Effects of low steady summer flows on rainbow trout in the Lee's Ferry tailwater, 2000

David W. Speas, William R. Persons, R. Scott Rogers, David L. Ward, Andrew S. Makinster, and Joe E. Slaughter, IV

Arizona Game and Fish Department
Research Branch (WMRS)
2221 West Greenway Road
Phoenix Arizona 85023

Submitted to:
Grand Canyon Monitoring and Research Center
2255 N. Gemini Drive, Room 341
Flagstaff, AZ 86001
Cooperative Agreement No. 1425-97-FC-40-22690 (c) [handwritten correction: 98]

March 2004

Abstract

To improve survival and growth of native fishes, an experimental combination of flows simulating seasonal floods and low, steady summer flows were conducted during March-September of 2000 in the Colorado River below Glen Canyon Dam, Arizona. Diel flow fluctuations were essentially zero and mean daily discharge was 8,000 cfs from June 1 through October 1. We electrofished the Lee's Ferry tailwater on four separate occasions during 2000 to assess impacts of the steady flow experiment on CPE, size structure, and condition factor of rainbow trout. Mean catch-per-unit-effort, condition, growth rates and proportional stock density values for 2000 show no significant departure from those observed in recent years (1997-1999), but seasonal peaks in condition and appearance of young-of-year in the catch occurred several months earlier during 2000 than during previous years (1991-1999). Previous studies and stock assessment models predicted enhanced survival of wild-spawned age ≤ 1 fish under low daily flow fluctuations, but CPE of age ≤ 1 fish during 2000 did not deviate significantly from those observed during the preceding 3 to 5 years. This lack of change may be attributed to both positive (stabilized flows) and negative (low flows) hydrologic forces acting simultaneously on early life history of trout, or it simply may be an artifact of low sample statistical power. We recommend that long-term monitoring sample sizes be increased in part to enhance statistical power for short-term experiments, and that future flow experiments consist of fewer hydrological treatments than those applied during 2000.

Introduction

Experimental low, steady flows were conducted during March-September of 2000 in the Colorado River below Glen Canyon Dam (GCD), Arizona. The low, steady summer flow (LSSF) experiment is an element of the Reasonable and Prudent Alternative to operations of GCD as a means to remove jeopardy from the endangered humpback chub *(Gila cypha)* populations residing in Grand Canyon (Gorman 1997). Such flows are scheduled for low water years (annual total releases of approximately 8.23 million acre-feet) such as 2000.

Recommendations for the LSSF hydrograph were made by SWCA, inc., Environmental Consultants (SWCA; Valdez et al 2000) under contract with the Grand Canyon Monitoring and Research Center (GCMRC). The GCMRC in turn funded a number of studies to evaluate flow-related effects on biological resources. Among those resources potentially impacted by LSSF was the Lees' Ferry rainbow trout fishery, which has been an important recreational fishery resource since closure of the dam in 1964.

The LSSF hydrograph (Figure 1) resembled a natural hydrograph and contained aspects targeting species-specific life history stages (Valdez et al 2000). High, steady releases conducted during April and May (mimicking historical peak runoff) were implemented to pond tributary inflows and provide thermal refugia for young fish, whereas the spring 31,000 cubic ft./sec. (cfs) spike flow was designed primarily to disadvantage small bodied non-native fish. The steady releases conducted from June through September were designed to enhance growth and survival of young native fish by providing warm, low-velocity near-shore habitats. To displace non-native fish that may have benefited from these habitat enhancements, a second 31,000 cfs spike flow was conducted during September. Following September 30th, peak-power generation releases from GCD resumed.

Relationships between dam discharge and rainbow trout population dynamics in the Lee's Ferry tailwater are well documented (McKinney et. al, 1999a b, 2001a). Inception of Interim and Modified Low Fluctuating Flows (MLFF) in 1991 and 1996, respectively, coincided with increases in RBT natural recruitment and standing stocks across all age classes. Analyses of fishery data collected from 1991-1999 indicate that recruitment of wild-spawned fish to the breeding population is inversely related to the magnitude of diel flow fluctuations and duration of flows less than 8,000 cfs (McKinney et al. 1999a, 2001). Increases in trout density took place during periods when mean annual flows increased from ca. 11,000 cfs (1991-1994) to almost 17,000 cfs (1995-1999), and daily fluctuations averaged approximately 5,500 cfs.

In the present study we sought to document short-term effects of sustained low, essentially stable flows on trout in the Lee's Ferry tailwater. Specifically, we sought to evaluate effects by testing the following hypotheses:

H_{o1}: Catch per effort (CPE) of all size classes of rainbow trout will not differ from that observed during 1991-1999.

H_{o2}: Relative condition factor (K_n) of rainbow trout will not differ from that observed during 1991-1999.

H_{o3}: Growth rate of rainbow trout will not differ from that observed during 1991-1999.

H_{o4}: Proportional Stock Density (PSD) or size structure of the population will not differ from that observed during 1991-1999.

H_{o5}: Relative gut volume (RGV) of major food taxa will not differ from that observed during 1991-1999.

Methods

Field collections

We sampled the trout fishery by electrofishing following standard monitoring procedures (McKinney et al. 1999) to assess changes in CPE, size structure, and condition factor. Originally, our sampling strategy called for three sampling trips in 2000 during April, August, and November, but we moved our normal April sample to March and added a June sample to increase our ability to detect responses to the LSSF test.

We captured rainbow trout by electrofishing between dusk and dawn at nine fixed transects sampled since 1991 (ca. 33 min electrofishing/transect). We used a complex pattern of pulsed direct current, applying 215 V and maintaining a 15 A average output to a 30 cm stainless steel anode system (Sharber et al. 1994). Fish were measured to the nearest millimeter total length (TL), weighed to the nearest gram, and released unless collected for analysis of food habits or growth (stocked fish, coded wire tags).

We collected 45 trout stomachs per trip and preserved them in 10% formalin in the field. We identified and measured stomach contents of trout in the laboratory using volumetric displacement (ml), and computed relative stomach volume (RGV, $mL\ food \cdot m^{-1} TL$; Filbert and Hawkins 1995) of total contents, *Cladophora glomerata*, and predominant macroinvertebrates (*Gammarus lacustris,* chironomidae, gastropod). We attempted to select stomach samples randomly from within established trout length groups (McKinney et al. 1999, 2001; see **Methods**, *Analysis*), but actual sizes obtained differed slightly from these groups and are as follows: small fish, 152-304 mm MTL; medium fish, 305-405 mm MTL; and large fish, 406-558 mm MTL.

Analysis

We tested H_{o1}, H_{o2}, and H_{o4} by comparing size-specific CPE [transformed to Ln (CPE + 1)], K_n and PSD data from 2000 with their counterparts from previous years (1991-1999; McKinney et al. 1999, 2001) through repeated measures ANOVA (Maceina et al. 1994) followed by orthogonal contrasts of annual mean CPE for 2000 with preceding years. To increase power of orthogonal contrasts, we set α equal to 0.10, and adjusted comparison-wise error rates for type I error probabilities through a sequential Bonferroni procedure described by Rice (1989).

Although not formally stated as hypotheses, we were also interested in seasonal variance in CPE, Kn and PSD during 2000 in relation to hydrologic components of the LSSF test and also in relation to seasonal trends documented during 1991 – 1999 (McKinney et al. 1999). Seasons were defined as winter (January – March), spring (April – June), summer (July – September) and fall (October – December). We evaluated seasonal changes in CPE, Kn and PSD during 2000 using one-way randomized ANOVAs. We did not perform repeated measures tests on the 2000 data because such tests were not appropriate for the 1991 – 1999 data subset, which (unlike 2000 data) was seasonally unbalanced. Hypotheses of no seasonal change during 2000 were rejected if test statistic probabilities were $\alpha = 0.10$ or less. Post-ANOVA multiple comparisons among seasons were essentially unplanned, so we identified differences in seasonal means by inspection of 95% confidence intervals (Day and Quinn 1989) and compared seasonal patterns from 1991 –1999 to those seen in 2000. Baseline seasonal trends from 1991 –1999 were estimated from an ANCOVA with years as the covariate and seasons as main effects. We calculated post-hoc statistical power of ANOVAs using G-power (Buchner et al. 1997), and interpreted results assuming desirable power was $(1 - \alpha) = 0.90$ (Cohen 1988).

We used rainbow trout length categories reported by McKinney et al. (1999 a, 2001), which are defined in relation to estimated fish age, age at maturity, and/or PSD length intervals: < 152 mm (Age-1), 152-304 mm (ages 2-3), 305-405 mm (age-4+; age at maturity; "stock"-size fish, PSD denominator), and > 405 mm (age > 4; "quality"-size fish, PSD numerator)[1].

Relative condition (K_n; Anderson and Nuemann 1996) was calculated as

$$Kn = W/W' * 100$$

where W′ is the standard weight relationship $10^{\wedge(-4.6 + 2.856*\mathrm{Log10(length)})}$ derived from Lee's Ferry specimens (McKinney et al. 2001). Proportional stock density (Anderson and Nuemann 1996) was defined as

$$PSD = (\#\ \text{fish} \geq 406\ \text{mm TL} / \#\ \text{fish} \geq 305\ \text{mm TL}) * 100$$

[1]Rainbow trout length-at-age classes were estimated through the Wang (1998) estimation procedure for mark – recapture data as

$$-(1/K) * \mathrm{Ln}[1 - (L_m / \acute{L}_\infty)]$$

where L_m is observed length at marking and $\acute{L}_\infty$ is length at infinite age for individual fish, and K is a metabolic parameter for the sampled sub-population estimated from the Wang growth rate procedure (Wang 1998). Resulting estimated lengths at age were: age ≤ 1: <152 mm TL; age-2: 152-246 mm TL; age-3: 247-304 mm TL; age-4: 305-339 mm TL; and age > 4: >339 mm TL.

where fish ≥ 406 mm TL represent "quality" fish and fish ≥ 305 mm TL represent the bulk of adult or "stock"-size fish (McKinney et al. 1999).

We assessed trends in rainbow trout growth by plotting their average annual instantaneous growth (IG; Busacker et al. 1990), calculated as

$$\ln(TL_r) - \ln(TL_m) / (t_r - t_m)$$

where TL_r is length at recapture and TL_m is mean length of hatchery-reared fish during stocking occasions (Roger Sorensen, AZ Game and Fish, Department, unpublished data) or length at marking occasion for wild-spawned fish, and $(t_r - t_m)$ is time elapsed (days) between mark and recapture occasions. The bulk of growth data is derived from returns of coded-wire tagged, hatchery-reared trout which were stocked during 1992 – 1998; a small number of PIT-tagged, wild-spawned fish were present in the 1999 and 2000 samples. We evaluated growth rate trends among years using simple linear regression, and tested H_{o3} by comparing mean growth for 2000 to preceding years using Bonferroni-corrected orthogonal contrasts.

Stomach Contents

Analyses of stomach content data were similar to McKinney et al. (1999) and are summarized below. As in previous years, trout RGV data were highly skewed. We used Kruskal-Wallis tests (K-W) to compare annual and seasonal differences in trout food habits according to length categories (small fish = 152-304 mm TL; medium fish = 305-405 mm TL; large fish = 406-558 mm TL). Percentages of empty stomach among years and seasons were compared using chi-square, and trends in the proportions of these empty stomachs among years were analyzed with Spearman Rank Order correlations. Frequency of occurrence for food habits was determined only for fish with ingested food items, while frequency of empty stomachs was calculated as the percent of all fish collected for diet analysis. Statistical significance for diet analyses were set at $\alpha = 0.05$.

Results

Catch per effort and length frequencies

Catch-per-effort of all RBT size classes has increased since 1991 ($df = 9$, $F \geq 10.3$, $P \leq 0.001$; Table 1 [Contrasts], Figure 2). There were few differences in CPE of all size categories during 2000 from values observed from 1994 – 2000 (Figure 2a-e; table 1). Catch-per-effort of all RBT size classes combined was greater in 2000 than in 1999 ($df = 1$, $F = 12.1$, $P = 0.001$). Bonferroni-corrected orthogonal contrasts indicated no significant change in mean CPE between 1999 and 2000 for individual RBT size classes (Table 1), but inspection of confidence intervals and a marginal *P*-value (0.047) suggested a slight increase in CPE of age ≤ 1 fish. Power of all non-significant contrasts among annual CPE, Kn and PSD values was ≤ 0.85.

Catch-per-effort of age ≤ 1 fish was lowest during autumn and winter months of 2000 ($df = 36$, $F = 2.1$, $P = 0.12$), whereas CPE of stock-size fish ($df = 36$, $F = 2.2$, $P = 0.11$) was stable for most of the year but declined in December (Figure 5). Sample power for detection of inter-annual trends during 2000 (total $N = 36$) was ≤ 0.63. During 1991 – 1999, CPE of age ≤ 1 and age 2-3 fish was also lowest during autumn and winter months ($df = 338$, $F \geq 2.9$, $P \leq 0.034$), but CPE quality size was greatest during winter and lowest during summer and fall ($df = 336$, $F = 6.6$, $P < 0.001$). CPE of stock-size fish and all fish combined did not vary significantly by season during 1991 – 1999. Age-0 fish appeared in the catch during April-June, which is about 3 months earlier than data from 1991-1999 suggest (Figure 5). Rainbow trout measuring 50-75 mm TL were more numerous in 2000 than in all previous years combined (Figure 3).

Relative Condition

Trends in relative condition varied among RBT size classes. Condition increased significantly in 1993 then declined for fish > 304 mm ($df = 9$, $F \geq 12.2$, $P \leq 0.010$) but declined significantly since 1991 for 152 – 304 mm fish ($df = 9$, $F = 16.1$, $P = 0.004$; Figure 4; Table 2). Relative condition of > 405 mm fish declined significantly from 1999 to 2000 ($df = 1$, $F = 10.5$, $P = 0.0143$), but did not change significantly for other RBT size classes.

Seasonally, K_n for all size categories except quality-size fish peaked during spring months of 2000 (April-June; df $\geq$ 688, F $\geq$ 10.5, P $\leq$ 0.001), whereas it had peaked during summer months (July-September) during previous years for all size groups (df $\geq$ 3041, F $\geq$ 9.2, P $\leq$ 0.001; Figure 6; McKinney et al. 1999).

Proportional Stock Density (PSD)

Proportional Stock Density has declined significantly since 1991 (df = 8, F = 47.5, P < 0.001; Figure 8) but did not change significantly from 1999 to 2000 (post hoc power = 0.24, Table 3). PSD did not vary significantly by season during 2000 (post-hoc power = 0.30), whereas it peaked in winter months during previous years (df = 342, F = 14.7, P < 0.001; Figure 9; McKinney et al. 1999).

Growth

Instantaneous growth of rainbow trout has declined by 92% since 1991 (df = 732, R^2 = 0.29, P < 0.001; Figure 7). Bonferroni-correct contrasts indicated that growth during 2000 was lower than any previous year (df = 1, Table 4).

Stomach Contents

Total RGV was similar in 2000 to the previous two years, but differed among all years since 1991 (χ^2 = 31.87, df = 8, P < 0.01; Figure 10). *Cladophora* were still the dominant food item present in rainbow trout diets, but the RGV content for this item was lower than 1999 (χ^2 = 56.56, df = 8, P < 0.01). *Gammarus* and gastropod RGV was higher in 2000 than 1999 (χ^2 = 85.53, df = 8, P < 0.01; χ^2 = 30.61, df = 8, P < 0.01, respectively), while chironomid RGV was similar to the previous 5 years, but differed among all years (χ^2 = 62.33, df = 8, P < 0.01). Seasonally, *Cladophora* RGV was higher in summer and fall, *Gammarus* RGV was lower in summer, fall, and winter, chironomid RGV was higher in summer, fall, and winter and lower in spring, and gastropod RGV was lower in summer and higher in winter and spring than seasonal means from 1991-1999 (Table 5).

Seasonal size-specific RGV was lower in spring for both small and medium sized rainbow trout, yet higher for large rainbow trout (Table 6; Figure 11). *Gammarus* RGV was higher for medium sized rainbow trout in winter and large rainbow trout in spring and lower for medium sized rainbow trout in fall and large rainbow trout in summer than seasonal means for the previous 9 years (Table 6; Figure 12). Gastropod RGV was higher in winter and spring for large size rainbow trout and lower in summer for small rainbow trout and summer and fall for medium size rainbow trout than seasonal means for the previous 9 years (Table 6; Figure 13). *Cladophora* RGV was relatively similar to seasonal means from the previous 9 years, except for being lower for small rainbow trout in spring and for medium size trout in winter and spring and higher for large rainbow trout in summer (Table 6; Figure 14). Chironomid RGV was higher in winter and fall and lower in spring for small rainbow trout, higher in winter for medium rainbow trout, and lower in spring for both medium and large rainbow trout than means for the previous 9 years (Table 6; Figure 15).

The percentage of empty stomachs was relatively unchanged in 2000 compared to previous years ($P = 0.27$; Figure 16). There were no seasonal differences in percentage of empty stomachs in 2000 ($P = 0.78$) or among 2000 and the previous 9 years (all $P > 0.13$). The most marked size-specific seasonal increases of empty stomachs were for large rainbow trout in winter and all size classes in spring (Figure 17).

Discussion

Data collected during 2000 indicate minimal immediate impacts of the LSSF experiment on the Lee's Ferry trout fishery. Mean CPE, condition, growth parameter and PSD values for 2000 show few significant departures from those observed in recent years (1997-1999), although increased CPE during 2000 (all sizes combined) is probably due to increases in CPE of fish < 152 mm relative to 1999. Previous studies (McKinney et al. 1999, 2001a) predict enhanced survival of wild-spawned fish < 152 mm under low daily flow fluctuations, but CPE of fish < 152 mm during 2000 was only marginally higher than 1999, and not different from CPE values observed during the preceding five years.

Recognizing that some passage of time may be necessary to evaluate recruitment from the 2000 yearclass, at present two explanations exist for the weak results. On one hand, the LSSF was comprised of hydrologic aspects which oppose each other in their influence on age ≤ 1 fish. McKinney et al. (1999, 2001a) showed that steady flows enhance survival of age ≤ 1 fish, but the authors also noted that duration of flows at or below 8,000 cfs have a negative impact on survival of these fish due to lower net habitat availability. Thus, gains in survival of age ≤ 1 fish due to stabilized flows could be offset by reduced near-shore habitat at 8,000 cfs, or for that matter, displacement by the spike flows. The simultaneous application of several types of hydrologic treatments during the LSSF complicates interpretation of results, but lack of response by age ≤ 1 fish is not entirely surprising.

On the other hand, changes in relative density of age ≤ 1 fish may have taken place but went undetected due to low short-term sample power. Magnitudes of "biologically significant" effects resulting from experimental flows are at present poorly understood (Hilborn and Mangel, 1997), and impacts of a particular flow regime on recruitment and ancillary variables are often not immediately detectable. In coordination with GCMRC, we have increased the Lee's Ferry monitoring sample size from 9 samples/trip (1991-2000) to 33-36 samples/trip (2001 and beyond). Our hope is to increase statistical power to detect changes in long-term fishery status and trends (as evidenced by CPE), but also to improve sensitivity to short-term effects resulting from experimentation (Culver et al. 2000). Power of short-term analyses of K_n, PSD and growth are contingent on numbers of fish captured and sample sizes are difficult to control.

During the LSSF experiment, CPE of age ≤ 1 trout did not change from June 30 to September 30, indicating little or no impact of the 31,000 cfs spike flows (Sept 5-9) on age ≤ 1 fish. Lack of response in age ≤ 1 trout relative density was also observed following the 1997 habitat maintenance flows (2 days @ approximately 28,000 cfs). By contrast, percentages of age ≤ 1 trout declined slightly following the Beach and Habitat Building Flow of 1996 (8 days @ approximately 45,000 cfs; McKinney et al. 1998). It is likely that brief spike flows of 31,000 cfs pose minimal threats to RBT recruitment in the tailwater when age ≤ 1 densities are relatively high, as they have been since 1997, but recruitment impacts sustained when densities are low have yet to be documented.

Density-dependent constraints have influenced trout growth trajectories throughout much of the 1990s (McKinney et al. 1999; McKinney and Speas 2001). McKinney and Speas (2001) demonstrated that energy deficits were present in adult (large) rainbow trout during the mid-1990s, a period when flows were comparatively high and fish densities were increasing. Low water conditions during 2000 likely exacerbated competition for food and space, resulting in continued declines in growth and (for stock size fish) condition. It is very possible, however, that antecedent, density-dependent growth trajectories evidenced in McKinney and Speas (2001) would have resulted in continually declining growth in 2000 regardless of flow conditions.

In 2000, the only significant departures from long term trends observed from 1991-1999 were shifts in the timing of seasonal trends in K_n and appearance of young-of-year in the catch. The latter fish were also among the smallest RBT ever captured in significant numbers at Lee's Ferry during a single year. Both K_n and age-0 occurrence peaked ca. 1-3 months earlier in the year than previous seasonal data indicate.

The peak in relative condition during 2000 coincided with the maximum observed drifting *Gammarus* density during 2000 (Rogers, personal communication). This observation is consistent with previous studies conducted during 1991-1997, in which RBT condition and food consumption was positively correlated with drift density of *Gammarus* (McKinney et al, 1999). Other studies (Leibfried and Blinn 1987; Blinn et al. 1995; Ayers and McKinney 1996) indicate that high drift densities are positively associated with fluctuating versus stable flows, suggesting that fish food availability and consumption rates are also higher under fluctuating flows as opposed stable flows.

We suspect that capture of large numbers of unusually small age-0 (ca. 50-75 mm TL) fish during June and September 2000 was directly and indirectly enhanced by the low, stable flow component of the LSSF. Lack of fluctuations provided conditions favoring development of dense aquatic macrophyte beds in near shore areas, providing a stable source of refuge for age-0 fish. Secondly, the density and hence catch rate of age-0 fish was likely enhanced due to consistently low discharge which probably concentrated the fish.

Lack of change among fishery variables during the past 4 or 5 years suggests some degree of stability in rainbow trout population parameters, yet growth rates continue to decline and relative condition remains below levels targeted by management objectives (target growth: 458 mm by age-3; target relative condition: 90). Comparative stability in PSD since 1995 (figure 7) indicate minimal variation in annual recruitment

(Carline et al. 1984; McKinney et al. 1997), but continual decline in RBT growth rate parameters suggests that over-recruitment and subsequent resource limitation remains a problematic aspect of the fishery (McKinney and Speas 2001). Efforts are ongoing to evaluate these hypotheses using our stock synthesis model. We should begin evaluation of feasibility and probability for success of management options in the Lee's Ferry tailwater fishery, with particular emphasis on flow regimes which may be employed to limit further RBT recruitment.

Recommendations

1. Design simplified flow experiments comprised of fewer hydrologic treatments. Interpretation of data from multi-faceted experiments is difficult, particularly when magnitudes of effects and interactions among components are unknown.
2. Evaluate statistical power of Lee's Ferry long-term trout monitoring program to detect short-term effects of experimental flows, with references toward defining "biologically significant" effects of such flows. The latter may be accomplished by utilizing power analysis in conjunction with synthesis model predictions of hypothetical population trends.
3. Continue refinement of stock assessment model by adding data from 2000; evaluate discrepancy between model predictions for age ≤ 1 trout and observations from electrofishing for lack of model predictive power, or lack of statistical power in monitoring program.
4. Begin evaluation of fishery and/or water management alternatives aimed at reducing or limiting RBT recruitment in the Lee's Ferry.

Acknowledgements

Grand Canyon Monitoring and Research Center funded the present study under Cooperative Agreement No. 1425-97-FC-40-22690. We thank numerous AGFD and GCMRC personnel for their assistance in collection of field data.

References Cited

Anderson, R.O. and R.M. Neumann. 1996. Length, weight and associated structural indices. Pages 447-481 *in* B.R. Murphy and D.W. Willis, editors. Fisheries Techniques. American Fisheries Society, Bethesda, MD.

Ayers, A.D. and T. McKinney. 1996. Lake Powell forebay and Glen Canyon Dam tailwater to Lee's Ferry during interim flows: particulate organic matter transport, nutrient content and periphyton standing stock. Final Report to U.S. Bureau of Reclamation, Glen Canyon Environmental Studies, Flagstaff, AZ. Arizona Game and Fish Department, Phoenix.

Blinn, D.W., J.P. Shannon, L.E. Stevens and J.P. Carder. 1995. Consequences of fluctuating discharge for lotic communities. Journal of the American Benthological Society 14:233-248.

Busacker, G.P., I.R. Adelman, and E.M. Goolish. 1990. Growth. Pages 363-387 *in* C.B. Schreck and P.B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Carline, R.F., B.L. Johnson, and T.J. Hall. 1984. Estimation and interpretation of proportional stock density for fish populations in Ohio impoundments. North American Journal of Fisheries Management 4:139-154.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences: second edition. Lawrence Erlbaum Associates, Publishers. Hillsdale, New Jersey.

Culver, D.A., B.L Kearns, M. Liermann, and G.R. Wilde. 2000. Final report of the Lee's Ferry rainbow trout monitoring peer review panel. Grand Canyon Monitoring and Research Center, Flagstaff, AZ.

Day, R.W. and G.P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59:433-463.

Filbert, R.B., and C.P. Hawkins. 1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. Transactions of the American Fisheries Society 124:824-835.

Gorman, O.T. 1997. Recommendations for research, monitoring and conservation of endangered and native fishes in Grand Canyon. Final Report. United States Fish and Wildlife Service, Arizona Fisheries Research Office, Flagstaff, AZ.

Hilborn, R., and M. Mangel. 1997. The ecological detective: Confronting models with data. New Jersey: Princeton University Press. 317 p.

Leibfried, W.C. and D.W. Blinn. 1987. The effects of steady versus fluctuating flows on aquatic macroinvertebrates in the Colorado River below Glen Canyon Dam, Arizona. Final Report to Arizona Game and Fish Department, Phoenix.

Maceina, M.J., P.W. Bettoli, and D.R. DeVries. 1994. Use of split-plot analysis of variance design for repeated-measures fishery data. Fisheries 19:14-20.

McKinney, T., R.S. Rogers and W.R. Persons. 1997. Lee's Ferry reach: Lower trophic levels and rainbow trout. 1997 annual report to U.S Bureau of Reclamation, Grand Canyon Monitoring and Research Center, Flagstaff, AZ. Arizona Game and Fish Department, Phoenix.

McKinney, T., R.S. Rogers, A.D. Ayers, and W.R. Persons. 1998. Community responses in the Lee's Ferry reach. Geophysical Monographs 110:249-258.

McKinney, T., D.W. Speas, R.S. Rogers and W.R. Persons. 1999a. Rainbow trout in the Lee's Ferry recreational fishery below Glen Canyon Dam, Arizona, following establishment of minimum flow requirements. Final Report. Arizona Game and Fish Department, Phoenix, AZ.

McKinney, T., R.S. Rogers and W.R. Persons. 1999b. Effects of flow reductions on aquatic biota of the Colorado River below Glen Canyon Dam, Arizona. North American Journal of Fisheries Management 19:984-991.

McKinney, T., D.W. Speas, R.S. Rogers, and W.R. Persons. 2001. Rainbow trout in a regulated river below Glen Canyon Dam, Arizona, following increased minimum flows and reduced discharge variability. North American Journal of Fisheries Management 21:216-222.

McKinney, T. and D.W. Speas. 2001. Observations of size-related asymmetries in diet and energy intake of rainbow trout in a regulated river. Environmental Biology of Fishes 61:435-444.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

Sharber, N.G., S.W. Carothers, J.P. Sharber, J.C. deVos, Jr., and D.A. House. 1994. Reducing electrofishing-induced injury of rainbow trout. North American Journal of Fisheries Management 14:340-346.

Valdez, R.A., S.W. Carothers, D.A. House, M.E. Douglas, M. Douglas, R.J. Ryel, K.R. Bestgen, and D.L. Wegner. 2000. A program of experimental flows for endangered and native fishes of the Colorado River in Grand Canyon. U.S. Department of the Interior, Grand Canyon Monitoring and Research Center, Flagstaff, AZ.

Wang, You-Gan. 1998. An improved Fabens method for estimation of growth parameters in the Von Bertalanffy model with individual asymptotes. Canadian Journal of Fisheries and Aquatic Sciences 55:397-400.

Table 1. Results from orthogonal contrasts among size-specific CPE during LSSF treatment year 2000 and preceding years (df = 1 per contrast) including F ratio, probability P, Bonferroni-adjusted or "critical" alpha (ά), and resulting significance (* indicates P < ά, "ns" indicates P > ά).

Size Category	Contrast	F	P	ά	Significance
<152 mm	1991 vs. 2000	21.0	0.002	0.011	*
152-304 mm	1991 vs. 2000	30.9	0.001	0.013	*
305-405 mm	1991 vs. 2000	1.4	0.277	0.100	ns
>405 mm	1991 vs. 2000	27.0	0.001	0.011	*
All fish	1991 vs. 2000	9.9	0.003	0.033	*
<152 mm	1992 vs. 2000	12.4	0.008	0.013	*
152-304 mm	1992 vs. 2000	27.1	0.001	0.014	*
305-405 mm	1992 vs. 2000	69.8	0.000	0.013	*
>405 mm	1992 vs. 2000	0.9	0.365	0.033	ns
All fish	1992 vs. 2000	60.0	0.000	0.013	*
<152 mm	1993 vs. 2000	10.8	0.011	0.014	*
152-304 mm	1993 vs. 2000	36.0	0.000	0.011	*
305-405 mm	1993 vs. 2000	78.1	0.000	0.011	*
>405 mm	1993 vs. 2000	2.6	0.145	0.020	ns
All fish	1993 vs. 2000	81.0	0.000	0.011	*
<152 mm	1994 vs. 2000	2.8	0.133	0.025	ns
152-304 mm	1994 vs. 2000	6.1	0.038	0.020	ns
305-405 mm	1994 vs. 2000	62.5	0.000	0.014	*
>405 mm	1994 vs. 2000	3.7	0.090	0.017	ns
All fish	1994 vs. 2000	35.5	0.000	0.014	*
<152 mm	1995 vs. 2000	0.2	0.687	0.100	ns
152-304 mm	1995 vs. 2000	9.9	0.014	0.017	*
305-405 mm	1995 vs. 2000	25.0	0.001	0.017	*
>405 mm	1995 vs. 2000	2.1	0.182	0.025	ns
All fish	1995 vs. 2000	21.4	0.000	0.020	*
<152 mm	1996 vs. 2000	2.9	0.126	0.020	ns
152-304 mm	1996 vs. 2000	4.3	0.071	0.033	ns
305-405 mm	1996 vs. 2000	12.5	0.008	0.020	*
>405 mm	1996 vs. 2000	0.4	0.542	0.100	ns
All fish	1996 vs. 2000	23.3	0.000	0.017	*
<152 mm	1997 vs. 2000	0.4	0.544	0.050	ns
152-304 mm	1997 vs. 2000	4.9	0.058	0.025	ns
305-405 mm	1997 vs. 2000	2.6	0.145	0.033	ns
>405 mm	1997 vs. 2000	6.2	0.038	0.013	ns
All fish	1997 vs. 2000	0.2	0.625	0.050	ns
<152 mm	1998 vs. 2000	2.4	0.157	0.033	ns
152-304 mm	1998 vs. 2000	0.4	0.530	0.050	ns
305-405 mm	1998 vs. 2000	1.7	0.230	0.050	ns
>405 mm	1998 vs. 2000	0.8	0.385	0.050	ns
All fish	1998 vs. 2000	0.2	0.644	0.100	ns
<152 mm	1999 vs. 2000	5.5	0.047	0.017	ns
152-304 mm	1999 vs. 2000	0.1	0.739	0.100	ns
305-405 mm	1999 vs. 2000	3.2	0.109	0.025	ns
>405 mm	1999 vs. 2000	5.0	0.057	0.014	ns
All fish	1999 vs. 2000	12.1	0.001	0.025	*

Table 2. Results from orthogonal contrasts among size-specific relative condition during LSSF treatment year 2000 and preceding years (df = 1 per contrast) including F ratio, probability P, Bonferroni-adjusted or "critical" alpha (ά), and resulting significance (* indicates P < ά, "ns" indicates P > ά).

Size Category	Contrast	F	P	ά	Significance
< 152 mm	1991 vs. 2000	0.2	0.646	0.050	ns
152 - 304 mm	1991 vs. 2000	39.2	0.000	0.014	*
305 - 405 mm	1991 vs. 2000	9.7	0.014	0.020	*
> 405 mm	1991 vs. 2000	0.6	0.476	0.100	ns
All fish	1991 vs. 2000	6.7	0.032	0.050	*
< 152 mm	1992 vs. 2000	3.9	0.084	0.011	ns
152 - 304 mm	1992 vs. 2000	34.1	0.000	0.017	*
305 - 405 mm	1992 vs. 2000	6.7	0.032	0.033	*
> 405 mm	1992 vs. 2000	0.6	0.460	0.050	ns
All fish	1992 vs. 2000	26.0	0.001	0.020	*
< 152 mm	1993 vs. 2000	3.5	0.097	0.013	ns
152 - 304 mm	1993 vs. 2000	96.0	0.000	0.011	*
305 - 405 mm	1993 vs. 2000	38.5	0.000	0.013	*
> 405 mm	1993 vs. 2000	8.6	0.022	0.033	*
All fish	1993 vs. 2000	50.4	0.000	0.014	*
< 152 mm	1994 vs. 2000	3.2	0.112	0.014	ns
152 - 304 mm	1994 vs. 2000	32.2	0.000	0.020	*
305 - 405 mm	1994 vs. 2000	187.7	0.000	0.011	*
> 405 mm	1994 vs. 2000	56.7	0.000	0.011	*
All fish	1994 vs. 2000	56.1	0.000	0.013	*
< 152 mm	1995 vs. 2000	0.7	0.428	0.033	ns
152 - 304 mm	1995 vs. 2000	27.7	0.001	0.025	*
305 - 405 mm	1995 vs. 2000	21.7	0.002	0.017	*
> 405 mm	1995 vs. 2000	9.4	0.018	0.025	*
All fish	1995 vs. 2000	34.2	0.000	0.017	*
< 152 mm	1996 vs. 2000	2.6	0.146	0.017	ns
152 - 304 mm	1996 vs. 2000	68.8	0.000	0.013	*
305 - 405 mm	1996 vs. 2000	29.9	0.001	0.014	*
> 405 mm	1996 vs. 2000	14.0	0.007	0.014	*
All fish	1996 vs. 2000	56.7	0.000	0.011	*
< 152 mm	1997 vs. 2000	0.8	0.387	0.025	ns
152 - 304 mm	1997 vs. 2000	<0.1	0.878	0.050	ns
305 - 405 mm	1997 vs. 2000	6.7	0.032	0.025	ns
> 405 mm	1997 vs. 2000	15.4	0.006	0.013	*
All fish	1997 vs. 2000	8.6	0.019	0.033	*
< 152 mm	1998 vs. 2000	0.9	0.358	0.020	ns
152 - 304 mm	1998 vs. 2000	23.8	0.001	0.033	*
305 - 405 mm	1998 vs. 2000	3.7	0.090	0.050	ns
> 405 mm	1998 vs. 2000	12.3	0.010	0.017	*
All fish	1998 vs. 2000	12.5	0.008	0.025	*
< 152 mm	1999 vs. 2000	0.1	0.727	0.100	ns
152 - 304 mm	1999 vs. 2000	<0.1	0.978	0.100	ns
305 - 405 mm	1999 vs. 2000	2.7	0.137	0.100	ns
> 405 mm	1999 vs. 2000	10.5	0.014	0.020	*
All fish	1999 vs. 2000	<0.1	0.913	0.100	ns

Table 3. Results from orthogonal contrasts among proportional stock density during LSSF treatment year 2000 and preceding years (df = 1 per contrast) including F ratio, probability P, Bonferroni-adjusted or "critical" alpha (ά), and resulting significance (* indicates P < ά, "ns" indicates P > ά).

Contrast	F	P	ά	Significance
1991 vs. 2000	460.6	0.000	0.011	*
1992 vs. 2000	72.2	0.000	0.013	*
1993 vs. 2000	33.3	0.000	0.014	*
1994 vs. 2000	24.7	0.001	0.017	*
1995 vs. 2000	4.9	0.058	0.033	ns
1996 vs. 2000	6.4	0.036	0.025	ns
1997 vs. 2000	8.5	0.019	0.020	*
1998 vs. 2000	0.0	0.994	0.100	ns
1999 vs. 2000	0.9	0.382	0.050	ns

Table 4. Results from contrasts among instantaneous growth rates during LSSF treatment year 2000 and preceding years including difference between means, standard error (SE) of difference, probability (P) that the difference contains zero, Bonferroni-adjusted or "critical" alpha (ά), and resulting significance (* indicates P < ά, "ns" indicates P > ά).

Contrast	Mean Difference	SE	P	ά	Significance
1992 vs. 2000	-0.0035	0.0003	0.000	0.014	*
1999 vs. 2000	-0.0007	0.0002	0.002	0.100	*
1993 vs. 2000	-0.0018	0.0003	0.000	0.050	*
1997 vs. 2000	-0.0010	0.0001	0.000	0.033	*
1998 vs. 2000	-0.0012	0.0002	0.000	0.025	*
1995 vs. 2000	-0.0015	0.0001	0.000	0.020	*
1996 vs. 2000	-0.0014	0.0001	0.000	0.017	*
1994 vs. 2000	-0.0018	0.0001	0.000	0.013	*

Table 5. Seasonal frequencies of occurrence for predominant items in stomachs of rainbow trout captured by electrofishing, Lee's Ferry reach, 1991-2000. CG = *Cladophora glomerata*; GL = *Gammarus lacustris*; CH = total chironomids; GT = gastropods.

	1991-1999				1999	1999	2000	2000
	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring
CG	55.8	16.6	52.8	56.0	92.9	25.0	55.9	54.5
GL	72.9	70.9	63.9	54.7	21.4	25.0	52.9	54.5
CH	53.8	35.2	56.9	67.5	75.0	70.8	73.5	42.4
GT	19.6	29.1	6.9	15.0	3.6	29.2	29.4	30.3

Table 6. Seasonal size specific comparison of annual relative gut volume data by taxa for the Lee's Ferry tailwater fishery 1991-2000. * indicates significant differences.

size group	season	taxa	X^2	df	P	significance
small	winter	all	5.39	3	0.15	
(<305 mmTL)		*Gammarus*	5.87	3	0.12	
		Cladophora	2.43	3	0.49	
		Chironomid	8.73	3	0.03	*
		Gastropod	6.77	3	0.08	
	spring	all	15.88	7	0.03	*
		Gammarus	15.77	7	0.03	*
		Cladophora	11.00	7	0.14	
		Chironomid	18.31	7	0.01	*
		Gastropod	6.95	7	0.43	
	summer	all	13.76	6	0.03	*
		Gammarus	24.23	6	<0.01	*
		Cladophora	23.50	6	<0.01	*
		Chironomid	38.25	6	<0.01	*
		Gastropod	11.05	6	0.09	
	fall	all	11.50	7	0.12	
		Gammarus	4.81	7	0.68	
		Cladophora	5.50	7	0.60	
		Chironomid	14.82	7	0.04	*
		Gastropod	3.05	7	0.88	
medium	winter	all	11.76	3	0.01	*
(305-405 mmTL)		*Gammarus*	9.47	3	0.02	*
		Cladophora	7.48	3	0.06	
		Chironomid	5.16	3	0.16	
		Gastropod	5.45	3	0.14	
	spring	all	6.31	8	0.61	
		Gammarus	14.72	8	0.07	
		Cladophora	8.27	8	0.41	
		Chironomid	5.12	8	0.75	
		Gastropod	19.38	8	0.01	*
	summer	all	18.06	6	0.01	*
		Gammarus	24.31	6	<0.01	*
		Cladophora	8.96	6	0.18	
		Chironomid	11.17	6	0.08	
		Gastropod	13.61	6	0.03	*
	fall	all	12.47	7	0.09	
		Gammarus	34.97	7	<0.01	*
		Cladophora	15.39	7	0.03	*
		Chironomid	35.50	7	<0.01	*
		Gastropod	5.05	7	0.65	

Table 6 continued. Seasonal size specific comparison of annual relative gut volume data by taxa for the Lee's Ferry tailwater fishery 1991-2000. * indicates significant differences.

size group	season	taxa	X^2	df	P	significance
large	winter	all	0.19	3	0.98	
(>405 mmTL)		*Gammarus*	2.02	3	0.57	
		Cladophora	1.76	3	0.62	
		Chironomid	1.13	3	0.77	
		Gastropod	1.30	3	0.73	
	spring	all	7.11	8	0.53	
		Gammarus	14.56	8	0.07	
		Cladophora	12.87	8	0.12	
		Chironomid	4.89	8	0.77	
		Gastropod	22.24	8	<0.01	*
	summer	all	9.24	6	0.16	
		Gammarus	14.71	6	0.02	*
		Cladophora	12.08	6	0.06	
		Chironomid	13.03	6	0.04	*
		Gastropod	8.05	6	0.24	
	fall	all	3.42	7	0.84	
		Gammarus	6.40	7	0.49	
		Cladophora	5.78	7	0.57	
		Chironomid	2.63	7	0.92	
		Gastropod	1.94	7	0.96	

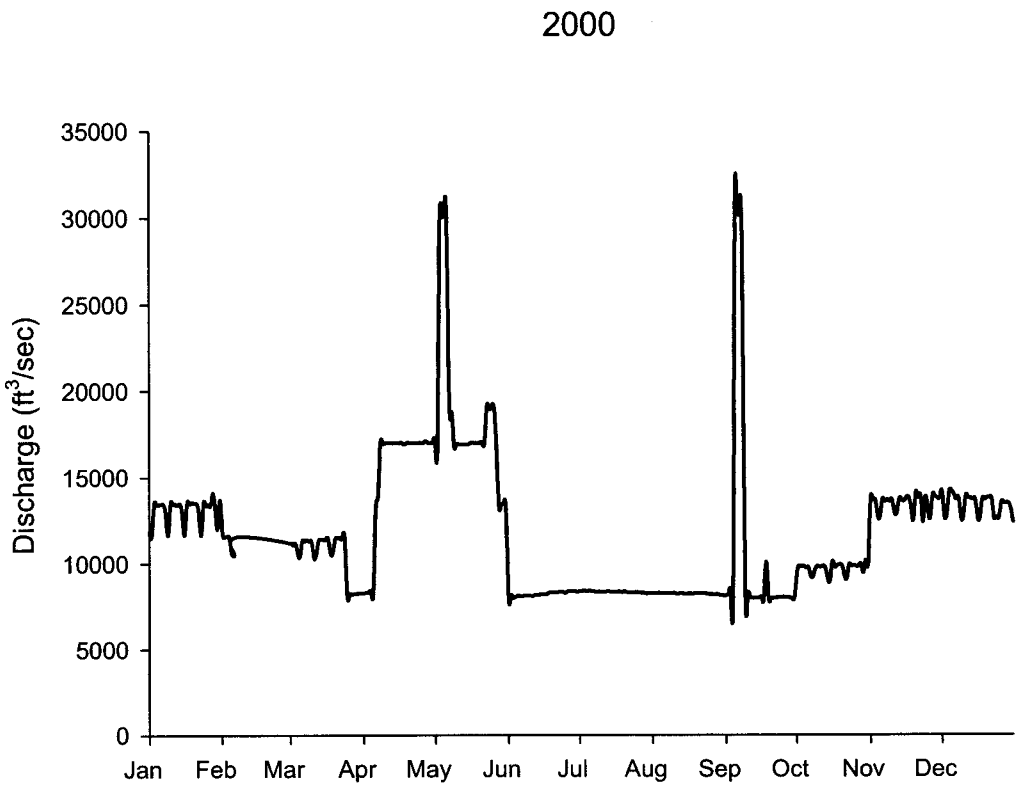

Figure 1. Mean daily discharge from Glen Canyon Dam, January 1- December 31, 2000.

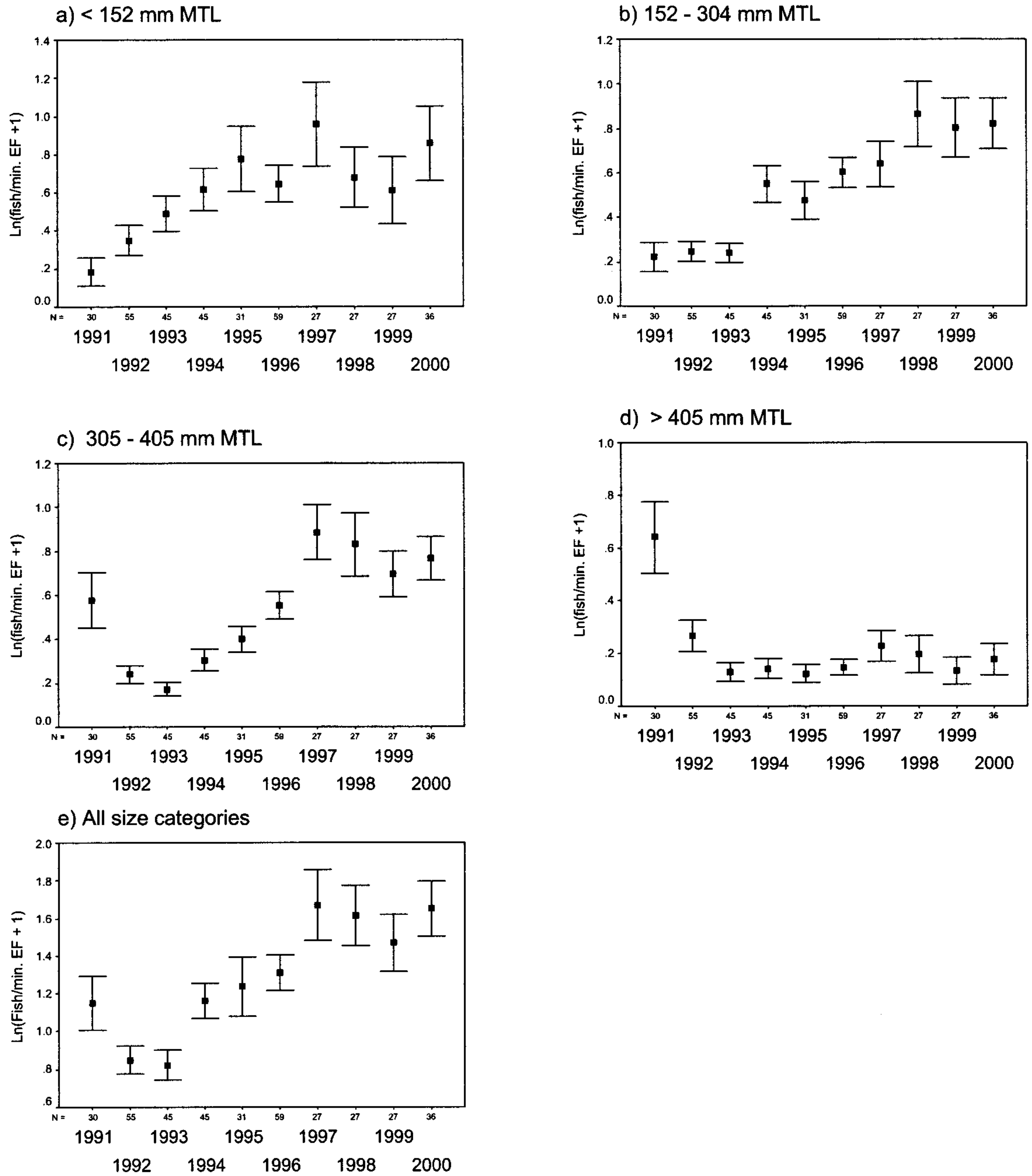

Figure 2. Apparent age-specific log-transformed CPE (fish/minute EF and 95% confidence intervals) of rainbow trout in the Lee's Ferry tailwater, 1991-2000.

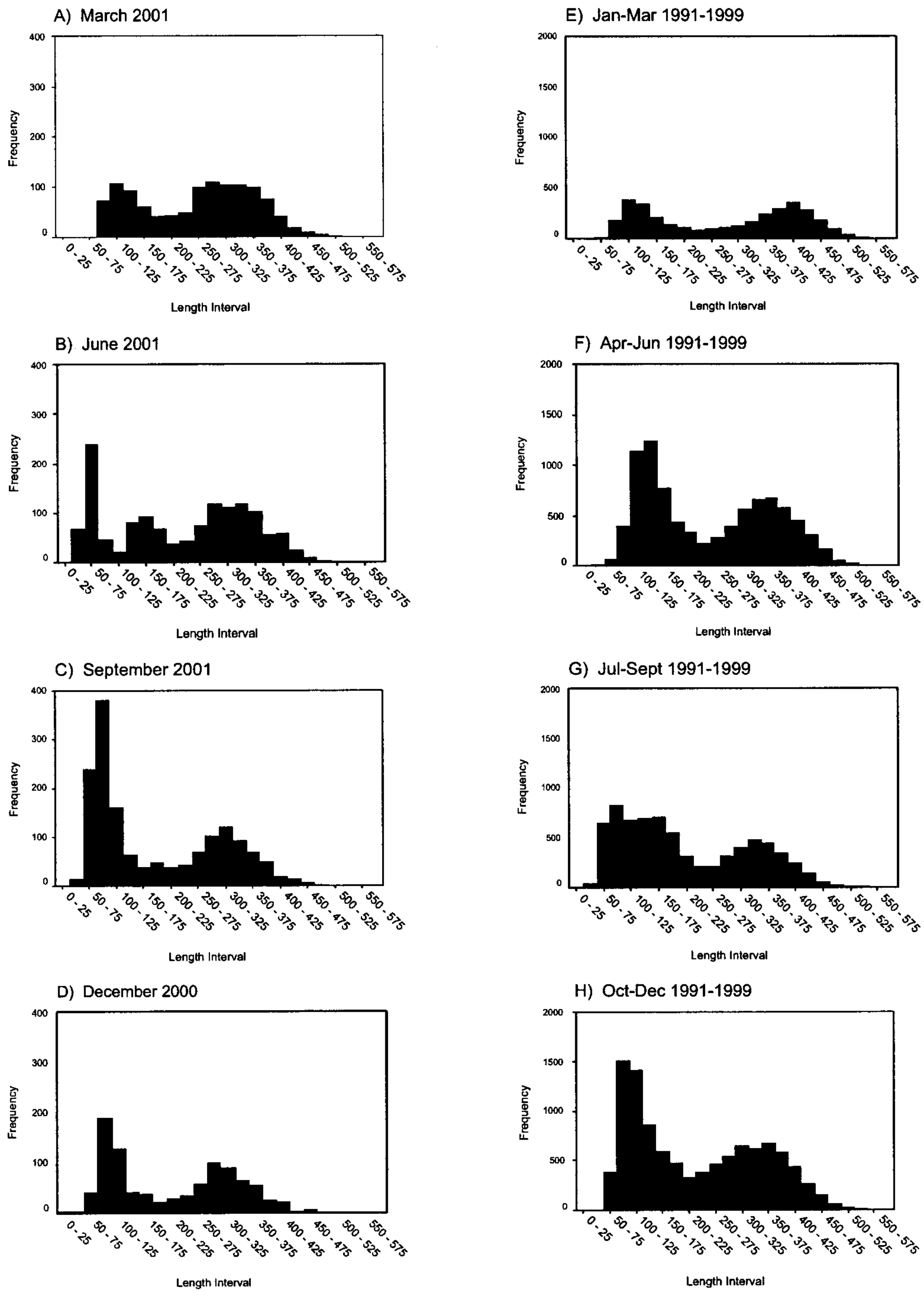

Figure 3. Seasonal length frequencies of rainbow trout captured in the Lee's Ferry tailwater during 2000 (3A-3D) and during 1991-1999 (3E-3H).

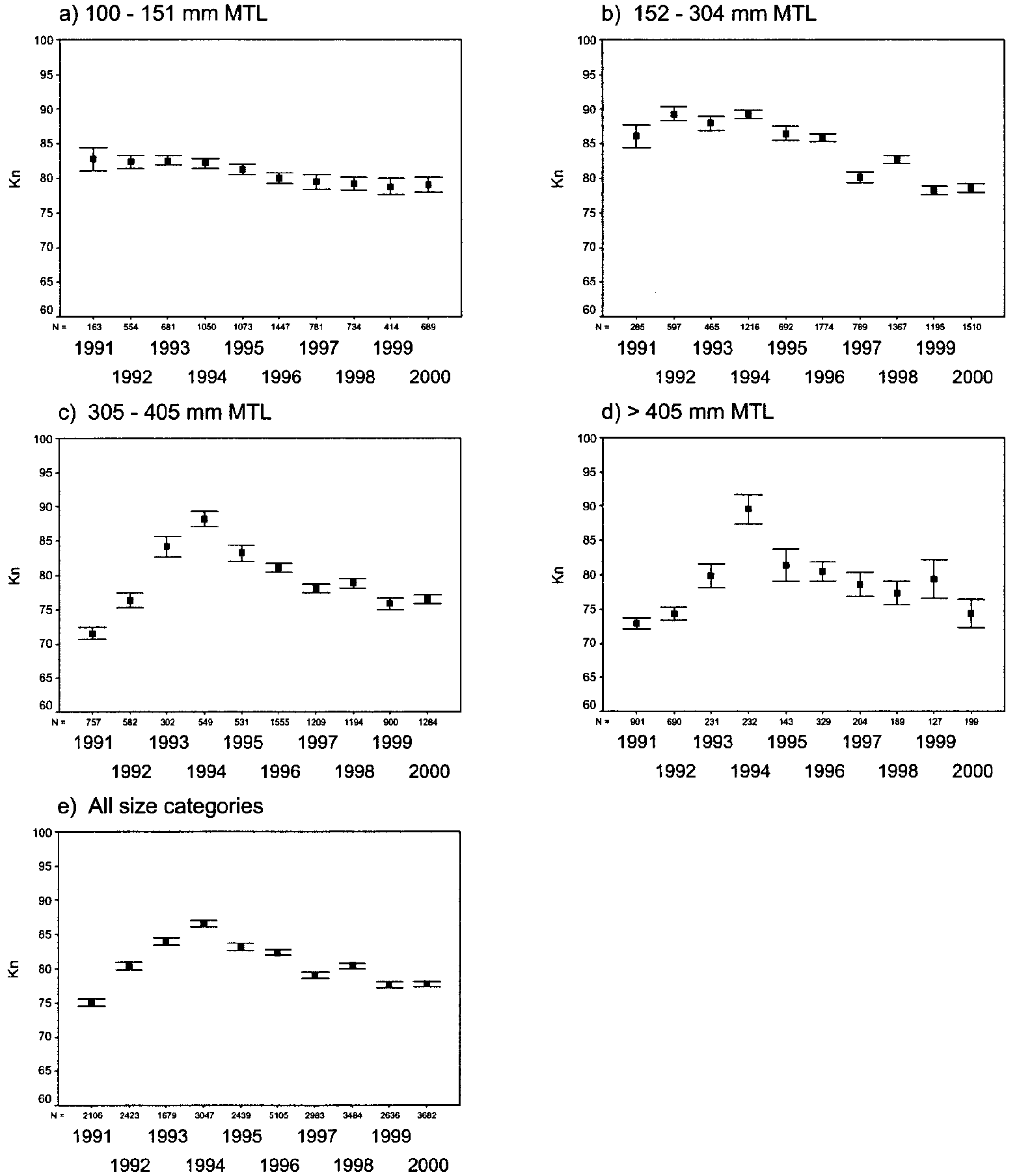

Figure 4. Mean relative condition and 95% confidence intervals of rainbow trout in the Lee's Ferry tailwater, 1991-2000.

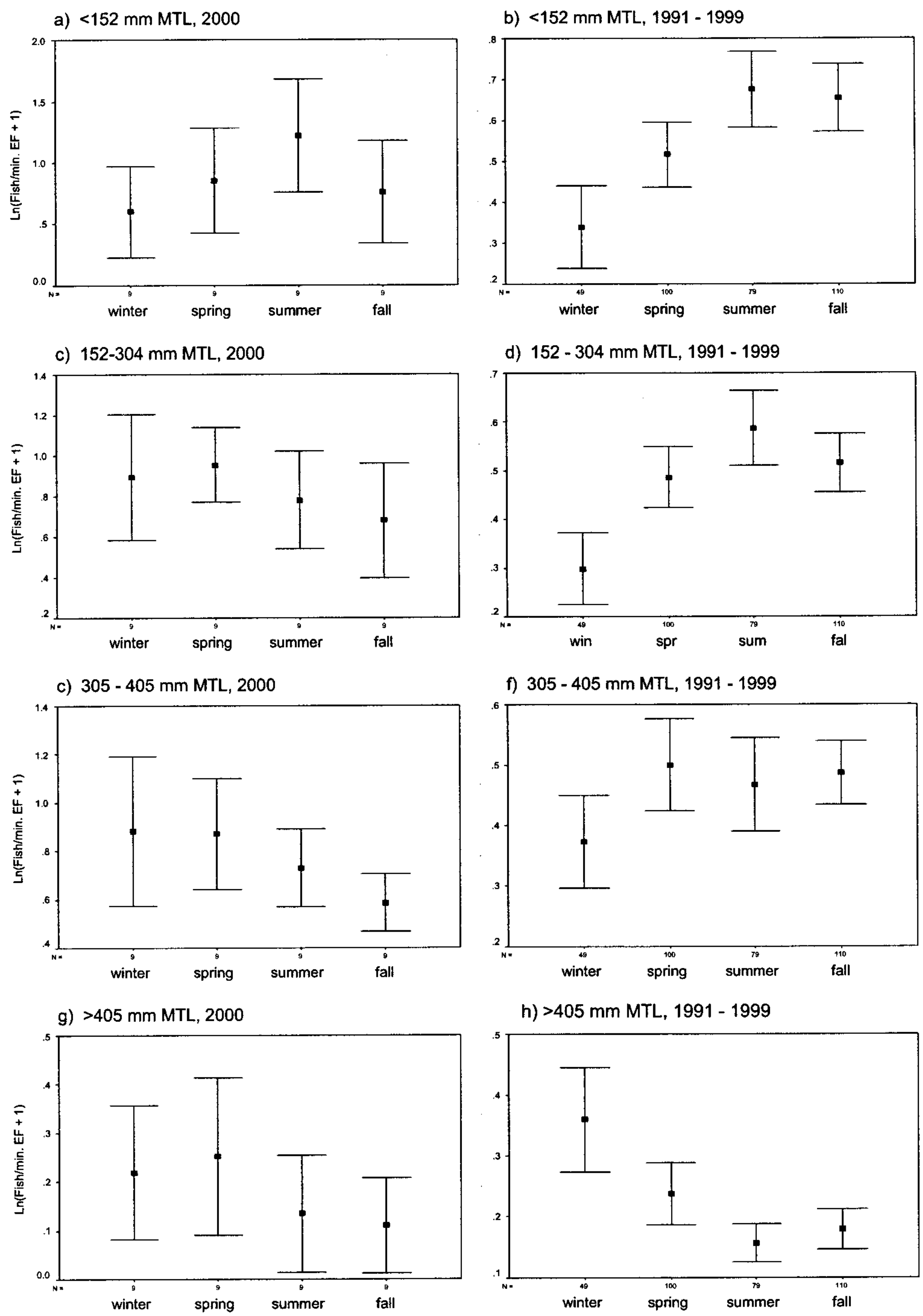

Figure 5. Apparent age-specific log-transformed CPE (fish/minute EF and 95% confidence intervals) of rainbow trout in the Lee's Ferry tailwater in 2000 by season.

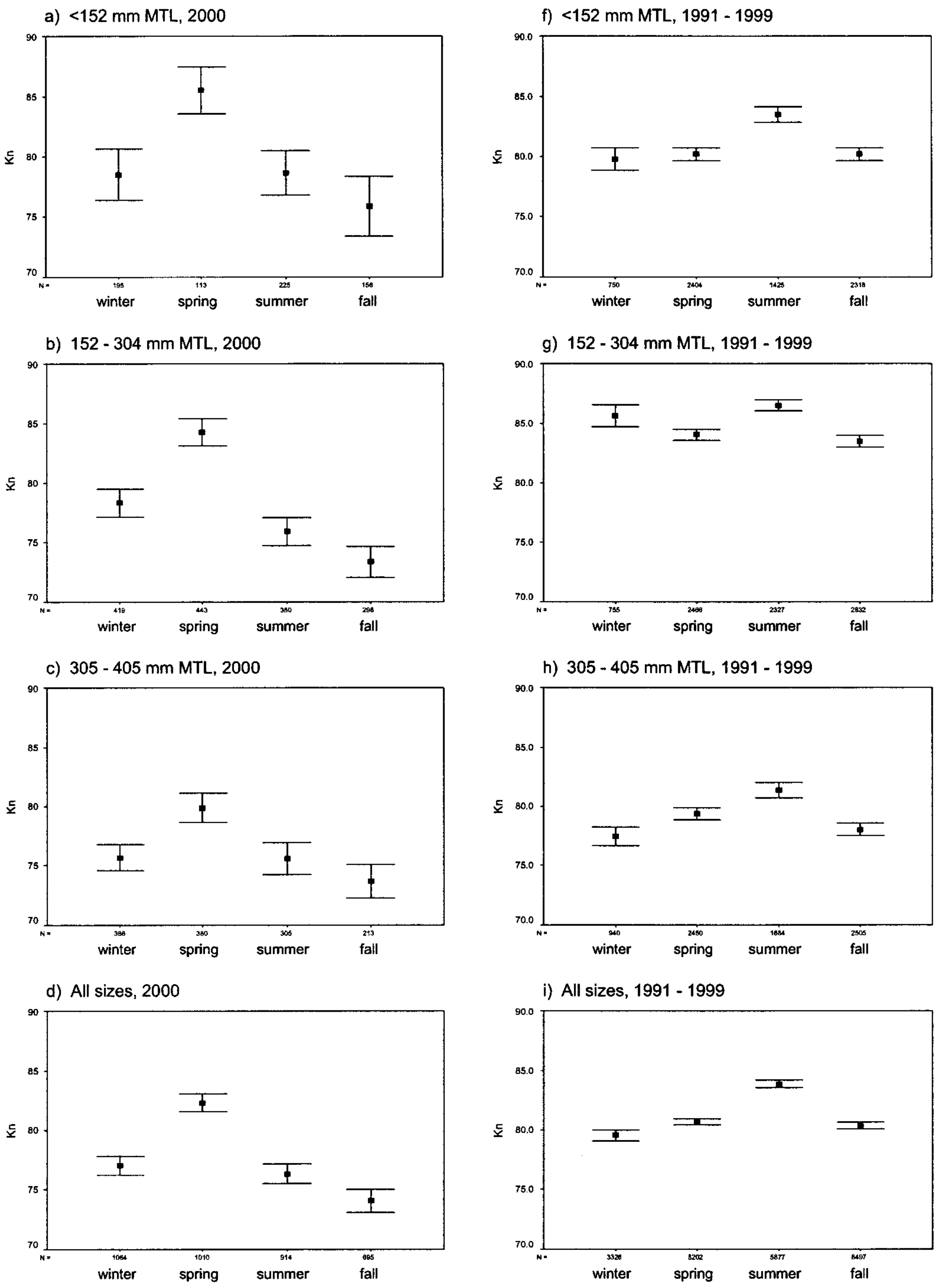

Figure 6. Apparent age-specific relative condition (Kn) of rainbow trout in the Lee's Ferry tailwater in 2000 by season

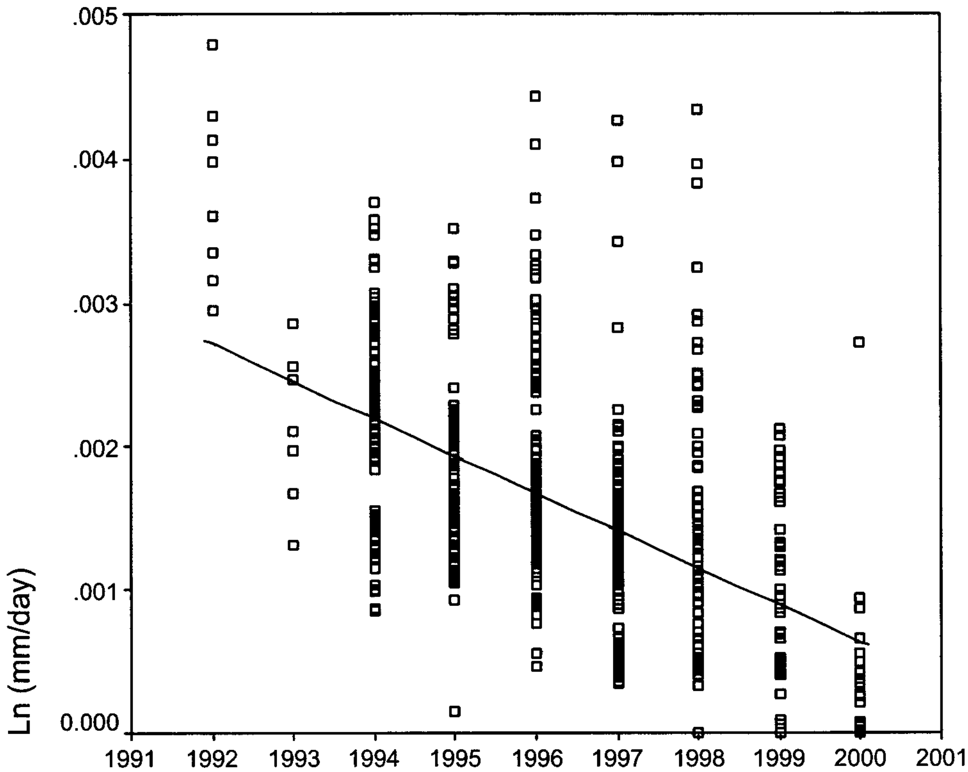

Figure 7. Instantaneous growth of rainbow trout in the Lee's Ferry tailwater during 1993 through 2000. Regression line ($y = 0.522 - 0.0003 * x$) is significant ($df = 732$, $R^2 = 0.29$, $P < 0.001$).

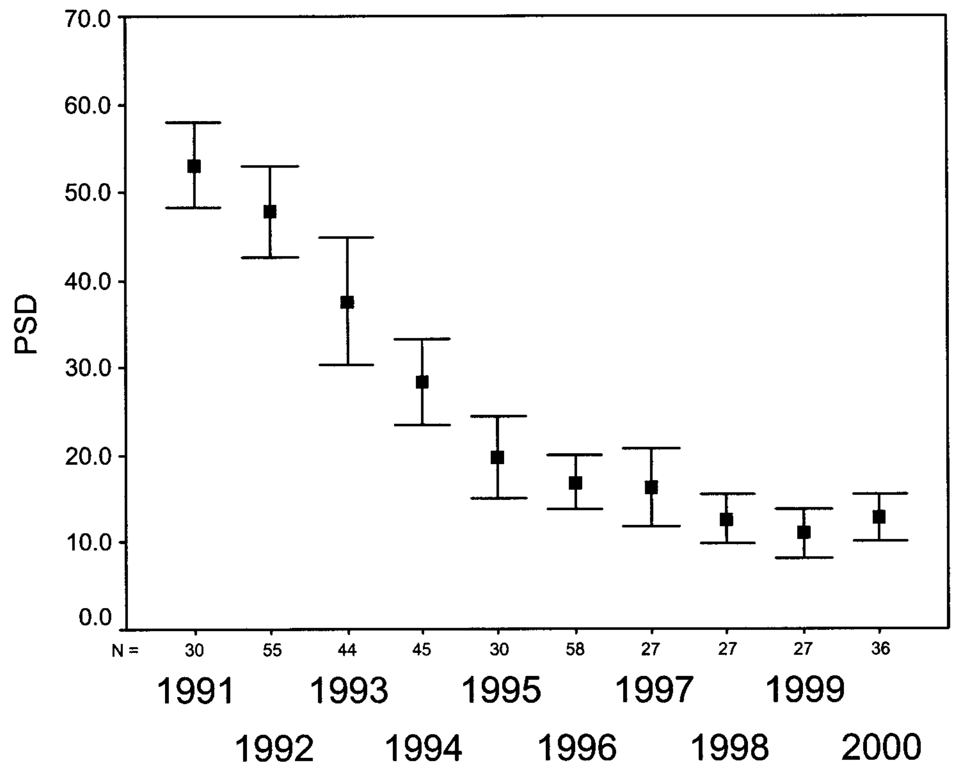

Figure 8. Proportional Stock Density (# fish >=406 mm TL/#fish >=305 mm TL * 100) and 95% confidence intervals of rainbow trout in the Lee's Ferry tailwater, 1991-2000.

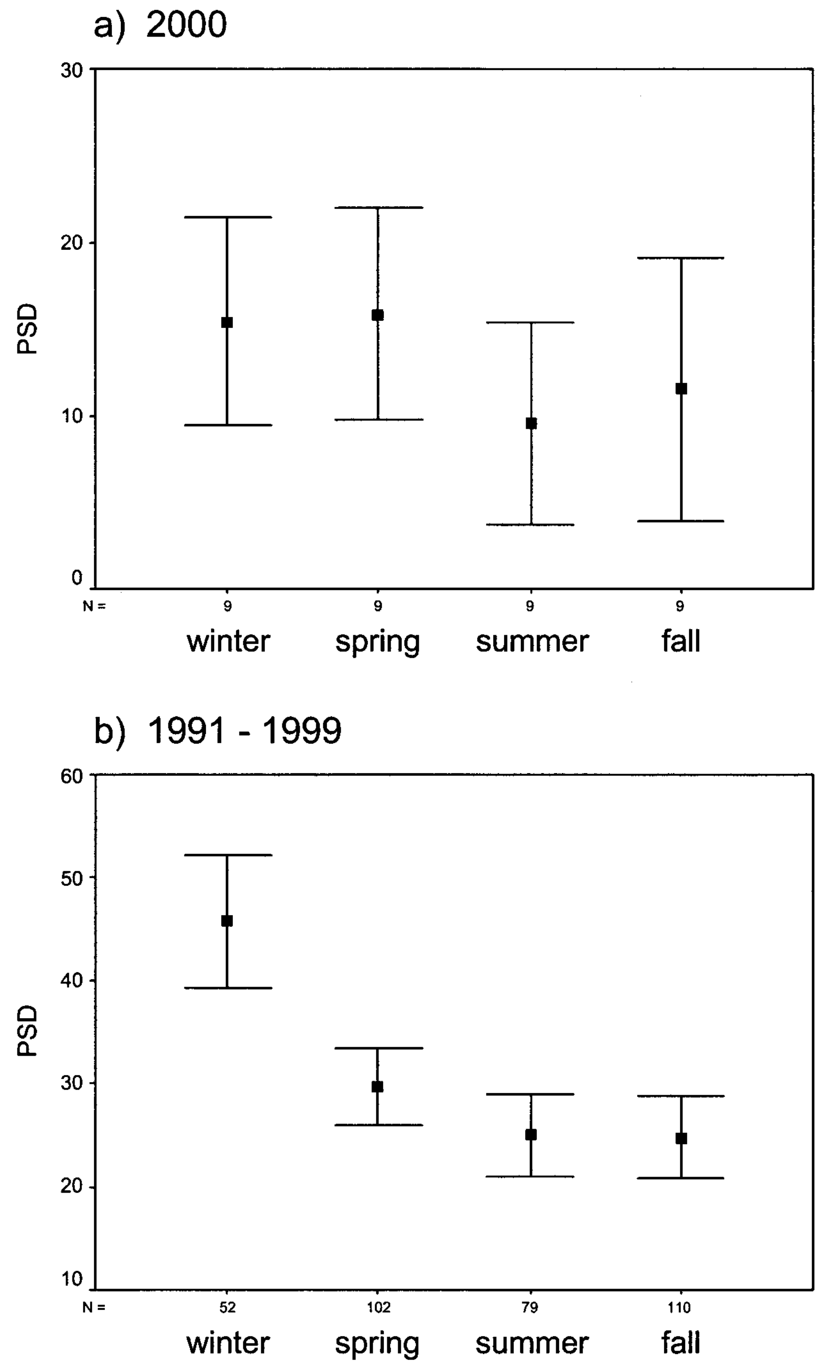

Figure 9. Seasonal Proportional Stock Density (# fish >=406 mm TL/#fish >=305 mm TL * 100) and 95% confidence intervals of rainbow trout in the Lee's Ferry tailwater, 2000 (a.) and 1991-1999 (b.).

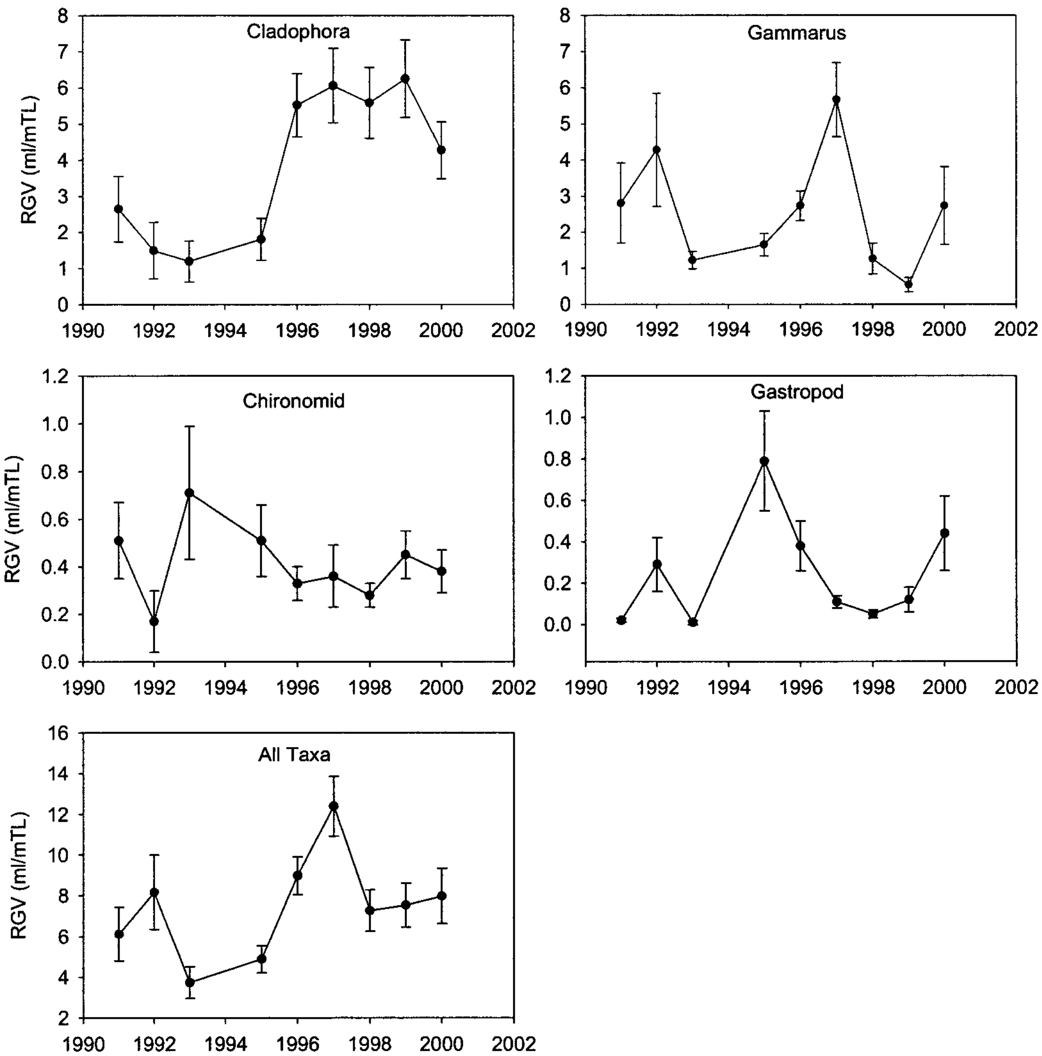

Figure 10. Mean relative gut volume (ml prey/m fish total length, ± 1 SE) of all rainbow trout for major prey taxa in the Lee's Ferry Reach, Colorado River, 1991-2000 (no samples were taken in 1994).

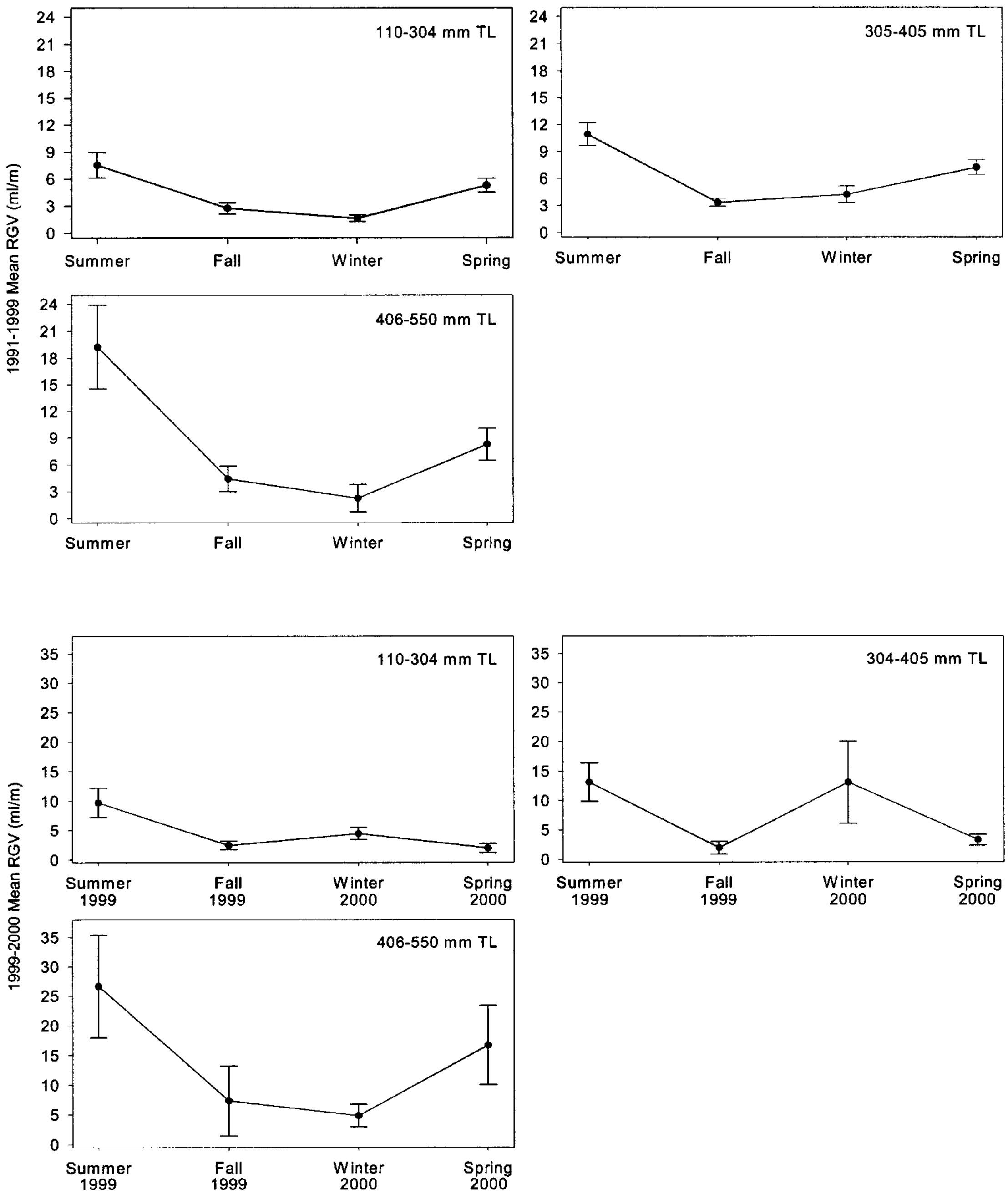

Figure 11. Seasonal size-specific total RGV (± 1 SE) of rainbow trout in the Lee's Ferry reach, Colorado River, 1991-1999 (top) and 1999-2000 (bottom).

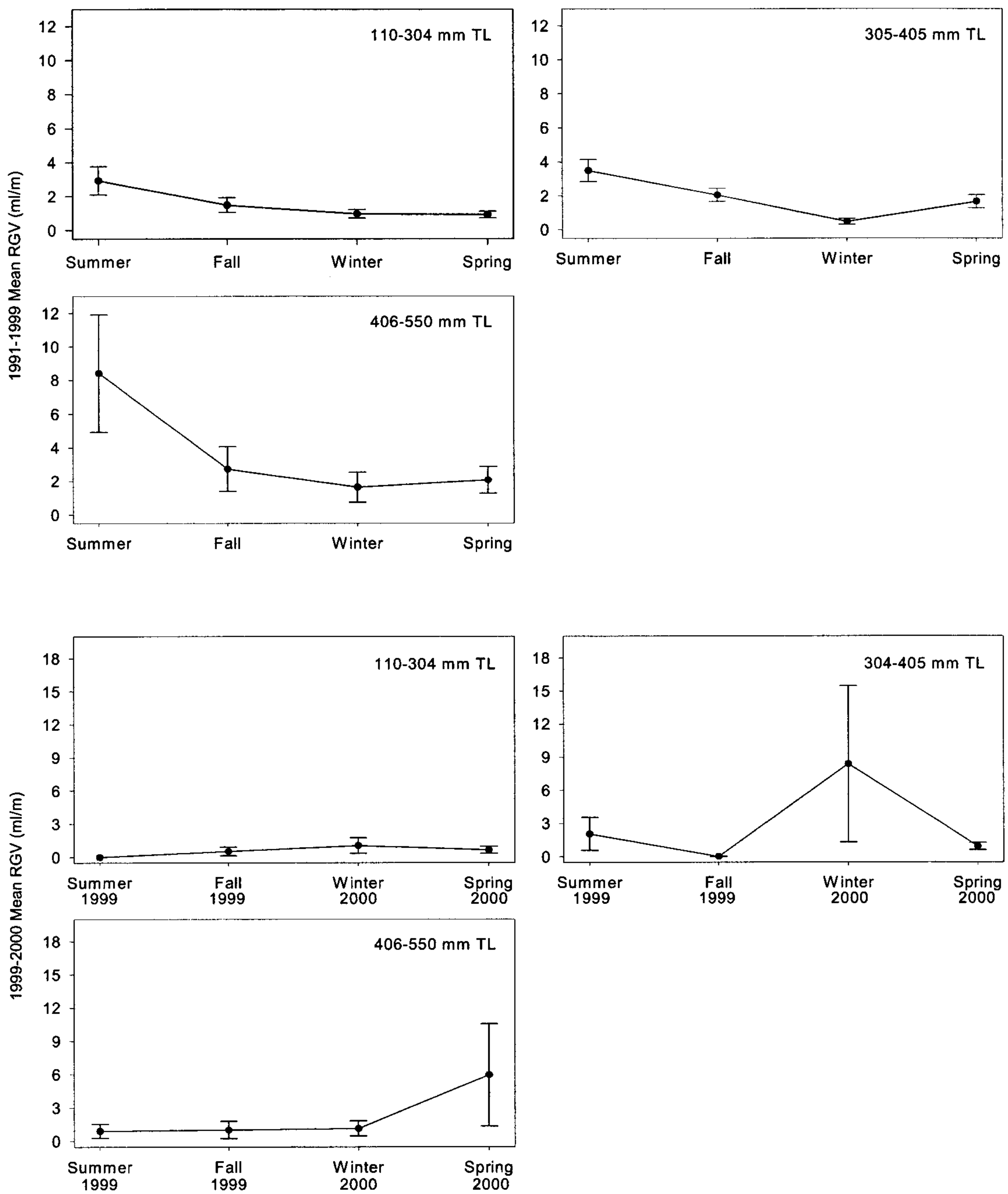

Figure 12. Seasonal size-specific *Gammarus* RGV (± 1 SE) of rainbow trout in the Lee's Ferry reach, Colorado River, 1991-1999 (top) and 1999-2000 (bottom).

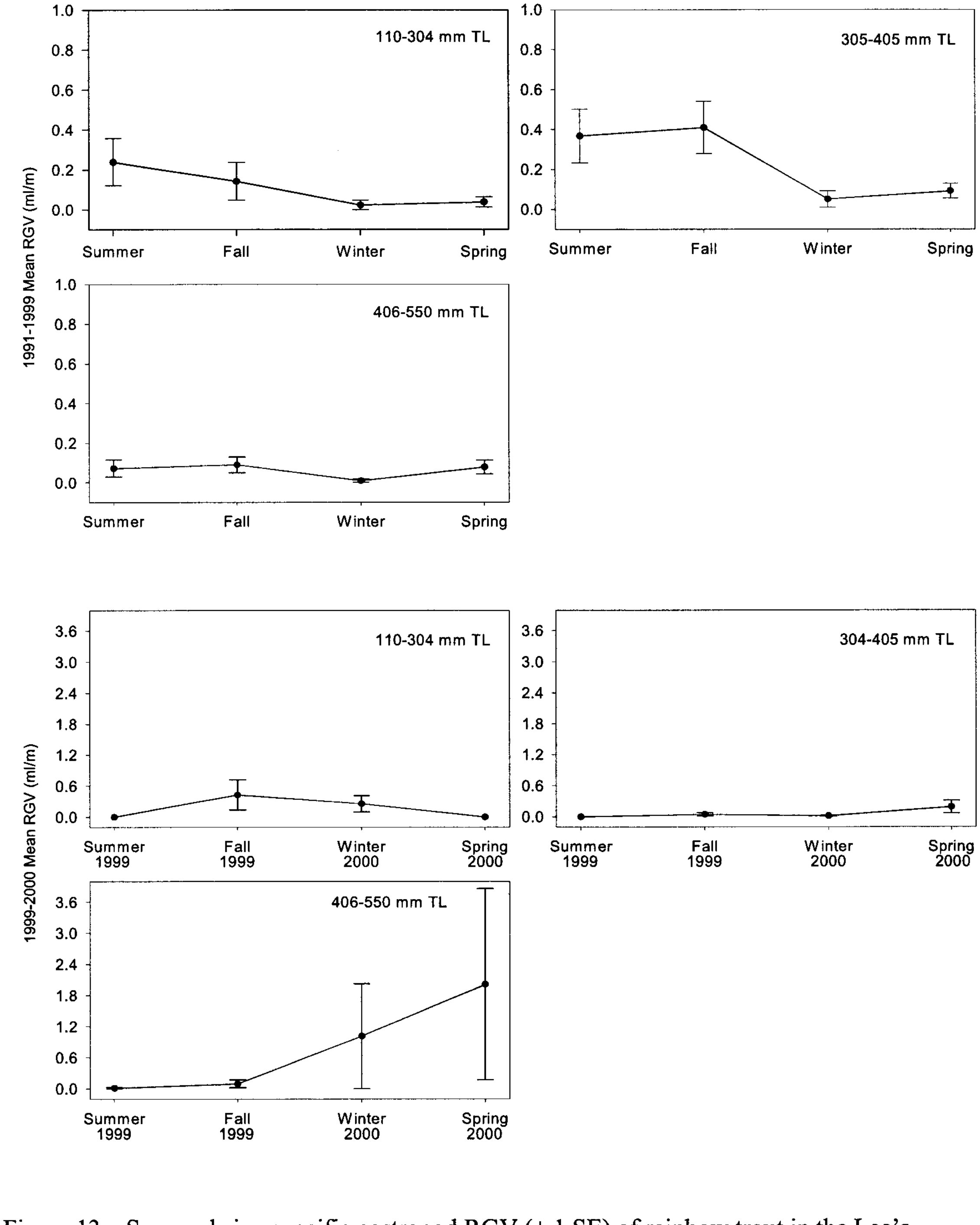

Figure 13. Seasonal size-specific gastropod RGV (± 1 SE) of rainbow trout in the Lee's Ferry reach, Colorado River, 1991-1999 (top) and 1999-2000 (bottom).

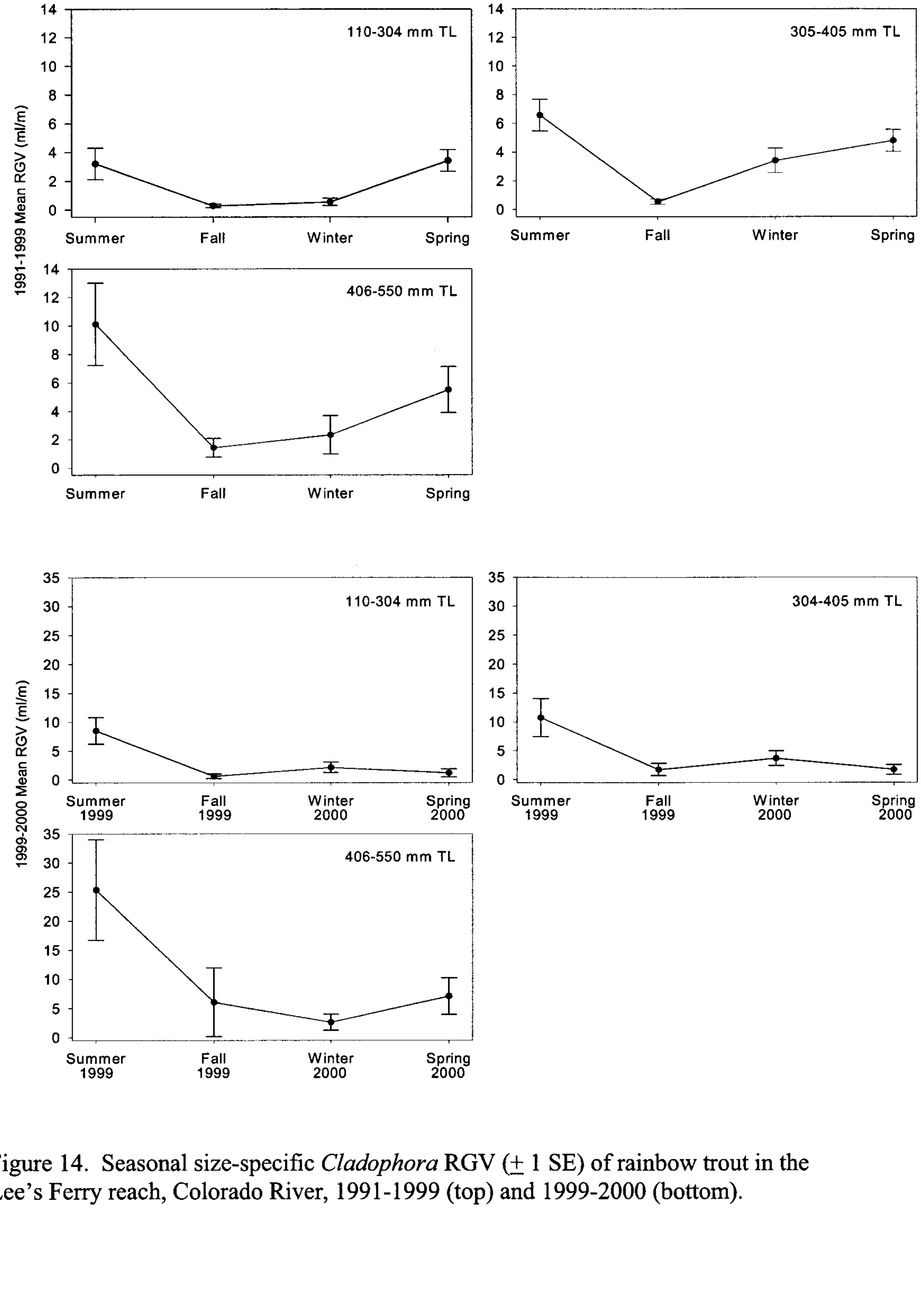

Figure 14. Seasonal size-specific *Cladophora* RGV (± 1 SE) of rainbow trout in the Lee's Ferry reach, Colorado River, 1991-1999 (top) and 1999-2000 (bottom).

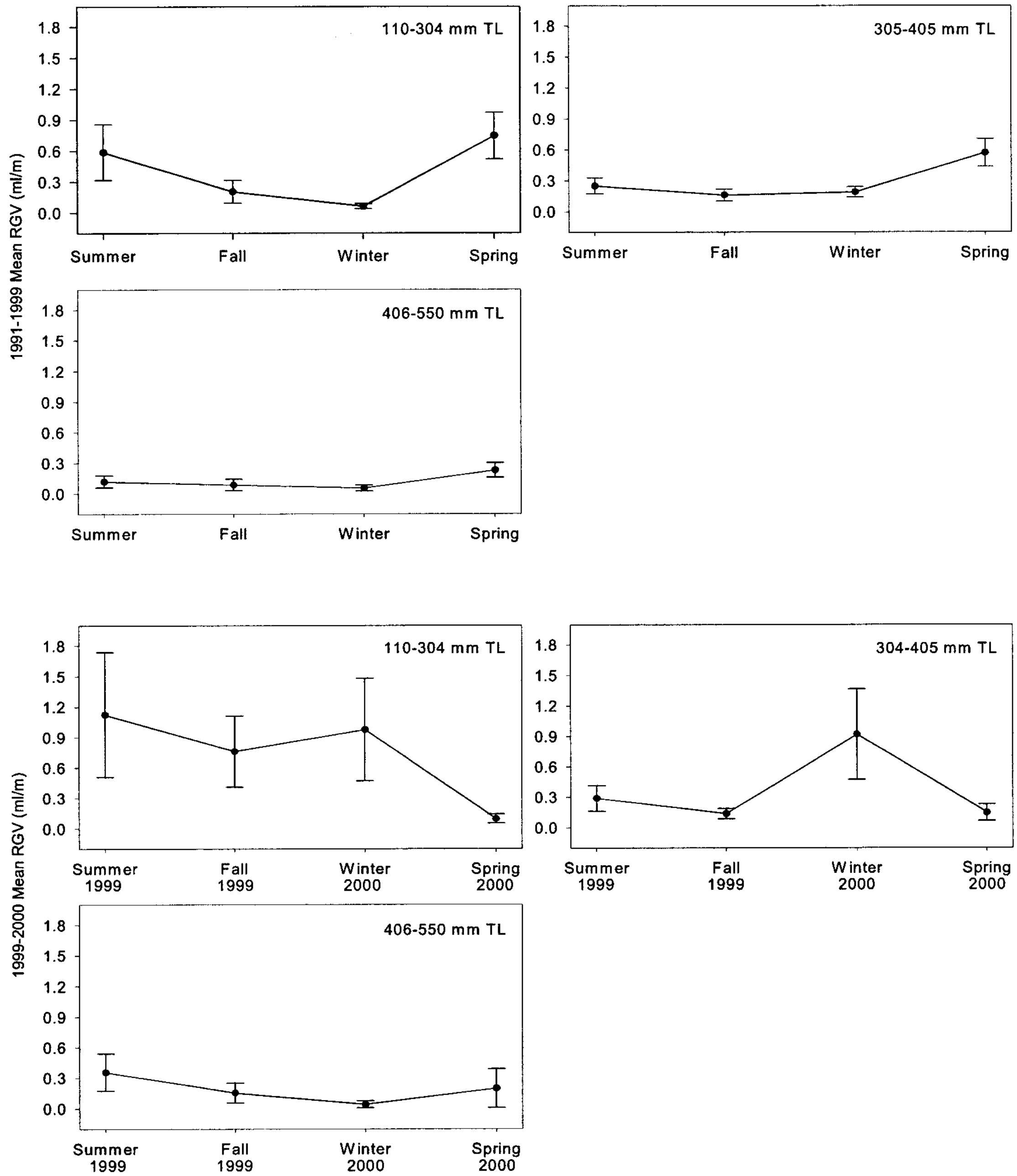

Figure 15. Seasonal size-specific chironomid RGV (+ 1 SE) of rainbow trout in the Lee's Ferry reach, Colorado River, 1991-1999 (top) and 1999-2000 (bottom).

% of Empty Stomach Samples

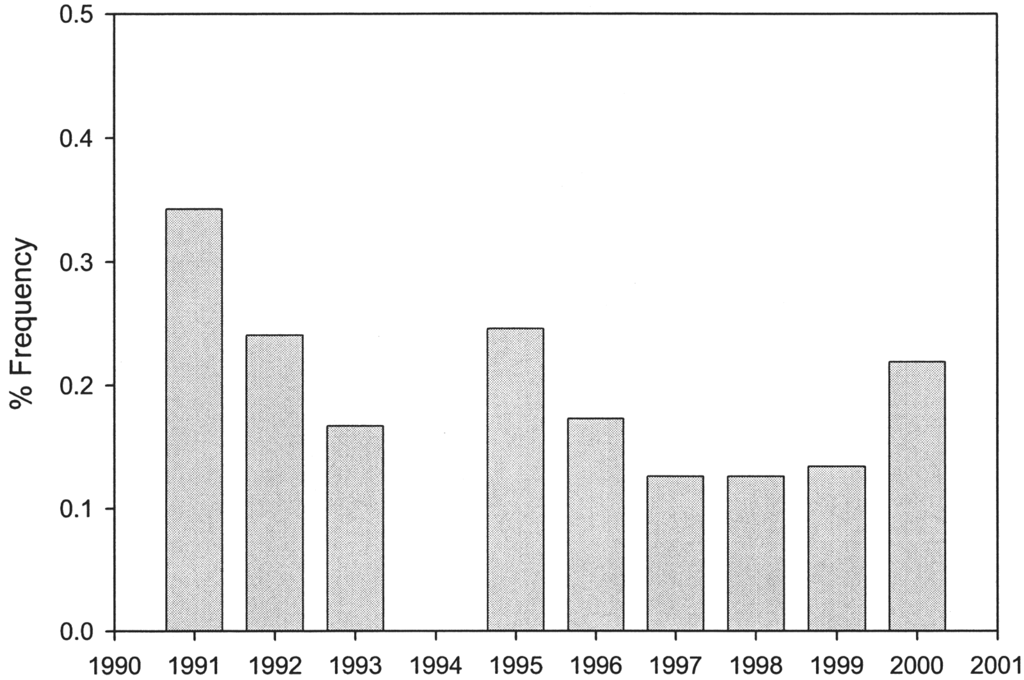

Figure 16. Percent empty stomachs from rainbow trout in the Lee's Ferry reach, Colorado River, 1991-2000.

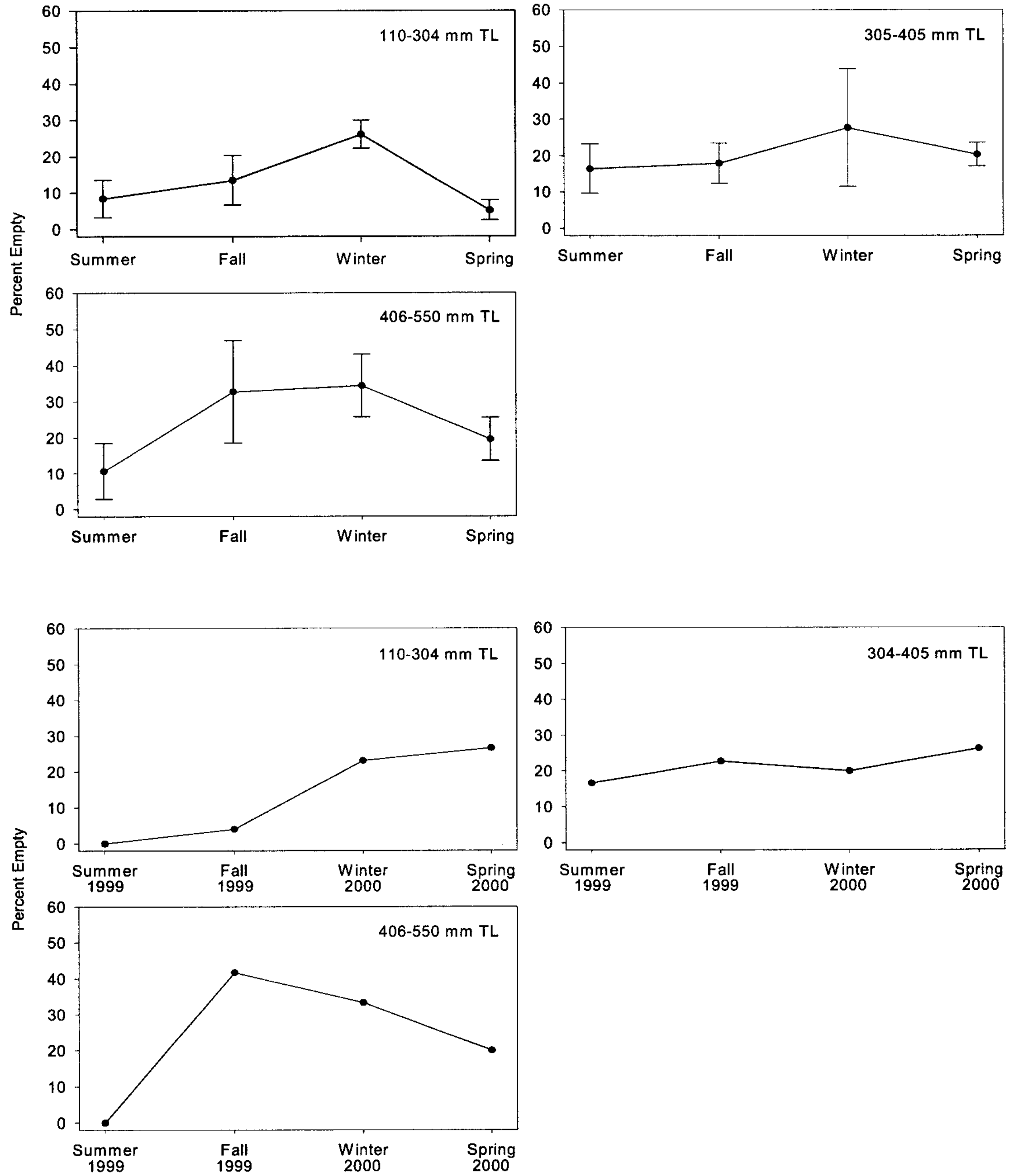

Figure 17. Length-specific seasonal percentages of empty stomachs (± 1 SE) of rainbow trout in the Lee's Ferry reach, Colorado River, 1991-1999 (top) and 1999-2000 (bottom).