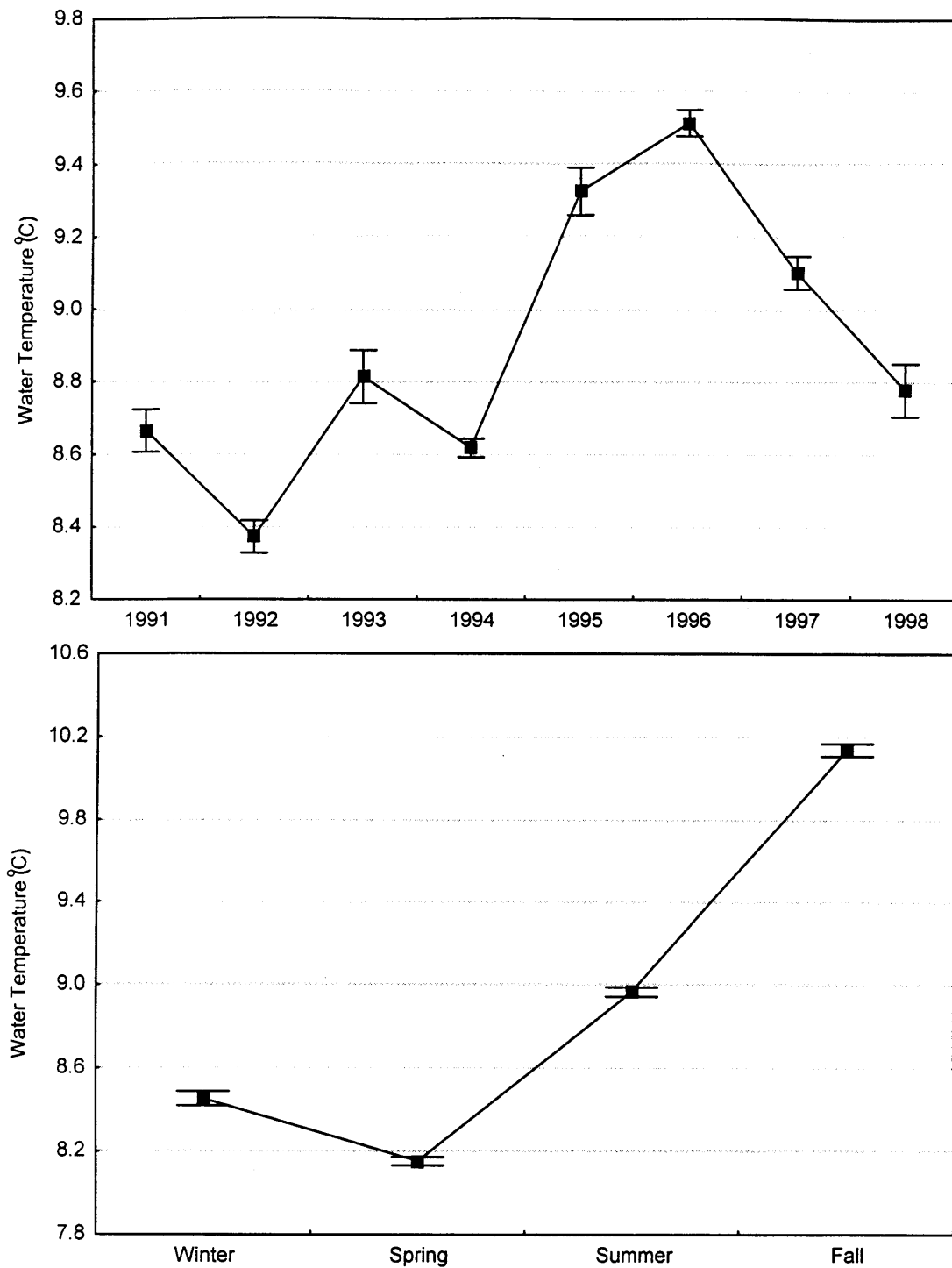


Figure 48. Yearly (top) and seasonal (bottom) mean water temperature ( $\pm 1$  SE) immediately below Glen Canyon Dam, Colorado River, 1991-1998.

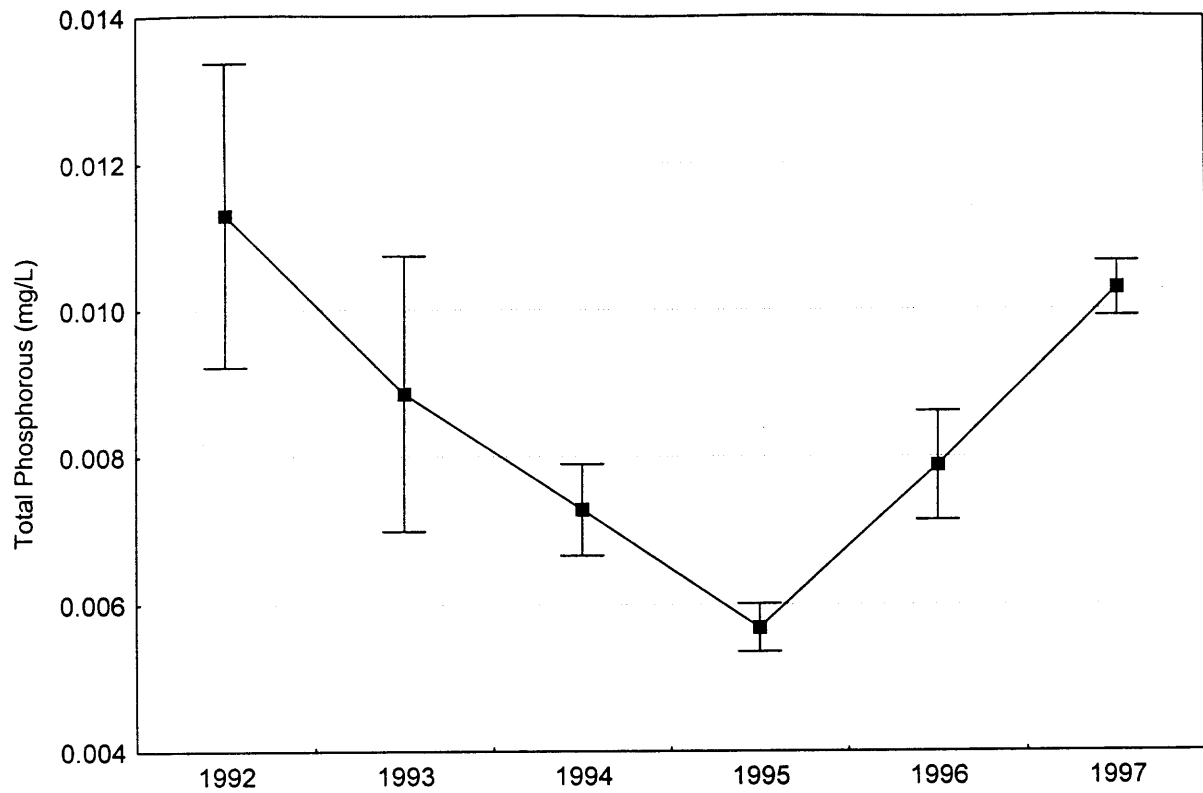


Figure 49. Yearly mean ( $\pm 1$  SE) total phosphorus in the Lee's Ferry reach, Colorado River, 1992-1997.