# Rainbow Trout and Lower Trophic Levels in the Lee's Ferry Tailwater Below Glen Canyon Dam, Arizona

## A Review

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## INTRODUCTION

The completion of Glen Canyon Dam (GCD) in March 1963 impounded the Colorado River, creating a large meromictic reservoir (Lake Powell) and significantly altering the hydrology, limnology and aquatic ecology of the downstream riverine environment. A popular rainbow trout (*Oncorhynchus mykiss*) recreational fishery developed in the 26 km Lee's Ferry tailwater immediately below GCD following introduction of trout soon after dam closure. However, the fishery declined in angler use and catch rates after the late 1970s, then recovered after about 1992.

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 and discussed operations of GCD (Hughes 1991, Ingram et al. 1991) relevant to ecology of the non-native rainbow trout.

Purpose of the present review is to describe and document the history (1966-1997) of management and research in the Lee's Ferry reach in relation to abiotic and biotic variables to provide synthesized information for fisheries and water resources managers. This review focuses on management, monitoring and research conducted in and relevant to the Lee's Ferry rainbow trout fishery in order to meet requirements of Grand Canyon Monitoring and Research Center (GCMRC), Cooperative Agreement No. 1425-97-FC-40-20810, Arizona Game and Fish Department (AGFD). Research Objective 1: Synthesize existing information (published and unpublished data) on the Glen Canyon/Lee's Ferry trout fishery and determine the fishery's likely response (growth, reproduction, recruitment, population structure, size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. Data and information included were obtained from unpublished and published sources available through mid-1998.

## HISTORY

Prior to construction of the dam, spring to early summer flooding was common, and seasonal floods typically ranged from 2,407 $m^3s^{-1}$ to 2,690 $m^3s^{-1}$ and reached maxima near 8,496 $m^3s^{-1}$ (Valdez and Carothers 1998). During late summer, fall and winter, base flows typically were 85 $m^3s^{-1}$ to 283 $m^3s^{-1}$. Pre-dam water temperatures ranged from near freezing in winter to 29.5$^0$C in late summer (Valdez and Ryel 1995). Post-dam water temperatures in the 26 km Lee's Ferry reach are clear and cold (8$^0$C to 10$^0$C) due to hypolimnetic releases from Lake Powell (Stanford and Ward 1991, Stevens et al. 1997). Glen Canyon Dam dramatically reduced downstream sediment load, resulting in low turbidity in the Lee's Ferry reach (Andrews 1991, Stanford and Ward 1991, Stevens et al. 1997).

Daily, monthly and yearly flows through Glen Canyon since closure of the dam differed dramatically from pre-dam conditions (Andrews 1991, Hughes 1991, Patten 1991, Stanford and Ward 1991, U.S. Department of Interior [USDI] 1995). Mean daily flows during the post-dam period have exceeded 852 $m^3s^{-1}$ only about 3% of the time (vs. 18% pre-dam) and have been less than 142 $m^3s^{-1}$ about 10% of the time (vs. 16% pre-dam), while daily variations in flow have increased (USDI 1995).

Filling of Lake Powell and dam operations are important to understanding ecology of the rainbow trout population and the recreational fishery in the Lee's Ferry reach. The following are major periods associated with reservoir filling and dam and reservoir operations following closure of GCD (Patten 1991, USDI 1995, Valdez and Ryel 1995, Collier et al. 1996, Valdez and Carothers 1998):

1) 1963-1964: Initial reservoir filling--Average flows <85 $m^3s^{-1}$.

2) 1965-1982: Long-term reservoir filling and operations--Daily flows fluctuated $\leq$566 $m^3s^{-1}$. Maintained summer releases $\geq$85 $m^3s^{-1}$, winter releases $\geq$28 $m^3s^{-1}$.

3) 1983-1986: Flood flows, spillway releases and high mean flows--Very high daily, monthly and annual flows. Flows commonly reached 1,278 $m^3s^{-1}$ to 1,420 $m^3s^{-1}$ during late spring and early summer. Minimum releases from dam ranged from 28 $m^3s^{-1}$ to 1,136 $m^3s^{-1}$, but releases often were in the range of 142-284 $m^3s^{-1}$. Maximum releases occurred June 1983 (2,756 $m^3s^{-1}$).

4) 1987-June 1, 1990: High fluctuating releases--Flows commonly ranged daily from <142 $m^3s^{-1}$ to >566 $m^3s^{-1}$. Weekends and holidays were characterized by up to 48 h of steady flows 142 $m^3s^{-1}$. Total and consecutive hours per month with flows <142 $m^3s^{-1}$ increased compared to prior months and years.

5) Research flows--June 1, 1990 to July 29, 1991: Characterized by 10-30 day periods of fluctuating flows ranging from <142 $m^3s^{-1}$ to 866 $m^3s^{-1}$. Fluctuations/24 h varied from 809 $m^3s^{-1}$ to 866 $m^3s^{-1}$. Fluctuating flow periods were followed by 3-11 days of steady flows ranging from 142 $m^3s^{-1}$ to 425 $m^3s^{-1}$. Minimum daily flows were maintained at 28 $m^3s^{-1}$ from Labor Day to Easter and 85 $m^3s^{-1}$ from Easter to Labor Day. Total hours per month with flows <142 $m^3s^{-1}$ increased dramatically.

(Note: Ramping rates were unrestricted during all periods described above)

6) August 1, 1991-September 1996: Interim Flow Alternative (IF) Flow parameters

a. Minimum 227 $m^3s^{-1}$ releases between 07:00 h and 19:00 h, 142 $m^3s^{-1}$ at night.

b. Maximum release 568 $m^3s^{-1}$.

c. Maximum daily fluctuation/24 h = 142 $m^3s^{-1}$ to 227 $m^3s^{-1}$.

d. Upramp $\leq$71 $m^3s^{-1}$/h; downramp $\leq$43 $m^3s^{-1}$/hr

7) September 1996 to present: Modified Low Fluctuating Flows Alternative and Record of Decision (MLFF) Flow parameters

a. Minimum 227 $m^3s^{-1}$ releases between 07:00 h and 19:00 h, 142 $m^3s^{-1}$ at night.

b. Maximum release 852 $m^3s^{-1}$.

c. Maximum daily fluctuation/24 h = 142 $m^3s^{-1}$ to 227 $m^3s^{-1}$.

d. Upramp $\leq$114 $m^3s^{-1}$/h; downramp $\leq$43 $m^3s^{-1}$/hr

(Note: No sustained flows <142 $m^3s^{-1}$ occurred during IF and MLFF.)

**The Fish Community**

Rainbow trout were introduced intermittently in tributaries to the Colorado River below Lee's Ferry by the National Park Service (NPS) and the U.S. Fish and Wildlife Service (USFW) between 1923-1972 but first were stocked in the Lee's Ferry reach by AGFD in 1964 (Table 1, Figure 1). Just prior to completion of the dam, channel catfish (*Ictatulus punctatus*) was the most abundant species in Glen Canyon and comprised about 90% of the fish community (Woodbury 1959, McDonald and Dotson 1960). Seven native and 10 non-native species occurred in the Glen Canyon area during the 1950s, but rainbow trout were absent (McDonald and Dotson 1960). Stone and Queenan (1967) collected 21 species and assessed relative abundance in the Lee's Ferry reach during July 1, 1966 to June 30, 1967 (scientific names are as presented in the original report):

| Species | Relative Abundance |
|---|---|
| Rainbow trout (*Salmo gairdneri*) | Abundant |
| Flannelmouth sucker (*Catostomus latipinnis*) | Abundant |
| Carp (*Cyprinus carpio*) | Abundant |
| Green sunfish (*Lepomis cyanellus*) | Abundant |
| Channel catfish *(Ictalurus punctatus)* | Abundant |
| Bonytail chub (*Gila robusta*) | Common |
| Largemouth bass (*Micropterus salmonides*) | Common |
| Speckled dace (*Rhinichthys osculus*) | Common |
| Red shiner (*Notropis lutrensis*) | Common |
| Fathead minnow (*Pimephales promelas*) | Common |
| Mountain sucker (*Pantosteus delphinus*) | Common |
| Roundtail chub (*G. robusta*) | Rare |
| Humpback chub (*G. cypha*) | Rare |
| Kokanee salmon (*Oncorhynchus nerka*) | Rare |
| Brown trout (*Salmo trutta*) | Rare |
| Black crappie (*Pomoxis nigromaculatus*) | Rare |
| Cutthroat trout (*Salmo clarki*) | Rare |
| Walleye (*Stizostedion vitreum*) | Rare |

| | |
|---|---|
| Black bullhead (*Ictalurus melas*) | Rare |
| Gambusia (*Gambusia affinis*) | Rare |
| Colorado River squawfish (*Ptychocheilus lucius*) | Very rare |

By 1968, rainbow trout likely comprised about 40% of the fish community in the Lee's Ferry reach (Stone and Rathbun 1968). During 1968-1972 (Stone and Rathbun 1969, Rathbun 1970, Stone and Bruce 1971, Stone 1972) and 1980-1993 (Persons et al. 1985, Reger et al. 1988, 1995), respectively, 4-15 and 6-8 species of fish were collected in the tailwater. Rainbow trout and flannelmouth sucker, respectively, comprised more than 50% and 27% of fish collected in 1980-1981 (when Lake Powell filled), and brook trout (*Salvelinus fontinalis*), cutthroat trout, bluehead sucker (*Catostomus discobolus*) and carp made up 1.1%-7.9% of fish (Persons et al. 1985). By 1984-1988, estimated proportion of trout increased to more than 80-90% (Maddux et al. 1987, Reger 1990) and equaled or exceeded that level in 1997, when only rainbow trout, flannelmouth sucker (McKinney et al. 1998c) and carp (AGFD unpublished data) were found in the Lee's Ferry reach. Although sampling methods varied between 1959 and 1997, results suggest a decline in species richness within the fish assemblage in the Lee's Ferry tailwater.

**The Fishery**

Following intermittent creel surveys since 1963, a systematic creel census program was initiated by AGFD in 1977 (Janisch 1985). Angler catch rates generally corresponded with changes in angler use (Table 2, Figures 2, 8). Angler use increased dramatically between 1972 and 1983, declined to 1986, increased during 1987-1991 and reached a low in 1993. During 1993 to 1997, angler use more than tripled but reached only about one-half the peak levels of 1982-1983. Angler catch rates also declined between 1970 and 1980, then increased to maxima in 1996-1997 (Table 2, Figure 2). The 1990-1991 research flows corresponded with declines of about 50% in angler use and catch rates.

Average lengths of fish creeled tended to increase between 1966 and 1983 and length was maximal during in 1978 to 1983 (Table 2). Average weights of creeled trout showed a general trend of increase between 1966 and 1983 but declined about 56% between 1983 and 1997, while mean lengths declined by about 15% during this period. Trout >635 mm TL disappeared from the creel after 1983, and fish >508 mm TL declined from 25% of the harvest in 1979-1983 to less than 10% in 1985-1988 (Reger et al. 1989). The period of 1990-1991, when the dam was operated with research flows, was characterized by abundance of emaciated trout, as fish condition deteriorated (Figure 3, Reger et al. 1995). During 1964-1971, average weight of fish harvested by anglers was 0.3 kg (0.75 lb). Average weight of creeled fish peaked at 1.6 kg (3.5 lb) by 1978, declined to 1.3 kg (2.8 lb) during 1979-1984, and continued a downward trend to 1997, when average weight creeled was 0.4 kg (0.9 lb) ( Table 2, Janisch 1985, Reger et al. 1989, 1995, Reger et al. 1997). The slot limit imposed in 1990 influenced size of fish creeled since that time, but weights and lengths of creeled fish continued their downward trends since about 1983.

The Lee's Ferry reach was managed primarily as a put-and-take fishery between 1964-1976, and rainbow trout were stocked as catchables (ca. 305 mm TL; Reger et al. 1989). Management strategy shifted in 1976 from introducing catchables to stocking fingerlings "as a supplement to natural reproduction" (Table 1, Reger et al. 1995). However, total numbers and salmonid species stocked and proportional composition of fingerlings and catchable fish varied during 1964-1997 (Table 1, Figure 1). Fingerlings ≤120 mm TL were first stocked in the reach in 1964 (Table 1), and catchable fish were last stocked in 1994 (Reger et al. 1997).

Early stockings of rainbow trout were made on the basis of availability of healthy, low cost eggs, regardless of strain (Reger et al. 1997). Considerable effort was expended between about 1989 and 1994 to determine a strain of rainbow trout suited to management objectives for the Lee's Ferry fishery (Davis 1989, 1994, Reger et al. 1995, 1997). The Eagle Lake strain was considered because it exhibited better performance characteristics and capability to achieve trophy size (Davis 1989, 1994). However, Davis (1994) warned against using hatchery characteristics to predict performance in a natural riverine environment. A Kamloops strain (Duncan River) was introduced and evaluated during 1985-1988 but was discontinued due to poor return-to-creel, and stockings of cutthroat and brook trout, respectively, were terminated in 1980 and 1988. Coho salmon (*Oncorhynchus kisutch*) were stocked in 1971 (Persons et al. 1985) but proved unsuccessful. Bel-Aire strain rainbow trout have been stocked extensively by AGFD, and only Bel-Aire strain has been stocked since 1986.

Stocking rates before 1987 averaged about 73,400 fish annually and were reduced to 20,000-25,000 yearly in 1996-1997 (Table 1, Figure 1). Prior to 1986, trout were stocked at the Lee's Ferry loading ramp, but since that time, plantings have been distributed between the loading ramp and GCD (Reger et al. 1989). Most rainbow trout in the Lee's Ferry reach were recaptured in the same areas where they were marked originally, but some occasionally moved downstream into Grand Canyon (Maddux et al. 1987, Niccum and Reger 1998). Reger et al. (1997) suggested that termination of stocking and subsequent development of a self-sustaining fishery would allow assessment of a Lee's Ferry strain of trout but would increase susceptibility of the fishery to catastrophic events and prohibit assessment of age (standard methods for determining age of wild-spawned trout in the tailwater are not feasible) and growth (due to lack of coded wire-tagged fish). Janisch (1985) described four distinct periods for the Lee's Ferry trout fishery by 1985:

1964-1971: Put-and-take era

1972-1978: Trophy fish era

1978-1984: Quality fishing era

1985: Something less than quality but not put-and-take

Interpretation of average weight of fish harvested by anglers, as well as fishing pressure and catch rates, is confounded by multiple changes in fishing regulations during 1964-1997. The following summarizes regulation and management changes potentially affecting the rainbow trout fishery (Janisch 1985, Reger 1990, Reger et al. 1989, 1995, 1997, Persons et al. 1985):

1976--Implemented general policy of all-fingerling stocking.

1978--Reduced bag limit from 10 to 4 fish.

1980--Implemented immediate kill regulation, no size limit.

1986--Implemented artificial lures only regulation and a constant high stocking level.

1990--Implemented a "no-kill" slot (406-559 mm) limitation to increase catch of larger fish. Bag limit reduced from 4 to 2 trout. Stocking was reduced in 1990 to about 60,000-80,000 annually to avoid accumulation of trout within the slot and reduce potential for negative effects on growth rates.

1996--Implemented barbless hook regulation to reduce injury. Stocking rates were reduced to 20,000-25,000 annually.

The 1978 bag limit reduction was based on the decision that the trophy fishery could not sustain increasing angler pressure in the Lee's Ferry reach as the recreational fishing community "discovered" the resource (Reger et al. 1989). The immediate kill regulation in 1980 was intended to prevent mortality due to prolonged "in-creel" possession and subsequent release by anglers, requiring them either to keep or release a fish immediately upon capture. Increased fishing pressure, harvest and percentage of fish released by bait fishermen were considered to be possible factors impairing the sport fishery prior to 1986 (Persons et al. 1985). Therefore, use of artificial lures only was required initially in 1986 to reduce hooking injuries and mortality in the growing percentage of fish caught and released (Reger 1990, Reger et al. 1989). The no-kill slot limit regulation and reduced bag limit were imposed in 1990 to increase catch of larger fish and improve recreational value of the fishery. The barbless hooks restriction in 1996 also was intended to reduce hooking injuries.

Angler use (hours/year) was low and catch rates were high during the "put-and-take" and "trophy fish" eras and increased fivefold between 1977 and 1983 (Table 2). Angler use peaked late in the "quality fishing" era, then declined to 1986, early in the "less than quality" era. Angler use in 1997 remained generally lower than during the "quality fishing" period but was about double that during the "trophy trout" era. Between 1980-1984, anglers voiced increasing concern over "decline" of the fishery, and AGFD became concerned when peak power production from the dam was announced to follow filling of Lake Powell (Janisch 1985, Reger et al. 1989).

Angler catch rates increased during 1981-1990, declined in 1991 and 1992, then increased through 1996-1997, when they exceeded those of previous years. Thus, little long-term correspondence is apparent between angling pressure, size of trout and changes in regulations. However, angler use increased dramatically to 1983, following the initial bag reduction and immediate kill restrictions in 1978 and 1980, respectively. Similarly, artificial lures and slot limit regulations were followed by upward trends in angler catch rates and use between 1986 and 1990 (Figure 7). These comparisons indicate that management efforts to reduce angling-related injury and mortality benefitted the fishery.

Angler surveys were conducted between 1982 and 1984 to enhance understanding of angler attributes and perception of the fishing experience (Caylor 1986, Bishop et al. 1987). Trends in angler use, catch rates and size of creeled fish since 1977 support the conclusion that anglers like to catch fish, especially those of "reasonable size" (e.g., 305 mm TL) but like to have the possibility of catching larger trout (Bishop et al. 1987, Reger et al. 1989). Catching no fish was the most frequently cited attribute of a poor fishing trip in the Lee's Ferry reach, while not catching a trophy trout ranked near the bottom of attributes evaluated.

Management objectives of AGFD in 1990 were to maintain for Lee's Ferry reach an angler catch rate of 0.6-0.9 fish per hour and to increase the average size of trout available to the angler (Reger 1990). Reger et al. (1995) recommended that goals and objectives should be: 1) Age 3 fish should be at least 50% wild-spawned, 2) the estimated population of age 2 and older fish should be maintained at or above about 100,000, and 3) growth rates of trout should be maintained to produce age 3 fish that are 457 mm TL with relative weights (Anderson and Neumann 1996, Simpkins and Hubert 1996) of at least 80. In 1995, Reger et al. (1995) noted that average size of trout in the Lee's Ferry reach was declining and recognized needs to reduce capture- and handling-related stress of angling and to protect larger, "trophy" fish (i.e. slot size and larger) by increasing potential harvest of fish below 457 mm TL. Present angler use and catch rates in the Lee's Ferry reach compare favorably with those reported for put-and-take tailwater fisheries (Swink 1983, Weiland and Hayward 1997).

Table 1. Numbers and size ranges (mm; in parentheses) of trout stocked by Arizona Game and Fish Department in Lee's Ferry reach, 1964-1997. RBT = rainbow trout; BT = brook trout; CT = cutthroat trout. Data taken from Persons et al. 1985, Maddux et al. 1987, Reger et al. 1989, 1995, Reger et al. 1997. (Note: Stocking only of fingerling [≤120 mm total length; TL] rainbow trout from 1976 to 1997).

| Year | RBT | BT | CT | Total |
|---|---|---|---|---|
| 1964 | 35,200 (140-279) | --- | --- | 35,200 |
| 1965 | 22,830 (76-279) | --- | --- | 22,830 |
| 1966 | 14,500 (76-279) | --- | --- | 14,500 |
| 1967 | 20,600 (102-318) | --- | --- | 20,600 |
| 1968 | 38,300 (127-279) | --- | --- | 38,300 |
| 1969 | 64,895 (127-241) | --- | --- | 64,895 |
| 1970 | 24,375 (152-229) | --- | --- | 24,375 |
| 1971 | 5,110 (229-241) | --- | --- | 5,110 |
| 1972 | 4,585 (254-267) | --- | --- | 4,585 |
| 1973 | 3,675 (216-241) | --- | --- | 3,675 |
| 1974 | 3,990 (216) | --- | --- | 3,990 |
| 1975 | 34,500 (76-229) | --- | --- | 34,500 |
| 1976 | 100,000 (51-76) | --- | --- | 100,00 |
| 1977 | 95,000 (76) | 47,880 (64) | --- | 142,800 |
| 1978 | 50,000 (102) | 142,700 (>64) | 60,000 (76) | 252,700 |
| 1979 | --- | --- | --- | 0 |
| 1980 | 87,596 (102) | 40,886 (76-229) | 857 | 129,339 |
| 1981 | 50,000 (102) | 60,096 (102-127) | --- | 110,096 |
| 1982 | 50,000 (102) | 50,000 (76) | --- | 100,000 |
| 1983 | 98,583 (102-114) | 50,000 (89) | --- | 148,353 |
| 1984 | 127,952 (76-102) | --- | --- | 127,952 |
| 1985 | 121,000 | 50,000 | --- | 171,000 |
| 1986 | 128,000 | 40,000 | --- | 168,000 |
| 1987 | 121,000 | 25,000 | --- | 146,000 |
| 1988 | 150,000 | --- | --- | 150,000 |
| 1989 | 129,000 | --- | --- | 129,000 |
| 1990 | 61,000 | --- | --- | 61,000 |
| 1991 | 72,000 | --- | --- | 72,000 |
| 1992 | 78,000 | --- | --- | 78,000 |
| 1993 | 73,000 | --- | --- | 73,000 |
| 1994 | 103,000 | --- | --- | 103,000 |
| 1995 | 73,000 | --- | --- | 73,000 |
| 1996 | 20,000 | --- | --- | 20,000 |
| 1997 | 25,000 | --- | --- | 25,000 |

Table 2. Creel survey statistics for trout in the Lee's Ferry reach 1966-1997 (creel surveys were not conducted during 1973-1979). Angler use (hours/year) based on National Park Service public use data. Other data taken from Stone 1965, 1966, Stone and Queenan 1967, Stone and Rathbun 1968, 1969, Rathbun 1970, Stone and Bruce 1971, Stone 1972, Reger et al. 1989, 1995, 1997. *Annualized estimate based on January-May data.

| Date | Angler hours/Year (x1000) | Angler catch rate (fish/hour/angler) | Average weight (g) of trout creeled | Average length (mm) of trout creeled |
|---|---|---|---|---|
| 7/66-6/67 | 19.0 | 0.46 | 318 | 305 |
| 7/67-6/68 | 22.8 | 0.39 | 309 | 310 |
| 7/68-6/69 | 11.7 | 0.43 | 263 | 274 |
| 7/69-6/70 | 17.6 | 0.46 | 295 | 300 |
| 7/70-6/71 | 15.6 | 0.53 | 276 | 300 |
| 7/71-6/72 | 16.6 | 0.53 | --- | 371 |
| 1977 | 72.2 | — | 735 | 398 |
| 1978 | 67.9 | — | 1,015 | 445 |
| 1979 | 150.2 | — | 926 | 431 |
| 1980 | 129.1 | 0.13 | 1,153 | 465 |
| 1981 | 195.7 | 0.22 | 957 | 436 |
| 1982 | 333.2 | 0.19 | 1,024 | 449 |
| 1983 | 358.5 | 0.27 | 926 | 431 |
| 1984 | 273.2 | 0.37 | 595 | 370 |
| 1985 | 183.6 | 0.60 | 548 | 370 |
| 1986 | 122.8 | 0.39 | 827 | 426 |
| 1987 | 212.7 | 0.68 | 770 | 416 |
| 1988 | 241.0 | 0.78 | 731 | 412 |
| 1989 | 222.4 | 0.76 | 663 | 395 |
| 1990 | 267.9 | 0.80 | 514 | 385 |
| 1991 | 242.4 | 0.56 | 503 | 380 |
| 1992 | 110.4 | 0.41 | 499 | 371 |
| 1993 | 55.4 | 0.49 | 476 | 363 |
| 1994 | 79.5 | 0.74 | 475 | 354 |
| 1995 | 100.1 | 0.88 | 454 | 360 |
| 1996 | 132.8 | 1.11 | 432 | 360 |
| 1997* | 177.9 | 1.10 | 407 | 364 |

### Aquatic Food Base

Little information is available on abundance or composition of benthic algal and invertebrate communities in Glen Canyon before dam construction (Blinn and Cole 1991). McDonald and Dotson (1960) reported a sparse and depauperate (20 species) aquatic insect community in the Colorado River mainstem in the Glen Canyon area in 1958. Assemblage composition and densities of benthic macroinvertebrates after dam construction were typical of the pre-dam Colorado River (Persons et al. 1985). Densities were low, species were limited to a black snail (*Helisoma* sp.) and chironomids (Stone 1964, 1972), and benthic macroinvertebrates were believed to contribute little to food resources of rainbow trout (Stone and Queenan 1967). As a consequence, AGFD introduced numerous invertebrate taxa into the tailwater between 1966-1969, primarily organisms known to be major food sources for trout (Stone and Queenan 1967, Stone and Rathbun 1968, 1969). Most introduced species were unsuccessful, but *Gammarus lacustris*, chironomids and snails persisted (Persons et al. 1985, Angradi and Kubly 1993, Blinn et al. 1992, 1994, Ayers and McKinney 1997a, 1997b, McKinney et al. 1996, 1997) and currently represent a depauperate but important food base for rainbow trout (Angradi 1994, McKinney et al. 1996, 1997, Stevens et al. 1997).

McDonald and Dotson (1960) identified three species of *Cladophora*, one species of *Oscillatoria*, and six species of *Spirogyra* in the Glen Canyon area before dam construction. They also identified eight diatom taxa which are relatively abundant in the 1990s (Ayers and McKinney 1997a, McKinney et al. 1996), but they found no *Diatoma* or *Rhoicosphenia* species, which now are common. Benthic algae (unidentified) occurred to about 0.8 km below GCD in 1968 (Stone and Rathbun 1968). *Cladophora glomerata* and the amphipod *Gammarus lacustris* were introduced simultaneously into the Lee's Ferry tailwater in 1968 (Maddux et al. 1987), and the filamentous alga had established in large beds to about 8 km below the dam by 1969 (Mullan et al. 1976). Biologists speculated that the spread of *Cladophora* was the key to the establishment of benthic macroinvertebrates (Stone and Rathbun 1969). However, densities of benthic macroinvertebrates remained very low at least to 1972 and occurred only near diversion tunnels below the dam (Stone 1972). *Cladophora* had established in large beds to more than 124 km below the dam by 1981 (Persons et al. 1985). *Cladophora* remains the dominant filamentous green alga on rocky substrata in the Lee's Ferry reach, but submerged macrophytes (*Chara contraria* and *Potamogeton pectinatus*) established extensively since 1993 (Ayers and McKinney 1996b, McKinney et al. 1996, 1997). Presently, the 26 km clear-water Lee's Ferry reach supports more than 60% of the primary producer mass and more than 85% of the benthic macroinvertebrate mass throughout Glen and Grand Canyons (Blinn et al. 1994, Stevens et al. 1997).

## MONITORING AND RESEARCH

The Glen Canyon Environmental Studies (GCES Phase 1) program was initiated in 1982 in association with upgrading the dam's generators. Ecological knowledge of large riverine systems in response to dam operations was poor when the GCES program was initiated (Walburg et al. 1981, 1983, Cushman 1985, Persons et al. 1985, Leibfried and Blinn 1987, Usher et al. 1987, Blinn and Cole 1991, Wegner 1991), and the program was developed to obtain data necessary for making decisions regarding operating criteria of the dam. Subsequently, studies were extended in 1990 (GCES Phase 2) to collect additional data relevant to identifying and understanding effects of dam operations on the downstream ecosystem, identifying critical habitats for fishes, and understanding magnitudes of influence of abiotic, biotic and hydrologic variables on lotic biota (Patten 1991).

Grand Canyon Monitoring and Research Center has coordinated most monitoring and research in the tailwater since 1996.

Limnology of Lake Powell, coupled with dam operations, determines limnology of the Colorado River downstream from the dam (Stanford and Ward 1991, Hart and Sherman 1996). Nutrient levels and physicochemical variables in the reservoir and the Lee's Ferry tailwater generally remained similar between 1967 and 1997 (Stone 1966, Stone and Queenan 1967, Stone and Rathbun 1968, 1969, Stone and Bruce 1971, Stone 1972, Persons et al. 1985, Grimm and Fisher 1986, Maddux et al. 1987, Blinn et al. 1992, Ayers and McKinney 1996c, Hart and Sherman 1996, Stevens et al. 1997 [but see Cole and Kubly 1976, Wegner 1989]). However, concentrations of total phosphorous have declined in the tailwater since 1993, corresponding with high inflows to Lake Powell during 1993, 1995, 1996, 1997 and the 1996 controlled flood (Susan Hueftle and Bill Vernieu, GCMRC, personal communications and unpublished data). Primary production in the Lee's Ferry tailwater is nutrient-limited (Gloss et al. 1980, Grimm and Fisher 1986, Angradi et al. 1992, Ayers and McKinney 1996b, 1996c).

Physicochemical variables (pH, dissolved oxygen, conductivity, salinity, temperature, turbidity) in the clear-water Lee's Ferry reach are within ranges suitable for reproduction, growth and survival of trout (Wiley and Dufek 1980, Persons et al. 1985, Maddux et al. 1987, Davis 1989, Griffith 1993, Davis 1994, Walters et al. 1996). Rainbow trout, algae and benthic macroinvertebrates are closely-linked components of the trophic web in the Lee's Ferry reach (Blinn et al. 1992, Angradi 1994, Shannon et al. 1994, Stevens et al. 1997). Within comparatively stable water quality constraints, dam operations, composition and relative abundance of the aquatic food base, intraspecific factors, habitat, angling pressure (angler use and catch rates), and resource management (e.g., stocking, regulations) are variables influencing the Lee's Ferry rainbow trout fishery.

Investigators in lotic systems have considered relations among stocking rates, angler harvest, intraspecific factors, food base and water temperature and quality as variables influencing trout populations (Binns and Eiserman 1979, Orth and Maughan 1982, Cada et al. 1987, Conder and Annear 1987, Ensign et al. 1990, Bohlin et al. 1994, Filbert and Hawkins 1995, Kwak and Waters 1997, Weiland and Hayward 1997). Persons et al. (1985), Maddux et al. (1987), Leibfried and Blinn (1987), Usher et al. (1987), Angradi et al. (1992) and Angradi and Kubly (1993) conducted the earliest investigations regarding effects of dam operations on lotic biota in the Lee's Ferry tailwater and downstream, providing focus and foundation for much future research in the Glen Canyon reach. Andrews (1991), Blinn and Cole (1991), Dawdy (1991) and Stanford and Ward (1991) reviewed early GCES investigations of sediment transport, algal and invertebrate biota, hydrology and limnology of the Colorado River through Glen and Grand Canyons under pre- and post-dam environments.

## LAKE POWELL AND GLEN CANYON DAM

Circulation patterns of water in Lake Powell are characterized by strong advective overflow during late spring and early summer, interflow during late summer to early fall and underflow during late fall and winter (Mayer 1977, Merritt and Johnson 1977, Johnson and Merritt 1979, Gloss et al. 1980, Stanford and Ward 1991, Ayers and McKinney 1996c). Vertical mixing occurs in winter to about 60 m in depth, and thermal stratification is induced as early as March, persisting through September. Primary production in the reservoir is phosphorous-limited and dependent on seasonal advective nutrient renewal associated with the spring overflow plume (Gloss et al. 1980, Ayers and

McKinney 1996b, 1996c). Primary and secondary production varies seasonally but is concentrated within the reservoir trophogenic zone (Hansmann et al. 1974, Blinn et al. 1976, Stewart and Blinn 1976, Gloss et al. 1980, Haury 1986, Sollberger et al. 1988, Angradi et al. 1992, Ayers and McKinney 1996a, 1996b, 1996c).

Under present operations of GCD, hypolimnetic withdrawals from the reservoir penstock zone entrain living and dead organisms which are discharged through dam draft tubes (Petts 1984, Ayers and McKinney 1996a, 1996b, 1996c). Generally, physical, chemical and biotic variables characteristic of outflows through GCD draft tubes are similar to those of water at penstock depth in the reservoir forebay and at Lee's Ferry (Ayers and McKinney 1996b, 1996c, Hart and Sherman 1996). Rapid water turnover of water from the dam through Glen Canyon (Graf 1995) impedes changes in nutrient and physicochemical variables within the reach. Withdrawal currents in the reservoir encompass broad horizontal and vertical zones but may not lead to discharges of near-surface waters at reservoir elevations $\geq$ 1,100 m (Merritt and Johnson 1977, Johnson and Merritt 1979).

If implemented, selective withdrawal of near-surface waters from Lake Powell during spring and summer (USDI 1995) likely would result in increased discharge of plankton from the reservoir at that time (Ayers and McKinney 1996a, 1996b, 1996c). Epilimnial-release reservoirs tend to yield a greater abundance of plankton during periods of stratification, but hypolimnetic releases contain greater concentrations of bacteria and organic debris (Petts 1984) which contribute a nutrient-rich detritus to the dam tailwater system (Sedell et al. 1978, Kondratieff and Simmons 1984, Petts 1984, Lieberman and Burke 1993). Thus, selective withdrawal of near-surface waters, compared to hypolimnetic releases, likely would affect transport of fine particulate organic matter and influence food webs and structuring of biotic communities downstream from GCD (Vannote et al. 1980, Thorp and Delong 1994).

## LEE'S FERRY REACH

### Aquatic Food Base

***Benthos:*** Prior to about 1990, knowledge and understanding of ecology of the benthic communities in the Lee's Ferry reach were limited (Blinn and Cole 1991). The aquatic ecosystem in the Glen Canyon tailwater (Lee's Ferry reach) developed a depauperate macroinvertebrate community following closure of GCD and is dominated by introduced taxa, *Gammarus lacustris*, chironomids and, to a lesser extent, gastropods, which are key components of the aquatic food base for rainbow trout (Angradi et al. 1992, McKinney et al 1996, 1997, 1998a). *Cladophora glomerata* established throughout the Lee's Ferry reach between 1969 and 1981 (Mullan et al. 1976, Persons et al. 1985), and has been the dominant attached filamentous green alga in the tailwater since at least the early 1980s (Gosse 1981, Persons et al. 1985, Usher et al. 1987, Usher and Blinn 1990, Blinn and Cole 1991, Blinn et al. 1994, Ayers and McKinney 1997a, McKinney et al. 1997). *Cladophora* hosts abundant diatom epiphytes which provide food resources for benthic macroinvertebrates (Blinn and Cole 1991, Shannon et al. 1994, Ayers and McKinney 1997a, Stevens et al. 1997). Aquatic macrophytes (*Chara contraria, Potamogeton pectinatus*) became co-dominant with *Cladophora* in the Lee's Ferry reach by 1996 (Angradi and Kubly 1993, 1994, Blinn et al. 1994, Ayers and McKinney 1996a, 1996b, McKinney et al. 1996, 1997), increasing the food base and habitat for benthic invertebrate grazers and rainbow trout. Initially, *Chara contraria* dominated aquatic macrophytes in the tailwater, but *Potamogeton pectinatus*, previously less common, replaced the macroalga following the controlled flood in 1996 (Ayers and McKinney 1996a, 1996b, McKinney et al. 1996, 1997, Shannon et al. 1998).

Benthic macroinvertebrate assemblages in the Lee's Ferry reach consist predominantly of *Gammarus*, chironomids, gastropods and oligochaetes (Persons et al. 1985, Leibfried and Blinn 1987, Blinn and Cole 1991, Blinn et al. 1992, McKinney et al. 1996, 1997, Ayers and McKinney 1996a, 1997a, 1997b). Densities of benthic macroinvertebrates in recent years, relative to the early post-dam period, are high but are patchy and differ among seasons and years (Leibfried and Blinn 1987, Ayers and McKinney 1996a, 1997a, 1997b, Stevens et al. 1997). Macroinvertebrate densities correspond positively with periphyton mass in the tailwater (Gosse 1981, Leibfried and Blinn 1987, Blinn et al. 1992, Shannon et al. 1994, Stevens et al. 1997), but relations between benthic macroinvertebrates and macrophyte densities and species composition on soft-bottom habitats is poorly understood (Angradi et al. 1992, Ayers and McKinney 1996a, McKinney et al. 1996, 1997). Interactions between benthic algae and herbivory by grazing macroinvertebrates typically are complex and influenced by numerous factors (Biggs, 1996, Lamberti 1996). Algal biomass provides an index of how much food is potentially available to herbivores in a system at a point in time but provides no information on how large a herbivore population can be supported by that biomass (Steinman and Lamberti 1996). Generally, periphyton is strongly regulated by herbivores in lotic systems (Feminella and Hawkins 1995).

*Cladophora* and aquatic macrophytes in the Glen Canyon tailwater host assemblages of diatom epiphytes (Usher et al. 1987, Blinn et al. 1992, 1994, Ayers and McKinney 1997a, McKinney et al. 1996, 1997) consumed by grazing macroinvertebrates (Pinney 1991, Blinn et al. 1992, Angradi 1994, Shannon et al. 1994, Stevens et al. 1997). *Cladophora* does not provide direct nutritional benefit to macroinvertebrates but serves as structural host for diatom epiphytes (Pinney 1991, Blinn et al. 1992, Angradi 1994, Stevens et al. 1997, Weiland and Hayward 1997). Aquatic macrophytes provide important substrate for epiphytic diatoms and also may be consumed or damaged to some degree by invertebrate grazers (Humphries 1996, Lodge 1991, Newman 1991, Sand-Jensen and Madsen 1989). Diatom epiphyte assemblages on *Cladophora* and *C. contraria* in the Lee's Ferry reach frequently include *Achnanthes minutissima*, *Cocconeis* spp., *Synedra* spp., *Diatoma vulgare*, *Rhoicosphenia curvata*, *Gomphonema olivaceum* and *Tabellaria fennestrata* (Czarnecki and Blinn 1978, Blinn et al. 1989, 1992, Hardwick et al. 1992, Ayers and McKinney 1997a, McKinney et al. 1996, 1997). Large, upright taxa generally predominate over small and adnate species in the reach (Blinn et al. 1989, Hardwick et al. 1992, Shannon et al. 1994, McKinney et al. 1996, 1997), and the upright forms are more readily consumed by macroinvertebrate grazers, e. g., *Gammarus lacustris* (Blinn et al. 1989, Pinney 1991). During 1993-1994, however, small and adnate diatom epiphytes occurred in proportionally greater densities than large, upright species in assemblages on cobbles and sandstone tiles (Ayers and McKinney 1997a). Reasons for this shift in structure are unknown but may have been related to algal pathology (Peterson et al. 1993).

***Organic drift***: *Cladophora* is the predominant primary producer in drifting coarse particulate organic matter (CPOM; >1 mm) in the Lee's Ferry reach (Angradi et al. 1992, Angradi and Kubly 1994, Blinn et al. 1994, Ayers and McKinney 1996b, Shannon et al. 1996). Concentrations of *Cladophora* in the drift peak during late spring to fall (Angradi et al. 1992, Angradi and Kubly 1994, Blinn et al. 1994, Ayers and McKinney 1996b, Shannon et al. 1996), corresponding with seasonal changes in standing stock of the alga (Angradi et al. 1992, Ayers and McKinney 1996a, 1996b). Aquatic macrophytes in the drift increased prior to the 1996 experimental flood releases and provided a high proportion of drifting primary producers during fall-winter, when standing stock of the macroalga *Chara* was at seasonal maxima (Ayers and McKinney 1996a, 1996b).

*Gammarus* and chironomids (several species of chironomids; Blinn et al. 1992, Stevens et al. 1998) are the main macroinvertebrate components in the drift, and concentrations of chironomids exceed those of amphipods (Leibfried and Blinn 1987, Blinn et al. 1994, Ayers and McKinney 1996b, Shannon et al. 1996). Shannon et al. (1996) reported that chironomid larvae predominated in dipteran drift, and Ayers and McKinney (1996b) found that drift concentrations of adults exceeded those of larvae and pupae. Concentrations of total chironomids in the drift tend to be highest in spring or early summer (Leibfried and Blinn 1987, Blinn et al. 1994, Ayers and McKinney 1996b, Shannon et al. 1996), and Ayers and McKinney (1996b) reported that drift of adults, larvae and pupae peaked in the spring, while concentrations of adults also showed a winter peak. Seasonally, drift of *Gammarus* is higher in summer to fall and in winter than during spring (Leibfried and Blinn 1987, Blinn et al. 1994, Ayers and McKinney 1996b), corresponding with seasonal recruitment of young gammarids into the population during summer and onset of breeding in winter (Ayers and McKinney 1997b, Ayers et al. 1998). No correspondence occurred between benthic and drift densities of amphipods or chironomids, but sampling sites for drift and benthos were widely separated in the reach (Ayers and McKinney 1996b, 1997a, Ayers et al. 1998). Results are suspect due to inability to measure and correlate in a valid way and to the possibility of considerable and undocumented local variations (Filbert and Hawkins 1995).

Gastropods and oligochaetes, though present in benthic samples in the Lee's Ferry reach (Blinn et al. 1992, Ayers and McKinney 1997a), are negligible components of macroinvertebrate drift (Leibfried and Blinn 1987, Angradi 1994, Blinn et al. 1994, Ayers and McKinney 1996b, Shannon et al. 1996). Concentrations of entrained zooplankton are comparatively high in the tailwater, and copepods predominate (Haury 1986, Maddux et al. 1987, Ayers and McKinney 1996b). Copepod densities were lower at Lee's Ferry than in water from dam draft tubes, suggesting filtration by benthic flora and predation by young-of-the-year trout (Maddux et al. 1987, Ayers and McKinney 1996a, 1996c). Some production of cladocerans may occur in the reach during summer (Ayers and McKinney 1996b).

***Effects of Dam operations***: Physicochemical and hydrologic variables constrain species diversity, richness, assemblage composition and relative abundance of the aquatic food base in the Lee's Ferry reach (Leibfried and Blinn 1987, Usher et al. 1987, Blinn and Cole 1991, Stanford and Ward 1991, Blinn et al. 1994, 1995, Stevens et al. 1997). Regulated discharges from GCD constitute the primary driving variable influencing assemblage composition and standing stocks of the aquatic food base.

**Fluctuating flows:** Daily fluctuations in releases from GCD reduce mass and chlorophyll *a* content of *Cladophora* in the varial zone (area between daily minimum and maximum flow elevations), compared to permanently-inundated substrata. Among-site variability exists, but Angradi et al. (1992), Blinn et al. (1992, 1995) and Ayers and McKinney (1996a, 1996b) reported that standing stocks of *Cladophora* in the permanently-inundated zone exceeded those exposed to the atmosphere during all seasons. Mass and chlorophyll *a* content of submerged aquatic macrophytes also was lower in the zone of fluctuating flows, and submerged macrophytes tend to be more susceptible to atmospheric exposure than is periphyton (Ayers and McKinney 1996a, 1996b, Humphries 1996).

Usher et al. (1987) and Hardwick et al. (1992) reported reduced epiphytic diatom cell densities and a marked decrease in upright epiphytic diatom taxa associated with fluctuations in discharge. Angradi et al. (1992) and Ayers and McKinney (1997a) reported that colonization of chlorophytes on natural sandstone tiles was inhibited by atmospheric exposure, supporting the finding by Blinn et al. (1995) that colonization by *Cladophora* was slow on cobbles re-wetted following long-term (ca. 6 mo) desiccation.

Researchers confirmed experimentally the negative influences of atmospheric exposure and desiccation on algal assemblages. Experimental atmospheric exposure of epilithon in the field reduced gross primary productivity, and only 57% of initial chlorophyll *a* remained following 8 h of exposure (Angradi and Kubly 1993). Usher et al. (1987) and Blinn et al. (1995) showed in a complex series of field experiments that *Cladophora* mass was reduced 50% after two days of repeated 12 h atmospheric exposures in summer. Five days of repeated exposures resulted in a loss of more than 70% of *Cladophora* and more than 50% of epiphyton mass. One night time exposure in winter to freezing air temperatures reduced periphyton mass and chlorophyll *a* content by about 50%. Nutritional quality of the aquatic food base in zones exposed to the atmosphere during fluctuating flows is reduced by colonization of *Oscillatoria* sp. (Angradi and Kubly 1993, Shannon et al. 1994, McKinney et al. 1997, Shaver et al. 1997). Usher and Blinn (1990) reported losses of *Cladophora* mass following repeated 12 h exposures in stream tanks that were comparable to results observed in the field. Small and adnate epiphytic diatoms became numerically more abundant in stream tanks than large, upright forms at water temperatures (18$^0$C and 21$^0$C) elevated above those of hypolimnetic releases from GCD.

Effects of daily fluctuations in flow in the Lee's Ferry reach on benthic macroinvertebrate assemblages tend to parallel reported results for algae and macrophytes, underscoring strong linkages between primary and secondary producers and dam operations (Pinney 1991, Blinn et al. 1992, Angradi 1994, Shannon et al. 1994, Stevens et al. 1997). Leibfried and Blinn (1987) provided the first quantitative evidence that fluctuating flows reduced total macroinvertebrate standing stocks, but results were taxon-specific. Standing stocks of chironomids, oligochaetes and *Gammarus*, but not gastropods, were reduced during fluctuating flows relative to high steady discharges.

Blinn et al. (1992, 1995) found that nearshore cobbles in the permanently-submerged river channel supported a fourfold greater macroinvertebrate mass than the varial zone at Lee's Ferry. Annual production by *Gammarus* and chironomids associated with cobble habitat was reduced more than 80% in the varial zone (Blinn et al. 1994). Experimental exposure of periphyton to ambient conditions for only 12 h during summer or winter reduced macroinvertebrate mass by 85% or more (Blinn et al. 1992, 1995). Gastropods rapidly (1 wk) recolonized on resubmerged cobbles that were subjected to long-term (ca. 6 mo) desiccation, but standing stocks of *Gammarus* and chironomid larvae failed to reach control levels within four months (Blinn et al. 1992, 1995). Fluctuating water levels enhance colonization by *Oscillatoria* spp. and *Ulothrix zonata* in the varial zone (Angradi and Kubly 1993, Blinn et al. 1994, McKinney et al. 1997, Shaver et al. 1997), potentially reducing diatom epiphytes and macroinvertebrate mass (Blinn et al. 1992, 1994, 1995).

Macroinvertebrate standing stocks also were reduced by exposure at a minimum flow elevation level (repeated exposure but not always exposed daily) in the varial zone in both cobble and fine-sediment habitats, but effects were taxon-specific (Ayers and McKinney 1997a, 1997b, Ayers et al. 1998). Densities of *Gammarus*, gastropods and oligochaetes were significantly lower in the varial zone than in the nearshore permanently-submerged channel, but densities of chironomid larvae and pupae did not differ significantly between the flow zones. Fecundity of *Gammarus* (eggs per female) also is lower in the varial zone than the permanently-submerged channel (Blinn et al. 1994, Ayers and McKinney 1997b, Ayers et al. 1998). Moreover, densities of adult female amphipods and recruitment and survival of young were reduced in the varial zone in both cobble and fine-sediment habitats (Ayers and McKinney 1997b, Ayers et al. 1998).

**Stable Operating Alternatives:** The IF and MLFF regimes increased base flows and reduced discharge fluctuations and hourly ramping rates for releases from GCD. Higher, more stable flows contributed to increases in the aquatic food base by providing more permanently-wetted nearshore zones for colonization by benthos (Walburg et al. 1981, Shannon et al. 1998, Blinn et al. 1995). Increases in wetted perimeter of the river channel associated with IF and MLFF correspond with areal increases in periphyton, aquatic macrophyte and benthic amphipod standing stocks (Ayers and McKinney 1996b, 1997a, McKinney et al. 1996, 1997). However, concentrations of periphyton mass and benthic macroinvertebrate densities in the permanently-submerged river channel evidenced no clear yearly trends following inception of IF through 1996 (Ayers and McKinney 1996a, 1996b, 1997a).

Aquatic macrophytes occurred at low densities in the tailwater since the mid-1970s (Persons et al. 1985, Blinn et al. 1994) but dramatically increased in abundance and distribution following 1992 (Angradi et al. 1992, Ayers and McKinney 1996b, McKinney et al. 1996, 1997, 1998, Shannon et al. 1998), due to streamflow stability (Warburg et al. 1981, Gislason 1985, Ayers and McKinney 1996b) during and following IF. Recently, *Cladophora* has been replaced seasonally downstream from GCD by other algal taxa, including Chlorophyta: *Mougeotia* spp., *Oedogonium* spp., *Spirogyra* spp., *Stigeoclonium* spp.; Rhodophyta: *Batrachospermum* spp., *Rhodochorton* spp.; Cyanophyta: *Tolypothrix* spp.; and a diatom mucilage matrix (Benenati et al. 1997, Shannon et al. 1998). Blinn et al. (1994) observed that physical changes which shift dominance of benthic flora away from *Cladophora* to other taxa may generate profound changes in the aquatic food base.

**Flooding:** No information regarding influences of flooding in the Lee's Ferry reach on lotic biota was available before 1996. Maddux et al. (1987) conducted investigations during 1984-1986, when releases from GCD ranged from 41 $m^3s^{-1}$ to 1,993 $m^3s^{-1}$, but effects of flooding (i.e. greater than power plant capacity, ca. 852 $m^3s^{-1}$) were not assessed specifically. Experimental flood releases from GCD in spring of 1996 (McKinney et al. 1996, Rubin et al. 1998) were implemented during sustained high flows and provided an opportunity to evaluate influences of a disturbance of moderate duration and magnitude on lotic biota. During March 22-April 8, discharges of 1,278 $m^3s^{-1}$ were maintained for seven days and were preceded and followed by four days of steady 227 $m^3s^{-1}$ flows. Immediately following the post-flood low releases, dam operations returned to stable high flows. Standing stocks of benthic primary and secondary (primarily *Gammarus*) producers were reduced following the flood, but taxon- and habitat-specific recoveries occurred within 1-8 months. Biota associated with fine sediments in the river channel were influenced more adversely and recovered more slowly than biota on cobble bars (McKinney et al. 1996, 1998, Shannon et al. 1998). *Potamogeton pectinatus* replaced *Chara contraria* as the dominant submerged macrophyte following the 1996 controlled flood through 1997 (McKinney et al. 1996, 1997). Relative effects of the rising, peak and falling flows of the flood event, as compared to low steady flows just before and after the event, on standing stocks are uncertain (McKinney et al. 1996, 1997).

**Reduced discharges of moderate duration and magnitude:** Brief periods (3 day) of reduced discharges (227 $m^3s^{-1}$) from GCD have been incorporated within sustained high flows during IF and MLFF for aerial photo-documentation of river channel morphometry. Three days of exposure to the atmosphere reduced standing stocks of periphyton, aquatic macrophytes and some benthic macroinvertebrate taxa by more than 60% (McKinney et al. 1997). Macrophytes were negatively affected more than periphyton, and *Gammarus*, chironomids and gastropods were more adversely affected than other macroinvertebrate taxa by the brief flow reduction (McKinney et al. 1997). Losses of benthic standing stocks of periphyton and macroinvertebrates were proportionally comparable to those previously associated with fluctuating flows (Blinn et al. 1992, Ayers and McKinney 1996a, 1996b, 1997a, 1997b) and experimental exposures to the atmosphere (Usher and Blinn 1990, Blinn et al. 1992, Angradi and Kubly 1993, Blinn et al. 1995).

**Discharge and Organic drift:** Numerous investigations indicate that increased drift of benthos corresponds with fluctuating or rising discharges from GCD. Drift rates, densities and the proportion of juvenile (<7 mm) *Gammarus* increased during fluctuating flows (43-625 $m^3s^{-1}$) above levels associated with steady flows (227 $m^3s^{-1}$) in May-December 1985 (Leibfried and Blinn 1987). Drift increased only during rising periods of discharge after periods of low flows (<142 $m^3s^{-1}$). In contrast, drift of *Cladophora* and chironomids changed little during fluctuating flows.

Three days of steady releases (227 $m^3s^{-1}$) from the dam were followed by greater drift of algal and macroinvertebrate mass and densities during two immediately subsequent days of fluctuating (141-283 $m^3s^{-1}$) flows (Blinn et al. 1994, Shannon et al. 1996). Only drifting *Cladophora*, macrophytes, oligochaetes and snails correlated significantly with discharge. McKinney et al. (1997) also found greater mass and densities of *Cladophora*, macrophytes, *Gammarus* and chironomids during rising discharges following three days of steady releases (227 $m^3s^{-1}$) implemented during sustained high discharges (ca. 596 $m^3s^{-1}$) from GCD.

Angradi and Kubly (1994) reported that concentrations of coarse particulate organic matter (CPOM) in the Lee's Ferry reach varied as a function of flow and suggested that *Cladophora* sloughed from the permanently-submerged river channel was a major source of particulate organic matter in the drift. Usher and Blinn (1990) and Blinn et al. (1995) considered that detachment of *Cladophora* in the varial zone occurred during discharge fluctuations. Flow-related losses of benthic flora and macroinvertebrates result in downstream export from the Glen Canyon tailwater of large amounts of potential ecosystem energy (Blinn et al. 1995). Ayers and McKinney (1996b) also reported that CPOM mass was greatest during the peak flow stage of the daily hydrograph, but drift concentrations of *Gammarus* were greatest during the descending flow stage. Blinn et al. (1994) demonstrated experimentally that three nights of repeated exposure of *Cladophora* and its associated macroinvertebrate assemblage resulted in significant loss of periphyton mass to stream drift, including *Gammarus*, snails and lumbriculids.

Stable isotope analysis indicated that drift shifted from primarily autochthonous organic matter (phytobenthos) during normal dam operations to allochthonous terrestrial vegetation during the 1996 experimental flood (Shannon et al. 1998). Drift mass during the flood was an order of magnitude higher than that reported during normal dam operations (Shannon et al. 1996). More than 90% of benthos was removed within 24 hr from the start of the experimental flood, and drift was highest during the first two days. Drift densities of vegetation and macroinvertebrates increased at Lee's Ferry during IF and MLFF (J. P. Shannon and D. W. Blinn, personal communication, Ayers and McKinney 1996b).

## Rainbow Trout

**Population-related trends:** Arizona Game and Fish Department has utilized electrofishing (EF) routinely in trout studies and surveys since about 1980 (Persons et al. 1985, McKinney et al.

1996, 1997). Sharber et al. (1994) developed electrofishing technique during 1988-1991 and recommended a complex pulse pattern of direct current to produce low incidence of injury with good electrotaxis and narcosis. Since 1991, AGFD has employed this EF system to sample standardized transects distributed throughout the Glen Canyon tailwater.

Population attributes of trout in the Lee's Ferry reach have undergone considerable change between 1984 and 1997. Condition (Wr; Anderson and Neumann 1996, Simpkins and Hubert 1996) of trout declined from 1984 to 1991, rose through 1994 and declined about 10% since that time (Figure 3). Catch per unit effort (CPUE = catch per minute of EF) of rainbow trout, an index of density, declined following the 1990-1991 research flows to 1992, then increased through 1997 (Figure 4). Catch of biomass per unit EF also declined from 1991 through 1993 and showed and upward trend since that time (Figure 4). Results of McKinney et al. (1997) generally agree with results from an unregulated stream (Kwak and Waters 1997) in that young age classes contribute most to biomass in salmonid populations.

Proportional stock density (PSD) is a numerical descriptor of length-frequency data used in fish stock assessment (Anderson and Neumann 1996). This index of size structure has been used extensively by fisheries biologists but has found limited application in coldwater systems (Willis and Scalet 1989, Anderson and Neumann 1996). McKinney et al. (1997) computed PSD for rainbow trout captured by EF in the Lee's Ferry reach during 1991 to 1997, using the following formula:

$$PSD = (\text{number of fish} \geq \text{minimum quality length}/\text{number of fish} \geq \text{minimum stock length}) \times 100$$

McKinney et al. (1997) assumed for these calculations that minimum quality length = 406 mm TL and minimum stock length = 305 mm TL, similar to length categories presented by Simpkins and Hubert (1996). Quality and stock lengths, respectively, were defined as the minimum for the present slot limit and a presumed minimum for size of fish (i.e., "pan-size") that most anglers like to catch (Reger et al. 1997).

McKinney et al. (1997) considered a "balanced population" to be one dominated by fish intermediate between extremes in size and to have satisfactory rates of recruitment, growth and mortality (Anderson and Neumann 1996). High or low PSD values and wide variations over time are evident in populations with "functional problems" (Anderson and Neumann 1996). The PSD for trout captured by electrofishing declined continually between widely varying research flows in 1990-1991 (Patten 1991) and 1997 (Figure 5), reflecting "stockpiling" fish within the 305-405 mm TL category and reduced recruitment into larger size classes (Carline et al. 1984, Neumann and Murphy 1991, Reger et al. 1997). Seasonality of angler use of the resource and angling-related impacts on fish may be factors inhibiting accrual of slot-sized trout (Willis and Scalet 1989, Ferguson and Tufts 1992, Muoneke and Childress 1994, Reger et al. 1995).

Growth rates of trout in the cold Lee's Ferry reach are difficult to estimate because fish cannot be aged accurately due to absence of discrete annuli on scales and otoliths and year-round reproduction. Between 1964 and 1997, stocked trout have been tagged to allow mark-recapture studies and assess growth, recruitment and survival (Persons et al. 1985, Reger et al. 1995). Early efforts employed streamer tags, fin clipping and oxytetracycline dye to evaluate relative contributions of hatchery and natural reproduction to the fishery, but coded wire tags implanted in the nasal cartridge of stocked fish have been used exclusively since 1992. Only three wire-tagged trout stocked in the Lee's Ferry reach have been recaptured downstream from the tailwater (Valdez and Ryel 1995). Estimations of growth of trout during 1984-1997 have varied from about 7 mm/month to 12.7 mm/month (Maddux et al. 1987, Reger et al. 1995, 1997). MULTIFAN analyses (Fournier et al. 1990, 1991, Terceiro et al. 1992) were used in an attempt to model age and growth structures of the Lee's Ferry trout population, but quantification of age and growth remains problematic, in part due to inability to assess unmarked wild-spawned fish (AGFD unpublished data 1994). Mark-recapture studies of rainbow trout might offer potential in conjunction with angler surveys and population modeling to evaluate fishing regulations in the Lee's Ferry fishery (Luecke et al. 1994). Reger et al. (1995) estimated that 22% of stocked fingerling rainbow trout survived to exceed 405 mm TL after three years, and 23% of catchable stocked fish survived to exceed 405 mm TL after two years.

**Food habits:** Throughout the late 1960s and early 1970s, trout diets consisted primarily of zooplankton and algae (Stone 1966, Stone and Queenan 1967, Stone and Rathbun 1968, 1969, Rathbun 1970, Stone and Bruce 1971, Stone 1972). Zooplankton consumed by trout in these early years likely originated in Lake Powell (Haury 1986, Stanford and Ward 1991, Ayers and McKinney 1996c) and were comparatively abundant in water released from the dam from 1966 to 1995 (Stone and Queenan 1967, Rathbun 1970, Haury 1986, Maddux et al. 1987, Ayers and McKinney 1996c). Recent studies (AGFD unpublished data 1994) found low frequencies of occurrence and volumes of zooplankton in stomachs of rainbow trout ca. 100-150 mm TL, but multiple stable isotope analyses (Angradi 1994) indicated that adult trout (390-460 mm TL) in the Lee's Ferry reach consume zooplankton exported from Lake Powell. We are aware of no investigations to date that have evaluated zooplankton in trout of this length category. Maddux et al. (1987) also reported that during 1984-1985, zooplankton comprised about 40% ( numbers of food items for individual taxa) consumed by rainbow trout fry in the tailwater.

Algae occurred in stomachs of about 36% of trout examined during 1967-1969 (Stone and Queenan 1967, Stone and Rathbun 1968, 1969), and consumption of *Cladophora* by trout in the Lee's Ferry reach has remained high in subsequent years (Persons et al. 1985, Maddux et al. 1987, McKinney et al. 1996, 1997). *Gammarus lacustris* first was observed in trout stomachs (one amphipod in one fish) in 1969 (Stone and Rathbun 1969), and snails began occurring in stomachs in 1972 (Stone 1972). *Gammarus* became important in trout diets following about 1971, after which growth rates of stocked trout and size of fish creeled increased as the trophy fishery developed (Janisch 1985). Chironomids were introduced into the Lee's Ferry reach in 1966-1967 but were not reported as an important food component for trout until the 1980s (Stone and Queenan 1967, Stone and Rathbun 1968, 1969, Persons et al. 1985, Maddux et al. 1987).

Threadfin shad (*Dorosoma petenense*) were stocked in Lake Powell in 1969 and comprised a significant dietary component of trout during February-March 1970 (Rathbun 1970). Frequencies of occurrence between July 1969 and June 1970 were: algae 30.8%, fish 25.0%, zooplankton 21.5% (Rathbun 1970). However, fish were absent or infrequent and comprised low proportions in trout stomachs in previous (Stone and Queenan 1967, Stone and Rathbun 1968, 1969) and subsequent studies through 1997 (Persons et al. 1985, Maddux et al. 1987, Angradi et al. 1992, McKinney et al. 1996, 1997).

Trout food habits in the Lee's Ferry reach tend to correspond seasonally with concentrations of *Cladophora* and macroinvertebrates in the drift (Ayers and McKinney 1996b) and benthos (Ayers and McKinney 1997a, 1997b). The trout diet varies seasonally in the Lee's Ferry reach (Maddux et al. 1987, McKinney et al. 1996, 1997, 1998a), and diet composition has been consistent since about the 1980s, reflecting reliance on the depauperate benthos community and drift (Persons et al. 1985, Maddux et al. 1987, Angradi et al. 1992, McKinney et al. 1996, 1997, 1998a). Rainbow trout food habits tend to reflect composition of the drift (Elliott 1973, Wilzbach et al. 1986, Filbert and

Hawkins 1995). Unfortunately, drift samples were not collected in the Lee's Ferry reach coincident spatially and temporally with EF until 1997 (McKinney et al. 1997), when simultaneous EF and drift sampling was initiated to enhance determination of relations among trout diets, nutrition, energetics and drift and benthos concentrations (Elliott 1973, Cada et al. 1987, Ensign et al. 1990, Filbert 1991, Filbert and Hawkins 1995).

**Stocking and natural reproduction:** Persons et al. (1985) reported significant correlation between stocking rates and harvest of fish 1964-1981, indicating that the fishery was dependent on stocking. Prior to 1987, stocked fish comprised an estimated 72.5% of angler harvest (Maddux et al. 1987). During the period when bait fishing was allowed (prior to 1986), a stocking rate of 111,000 fish annually was estimated to be necessary to sustain 350,000 angler hours at a harvest rate of 0.15 fish/hour (Persons et al. 1985), but annual stocking exceeded that level almost every year between 1977 and 1989 (Table 1). Morgensen (1991) estimated that population size of trout ≥305 mm TL was about 98,000 near the beginning of IF. By about 1992 or 1993, the fishery was self-sustaining and no longer dependent on stocking. Since 1995, wild-spawned trout comprised more than 80%-90% of EF samples (Reger et al. 1997, McKinney et al. 1996, 1997), but reduced stocking rates influence this estimate. Angler catch rate corresponded with annual stocking rate during 1967-1972 and 1984-1993, but correspondence between stocking and catch rate was lacking in 1980-1983 and 1994-1997 (Figures 1, 2). Return-to-creel is generally low for stocked trout (Wiley et al. 1993a, 1993b, Walters et al. 1997), and higher densities and proportions of wild-spawned fish since about 1992 contributed to improved angler catch rates (Reger et al. 1995, McKinney et al. 1996, 1997; Table 2, Figure 2).

Length-frequency distributions of trout were unimodal prior to 1991 (Maddux et al. 1987, Reger 1989, 1990, Reger et al. 1995) but bimodal thereafter (Reger et al. 1995, McKinney et al. 1996, 1997), indicating extended and more successful spawning (Weatherly 1972) during IF and MLFF. Angler catch rate from 1987-1997 ranged from 0.4 to 1.1 fish per hour (Table 2, Reger et al. 1995, 1997), and reduced stocking rates starting in 1990 had no apparent detrimental effects on angler catch rates (Tables 1, 2, Figures 1, 2). However, high levels of stocking (128,000-171,000 fish/year) during 1984-1989 corresponded with a decline in relative weight of trout (Table 1, Figure 3), and Reger (1990) suggested that stocking rates during the period may have contributed to an apparent decrease in growth rates. Adverse effects of high stocking rates have been reported for other regulated rivers (Weiland and Hayward 1997).

**Regulations:** Regulations concerning fishing gear and bag and size limits implemented between 1978-1997 have had little clear long-term influence on the fishery (Tables 1, 2, Figures 3-5). The bag limit reduction in 1978 and the immediate kill regulation in 1980 were followed by upward trends in angler use and catch rates to 1990 (Table 2, Figure 7). Janisch (1985) estimated that hooking mortalities might be reduced by up to 50% if artificial lures only were used. The 1986 artificial lures only regulation corresponded with brief (2-3 yr) declines in angler use and catch rate, but the declines were followed by increased angler use (1987-1991) and catch rate (1987-1990) and return of larger fish (1986-1988) to the creel (Table 2, Figures 2, 3, 7, Reger et al. 1989). Restriction to flies and artificial lures also was accompanied by a one year increase in condition of fish which may have resulted from declines in angler use and catch rates (Figures 2, 3, 7).

Reger (1990) suggested that reduced stocking rates and regulations during 1986-1990 led to increased angler catch rate and size of fish harvested. The slot limit and bag reduction in 1990 was followed by declines in angler use and catch rates, likely reflecting effects of research flows rather than regulation changes, but the regulation had little apparent effect on longer-term trends in angling pressure and size of fish creeled (Table 2, Figures 2, 7). Angler use and catch rates increased from lows in 1992-1993 (Figures 2, 7), but size of fish creeled continued to decline to 1995-1997 (Table 2). Implementations of bag and slot limits were followed by a decline in relative weight to late 1991 and increasing body condition to 1994 (Figure 3), but CPUE and biomass per unit effort for trout captured by EF declined after the regulation and did not increase until 1993-1994 (Figure 4). Interpretation of correspondence between regulations and long-term differences in size of fish caught by anglers (Reger et al. 1997) and by EF (Persons 1996, Ayers et al. 1997, McKinney et al. 1997) is equivocal due to probable interactions among regulations, angler attitudes and preferences, flow regulation, aquatic food base and habitat. However, it seems clear that bag and size limits and gear restrictions (i.e., artificial lures only) reduced angler-related mortality of trout, recognizing that angler harvest during high resource use years of 1977-1983 ranged from about 31 kg to 120 kg/ha (Persons et al. 1985). This equates to a peak annual harvest of about 49,000 kg (108,000 lb) of trout from the Lee's Ferry fishery. Any influence on the fishery of the recent requirement for use of barbless hooks (1996) is uncertain, but the regulation change likely will have little impact on the trout fishery (Muoneke and Childress 1994).

**Angler use and catch rates**: Angler use, angler catch rates, relative densities of fish (CPUE) and dam operations were linked, particularly since about 1980 (Tables 1, 2, Figures 2, 4, 6-8). Angler use and catch rates declined following periods of widely fluctuating flows, then increased under more stable dam operating regimes. During the 1980-1986 period of fluctuating flows, no correlation occurred between angler catch rates and flow variability ( Persons et al. 1985, Maddux et al. 1987), except that catch rates for trout in the mid-1980s tended to be highest when mean daily flows were less than 398 $m^3s^{-1}$ (Maddux et al. 1987).

Angler attitudes began changing in the 1980s (Janisch 1985), and catching fish, particularly of moderate size (e.g., 305 mm to 405 mm TL), has been a major factor contributing to angler satisfaction since that time (Caylor 1986, Bishop et al. 1987, Pringle 1994). The percent of trout caught and released by anglers increased from 30% in 1980 to 80% in 1988 (i.e., direct harvest declined). Recreational benefit of the fishery was an estimated $5 million in 1982 (Janisch 1985, Reger 1990) and likely exceeds that value today (Table 2, USDI 1996).

Angler use and catch rate appear to be related to the long-term decline in PSD since 1991, suggesting that resource use influences structure of the trout fishery (Tables 1, 2, Figures 2, 5, 7, 8). Caylor (1986) discussed complexity of estimating recreational carrying capacity, i.e. a level of recreational use beyond which some value is unacceptably diminished. The seasonal periods of increase and decrease in PSD, respectively, correspond with periods of low and high angler use (Reger et al. 1995) and with seasonal recruitment (Carline et al. 1984, McKinney et al. 1997). Hooking stress, handling and air exposure in "catch and release" fisheries influence survival of released fish (Dotson 1982, Schill et al. 1986, Ferguson and Tufts 1992, Mitton and McDonald 1994, Muoneke and Childress 1994), possibly affecting trout within or near the slot limit more than smaller sizes (e.g., <305 mm). The seasonal trends in PSD correspond with results obtained in 1980-1981 (Persons et al. 1985) indicating greater angler harvest of fish >500 mm TL during August-February and lower catch of this size class during March-July. Recruitment influences seasonal changes in PSD (Carline et al. 1984), and increased fishing pressure may lead to smaller mean lengths of trout (Wiley and Dufek 1980). However, consideration of PSD alone can be misleading and should be integrated with other data (e.g., Wr, recruitment, length-frequency distributions, densities and growth and mortality rates) for interpretation (Carline et al. 1984, Gabelhouse 1984, Willis and Scalet 1989, Ney 1993, Anderson and Neumann 1996). Results obtained in the Lee's Ferry reach between 1991 and 1997 (Reger et al. 1995, Persons 1996, McKinney et al. 1996, 1997, Reger et al. 1997) indicate that increased densities of fish <406 mm TL are a major factor influencing PSD.

***Effects of Dam operations*:** Flow regulation is a major factor influencing reproduction, growth, recruitment, health and population abundance and structure of the Lee's Ferry rainbow trout fishery. During the late 1970s, declines in size and condition of trout in the tailwater raised concerns over possible effects of proposed peaking power production when Lake Powell filled (Persons et al. 1985). These concerns motivated and provided the focus of subsequent investigations to determine possible impacts of dam operations on the fishery.

Kondolf et al. (1989) reported that composition of gravel bars in the Lee's Ferry reach was adequate for successful spawning by trout. However, they noted that mainstem spawning gravels in the tailwater must be regarded as threatened by long-term transport of gravel downstream and reduction in suitably-sized spawning gravels in the absence of replenishment from upstream. Erosion of gravels and finer sediments occurs in the Glen Canyon tailwater (Howard and Dolan 1981), and the process has resulted in progressive armoring of the river bed by cobbles and reduction in suitable-sized spawning gravels below other large dams (Buer et al. 1981, Walburg et al. 1981).

**Fluctuating Flows:** During 1980-1981, flows typically fluctuated daily from 28 $m^3s^{-1}$ to 710 $m^3s^{-1}$, and Persons et al. (1985) reported that fluctuating discharges resulted in loss of suitable habitat for trout fry. They further found that year class strength was inversely correlated with the number of days annually that flows were below 85 $m^3s^{-1}$ and that fluctuating discharges resulted in stranding of trout fry. Wegner (1989), Anderson et al. (1986) and Maddux et al. (1987) confirmed that suitable habitat for trout was influenced negatively by widely fluctuating dam discharges.

Maddux et al. (1987) first documented use of mainstem gravel bars for spawning by trout in the Lee's Ferry reach and reported stranding and mortality of trout from 100 to >400 mm TL on cobble bars resulting from rapidly down-ramped releases from the dam. Fluctuating flows also exposed densely-aggregated redds on gravel bars (Maddux et al. 1987, Kondolf et al. 1989). Maddux et al. (1987) demonstrated experimentally that exposing redds for 10 h resulted in a 95% reduction in numbers of emerging fry and suggested that fluctuating flows could seriously inhibit natural recruitment.

Maddux et al. (1987) found more *Gammarus* in trout stomachs during a period of low flow than during fluctuating flows and suggested that fluctuating flow levels influence availability of amphipods for trout. Angradi et al. (1992) reported that mean total volume of stomach contents of trout collected during steady flows (142 $m^3s^{-1}$ and 426 $m^3s^{-1}$) was three to seven times greater than during fluctuating flows (85 $m^3s^{-1}$ to 781 $m^3s^{-1}$). Proportional volumes of *Gammarus* and gastropods in trout stomachs differed little, and diel feeding was similar, between fluctuating and steady discharges, but volume of chironomids was five to eight times greater during fluctuating flows. Relative volume of *Cladophora*, however, was 10 times greater during steady than fluctuating discharges.

Results obtained during steady 227 $m^3s^{-1}$ pre- and post-flood flows, peak flood discharges and following brief drawdown to steady 227 $m^3s^{-1}$ discharges suggest influences of fluctuating flows and rising and falling discharges on feeding and diets of trout (McKinney et al. 1996, 1997, 1998a, 1998b). Fish fed more on the first night of the 1996 flood than during pre-flood steady low flows (empty stomachs declined from 17% to zero; relative stomach volume increased three-fold), and trout diet shifted from chironomids to terrestrial invertebrates. Terrestrial invertebrates generally are absent in the drift in the Lee's Ferry reach (Ayers and McKinney 1996b, Shannon et al. 1996). Proportion of *Gammarus* in the diet were essentially unchanged during peak discharge. Trout also fed more during post-flood low steady discharge than on the final night of flooding. Empty stomachs decreased by 59%, and relative stomach volume increased two-fold. Proportion of *Gammarus* in the diet was unchanged, but proportion of chironomids declined by 50%, and proportion of *Cladophora* increased five-fold following the final night of the flood. McKinney et al. (1997) also found that consumption of *Gammarus* by trout increased during upramp releases following three days of steady low flows. Leibfried and Blinn (1987) and Blinn and Cole (1991) suggested that macroinvertebrates abandon periphyton in the varial zone during discharge fluctuations and enter the drift during periods of rising flows. Drift densities (McKinney et al. 1997) collected during upramp immediately following briefly-reduced flows support this hypothesis. While research results thus are somewhat equivocal, they indicate influences of discharge and ramping on feeding by trout.

Estimated growth of stocked rainbow trout also is linked to dam operations. Growth just prior to or during the trophy fish period was estimated at 7.4 mm/mo (Mullan et al. 1976). During flood releases (1984-1986), growth was estimated at 6.6 mm/mo (Maddux et al. 1987), and growth essentially ceased during the 1990-1991 research flows (Reger et al. 1997). Reger et al. (1989) and Reger (1990), in contrast to Maddux et al. (1987), reported that growth during 1984-1988 (flood and high fluctuating releases) averaged 12.7 mm/mo, corresponding with increases in fish condition during 1986-1988 (Figure 3). This discrepancy in estimated growth rates of stocked fish likely is explained by high total hours of flows $<142\ m^3s^{-1}$ during 1981-1982, even though consecutive hours $<142\ m^3s^{-1}$ were decreasing (Figure 7). During 1983-1988, both total and consecutive hours of flows $<142\ m^3s^{-1}$ were low, likely benefitting the food base, habitat and trout growth. Early during the IF regime (1992-1993), growth was estimated at 10 mm/mo, and it subsequently (1995-1997) increased to 12.5 mm/mo (Reger et al. 1997). Data indicate that growth of rainbow trout was inhibited during periods of widely fluctuating flows between the mid-1970s to mid-1991 and gradually increased with implementation of the more steady IF and MLFF flow regimes. Growth of fish in the Lee's Ferry reach compares favorably with that reported for rainbow trout in cool-water stream habitats in the West (Carlander 1969). However, growth rates in the tailwater are about half those in tailwaters below Navajo Dam in New Mexico (not thermally modified), Flaming Gorge Dam in Utah (prior to and following thermal modification) and Yellowtail Dam in Montana (prior to thermal modification) (Walburg et al. 1981, Wiley and Dufek 1980).

Relative weights of trout declined during periods of widely fluctuating discharge from GCD (1984-1991), then trended upward during more stable IF. The upward trend continued through 1994 but has declined somewhat since that time (Figure 3), possibly indicating density- or food-related effects, or influences of angling pressure on the fishery (Filbert and Hawkins 1995, Weiland and Hayward 1997). Relative densities (CPUE) and catch of biomass per unit effort for fish captured by EF also declined following the 1990-1991 research flows to about 1993 and subsequently increased dramatically during IF and MLFF flow regimes (Figure 4).

The 1990-1991 research flows were associated with high incidence of emaciated trout and levels of parasitic (Nematoda: *Bulbodacnitis ampullastoma*) infection (Landye 1993). Levels of parasitic infestation decreased by 1992 and remained low during the subsequent steady IF and MLFF flow regimes (AGFD unpublished data 1997), coincident with increased condition (Figure 3) and growth rates of trout. Hiscox and Brocksen (1973) demonstrated experimentally that inoculation of rainbow trout with *B. ampullastoma* inhibited growth. Arizona Game and Fish Department initiated preliminary studies in 1993 to identify the intermediate host for *B. ampullastoma*, and these investigations have been resumed recently (AGFD unpublished data 1998).

**Stable Operating Alternatives:** The above results indicate that implementation of the more stable IF and MLFF operating alternatives was followed by favorable change in the Lee's Ferry rainbow trout fishery (Figures 2-5, 8). Compared to conditions prior to and immediately following the period of research flows, natural reproduction, recruitment, relative densities, growth, condition and health of fish have increased. However, proportion of slot-size and larger trout remain lower than during the trophy fish era.

The percentage of trout larger than minimum slot size (406 mm TL) captured by EF was about 33% in 1993, declined to 25% in 1992, and remained about 5-11% from 1993 to 1997 (Persons 1996, McKinney et al. 1996, 1997). Angler catch rate also has increased to levels exceeding historical records, and angler use has tripled from a low in 1993. Janisch (1985) noted that the unique trophy fishery of the late 1970s resulted from a young and under-utilized resource. Calculated PSD values indicate an imbalanced trout population (Anderson and Neumann 1996) following the 1990-1991 research flows into 1997, due largely to increases in trout ≥305 mm TL. However, rate of decline in the PSD tended to be lower after 1993 (about two years following inception of the IF regime) (Figure 5), suggesting stability in proportion of trout ≥305 mm TL and a higher proportion of fish larger than minimum slot size.

**Pulse Disturbances:** Pulse disturbances are of limited and easily definable duration (e.g., floods, temporary discharge drawdowns), while press disturbances (e.g., fluctuating flow regimes) are longer in duration (Niemi et al. 1990). Results of short-term studies regarding pulse disturbances should be viewed with some caution, in view of possible long-term consequences for resilience and recovery which are not apparent during briefer periods. However, investigations to date in the Lee's Ferry reach indicate that pulse disturbances of moderate duration and magnitude during spring or late summer have little influence on the rainbow trout population, despite having dramatic short-term negative impacts on the aquatic food base (McKinney et al. 1996, 1997).

Average daily post-dam flows have exceeded power plant capacity (850 $m^3s^{-1}$) only about three percent of the time through 1994 (Graf 1995, Valdez and Ryel 1995), and consequences of discharges greater than power plant capacity for rainbow trout in the Lee's Ferry reach are poorly understood. The 1996 experimental flood (Rubin et al. 1998) had only limited short-term influences on rainbow trout in the Lee's Ferry reach but may have resulted in some downstream displacement of small (young-of-the-year; <152 mm TL) fish (McKinney et al. 1996, 1998a, 1998b, Valdez et al. 1998). Corresponding increases in catches of juvenile trout along shorelines and in backwaters in the vicinity of the Little Colorado River (river kilometer [RKM] 99) and Lava Falls Rapid (RKM 289) suggest downstream displacement, but these fish may have originated from local populations associated with tributaries below Lee's Ferry (Hoffnagle 1996, Hoffnagle et al. 1996, Valdez et al. 1998). Percentage of trout <152 mm TL increased in EF samples from the Lee's Ferry reach eight months after the flood, indicating no detrimental influence of the event on survival of fish <152 mm TL (McKinney et al. 1996, 1998, Valdez et al. 1998). Fishes often exhibit extended spawning or spawning and enhanced recruitment of fry following floods (Matthews 1986, Fausch and Bramblett 1991, Lamberti et al. 1991), but McKinney (T. McKinney unpublished data 1998) and McKinney et al. (1997) found no clear evidence of enhanced spawning in comparison with 1991-1996 data (Persons et al. 1996).

Body condition and organosomatic indices can be used to assess the degree of environmental stress experienced by fish (Goede and Barton 1990, Adams et al. 1993). McKinney et al. (1996) used the health assessment index (HAI; Goede and Barton 1990, Adams et al. 1993) to evaluate effects of the experimental flood on trout. The HAI was within a normal range throughout 1996, indicating no influence of the flood on health of trout. Normality indices exceeded 90%, and severity indices were below 0.05%. Total catch rates, condition indices and diet of adult rainbow trout in the Glen Canyon tailwater also were not significantly affected by the experimental flood (McKinney et al. 1996).

Three days of steady low releases (227 $m^3s^{-1}$) from the dam implemented during sustained high discharges (596 $m^3s^{-1}$) had no apparent negative influences on angler or EF catch rates or condition of rainbow trout (AGFD unpublished data 1998, McKinney et al. 1997). Electrofishing catch rates increased dramatically during the August-September 1997 (Labor Day weekend) discharge drawdown (Figure 4), possibly influenced by concentrations of fish. However, CPUE remained high during elevated discharges (596 $m^3s^{-1}$) in December 1997 (AGFD unpublished data 1997). Drift of *Gammarus* and chironomids increased significantly during upramp following the three days of reduced flows, due to drift from the varial zone as flows increased (McKinney et al. 1997). However, only *Gammarus* increased in stomachs of trout during upramp following the reduced flows, indicating that trout selected the amphipod. More trout also were feeding and they consumed more *Gammarus* during upramp, but proportions of *Cladophora*, chironomids and gastropods in the diet were unchanged in comparison to the reduced flows.

**Press disturbance:** Operations of GCD from 1963 to mid-1991 imposed a continual press disturbance on lotic biota below the dam, due to widely varying operating regimes, high ramping rates and extreme daily variation in releases from Lake Powell. Releases from the dam varied widely prior to inception of IF and MLFF operating alternatives (USDI 1995), often falling to 28 $m^3s^{-1}$ (Figure 6), but little quantitative information is available for earlier periods regarding effects of dam operations on the Lee's Ferry rainbow trout fishery (Gosse 1981, Gosse and Gosse 1985, Persons et al. 1985, Maddux et al. 1987). During 1980-1981, year class strength correlated negatively with discharges <85 $m^3s^{-1}$, and fluctuating flows resulted in loss of suitable habitat and stranding mortality of fry (Persons et al. 1985). Relationships between dam operations and the aquatic food base during 1985-1986 further demonstrated negative impacts of fluctuating flows (Leibfried and Blinn 1987).

Mean daily releases from GCD through 1994 were <142 $m^3s^{-1}$ only about 10% of the time (USDI 1995, Valdez and Ryel 1995), but low minimum discharges had important consequences for the Lee's Ferry trout fishery. Consecutive hours/year of flows <142 $m^3s^{-1}$ increased during 1976-1979 (Figure 7) and likely contributed to deterioration of the fishery during 1980-1984. During flood flows and spillway releases in 1984-1986, minimum releases from GCD tended to be high, total and consecutive hours per month with discharges <142 $m^3s^{-1}$ remained low, and angler catch rates and average size of fish creeled increased (Figures 6, 7). Minimum releases from GCD varied from about 28 $m^3s^{-1}$ to 1,136 $m^3s^{-1}$, and maxima varied from 1,278 $m^3s^{-1}$ to 2,630 $m^3s^{-1}$. Growth of stocked trout was low (Maddux et al. 1987), and relative weights declined as stocking rates increased (Figures 1, 3). However, relative weights and lengths of creeled fish increased briefly in 1986 when the artificial lures regulation was implemented (Table 2). Generally low angler catch rates (Table 2, Figure 2) were sustained by increased annual stocking rates of fingerlings (Table 1, Figure 1). Angler use declined by 55% during this period, but length of trout creeled remained generally stable (Tables 1, 2, Figure 3). Low total and consecutive hours/year of flows <142 $m^3s^{-1}$ during 1980-1988 corresponded with increasing angler catch rates and high angler use (Figure 7).

Highly fluctuating releases from GCD in 1987-1990 were associated with increased total and consecutive hours per month for discharges <142 $m^3s^{-1}$ (Figure 7), and flows often varied 425 $m^3s^{-1}$ daily. Growth of stocked fish was higher later in this period than during flood releases (Reger et al. 1989, Reger 1990), possibly related to declining annual stocking of fingerlings (Table 1, Figure

1). Angler use was generally stable, and catch rates increased, but size of fish creeled declined slightly (Table 2, Figure 2). Relative weights increased from 1987 to 1989, corresponding initially with lower stocking rates and fewer total and consecutive hours/year with flows <142 $m^3s^{-1}$, but declined in 1990-1991 as total and consecutive hours/year of flows <142 $m^3s^{-1}$ increased (Table 1, Figures 1, 3, 7).

Total and consecutive hours per month for flows <142 $m^3s^{-1}$ increased dramatically during the 1990-1991 research flows and were similar to those during 1977-1979 (Figure 7). During research flows, releases from GCD often varied daily by more than 800 $m^3s^{-1}$. Trout were emaciated and had high levels of parasite infestation, stocked fish exhibited no growth, and fish condition declined by 25% from late 1989 levels (Figure 3). Annual stocking rates were reduced by >50% during this period (Table 1, Figure 1). Angler use increased somewhat, but angler catch rates declined about 30%, while average weights of fish creeled declined (Table 2, Figures 2, 7).

Systematized monitoring and research to determine influences of dam operations on lotic biota were not implemented until about 1991 (Blinn et al. 1992, 1994, Angradi et al. 1992, Ayers and McKinney 1996b, 1996c 1997a, 1997b, McKinney et al. 1997). During IF and MLFF operating alternatives 1991-1997, there were no sustained releases <142 $m^3s^{-1}$ from GCD (Figures 6, 7, 8), and daily fluctuations were restricted to $\leq$227 $m^3s^{-1}$. Stocking of fingerlings was low (Table 1, Figure 1), growth of stocked trout increased to 10.0 mm/month, and fish condition increased to a peak in 1994, then declined slightly (Figure 3). Angler use more than doubled between 1993 to 1997 (Table 2, Figures 7, 8). Angler catch rate also increased more than twofold, but length of creeled fish declined slightly to 1996 (Table 2). Electrofishing studies initiated during IF also indicated that catch and biomass per unit effort declined from 1991 to about 1993 but increased more than fivefold by 1997 (Figure 4). Spawning by trout is influenced by dam discharges (Maddux et al. 1987, Dodge and MacCrimmon 1971) and became more successful than previously in the Lee's Ferry reach during IF and MLFF. Proportional stock densities may be stabilizing during IF and MLFF (Figure 5), corresponding with relative proportions of trout $\geq$305 mm TL, as well as slight increases in slot-sized fish (AGFD unpublished data 1998).

Stocking rates were low during 1996 and 1997 (Table 1, Figure 1), and angler catch rate remained higher during MLFF than since closure of the dam (Table 2, Figures 2, 7). Average weights of trout creeled declined about 19%, while average lengths declined about 4% (Table 2). Catch rates and biomass for EF samples increased steadily after about 1993, rose dramatically during the brief 1997 drawdown to 227 $m^3s^{-1}$ steady flows (Figure 4, McKinney et al. 1997) and remained unusually high in December 1997 during normal dam operations (AGFD unpublished data 1997).

Thus, monitoring and research results indicate that widely fluctuating releases from GCD adversely affect the Lee's Ferry rainbow trout fishery, and discharges <142 $m^3s^{-1}$ are particularly detrimental. Sustained higher and comparatively stable discharges benefit the fishery with respect to population-related attributes, recreational use and angler catch rates which correspond closely with dam operations (Figures 7, 8).

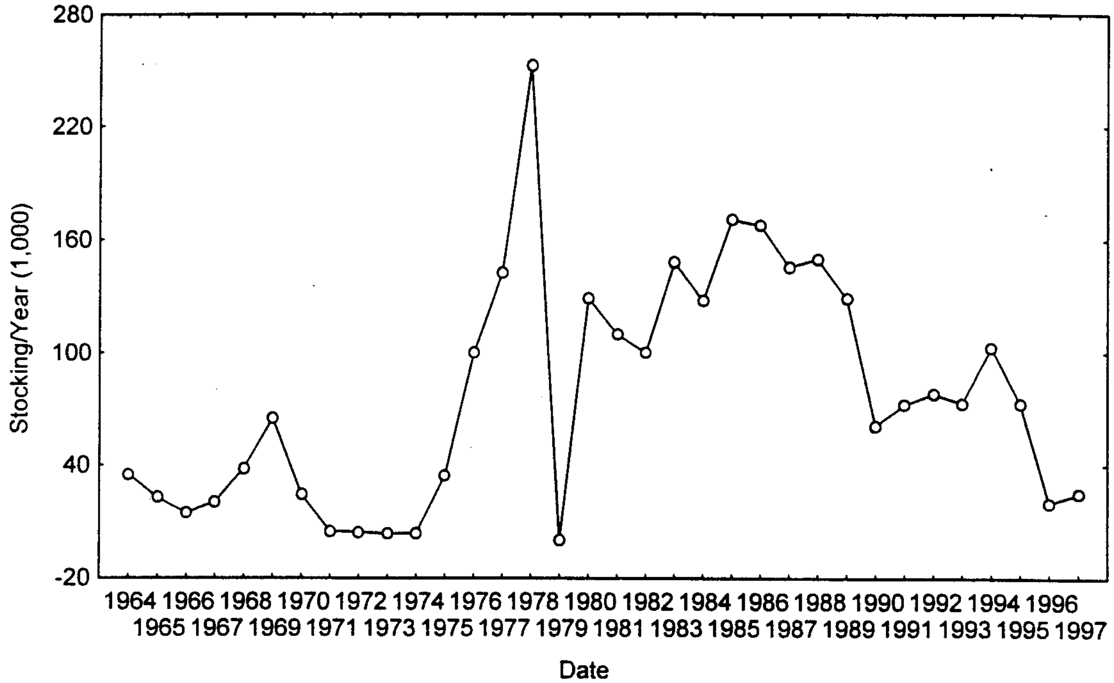


Figure 1. Annual stocking rates by Arizona Game and Fish Department for trout , Lee's Ferry reach, 1964-1997. (Data from Table 1; NOTE: Rainbow trout were stocked as catchables 1964-1976 and stocked as fry (<120 mm TL 1976-1997).

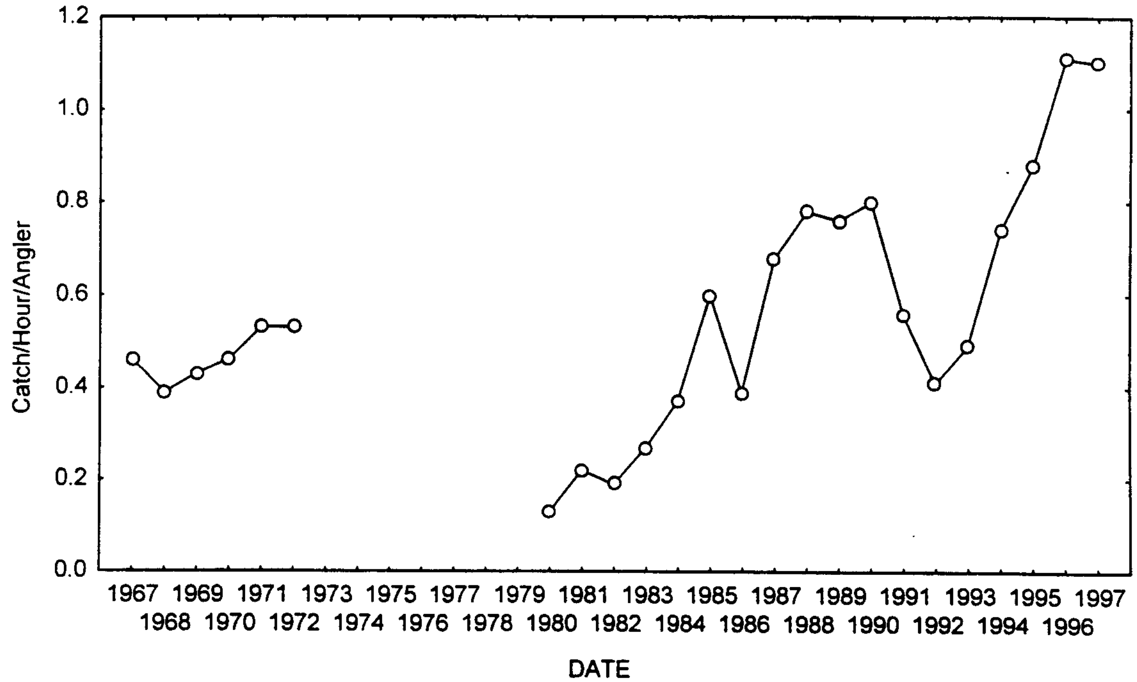


Figure 2. Angler catch rates based on creel survey data, Lee's Ferry reach, 1967-1997. (Data from Table 2).

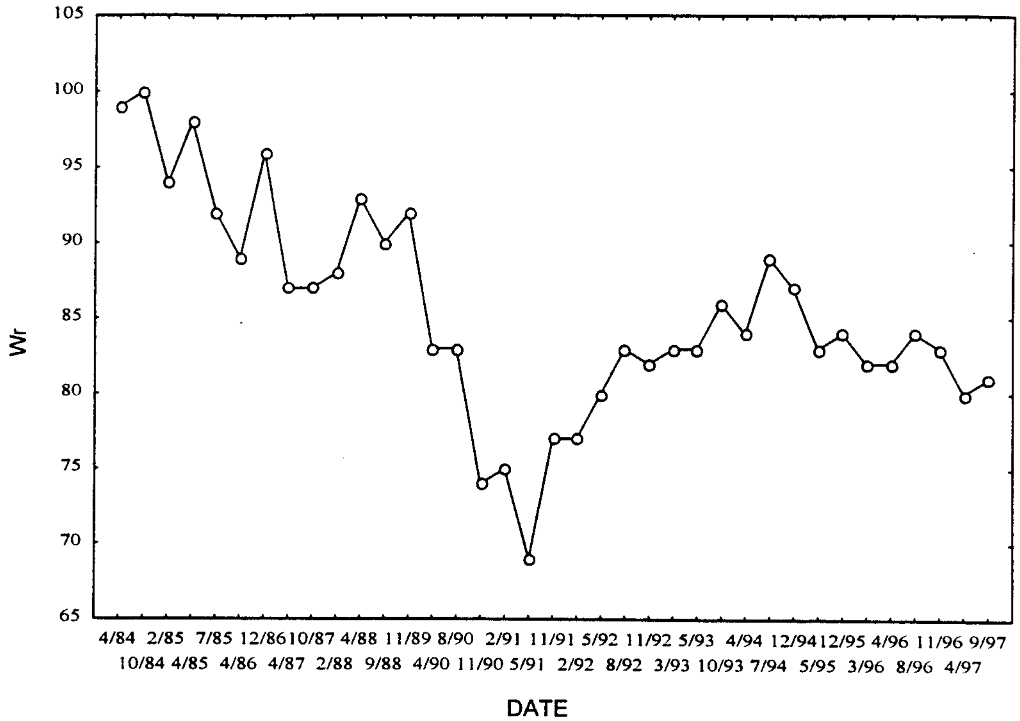


Figure 3. Relative weights (Wr) of rainbow trout captured by electrofishing April 1984 to September 1997, Lee's Ferry reach. (Data from Persons 1996, Ayers et al. 1997, McKinney et al. 1996, 1997).

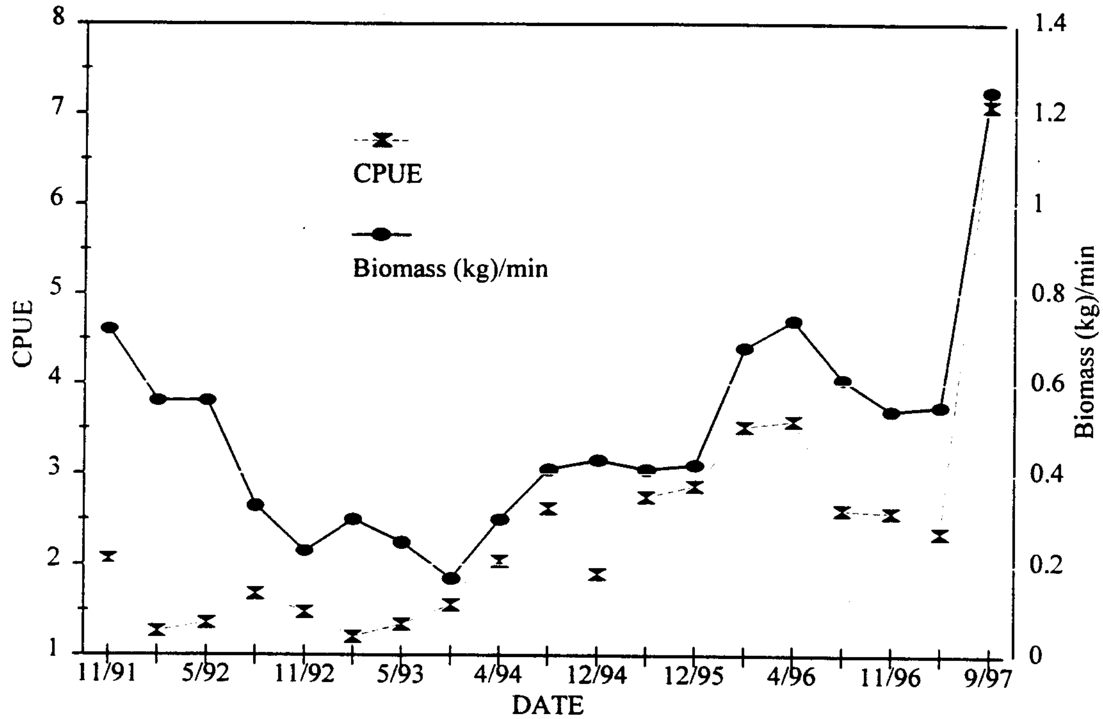


Figure 4. Catch per minute (CPUE) and biomass captured per minute by electrofishing for rainbow trout, November 1991-September 1997, Lee's Ferry reach. (Data from Persons 1996, McKinney et al. 1996, 1997).

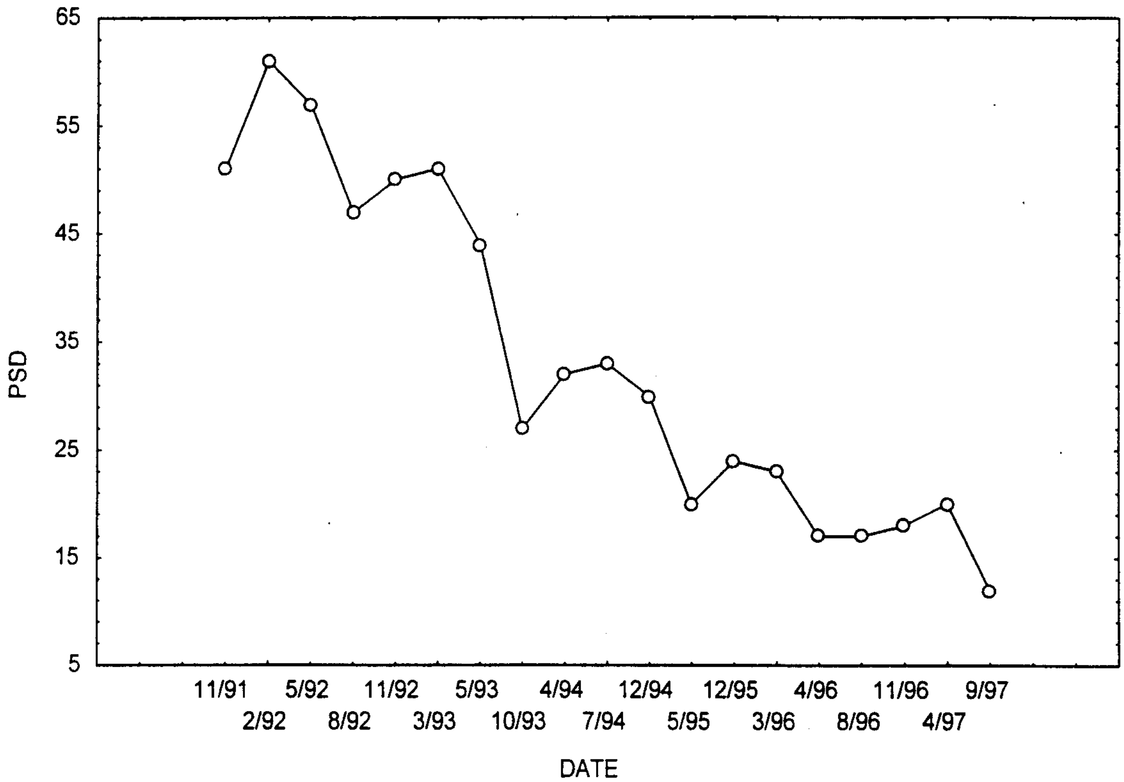


Figure 5. Proportional stock densities (PSD) for rainbow trout captured by electrofishing, Lee's Ferry reach, November 1991 - September 1997 (McKinney et al. 1997).

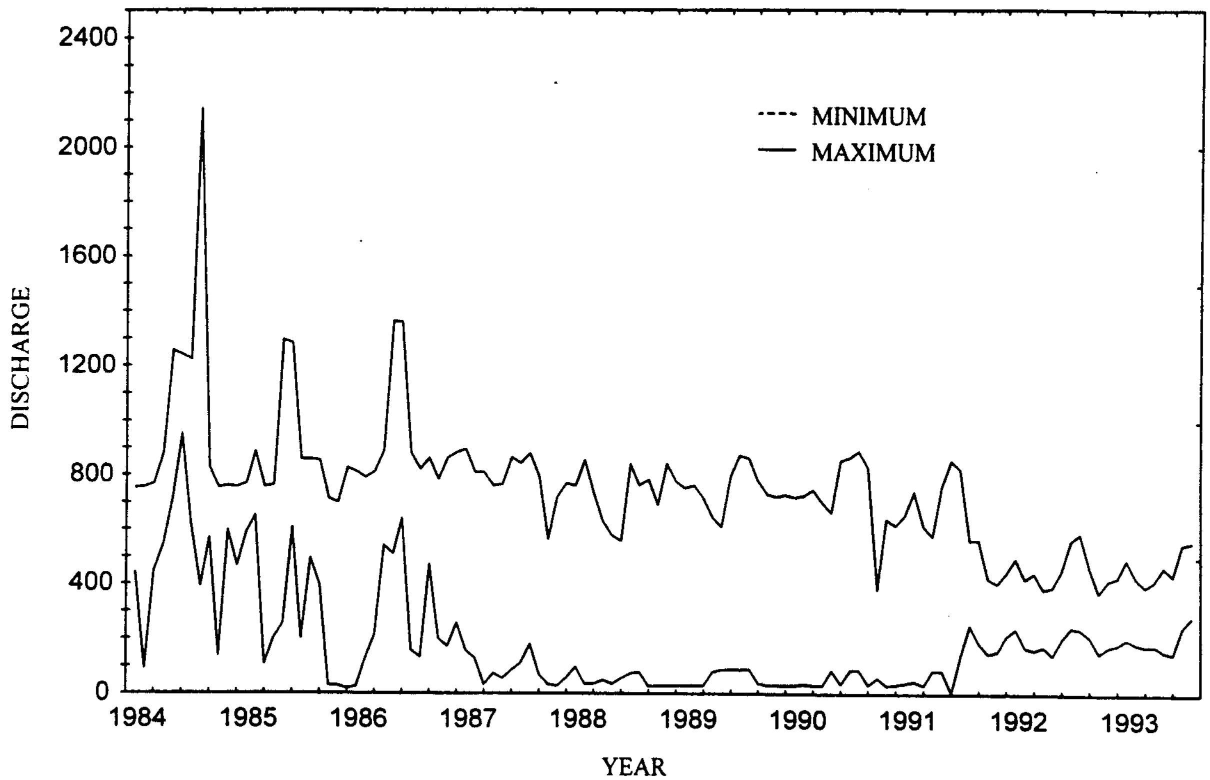


Figure 6. Mean monthly maximum and minimum releases ($m^3s^{-1}$) from Glen Canyon Dam, 1984-1993 (Bureau of Reclamation unpublished data).

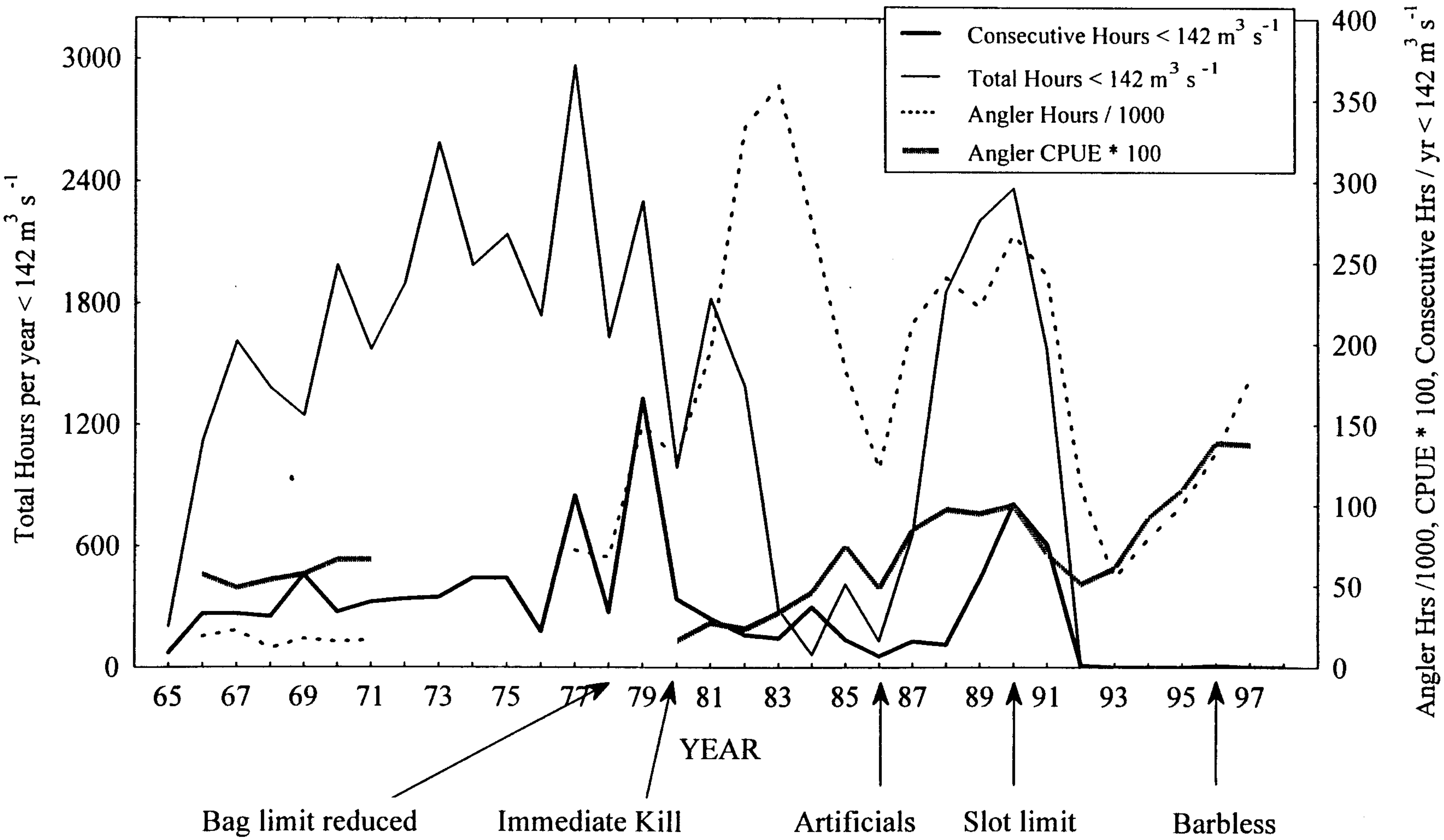


Figure 7. Angler hours/year (x 0.001), angler catch rates (CPUE; fish/h/angler*100), and maximum number of total and consecutive hours per year with flows less than 142 $m^3 s^{-1}$ released from Glen Canyon Dam, 1965-1997.

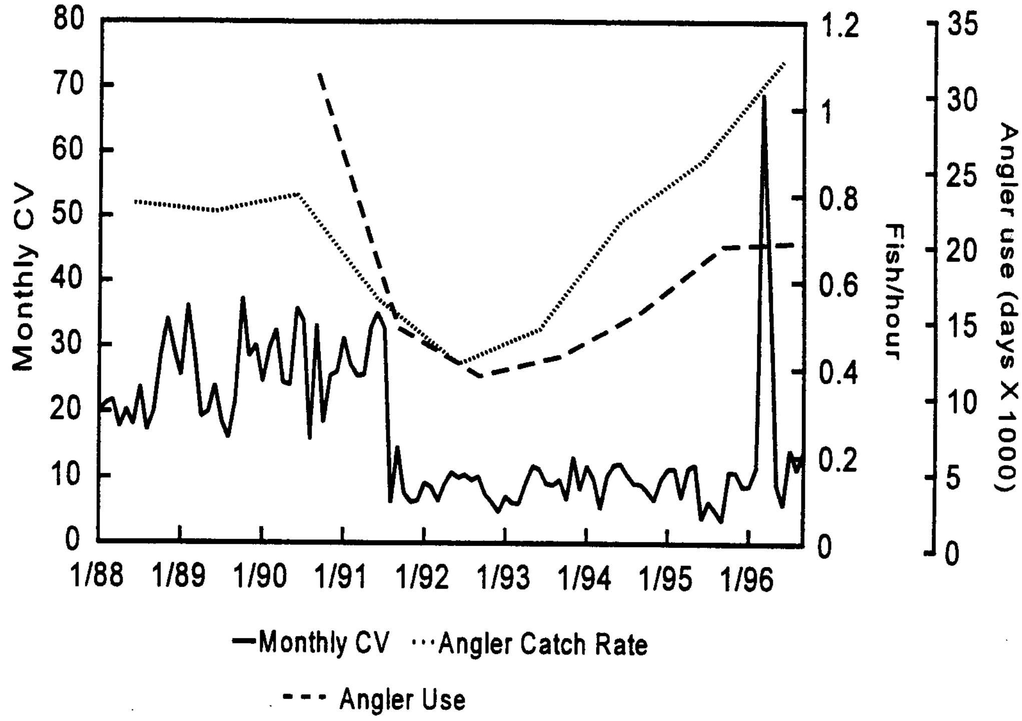


Figure 8. Coefficient of variation (CV) for monthly releases from Glen Canyon Dam, angler catch rates and estimated annual angler use, Lee's Ferry reach, 1988-1996. (Data from Table 2 and Bureau of Reclamation unpublished data).

## DISCUSSION

Investigations addressing relationships between dam operations, rainbow trout and lower trophic levels in the Lee's Ferry reach were initiated little more than a decade ago (Persons et al. 1985, Leibfried and Blinn 1987, Maddux et al. 1987). Integrating resource management for trout, benthic food base and flow regulation is an ongoing learning process, since attributes of the lotic environment below GCD are characteristically dynamic and complex in responses to dam operations, resource use and fishery management. Integrating and understanding variables affecting tailwater fisheries often is difficult (Caylor 1986, Fryer 1987, Minshall 1988, Maceina et al. 1994, Palmer 1993, Peterman 1990, Filbert and Hawkins 1995, Stevens et al. 1997, Weiland and Hayward 1997). As adaptive management emerges and numbers of variables requiring attention of resource managers expand (Walters 1997), a level of integration which is conceptually new to fisheries biologists is necessary (Anderson and Neumann 1996).

Most rainbow trout fisheries in cold North American tailwaters are managed as put-and-take or put-grow-and-take resources (Wiley and Dufek 1980, Filbert and Hawkins 1995, Weiland and Hayward 1997). Declines in tailwater trout fisheries are documented, but causes and mechanisms associated with declines are difficult to determine with certainty (Holden and Crist 1981, Walters et al. 1996, Weiland and Hayward 1997). Monitoring and research results indicate that operations of GCD influence growth, reproduction, recruitment, population structure and densities of trout in the Lee's Ferry tailwater. Dam operations contributed to declines of the fishery between about 1979-1992 but also were paramount in subsequent recoveries. Widely fluctuating discharges negatively influenced trout year class strength and fry survival in 1980-1981 (Persons et al. 1985). During flood and high fluctuating releases from the dam in 1984 to early 1990, growth of trout was reduced, and condition of fish declined about 17% but remained within acceptable levels (i.e., Wr $\geq$80). Late during flood and spillway releases, condition and growth of trout increased briefly, then fell dramatically.

Total and consecutive hours of flows <142 $m^3s^{-1}$ increased during 1976-1979, were low during 1982-1986, then increased during 1987 to mid-1991. Wetted perimeter of the reach, suitable habitat for fry (Persons et al. 1985, Maddux et al. 1987, Wegner 1989) and the food base (Blinn et al. 1995, Ayers and McKinney 1997a, 1997b, McKinney et al. 1996, 1997) increased during 1983-1988 flood flows and high fluctuating releases from the dam due to high frequency of discharges $\geq$142 $m^3s^{-1}$, resulting in a brief increase in fish condition and growth. However, wetted perimeter of the reach and suitable habitat generally were reduced during 1976-1979 and 1989 to mid-1991 (Persons et al. 1985, Maddux et al. 1987, Wegner 1989) due to increased total and consecutive hours of flows <142 $m^3s^{-1}$, resulting in reduced available food base, since periphyton and macroinvertebrate colonization is inhibited in the varial zone (Blinn et al. 1992, 1995, Ayers and McKinney 1997a, 1997b, McKinney et al. 1996, 1997). Increased total and consecutive flows <142 $m^3s^{-1}$ in each of these periods were followed by declines in the fishery. Conversely, low total and consecutive flows <142 $m^3s^{-1}$ during 1980-1988 and after 1991 corresponded with periods of recovery of the fishery.

Reductions in wetted perimeter, suitable habitat and the food base likely were exacerbated during the 1990-1991 research flows, when trout growth ceased, and condition and health of fish fell dramatically. Condition indices have been used widely by fisheries managers to assess relative food availability (Bolger and Connolly 1989, Filbert and Hawkins 1995, Porath and Peters 1997).

However, many fishes show rapid compensatory growth in recovering from periods of lower food supply (Bove et al. 1997), and decreasing fish condition may not necessarily correspond with reduced fish growth (Liao et al. 1995). During 1986-1989 and 1991-1994, but not in 1995-1997, increasing body condition corresponded with increasing growth of trout in the Lee's Ferry reach.

Stocking policy and angling-related impacts are important variables influencing the fishery (Wiley and Dufek 1980, Willis and Scalet 1989, van den Avyle 1993, Weiland and Hayward 1997). Interpreting effects of dam operations prior to 1991 on the Lee's Ferry trout fishery is confounded by potential interactions among dam operations, the food base, regulations, annual stocking rates and angler use and catch. Changes in fishing regulations between 1984 and 1987 had apparent short-term influences, but regulations have had no clear longer-term effects on population trends. Annual stocking of trout corresponded with angler catch rates and sustained the fishery through about 1992 but since then has not corresponded with increasing densities of fish and angler catch rates. High stocking rates and moderate angler catch persisted through flood and high fluctuating releases, and both declined during research flows, paralleling changes in fish condition. High stocking rates in 1976-1977, coupled with increasing angler use and consecutive hours of flows <142 $m^3s^{-1}$ and high total hours of flows <142 $m^3s^{-1}$, corresponded with decline of the fishery. Therefore, stocking cannot overcome dramatically varying dam operations, and more stable flow regimes reduce the need for stocking.

Declining fish condition during 1984-1991 may have resulted from negative effects of high stocking rates and discharge-related variables on the food base (Elwood and Waters 1969, Goede and Barton 1990, Blinn et al. 1995, Weiland and Hayward 1997) and suggests food limitation (Cada et al. 1987, Ensign et al. 1990, Hewett and Kraft 1993, Blinn et al. 1995, Filbert and Hawkins 1995, Porath and Peters 1997). Low growth rates may have been due to inadequacy of a diet comprised largely of *Cladophora* (adult trout) or zooplankton and chironomids (trout fry) (Walburg et al. 1981, Maddux et al. 1987, Weiland and Hayward 1997). Lower fish condition and growth rates also might have resulted from increased density-related stress (Chapman 1966, Piper et al. 1982, Pickering 1992) as fish concentrations increased under conditions of greater number of hours with flows <142 $m^3s^{-1}$ and quantitatively and qualitatively degraded habitat. Particularly high levels of parasitic infestation and incidence of emaciated trout during 1990-1991 research flows likely resulted from poor nutrition and density-related stress (Wedemeyer et al. 1976, Piper et al. 1982, Pickering 1992, Blinn et al. 1995).

Relationships among food habits, diet and bioenergetics of rainbow trout and drift and benthic standing stocks are poorly understood for the Lee's Ferry reach. Drift concentrations are potentially influenced by discharge fluctuations (Leibfried and Blinn 1987, Blinn et al. 1994, Shannon et al. 1996, McKinney et al. 1997), and food intake by trout generally corresponds with drift concentrations (Elliott 1973, Cada et al. 1987, Filbert and Hawkins 1995, McKinney et al. 1997). Drift concentrations of macroinvertebrates are comparable to or higher in the Lee's Ferry reach than in some regulated rivers (Filbert 1991, Blinn et al. 1994, Shannon et al. 1996, Young et al. 1997). *Cladophora* comprises a major proportion of drift below Glen Canyon Dam (Leibfried and Blinn 1987, Blinn et al. 1994, Ayers and McKinney 1996b, Shannon et al. 1996). The alga is a significant component in trout stomachs in the Lee's Ferry reach (Angradi et al. 1992, McKinney et al. 1996, 1997) and elsewhere (Angradi and Griffith 1990, Weiland and Hayward 1997). However, the alga provides negligible nutritional value (Leibfried 1988, Angradi 1994, Weiland and Hayward 1997), and Weiland and Hayward (1997) suggested that relative biomass of *Cladophora* in stomachs of rainbow trout may indicate sub-optimal food supply in tailwater environments. Angradi and Griffith (1990) suggested that algae are ingested accidentally by trout during epibenthic foraging.

Interactions among trout diets and condition, drift, benthos, water temperatures and dam operations are complex (Waters 1961, Allan 1982, Brittain and Eikeland 1988, Angradi and Griffith 1990, Sagar and Glova 1992, Feminella and Hawkins 1995, Koetsier et al. 1996, McKinney et al. 1996, 1997). Effects of food availability on trout growth are different at optimal compared to sub-optimal temperatures (Brett et al. 1969, Filbert and Hawkins 1995). The thermal optimum for growth of rainbow trout in laboratory studies is about 17$^0$C (Hokanson et al. 1977). Comparisons of water temperatures and trout growth rates between Lee's Ferry reach and the tailwater below Flaming Gorge Dam in Utah (Wiley and Dufek 1980) suggest that low water temperatures in Glen Canyon inhibit trout growth.

Sustained wetted perimeter of the Lee's Ferry reach increased dramatically under IF and MLFF operating alternatives initiated since mid-1991. Morphometry of the tailwater suggests that increasing discharges from 142 $m^3s^{-1}$ to 793 $m^3s^{-1}$ results in an increase of 15.8 ha in wetted perimeter of the river channel (Blinn et al. 1995). The aquatic food base increased (Blinn et al. 1994, Ayers and McKinney 1996b, 1997a, McKinney et al. 1996), providing greater potential availability of food-related energy for trout (Blinn et al. 1995). Increases in wetted perimeter and reductions in amplitude and duration of power-peaking flow fluctuations can enhance standing stocks of aquatic invertebrates and benefit fish populations (Gislason 1985, Schlosser 1985, Bain et al. 1988, Weisberg and Burton 1993, Travnichek et al. 1995). Quantitative data on the fishery are limited prior to inception of IF, but declines in daily flow variation, absence of total and consecutive hours of flows <142 $m^3s^{-1}$, increased habitat and aquatic food base since 1991 correspond with dramatic recovery of the fishery.

During IF, suitable habitat for trout increased, the fishery shifted from reliance on stocked fish to natural reproduction, and stranding of fish and desiccation of redds were essentially precluded (AGFD unpublished data 1998). However, increased densities of submerged macrophytes during IF and MLFF might harm quality of the fishery and contribute to higher densities of smaller fish (Olson et al. 1998). Although armoring of gravel beds remains a potential threat to spawning success of trout in the Lee's Ferry reach (Kondolf et al. 1989), the process currently does not appear to present a problem (e.g. McKinney et al. 1996, 1997, Valdez et al. 1998).

Initiation of steadier, high sustained flow regimes during 1991 to 1997 was followed, in spite of greatly reduced annual stocking rates, by increases in angler use and catch rates and fish densities and biomass in electrofishing samples. Average sizes of fish creeled by anglers continue a slight downward trend, but average lengths and weights of trout creeled in 1996-1997 are greater than prior to 1973. Catch of trophy (slot-sized) fish by EF and reported by anglers remains comparatively low, possibly due partly to increased angler use of the fishery resource (Muoneke and Childress 1994). Similarly, average size of trout creeled declined in 1980-1984 as angler use of the resource nearly tripled. Average length of trout creeled during 1992-1997 was essentially stable, although angler use nearly doubled and average weight of fish creeled decreased about 18%. In contrast, size of fish captured by EF declined during 1991-1994 but increased slightly since that time (AGFD unpublished data 1998).

The decline of PSD since 1991 suggests imbalances in the Lee's Ferry fishery and indicates structural shifts in the population corresponding with high angler use prior to 1991 and increasing angler catch rates and use during 1994-1997. Angling-related injury and stress may be a mortality factor in catch-and-release fisheries (Dobson 1982, Schill et al. 1986, Ferguson and Tufts 1992). However, the trend of PSD appears to be more stable since about 1993, suggesting more stable proportions of trout ≥305 mm and possibly increased relative abundance of slot-sized fish (but see Carline et al. 1984, Willis and Scalet 1989, Anderson and Neumann 1996). In general, relations between PSD, density indices and size of trout support the energy equivalence hypothesis (Bohlin et al. 1994) that population abundance and body size of salmonids are inversely related. However, one would expect that apparent stabilization of PSD since about 1994 would correspond with stability, rather than decline, in the ponderal index (Willis and Scalet 1989). Slight downward trends since 1991 in periphyton mass and *Gammarus* and gastropod benthic densities (AGFD unpublished data 1998, Ayers and McKinney 1996a, 1997a, 1997b, McKinney et al. 1996, 1997, 1998), along with increased trout densities and declining fish condition and nutrients since about 1993-1994, suggest that density-dependent factors or food limitation may be operative in the Lee's Ferry trout fishery during 1995-1997, but this hypothesis remains to be tested. Trout populations in unregulated streams (Cada et al. 1987, Ensign et al. 1990) and tailwaters (Filbert and Hawkins 1995, Weiland and Hayward 1997) often may be food-limited.

## CONCLUSIONS

Alterations in flow regimes in regulated rivers profoundly influence fish populations (Bain et al. 1988, Weisberg and Burton 1993, Travnichek et al. 1995, Bowen et al. 1998). Our review similarly indicates that operations of Glen Canyon Dam influence the Lee's Ferry rainbow trout population. Widely fluctuating discharges, and particularly extended periods of flow reductions to between about 28 $m^3s^{-1}$ and 142 $m^3s^{-1}$, are detrimental to trout health, condition, growth, reproduction, recruitment, and population size and structure. Negative impacts of dam operations result from the following influences:

1) Disrupted or seasonally restricted spawning
2) Desiccation of redds
3) Stranding mortality of larvae, fry and older fish
4) Reduced suitable habitat, influencing survival of fry, environmental stress and lowered health and condition of fish
5) Reduced available food base due to losses and slow re-colonization of periphyton, submerged macrophytes and benthic macroinvertebrates in the varial zone
6) Increased metabolic demands associated with local displacements and greater density-related stress (competition for food and space)
7) Reduced recruitment to sexual maturity associated with lower growth rates

Conversely, more stable daily and seasonal flow regimes such as provided by IF and MLFF operating alternatives for GCD benefit the rainbow trout fishery through the following influences:

1) Increased suitable habitat for fry and older fish
2) Extended spawning
3) Reduced desiccation of redds
4) Prevention of stranding mortality due to restricted ramping rates and magnitude of daily flow fluctuations
5) Improved health and condition

6) Increased aquatic food base due to greater permanently-wetted perimeter of river channel
7) Reduced local displacement, density-related stress and metabolic demands
8) Greater recruitment due to increased growth rates

Minimum flow elevations of 142 $m^3s^{-1}$ or more and restricted daily flow variability and ramping rates during IF and MLFF were followed by dramatic increases in trout densities, condition and health and angler use and catch rates. The pattern of change for fish condition altered in late 1994, suggesting that factors other than discharge-related (e.g., density- or food-related) may have become operative in affecting the trout fishery. However, PSD appears to be stabilizing, suggesting that the fishery may be achieving better balance from a management perspective. Increasingly, angling pressure will require consideration by resource managers, and regulations, such as those affecting slot limits (Luecke et al. 1994) and angler-related impacts (Wiley and Dufek 1980, Ferguson and Tufts 1992, Weiland and Hayward 1997), will necessarily be integrated with dam operations to achieve management goals and objectives. Stocking rates and natural reproduction can affect population size, angler catch rates and the aquatic food base. The present stocking policy appears to address current goals and objectives satisfactorily, but increased standing stocks of rainbow trout may have reached carrying capacity of the lotic system. Moreover, declining nutrient concentrations in the Lee's Ferry tailwater may impose important limitations for productivity and management of the trout fishery and lead to a "bottoms up" reduction in trout condition. Under IF, MLFF or similar operating alternatives for GCD, and with careful monitoring and effective management of regulations and angler use and catch, the Lee's Ferry recreational fishery likely will continue to be self-sustaining for the foreseeable future, and present management goals and objectives for the resource likely will continue to be achieved.

The Bureau of Reclamation recently proposed installation of a multilevel intake structure (MLIS) on GCD to provide the option of increasing downstream water temperatures seasonally through selective withdrawal of water from Lake Powell (USDI 1995). Potential effects of warming the river seasonally on the rainbow trout fishery are an important consideration. Elevation of water temperatures may result in increased population size of rainbow trout downstream from GCD (Hokanson et al. 1977). Previous research in the Lee's Ferry tailwater provides little information regarding possible influences of MLIS operations. Blinn et al. (1989) found that warming water temperatures resulted in smaller and more adnate diatom taxa becoming numerically predominant over large, upright taxa. Thermal modification (MLIS) of the Lee's Ferry reach could impact standing stocks and composition of primary and secondary producers, affecting food resources for benthic macroinvertebrates and rainbow trout (Holden and Crist 1981, Walburg et al. 1983).

An MLIS was installed on Flaming Gorge Dam in 1978 to selectively withdraw warmer water and increase trout productivity in the Green River tailwater following a period of decline in the fishery (Wiley and Dufek 1980, Holden and Crist 1981). Thermal modification dramatically changed macroinvertebrate assemblage composition but had no apparent effects on abundance or distribution of *Chara* sp. (Mark Vinson, Utah State University, personal communication, Holden and Crist 1981). Abundance of *Gammarus lacustris* increased initially in the 27 km tailwater below the dam following installation of the MLIS, but the rainbow trout fishery declined dramatically (Holden and Crist 1981). Growth rates of trout in the thermally-modified tailwater, however, were more than double those observed in the Lee's Ferry reach (Wiley and Dufek 1980). Filbert and Hawkins (1995) concluded about 10 yr after thermal modification that rainbow trout were food-limited in the Green

River tailwater. Food resources were abundant, but invertebrate diversity was low. Walburg et al. (1983) found that benthic macroinvertebrate densities, mass and species richness were greater in seven tailwaters located in Arkansas, Georgia-South Carolina, Kentucky and Oklahoma when warmer waters were discharged from dams. Since about 1993, the amphipod *Hyallela azteca* increased dramatically in abundance in the Green River tailwater, replacing *Gammarus lacustris* (Mark Vinson, Utah State University, personal communication). The fishery has been managed as a put-grow-and-take trophy resource, with a slot limit similar to that for the Lee's Ferry reach (Wiley and Dufek 1980, Filbert and Hawkins 1995).

In summary, the IF and MLFF operating alternatives benefitted the Lee's Ferry recreational fishery by development of a self-sustaining rainbow trout population and increased fish densities and recreational use by anglers. Present resource quality likely will be sustained within the foreseeable future under current policies of dam operations (MLFF) and fisheries management. However, importance of density- and food-related factors and changing nutrient concentrations since 1993-1994 in affecting the fishery remain to be evaluated. Continued monitoring, research and management efforts are essential to increase the knowledge base from which to manage the fishery in relation to operations of GCD. Greater consideration of habitat suitability, the aquatic food base and energetic conditions for rainbow trout than in the past should enhance management capabilities.

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