Draft Report

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IMPACT OF FLUCTUATING WATER LEVELS ON EARLY LIFE HISTORY OF RAINBOW TROUT

by

COPY

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Prepared for

Bureau of Reclamation

Glen Canyon Environmental Studies

Under Contract CA 0-FC-40-09620

GLEN CANYON ENVIRONMENTAL
STUDIES OFFICE

AUG 6 1993

RECEIVED
FLAGSTAFF, AZ

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

Many individuals and agencies contributed to completion of this research. Glen Canyon Environmental Studies (GCES), Bureau of Reclamation, provided most of the funding. David Wegner, Michael Yard and various other GCES personnel were extremely helpful in facilitating and supporting many phases of the work. One of the Living Stream tanks was graciously provided by Anglers United, Phoenix, Arizona, the other by David Wegner, GCES. GCES also provided boat transportation at Lees Ferry, arranged for research permits, and set and downloaded data from thermographs. Personnel of the Arizona Game and Fish Department, particularly Scott Reger, Charles Benedict, Phil Heins, and other personnel from Region 2 and the Page Springs and Sterling Springs Fish Hatcheries, conducted habitat surveys and the fry release experiment, and provided rainbow trout eggs for laboratory and field experiments. Carey Conover and Susan Schroeder, Office of Grants and Contracts Administration, Northern Arizona University (NAU), assisted with monitoring and handling contract funds. The Department of Biological Sciences, provided laboratory space; Pat Donnelly of the Department handled personnel and travel matters. Doug Van Cleave and Peg Campbell, Animal Care Facility, NAU, arranged for space for the stream tanks during the several months of experiments. Dr. Dean Blinn and Dr. Kiisa Nishikawa (NAU) assisted with research design and planning and data analysis. Sally Evans assisted with data manipulation and graphics. Colin Spring helped with library research and laboratory and field experiments.

INTRODUCTION

The Colorado River changed dramatically after closure of Glen Canyon Dam in 1962 (Carothers and Brown 1991). Pre-dam water temperatures ranged 0-30 C. Now, due to hypolimnetic release of deep water from the dam, water temperatures are both lower and less variable (6-12 C). Prior to the dam, river discharge varied seasonally, but gradually, from lows of 700 cubic feet per second (cfs) to highs of 7,300,000 cfs. In recent years, flows controlled by the dam have ranged from 1000 cfs to >30,000 cfs, often spanning changes in discharge of $\geq$ 20,000 cfs daily, but with little seasonal change. The amount of sediment carried by the river has also changed since the completion of the dam. Pre-dam sediment loads in the Grand Canyon averaged 380,000 tons per day. Now, most of the sediment in the upper Grand Canyon derives from the Paria River and the Little Colorado River, which collectively contribute only 40,000 tons per year. All of the present sediment load is produced by tributaries downstream from Lees Ferry, 15 miles below Glen Canyon Dam; the water between the dam and Lees Ferry runs clear and cold.

Provided with a "new" reach of cold, clear water, the Arizona Game and fish Department began stocking rainbow trout in the fifteen mile stretch of the Colorado River between the dam and Lees Ferry in 1963. The number of trout stocked generally exceeded 100,000 annually (Reger 1989), but appears to have been considered as a mere supplement to what was believed to be active spawning by resident trout. During the late 1970's and early 1980's, Lees Ferry gained nationwide notoriety as a trophy trout fishery, and experienced a tremendous increase in fishing pressure. Then, during a short period in the early-mid 1980's, the fishery crashed. Subsequent research and review of stocking records demonstrated that stocked fish formed the foundation for the fishery, and that there was little recruitment from naturally spawned eggs even though trout spawned actively and viable eggs were laid at a number of spawning sites. Mark-recapture studies during Phase I of the Glen Canyon Environmental Studies estimated that only 27% of fish caught at Lees Ferry were the result of reproduction of rainbow trout in the Colorado River (Maddux et al. 1987).

The poor natural recruitment of rainbow trout may be related to the fluctuating water levels caused by the hydroelectric power operations of Glen Canyon Dam. Although food and adult trout habitat appear ample to support large trout populations, fluctuating water levels could harm developing eggs or sac fry (alevins), as well as eliminate proper fry rearing habitat along the shore.

This study was designed to assess the impact of fluctuating water levels on developing eggs, sac fry, and free-swimming fry at Lees Ferry. Four major factors could account for the failure of natural recruitment at Lees Ferry. First, despite frequent observation of trout that were actively maintaining redds or spawning, physical characteristics of the substrate could be insufficient to support survival of eggs or alevins independent of the effects of fluctuating water levels and exposure. Second, survival of eggs could be reduced by exposure. Third, survival of alevins could be reduced by exposure. Fourth, survival of recently emerged fry or their ability to remain in proper habitat could be reduced by fluctuating discharge.

In this report, we provide a descriptive summary of the spawning and early life history of fishes in the family Salmonidae (trout and salmon), review pertinent recent literature dealing with spawning habitat and early life history of various trout and salmon, and present descriptive and experimental data relating to: potential spawning habitat; egg and alevin survival under fluctuating water levels; and the likely fate of recently-emerged trout fry in the Colorado River above Lees Ferry.

SALMONID SPAWNING AND EARLY LIFE HISTORY: A SUMMARY

The basic salmonid life cycle (see Behnke 1992, Margolis and Groot 1991) begins when an adult female selects a location for deposition of eggs and digs an oval depression, termed a "redd," in stream bed gravels by turning on her side and beating her caudal fin against or close to the substrate. This process loosens the sediment and allows it to be swept downstream with the current. Eggs and sperm are released into the redd by the spawning adults. The female then moves slightly upstream to dig again, covering the spawned eggs with gravel and, if she possesses additional eggs, preparing another site for deposition of these eggs.

Salmonid eggs develop for various periods of time depending on temperature and oxygen levels. The eggs hatch to release embryos (sac fry, alevins) with an extensive yolk sac. These fish remain in the redd until the yolk sac is largely or completely absorbed, then rise through the overlying gravel and emerge as free-swimming fry. Shortly after emergence, these negatively buoyant fry make repeated forays to the water's surface to gulp air and thereby fill their air bladders and achieve neutral buoyancy. Fry generally move into shallow, still or slowly-flowing water near shore, often into backwaters or emergent vegetation, where they feed and grow to sizes at which they move into the river.

Thus, successful production of young that recruit into river populations of rainbow trout depends on several factors. First, proper spawning substrate must be available to adults in accessible locations. Second, conditions must be present to support survival of eggs and sac fry. Third, proper habitat must be consistently available for fry following their emergence. Below we describe general patterns in conditions of substrate, egg and alevin rearing habitat, and emergent fry habitat that support successful spawning by various salmonid fishes. We have expanded this review beyond the limits of rainbow trout for two reasons. First, few data exist for rainbow trout relative to certain features of spawning and early life history. Second, as recognized by Behnke (1992) and others, spawning characteristics for trout and other salmonids largely reflect size of the fish and environmental conditions, not species-specific differences in preferred spawning habitat or behavior.

SALMONID SPAWNING AND EARLY LIFE HISTORY: A REVIEW OF RECENT LITERATURE

SPAWNING SITES

A broad array of salmonids spawn in < 2 m of water and many in < 1 m (Table 1), but steelhead (sea-run rainbow trout) may spawn in water circa 2 meters deep and chinook salmon at >7 m. In many cases, water depth may be insufficient to cover the backs of spawning adults, although in all but one case water depth exceeded body depth of the female in a study of spawning brown trout (resident and sea-run) and Atlantic salmon (Crisp and Carling 1989). The rarity of reports of spawning depths >2 m may reflect sampling error, as few workers have performed diving surveys in deep sections of rivers. Chapman et al. (1986) performed such surveys in the Central Columbia River, and recorded chinook salmon redds as deep as 7 m at low flow (1,020 m^3/second; flows ranged from 1,020 to 4250 m^3/sec on most days), leading Chapman et al. (1986) to suggest that depth was not a major influence on position of redds in chinook salmon.

Water velocities above redds range from almost slack water (0.01 m/sec) to relatively swift currents (1.89 m/sec in studies we reviewed; 1 m/sec = 3.6 km/hr $\simeq$ 2.2 mi/hr), although most salmonids appear to spawn at flows < ~ 0.5 m/sec (Table 1). Beland et al. (1982) felt that currents up to 0.9 m/sec were not excessive for adult

Table 1. Water depth and velocity over spawning sites for various salmonids. Single values indicate means. In this and subsequent tables, some sources are reviews and not the original sources for data. Also in this and subsequent tables, data for rainbow trout (Oncorhynchus mykiss) precede those for other species of Oncorhynchus, followed by data for species in other genera. See Appendix for common and scientific names of fishes.

SPECIES	VELOCITY (m/s)	DEPTH (m)	SOURCE
Oncorhynchus mykiss	0.31-0.99	0.78	Sams and Pearson 1963
	0.39-0.91	0.37	Smith 1973
	0.49-0.91	0.34	Beland et al. 1982
O. tshawytscha	0.08-1.14	0.22-1.98	Chambers et al. 1955
	0.23-0.76	0.26-0.30	Sams and Pearson 1963
	0.19-0.81	0.31-0.39	Smith 1973
	0.67	≥ 7	Chapman et al. 1986
	0.10-1.89	0.05-7.2	Healey 1991
O. kisutch	0.25-0.71	0.25	Sams and Pearson 1963
	0.19-0.69	0.22	Smith 1973
	0.30-0.75	0.04-0.33	Sandercock 1991
O. keta	0.45-1.00	0.30	Smith 1973
	0.20-0.80	0.13-0.5	Salo 1991
O. nerka	0.14-0.73	0.23	Smith 1973
Salmo salar	0.53	0.17-0.76	Beland et al. 1982
Salmo trutta	0.20-0.68	0.43	Smith 1973
Salvelinus fontinalis	0.01-0.23	0.25	Smith 1973

Atlantic salmon, but noted that their specimens were relatively large (75 cm fork length, 4.5 kg, 2-sea-winter fish), and that larger salmonids probably have greater endurance in strong currents than smaller fish (Weaver 1963, in Beland et al. 1982). Average velocity over redds of these 2-sea-winter Atlantic salmon was 0.53 m/sec (Beland et al. 1982).

Reports of size distributions for gravels on spawning sites of salmonids are difficult to compare due to differences in size classes of sediment distinguished and to inconsistent definitions for categories of sediments. For example, McNeil and Ahnell (1964, in Heard 1991) reported gravel sizes for pink salmon redds as: 14.3% < 0.8 mm diameter, 31.4% 0.8-6.7 mm, and 54.1% > 6.7 mm. A Russian worker (Rukhlov 1969, in Heard 1991) classified sediments from pink salmon redds and unspawned areas as "sand," "gravel," "shingle," and "cobble;" only cobble was defined (> 100 mm). Wide reading, however, leaves the impression that many species of salmonids can and do spawn in those conditions available to them; when spawning gravels are unavailable, for example, sockeye salmon (and occasionally other salmon species) may simply drop eggs into crevices around boulders too large to dislodge (see chapters in Groot and Margolis 1991). Behnke (1992) also cites cases where "preferences" for reproductive sites identified by authors are in fact simple descriptions of the spawning habitat available to the fishes.

Kondolf et al. (1989) described stream gravels from redds and unspawned areas on three gravel bars (4-, 8-,and 12-mile) between Glen Canyon Dam and Lees Ferry, and compared distributions of gravel size from these locales with those reported from tributary streams in the Grand Canyon and elsewhere. In the area above Lees Ferry, geometric mean gravel size was similar for two redds (5.5 mm) and one unspawned site (5.2 mm), although the geometric standard deviation was higher (10.5) for the unspawned site than the redds (5.4). Unspawned gravels had a higher fraction of small particles (<3.4 mm, 25%) than the redds (15.2%). This is consistent with reports by Rukhlov (1969, in Heard 1991) for pink salmon and is widely reported for other species. The Lees Ferry gravels tended to be smaller than those from unspawned gravels in Grand Canyon tributaries (14.9 mm) or rivers elsewhere (8.3-14.7; Montana, Idaho, British Columbia). Kondolf et al. (1989) assessed even the small gravels above Lees Ferry as sufficient to support successful spawning of rainbow trout.

The depths at which eggs are laid in gravels appears to depend on average size of the species and size of the female, but is generally less than 20 cm in smaller species (Hobbs 1937, in Chapman 1988; Table 2). Crisp and Carling (1989) found that depth of eggs was a linear function of female length at several of their study sites. Probably related to this relationship is the tendency for small species (rainbow and brown trout) to deposit eggs at shallower depths (5-30 cm) than larger species (chinook salmon, to ~ 80 cm). At Lees Ferry, Kondolf et al. (1989) reported eggs at depths of 10-15 cm.

SURVIVAL OF EGGS

Temperature influences both survival and developmental rates of fertilized eggs. In general, salmonid eggs are capable of tolerating and hatching over a relatively wide range of temperatures (Table 3). For example, Crisp (1981) and Dwyer (1987) reported hatching success of rainbow trout of 62-66% at temperatures from 1.8 to 16 C. In coho salmon, hatching exceeded 80% at 1.3-12.5 C, but dropped significantly above and below those temperatures, with complete mortality at $<$1.3 and 17 C.

Within tolerance limits for hatching, temperature exerts strong influence on developmental rates (Table 4). Cooler temperatures slow development, warmer temperatures accelerate it. In rainbow trout, Embody (1934, in Wales 1941) reported a 5-fold increase in developmental rate (80 days to 19 days) with an 11.6 C increase in

Table 2. Depths (cm) at which various salmonids deposited pockets of eggs below surface of gravel in redds.

SPECIES	DEPTH (cm)	SOURCE
Oncorhynchus mykiss	10-15	Kondolf et al. 1989
	~20	Chapman 1988
O. gorbuscha	15-50	Heard 1991
O. keta	7.5-43	Sago 1991
O. kisutch	15-39.1	Sandercock 1991
O. tshawytscha	18-43	Chapman 1988
	10-80	Healey 1991
Salmo salar	5-30	Jensen et al. 1989
	5-~25	Crisp and Carling 1989
Salmo trutta	5-30	Jensen et al. 1989
	8-22	Chapman 1988

Table 3. Percent of eggs that hatched at various water temperatures for several species of salmonids.

SPECIES	TEMPERATURE (C)	HATCH (%)	SOURCE
Oncorhynchus mykiss	3.2-16	62	Crisp 1981
	1.8	63	Dwyer 1987
	6.4	66	
	9.8	62	
O. kisutch	<1.3	0	Tang et al. 1987
	1.3	90	
	2.4	90-94	
	3.1	94-96	
	4.7	92-94	
	6.5	83-94	
	8.3	88-93	
	10.9	81-91	
	12.5	79-87	
	14.4	1.0-14	
	17.0	0	
O. tshawytscha	6.0	93	Heming 1982
	8.0	92	
	10.0	91	
	12.0	89	
Salvelinus fontinalis	6.0	78-92	Hokanson et al. 1973
	9.0	63-68	
	15.0	12-40	
	18.0	0	

Table 4. Days required for eggs to hatch at various water temperatures for several species of salmonids.

SPECIES	DAYS	TEMPERATURE (C)	SOURCE
Oncorhynchus mykiss	80	4.4	Wales 1941
	48	7.2	
	31	10	
	24	12.8	
	19	16	
O. gorbuscha	130 (to 50% emergence)	3.4	Heard 1991
	106	5.0	
	77.5	7.9	
	61.5	9.9	
	61.0	12.3	
	35.8	15.0	
O. keta	182	2.8	
	118	4.8	
	86	7.2	
O. kisutch	196 (to 50% hatch)	1.3	Tang et al. 1987
	176	2.4	
	103	4.7	
	60	8.3	
	42	10.9	
	37	12.5	
	32	14.4	
	0	17.0	
O nerka	119 (to 50% hatch)	5.0	Burgner 1991
	80	8.0	
	57	11.0	
Salmo trutta	156	1.7	Wales 1941
	100	4.4	
	64	7.2	
	41	10	

Table 4. (continued)

Salvelinus alpinus	14-23	4	Gruber and Wieser 1983
	6-13	8	
S. fontinalis	144	1.7	Wales 1941
	103	4.4	
	68	7.2	
	44	10.0	
	35	12.8	
S. namaycush	196	1.8	Dwyer 1987
	90	6.4	
	58	9.8	
	162	1.7	Wales 1941
	108	4.4	
	72	7.2	
	49	10.0	

temperature from 4.4 C to 16.0 C. This exceeds the expected change in rate based on a common vertebrate Q^{10} for many metabolic processes of ~2. Some tests over a broad temperature range suggest an asymptotic approach to a minimum time required for development as temperature increases toward upper lethal limits; coho salmon accelerated development from 103 days to 60 days with a 3.6 C increase from 4.7 to 8.3 C, but accelerated only from 42 to 32 days with a 3.5 C shift from 10.9 to 14.4 C.

We found no data dealing with the effects of short-term fluctuations in temperatures. Unfortunately, this problem is probably more relevant to the system at Lees Ferry than estimates of hatching success and development rates based on stable experimental temperatures (see thermograph data presented below). Temperatures may vary within redds when gravels are exposed (Neitzel and Becker 1985). Reiser and White (1983) found that rainbow trout eggs exposed while buried in spawning gravels hatched 11 days earlier than submerged controls. Eggs in advanced stages (eyed stage) were more tolerant of extreme temperatures than those in early developmental stages (Hokanson et al. 1973), but we know of no work addressing differences among developmental stages in tolerance to short-term fluctuations in temperature.

Associated with increased temperature that might occur when spawning sites are exposed is the potential for drying of eggs and alevins. According to Reiser and White (1983; Table 5), exposure of salmonid eggs in redds has little effect on hatching of eggs, provided that the gravel retains a moisture content of at least 4%.

SURVIVAL OF ALEVINS

Alevin survival appears to be influenced little by temperature within the range of temperatures allowing normal development and hatching of eggs (Table 6). Chinook and coho salmon exhibited high survivorship (> ~85%) at temperatures from ~3 to ~12 C. Coho alevin mortality increased above 12.5 C, as did mortality of coho eggs.

Table 5. Effects of exposure of varying duration on hatching success of salmonid eggs in experimental redds.

SPECIES	DURATION	HATCH (%)	SOURCE
Oncorhynchus mykiss	26 days	0-7.3	Reiser and White 1981
	1 week	45	Reiser and White 1983
	2 weeks	97	
	3 weeks	90	
	4 weeks	88	
O. tshawytscha	26 days	28.4-97.7	Reiser and White 1981
	2 weeks	78	Reiser and White 1983
	3 weeks	78	
	4 weeks	76	
	5 weeks	73	
	121 days	87-99	Reiser and White 1990
	12 days	92-98	Becker et al. 1983
	16 days	64	
	20 days	53	
	6 hours	0 (survival of alevins)	

Table 6. Survival of alevins (sac fry) at various water temperatures for two species of salmonids.

SPECIES	TEMPERATURE	SURVIVAL (%)	SOURCE
Oncorhynchus tshawytscha	6.0	93	Heming 1981
	8.0	93	
	10.0	90	
	12.0	85	
O. kisutch	3.1	97-100	Tang et al. 1987
	4.7	97-100	
	6.5	98-100	
	8.3	98-100	
	10.9	95-100	
	12.5	41-95	
	14.4	0-65	

In contrast to its effects on eggs, exposure causes high mortality among alevins (Reiser and White 1983; Table 6). Becker et al. (1982) showed that 96% of alevins were killed by 1 hour of exposure daily over a 22 day period. Becker et al. (1982, 1983) also recognized that pre-emergence alevins were more sensitive to exposure than either advanced embryos (eleutheroembryos) or cleavage eggs and early embryos. As with eggs, changing temperatures in exposed redds may also influence alevins; alevins survived 4 hours at 23.5 C, but only 1 hour at 25.0 C (Neitzel and Becker 1985).

BEHAVIOR AND SURVIVAL OF FREE-SWIMMING FRY

As noted above, recently emerged fry often move into quiet waters near shore. Fluctuating water levels at Lees Ferry could have two critical effects on such habitats. First, fluctuating water levels would alternately flood and expose shoreline zones and threaten fry with stranding. Second, depending on the position of emergent vegetation, which reduces current speeds along shorelines, and the structure of the river bed (slope of substrata and position of channels), changes in water levels may greatly alter current speed along the short. Although we lack quantitative data about the effects of stranding on fry, it is clear that marked increase in current speed above certain levels will rapidly displace fry downstream.

At least three factors increase the threat of downstream displacement of fry. First, fry must move from locations of redds, with often swift currents (Table 1), to stream margins. Second, recently emerged fry tend to be most active at night, taking refuge in crevices and sediments during the day. The inability of these small (25-35 mm upon emergence) animals to maintain a station relative to particular physical landmarks in the dark tends to result in their downstream displacement. Third, after emergence, negatively buoyant fry dart to the surface and gulp air; this behavior, which fills the air bladder and leads to neutral buoyancy, may be repeated several times and would take the animals from areas of low flow near the bottom into the higher flows of the water column.

Heggenes and Traaen (1988) concluded that salmonid fry entering the free-feeding stage are the most vulnerable to downstream displacement caused by increased water velocities, and downstream displacement of fry occurs in many species (see chapters in Groot and Margolis 1991). Increases of as little as 4-14 cm/s in water velocity displaced brown trout (Heggenes 1988). Irvine (1986) reported that fluctuating discharge appeared to increase the number of chinook salmon fry (size = 38-40 mm) moving downstream, and that the increase in downstream movement occurred when flows exceeded 25 cm/s. This value concurs with an overview of many species (Table 7) that failed to find fry inhabiting any areas where current exceeded 24 cm/sec.

It is clear that the threat of downstream displacement is size-dependent. Experiments with sockeye and kokanee salmon demonstrated that larger fry (70-85 mm) are able to withstand faster water velocities (53 and 60 cm/s; Taylor and Foote 1991). Young brown trout (67-160 mm) in a stream in Norway were not displaced by either induced or natural high flows (Heggenes 1988).

Depths inhabited by fry are also generally less than those inhabited by adults (Table 7), and are consistent with occupation of stream margins and backwaters. Although salmon fry have been recorded from depths up to 85 cm, most reports for rainbow trout and several other species indicate that fry tend to occupy water <25-30 cm in depth.

Comparison of data describing depth and current conditions for redds (Table 1) with those for fry habitats (Table 7) make it clear that fry must be exposed upon emergence to currents exceeding their usual abilities to hold a position in the stream, and that they must move some distance to stream margins. For example, most spawning sites were

Table 7. Velocity and depth of water occupied by free-swimming fry of various salmonids

SPECIES	WATER VELOCITY (m/sec)	DEPTH (m)	SOURCE
Oncorhynchus mykiss	<0.15	<0.15	Everest et al. 1972
	0.09-0.21	0.09-0.15	Sheppard et al. 1985
	<0.20	<0.20	Bustard and Narver 1975
	<0.20	<0.15	Mundie and Traber 1983
	0.14		Bugert et al. 1991
	0.19-0.24	0.21	Gosse 1984
O. tshawytscha	<0.15	<0.15-0.30	Everest et al.1972
O. kisutch	0.09-0.21	0.61-0.73	Sheppard et al.1985
	0.00-0.09	0.46-0.85	Bugert et al. 1991
	0.15	0.24	Bustard and Narver 1975
	0.00-0.15	>0.15	Bisson et al. 1988
Salmo salar	<0.15		Hearn and Kynard 1986
	0.16-0.18	0.18-0.21	Heggenes et al. 1990
	0.23	0.47	Heggenes et al. 1991
	0.20		Wankowski et al. 1979
	0.10-0.30	0.24-0.36	Rimmer et al. 1984
Salmo trutta	0.03-0.19	0.11-0.23	Heggenes et al. 1990

SUMMARY

	Range of Velocity	Range of Depth
O. mykiss	0.03-0.24	0.09-0.21
O. tshawytscha	<0.15	<0.15-0.30
O. kisutch	0.00-0.21	0.15-0.85
Salmo salar	0.10-0.23	0.18-0.47
Salmo trutta	0.03-0.19	0.11-0.23
All species	0.00-0.24	0.09-0.85

characterized by currents exceeding 30 cm/sec, above the 24 cm/sec that seems to characterize the maximum tolerable flow for newly emerged fry. Furthermore, depths of water over redds (~30 cm to > 7 m) generally exceeded depths in fry habitats (usually < 30 cm).

RESEARCH OBJECTIVES

Our research investigated the possible bases for low recruitment of naturally spawned rainbow trout at Lees Ferry and the role fluctuating water levels might play in causing low recruitment. If the problem resides with factors influencing early life history stages, then poor recruitment may result from any or a combination of three primary phenomena:

a. poor survival or hatching of eggs;

b. poor survival of alevins (sac fry);

c. poor survival or retention of recently emerged fry.

Here we list primary objectives of this research and provide a short statement of how each relates to possible causes for low recruitment.

I. Describe size distribution of sediments on research sites at Lees Ferry.

Spawning by rainbow trout has been reported frequently from the Lees Ferry area by scientific and management personnel, professional fishing guides, and other observers. We wished to insure that sediments on the research sites were compatible with spawning by trout, and that both laboratory and field experiments could be designed to mimic conditions at Lees Ferry where possible.

IIa. Describe moisture content in sediments exposed for long periods at Lees Ferry.
IIb. Describe drying rates of sediments of different sizes.

Reiser and White (1983) stated that 4% moisture content in sediments was sufficient to support normal hatching of salmonid eggs. We wished to determine if similar levels of moisture were available in near-surface sediments at Lees Ferry after extended periods of exposure. Furthermore, we wished to investigate rates of drying of loosely packed sediments experimentally, in order to obtain a better idea of how drying might influence eggs and alevins.

III. Describe daily cycles and long-term changes in air temperature and sediment temperatures at different levels of exposure during a period when active spawning or development might take place.

Temperature influences survival and hatching of eggs as well as survival of alevins in redds, but we could find little information about the impact of short-term fluctuations in temperature on these phenomena.. We assumed that changes in water levels associated with fluctuating discharges from Glen Canyon Dam would result in changes in temperature of exposed sediments, but the depth to which these effects might be felt and the nature of fluctuations at depths where eggs might be deposited by rainbow trout at Lees Ferry were unknown. We wished to compare published records of temperature tolerance limits for salmonids with conditions experienced in redds in the Lees Ferry area.

IV. Estimate hatching success and mortality of eggs and mortality of sac fry under controlled conditions for different periods of exposure.

Previous studies indicated that extended exposure of eggs in moist gravels had little effect on hatching success of eggs, but that alevins (sac fry) were very sensitive to exposure. The existing literature, however, does not allow prediction of levels of mortality for different periods of daily exposure similar to those encountered under the fluctuating flow regime at Lees Ferry. Our experiments were designed to generate simple predictive models of the effect of exposure on egg and alevin mortality.

V. **Test predictions from laboratory experiments by subjecting eggs and alevins to known daily exposures in sediments at Lees Ferry.**

We wished to experimentally test predictive models generated by Objective IV, and to determine if laboratory protocols approximated field conditions sufficiently to warrant their use in future studies of the effects of exposure on early life history stages of trout.

VI. **Describe characteristics of habitat available to recently emerged fry near known spawning sites at Lees Ferry.**

Habitat occupied by recently emerged fry differs in depth and current velocity from habitat where redds are constructed and eggs laid. We wished to assess the availability of habitat that might be occupied by recently emerged fry, and how this habitat changed with fluctuating river discharge.

VII. **Introduce trout fry to proper habitat at Lees Ferry and track their fate during a period of fluctuating river discharge.**

In an extension of studies on availability of tolerable habitat, we wished to determine if fry are able to hold station under fluctuating flows at Lees Ferry.

MATERIALS AND METHODS

POTENTIAL SPAWNING GRAVELS

Methods used to collect sediment samples followed those of Kondolf et al. (1989). At each site (9-mile, 13.5-mile), three sampling reaches were laid out along the 5000 cfs and 10,000 cfs water lines. At haphazardly chosen sampling points along each reach, a 25 cm diameter bucket with its bottom removed was driven into the sediment. Sediment was then dug from the bucket to a depth of 11-15 cm, air dried, and sequentially sifted through standardized sorting screens of 4.85, 2.75, 1.00, and 0.63 cm square mesh. Subsamples were then weighed to 0.01 kg.

Proportion of total weight was calculated for each size category for each sample, and then proportional measures were natural-log transformed for analyses. Distributions of transformed data were checked for normality with the Lilliefors-standardized Kolmogorov-Smirnov test (Zar 1984). The transformation normalized all but 17 of the 60 subsets (2 sites x 2 discharges x 3 reaches x 5 sediment categories) of the data; 9 of the 16 nonnormal distributions were due to zero values for sediments in the largest size class. We applied 2-way Analysis of Variance and Tukey's HSD tests to the transformed data in order to assess possible differences between sediments at different discharge levels and differences among reaches.

MOISTURE CONTENT OF SEDIMENTS: FIELD ASSESSMENT

Sediment samples were collected at the 13.5 mile site after 13 and 16 hrs of exposure and at the 9 mile site after 11 hrs of exposure. At each exposure level, a 50 m transect was laid out parallel to the water's edge. Single (13 and 16 hrs exposure at 13.5 mile) or duplicate (11 hrs at 9 mile) samples were collected at 5 m intervals along each transect line. All samples contained sediments from the surface to a depth of 11 cm. Samples were sealed in Whirlpak bags and held on dry ice until they were weighed in the lab at Northern Arizona University. After determination of initial weight (to 0.001 kg), samples were spread on dry surfaces at room temperature and ambient humidity. As we wished to get a crude assessment of drying in exposed sediments under field conditions, we made no attempt to dry samples to constant weight at high temperature and unusually low humidity. Several days after exposure to air, samples were again weighed and the weight loss taken as a measure of water loss.

MOISTURE CONTENT OF SEDIMENTS: LABORATORY ASSESSMENT

As before, gravel samples were collected from the 9 and 13.5 m study sites. For laboratory studies, however, samples were air dried and separated into 4 categories based on particle size: < 1.0 cm, 1.0-2.8 cm, 2.8-4.9 cm, and >4.9 cm. An additional category comprised a mixture of gravels similar in composition to that encountered at Lees Ferry. One liter (~0.5 kg) samples of each gravel category were placed into bags constructed of cotton cloth. Three replicate subsamples of each sediment category were placed in a Living Stream tank with circulating water held at 11.5 C, representative of water temperature at Lees Ferry. The tank was maintained in a closed room with rapidly circulating air in the Live Animal Facility at Northern Arizona University. Room temperature ranged 17-19 C during the study. Bags of sediment were removed after 24 hours, immediately weighed (to 0.001 kg), then placed on screen racks to dry. Bags were reweighed every 3 hrs up to 15 hrs.

SEDIMENT TEMPERATURES

Beginning 13 October 1990, five thermographs that recorded temperature hourly to within 0.01 C were placed at the 9 mile site. Thermographs were buried to a depth of 11-15 cm [Kondolf et al. (1989) reported pockets of eggs at 11-15 cm depth from Lees Ferry] at the 3000 (continuously immersed), 5000, 10,000, and 15,000 cfs waterlines. A fifth thermograph was placed in vegetation well above high water lines to measure air temperatures near the shaded substrate.

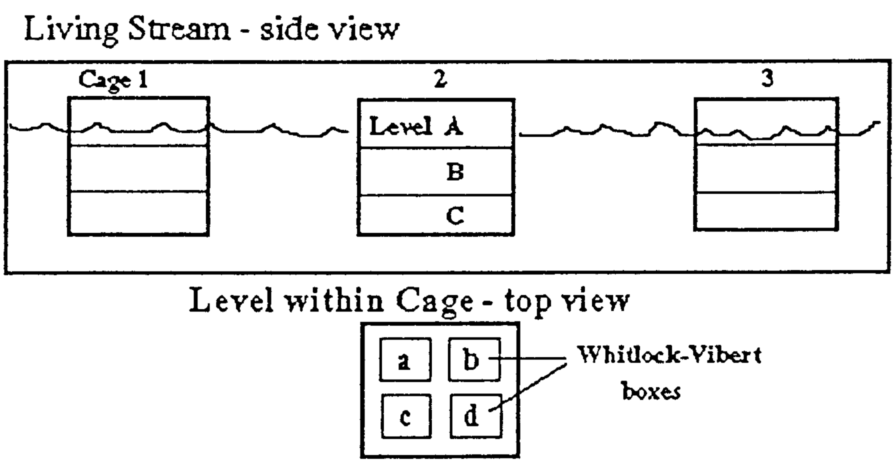
Data were downloaded as ASCII files, then transformed to formats compatible with SYSTAT. Only data from 16 March-7 April 1991 are presented. Field experiments were performed on egg survival and hatching and alevin survival during these same dates in

1990, but attempts to measure sediment temperatures using different techniques during that period failed. The 1991 data are, therefore, presented as the best possible estimate of conditions in sediments during the period of the earlier experiments.

TOLERANCE TO EXPOSURE: LABORATORY EXPERIMENTS

Two Living Stream recirculating aquaria were employed in our experiments. Each stream tank contained three PVC frames, termed cages, and each cage had three levels (Figure 1). Each level contained four artificial redds, each comprising a Whitlock-Vibert box buried in gravel. Gravel was collected from the 9 mile study site at Lees Ferry and sorted as described above; only gravels falling into the 2.75-4.85 cm size category were used in experimental redds. Thus, 4 boxes were buried on each of 3 levels in 6 cages, for a total of 24 boxes per treatment and 72 boxes per experiment.

Figure 1. Arrangement of Cages, Levels and Redds containing Whitlock-Vibert boxes in Living Stream tanks.



Cages were hung on from a frame by pulleys and were raised out of and lowered into water at designated times, thus exposing different levels within cages for different periods that simulate fluctuating flows at Lees Ferry. The bottom Level (C in Figure 1) served as a control, in which eggs were completely submerged for 24 hrs daily. Levels A and B received experimental treatments, with Level A being exposed longer than Level B.

Both stream tanks were filled with aged, dechlorinated water for three days prior to the experiments. Water temperature of both stream tanks was kept at 11 C and was checked daily with a YSI salinity-conductivity-temperature meter. Room temperature fluctuated between 13 and 18 C. Relative humidity was not monitored.

Rainbow trout eggs (Bellaire strain, to insure similarity with fish commonly stocked at Lees Ferry) were obtained from the Sterling Springs Hatchery, Arizona Game and Fish Department. Upon arrival of the eggs in the laboratory, they were placed into the egg-chamber of Whitlock-Vibert boxes (S. Howell, Pullman, WA; 25 eggs per box), buried in the artificial redds, and allowed to remain undisturbed and fully immersed for at least 24 hrs prior to the start of the experiments. During Experiment I, the boxes were lined loosely with fiberglass window screen in an attempt to reduce escapism of alevins. When this technique proved only marginally successful, screen was glued to the box walls with silicone aquarium cement in Experiments II and III. The boxes were then cleaned and soaked in aged water to avoid contamination to the eggs and sac fry.

Eggs were placed in boxes and redds on Day 1 and experimental exposures began on Day 3 of the experiments. Two boxes from each level were checked every other day, and the number of live eggs, dead eggs, live sac fry, and dead sac fry were recorded.

TOLERANCE TO EXPOSURE: FIELD EXPERIMENTS

The experiment began 16 March 1990 on the 13.5 mile site and on 17 March at the 9 mile site. Experimental plots were established at four different water levels: 1000 cfs (control, 0 hours of exposure per day). 5000 cfs (6 hours of exposure), 10,000 cfs (10 hours of exposure), and 15,000 cfs ($\geq$ 15 hours of exposure). These exposures were similar to those used in laboratory experiments (0, 6, 11, 12, and 15 hours). There were 4 plots per water level, each with 3 holes dug in sediments and lined with gravel 2.75-4.75 cm in diameter. Each hole contained 2 Whitlock-Vibert boxes, each with 25 Bellaire rainbow trout eggs. Plots were 3 m apart, while holes within a plot were 1 m apart. A plot with its 6 boxes (3 holes, each with 2 boxes) was excavated from each water level on 20, 23, 28 March and 6 April at the 13.5 mile site and on 21, 24, 29 March and 7 April at the 9 mile site. Live eggs, dead eggs, live sac fry and dead sac fry were counted.

HABITAT AVAILABLE FOR FRY

The 13.5 mile and 9 mile gravel bars were sampled during November 1991 and January 1992. Three transects were established perpendicular to the water's edge at the 5000 and 20,000 cfs water lines, near areas where active construction of redds and spawning had been observed the previous Spring. Each transect contained 5 sampling points at 1 m intervals from the water line (water line = Point 0). At each sampling point, velocities were measured at surface, 60% of depth and bottom with a Swoffor 2100 flow meter, depth was measured to 1 cm, and substrate was described.

ABILITY OF YOUNG FISH TO HOLD POSITION

On 17 July 1991, one thousand juvenile rainbow trout (60-70 mm TL) from Sterling Springs Fish Hatchery, Arizona Game and Fish Department, were adipose fin-clipped and released at 1600 hrs near shore at the 9 mile site. Sampling was conducted the same evening between 2100 and 2200 hrs at a discharge of ~ 20,000 cfs, as well as the next morning (0700-0800, ~ 5000-7000 cfs) and afternoon (1300-1400, ~ 20,000 cfs). Sampling involved triplicate seine hauls with a 10 m seine at the release site as well as a series of seine hauls to ~ 100 m upstream and downstream of the release site.

RESULTS

POTENTIAL SPAWNING GRAVELS

Sediments were quite similar at both study sites (Table 8). The 2.75-4.85 size category prevailed at both sampling sites (64.7-73.6%), followed by the <0.63, 4.85, 0.63-1.0 and 1.0-2.75 cm size classes. This pattern was consistent at both water lines as well; the only between-water line differences detected by ANOVA were a slightly higher level of 0.63-1.0 cm particles at the 10,000 cfs water line on the 13.5-mile site ($F = 8.94$, $p = 0.005$, error df = 38) and a slightly higher proportion of sand at the 10,000 cfs water line on the 9-mile site ($F = 5.91$, $p = 0.02$).

Table 8. Composition of sediments collected from the 9- and 13.5-mile study sites above Lees Ferry. Sediments were sorted through screens of 0.63 cm, 1.0 cm, 2.75 cm, and 4.85 cm square mesh. Values are means of percentages. Statistical analyses based on natural log transformed values are discussed in text.

			Size of Particles (as % of total)			
Site	*Discharge*	*≤ 0.63 cm*	*0.63-1.0*	*1.0-2.75*	*2.75-4.85*	*≥4.85*
9-mile	5,000 cfs	21.6	5.9	3.8	67.9	12.5
	10,000	24.0	6.5	3.5	64.7	12.7
13.5-mile	5,000	25.1	3.8	2.9	73.6	17.4
	10,000	21.9	6.3	3.4	68.6	13.6

MOISTURE CONTENT OF SEDIMENTS: FIELD ASSESSMENT

Crude moisture content was approximately 9% of initial sample weight at both sites and all conditions of exposure (Table 9). Variation among samples was low (coefficient of variation = 3.1-5.5%). There was close agreement between the mean and median, both measures of central tendency in the data and equal in normally-distributed populations, despite the Kolmogorov-Smirnov test's determination that samples from 11 and 13 hrs exposure deviated significantly from normality. Kruskal-Wallis nonparametric analyses of variance failed to detect effects either of position along transects at different exposures (11 hrs: $p = 0.32$; 13 hrs: $p = 0.44$; 16 hrs: $p = 0.44$) or of hours of exposure ($p = 0.18$). Parametric analyses of variance similarly failed to find an effect of position along transects when nested within hours of exposure ($F = 2.02$, 20 df, $p = 0.07$) or of hours of exposure ($F = 1.59$, 2 df, $p = 0.22$).

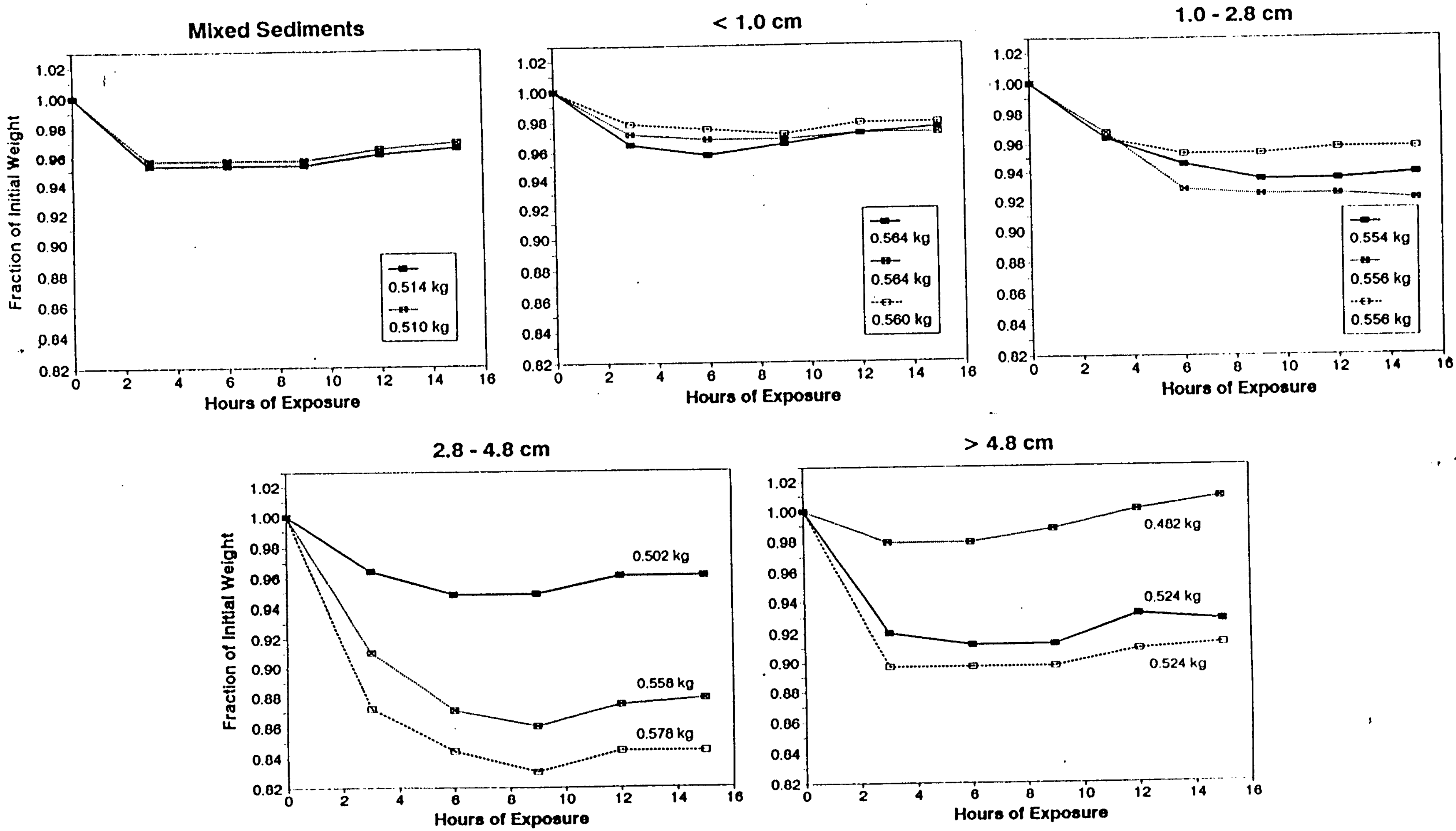
Table 9. Summary of crude estimates of moisture content (percent of initial sample weight) for sediments collected at Lees Ferry, 6-7 April 1991.

Mile	Exposure	Mean	Median	Range	S.D.	C.V.	N
8	11 hrs	9.2 %	9.2 %	7.9-9.7 %	0.4%	4.1 %	20
13.5	13	9.0	9.1	7.8-9.6	0.5	5.5	10
13.5	16	9.3	9.3	8.9-9.8	0.3	3.1	10

MOISTURE CONTENT OF SEDIMENTS: LABORATORY ASSESSMENT

Drying rates for both sorted and mixed-size sediments (Figure 2) were most rapid in the first 3-6 hrs of exposure. Small (<1.0 cm) and mixed sediments lost the least weight (2-4% and 4-5%, respectively), and the mixed sediments lost only half as much moisture as the field collected materials discussed above. Larger sediments, in general, lost a larger fraction of their initial weight.

Figure 2. Drying of mixed and size-sorted sediments from Lees Ferry. Insets or labels provide initial weights (kg) of samples. Samples were held in cloth bags, immersed for 24 hrs, then dried at room temperature and humidity.


Mixed Sediments
Fraction of Initial Weight
Hours of Exposure
0.514 kg
0.510 kg
< 1.0 cm
0.564 kg
0.564 kg
0.560 kg
1.0 - 2.8 cm
0.554 kg
0.556 kg
0.556 kg
2.8 - 4.8 cm
0.502 kg
0.558 kg
0.578 kg
> 4.8 cm
0.482 kg
0.524 kg
0.524 kg

SEDIMENT TEMPERATURES

Air temperatures ranged more widely and exhibited much greater variation (reflected by the standard deviations; Figures 3-5, Table 10) than constantly or intermittently submersed sites.

At all sites, the lowest temperatures occurred in the morning (0600-0800), the highest in late afternoon (1500-1600), and the highest rate of change between those times, particularly 0900-1200 (Figures 3-5, Table 10). Even at the 3000 level, rising and falling temperatures roughly tracked the pattern of changes in air temperature. Somewhat contrary to expectations, hourly means and the amount of variation were quite similar for the exposed sites (5000-15,000 cfs), although variation at the 5000 cfs site was slightly lower than at the other sites. Finally, variation was greatest in the afternoon for all exposed sites, but was greatest in the morning at 3000 cfs.

Table 10. Summary of temperature data 11-15 cm below sediment surface at the 9-mile site, 16 March-7 April 1991. Hourly means are plotted in Figure 3. Temperature maxima and minima (Columns 2 and 3) are the absolute daily maxima and minima for the entire period. Mean maxima and minima were calculated from daily summaries (see Figure 5; n = 23), and were used to calculate a maximum rate of change in temperature (Δ temperature/Δ time). Means, maxima and minima of daily ranges are also presented. All data and summaries are in degrees Celsius.

	Temperature		*Mean Minima and Maxima*				*Rate of*	*Daily Range*		
Discharge	max.	min.	min	time	min	time	*Change*	mean	min	max
3000 cfs	10.5	5.4	7.2	0700	8.5	1600	0.14	1.4	0.3	3.2
5000	14.4	4.2	5.7	0800	8.4	1500	0.38	2.9	1.0	9.5
10,000	16.8	3.3	5.1	0800	9.0	1600	0.56	4.2	1.4	12.5
15,000	14.5	3.7	5.3	0600	9.0	1600	0.46	4.0	1.1	9.8
Air	30.1	0.3	3.69	0600	18.54	1500	1.65	15.8	8.0	20.4

Daily fluctuations were slightest at the 3000 cfs level, where immersion was essentially continuous (Figures 3-5). The range in temperature at 3000 cfs for the study period was from 5.4 to 10.5 C, well within tolerance limits for normal development of trout eggs and alevins. Furthermore, the 3000 cfs site had the lowest mean, minimum

Figure 3. Hourly temperatures 11-15 cm below sediment surface at the 9-mile research site, Lees Ferry. Plots are for temperature dynamics at water lines associated with four river discharges. Values are means $\pm$ 1 standard deviation, calculated from daily records for 16 March-7 April 1991. Approximate periods of daily exposure at each water line: 0 hrs @ 3000 cfs; 6 hrs @ 5000 cfs; 10 hrs @ 10,000 cfs; $\geq$ 15 hrs @ 15,000 cfs.

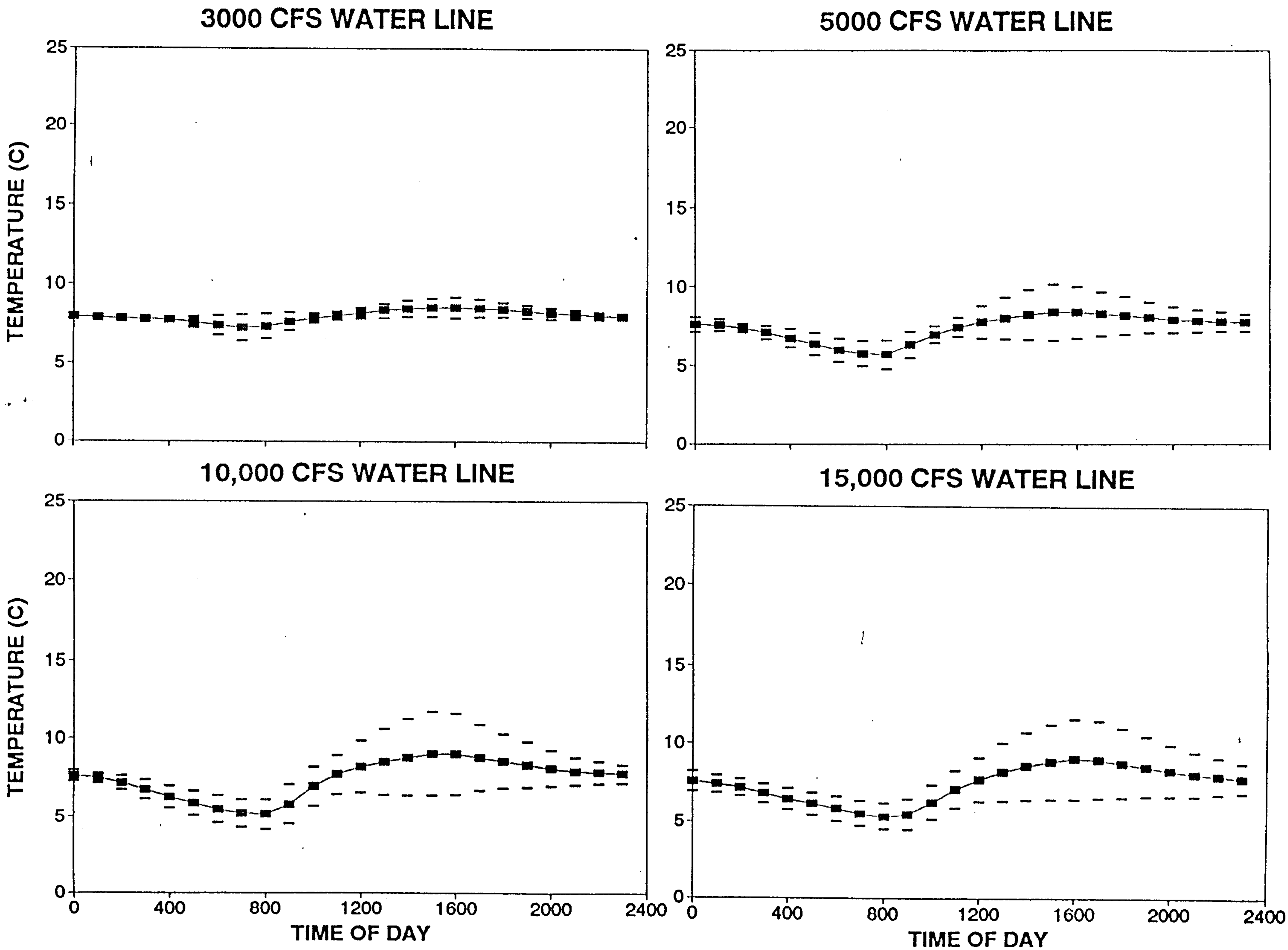
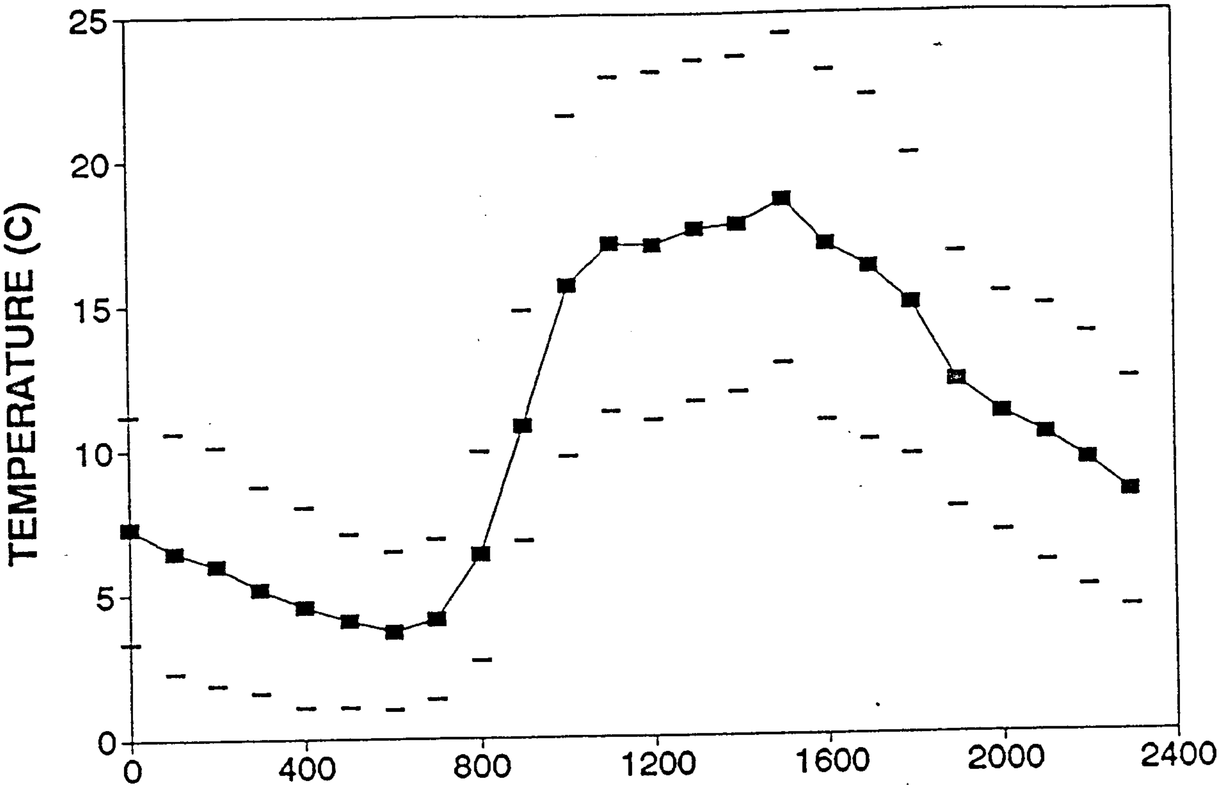

3000 CFS WATER LINE
5000 CFS WATER LINE
10,000 CFS WATER LINE
15,000 CFS WATER LINE
TEMPERATURE (C)
TIME OF DAY
0
5
10
15
20
25
0
400
800
1200
1600
2000
2400

Figure 4. Hourly air temperatures and standard deviations for hourly sediment and air temperatures, 16 March-7 April 1991, 9-mile research site, Lees Ferry. Air temperature values are means $\pm$ 1 standard deviation.

AIR TEMPERATURE



STANDARD DEVIATION FOR TEMPERATURE

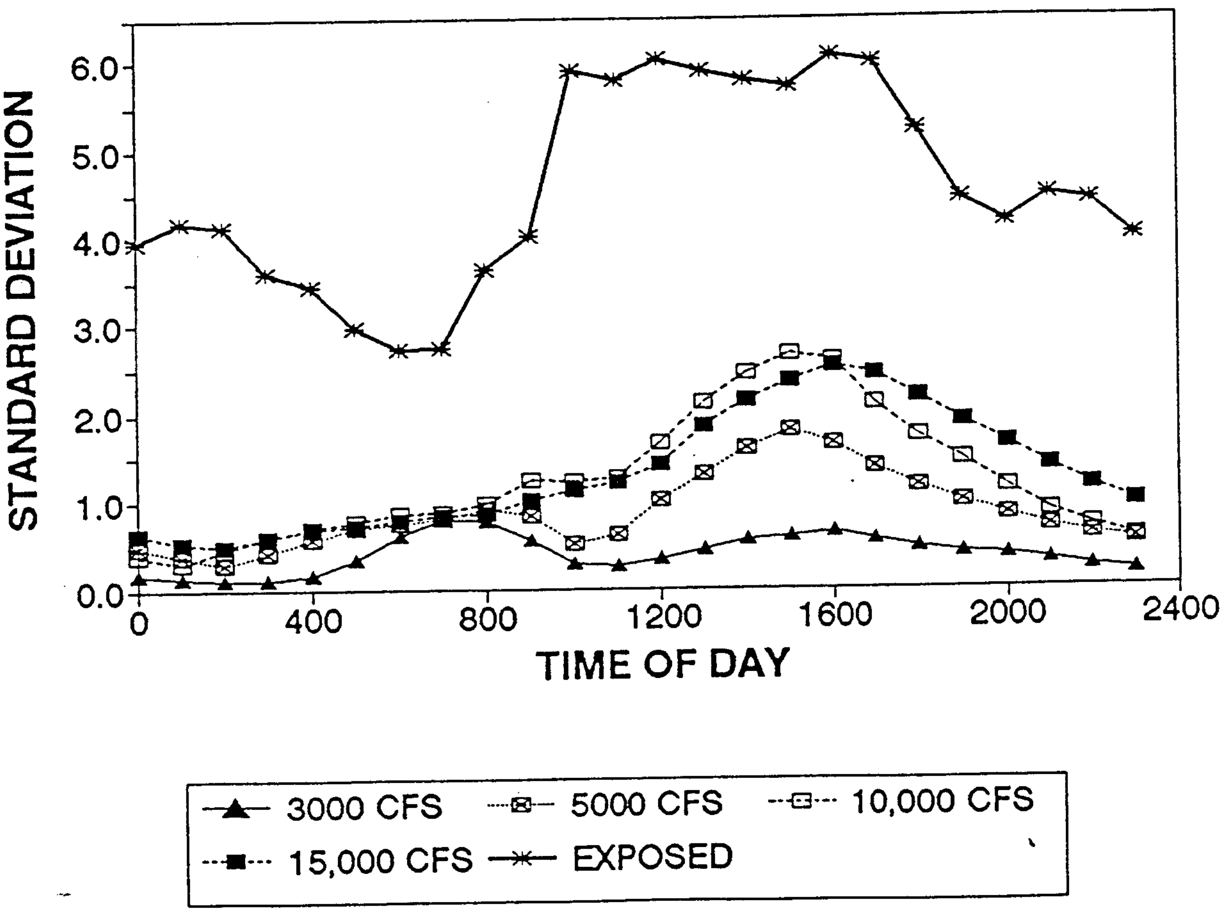
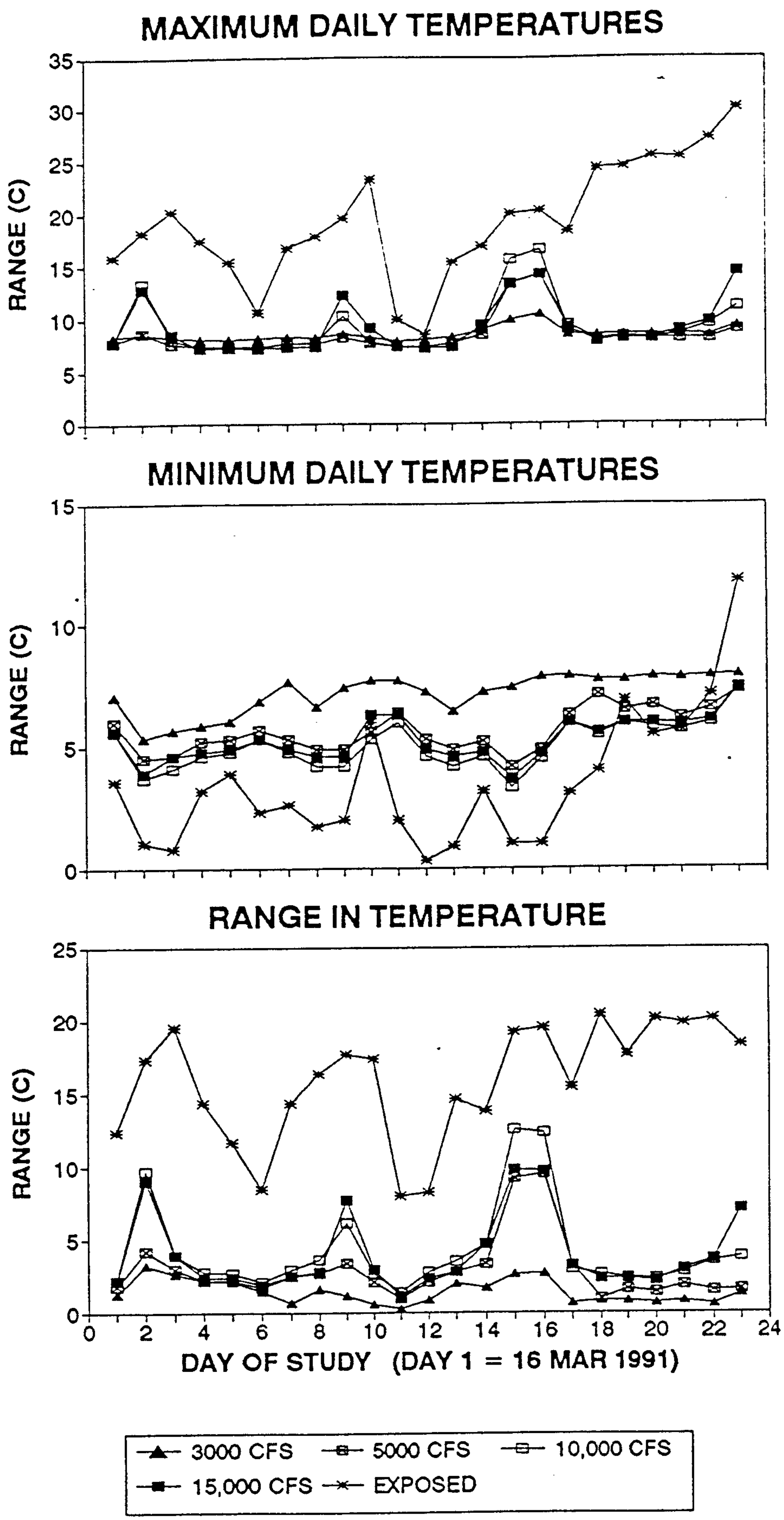


Figure 5. Daily maxima, minima and range for air and sediment temperatures, 16 March-7 April 1991, 9-mile research site, Lees Ferry.


MAXIMUM DAILY TEMPERATURES
RANGE (C)
MINIMUM DAILY TEMPERATURES
RANGE (C)
RANGE IN TEMPERATURE
RANGE (C)
DAY OF STUDY (DAY 1 = 16 MAR 1991)
3000 CFS
5000 CFS
10,000 CFS
15,000 CFS
EXPOSED

and maximum daily ranges in temperature of all sites, and the mean rate of change of temperature was least (Table 10) during the morning, when temperatures at all sites changed most rapidly (Figures 3-5).

Conditions at intermittently exposed sites were similar (Figures 3-5, Table 10). Temperatures were nearly identical at 10,000 and 15,000 cfs and slightly higher than at 5000 cfs. Average daily range was somewhat lower at 5000 cfs (2.9 C) than 10,000 or 15,000 cfs (4.2, 4.0, respectively), but minimum and maximum ranges were similar. Average rates of change were much higher for exposed sites than at 3000 cfs.

TOLERANCE TO EXPOSURE: LABORATORY EXPERIMENTS

Experiment I

Experiment I began on 17 October and ended on 2 November. The exposure treatments (0, 6 and 12 hrs per day) began on 19 November. Due to considerable and unpredicted escape of alevins from the Whitlock-Vibert boxes, we present data for hatching success only.

Hatching success was estimated as the number of eggs hatched, out of 25 initially placed in each Whitlock-Vibert box, by Day 9, as no additional hatching occurred in any treatment after Day 9 and all boxes were checked on Day 9 (Table 11). We performed an initial Analysis of Variance on from Day 9 using Cage, Exposure and Redd as factors, with Redd nested within Exposure (small sample sizes precluded a complete design that examined Stream Tank effects in this analysis). There was no detectable effect of Redd ($F = 1.39$, 9 df, $p = 0.217$), so values for individual redds were combined for calculations of means in Table 11. As expected, there was a strong effect of exposure ($F = 12.43$, 2 df, $p << 0.001$); a Tukey multiple comparison test distinguished the 12 hour exposure, with somewhat lowered hatching success, from the 0 and 6 hour exposures, but did not

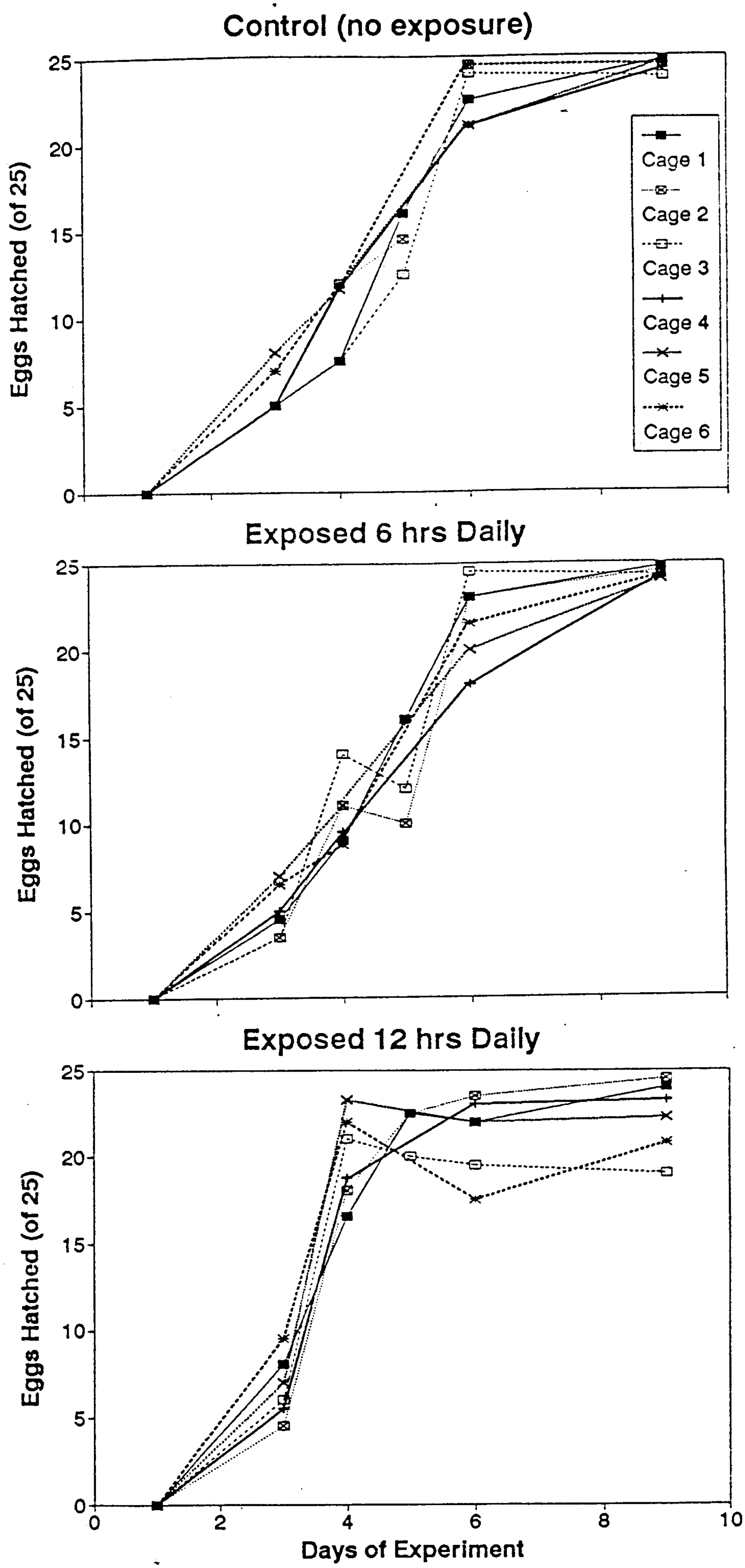
Table 11. Hatching success during laboratory Experiment I. Data are the average number of eggs that had hatched, out of 25 initially placed in the Whitlock-Vibert boxes, on Day 9. No additional hatching occurred after Day 9. Cages 1-3 and Cages 4-6 were in separate tanks, and Cages 1 and 4 were at the upstream end of their respective tanks, Cages 3 and 6 at the downstream end. [a] and [b] indicate two distinct groups identified by Tukey multiple range test ($p \leq 0.01$).

Exposure	Cage 1	Cage 2	Cage 3	Cage 4	Cage 5	Cage 6
12 hrs						
mean	24.00[A]	24.50[A]	19.00[B]	23.25[A]	22.25[B]	20.75[B]
sd	0.82	1.00	3.83	1.26	1.25	3.95
n	4	4	4	4	4	4
6 hrs						
mean	24.75[A]	24.50[A]	24.25[A]	24.25[A]	24.00[A]	24.25[A]
sd	0.50	0.58	0.96	0.96	0.82	0.96
n	4	4	4	4	4	4
0 hrs						
mean	24.75[A]	24.50[A]	23.75[A]	24.25[A]	24.67[A]	24.50[A]
sd	0.50	1.00	1.89	0.50	0.58	0.58
n	4	4	4	4	3	4

distinguish the latter two exposures ($p<0.0004$). There was also a significant effect of cage ($F = 3.02$, 5 df, $p = < 0.02$), with Cages 3-6 distinguished from Cages 1-2 (Tukey test, $p < 0.03$). A subsequent Analysis of Variance, with Tank, Exposure and Cage nested within Tank as factors, found no effect of Tank ($F = 0.276$, 1 df, $p = 0.60$).

Two other indicators of the effect of extended exposure on hatching success are evident. First, the variability in samples exposed for 12 hours was generally higher than for samples exposed for 0 or 6 hours per day (Table 11 and Figure 6). Second, eggs exposed for 12 hrs hatched earlier than those exposed for 0 or 6 hrs per day (Figure 6). Virtually all treatments had reached maximal hatch by Day 4 at 12 hrs exposure, while near-maximal hatch was not attained until Day 6 for other treatments.

Figure 6. Hatching success of rainbow trout eggs during Laboratory Experiment I. Data are the aggregate number of eggs that had hatched by a given day, out of 25 eggs originally placed in each box. Each point is the mean of values for 2 boxes. On each sampling day, only 2 of 4 boxes were scored from a given exposure and cage; this resulted in some cases where apparent hatching success was higher on one day then the next. Cages 4-6 were in Tank 1 and Cages 1-3 in Tank 2 (see Materials and Methods).



Control (no exposure)
Eggs Hatched (of 25)
0
5
10
15
20
25
Cage 1
Cage 2
Cage 3
Cage 4
Cage 5
Cage 6
Exposed 6 hrs Daily
Eggs Hatched (of 25)
0
5
10
15
20
25
Exposed 12 hrs Daily
Eggs Hatched (of 25)
0
5
10
15
20
25
0
2
4
6
8
10
Days of Experiment

Experiment II

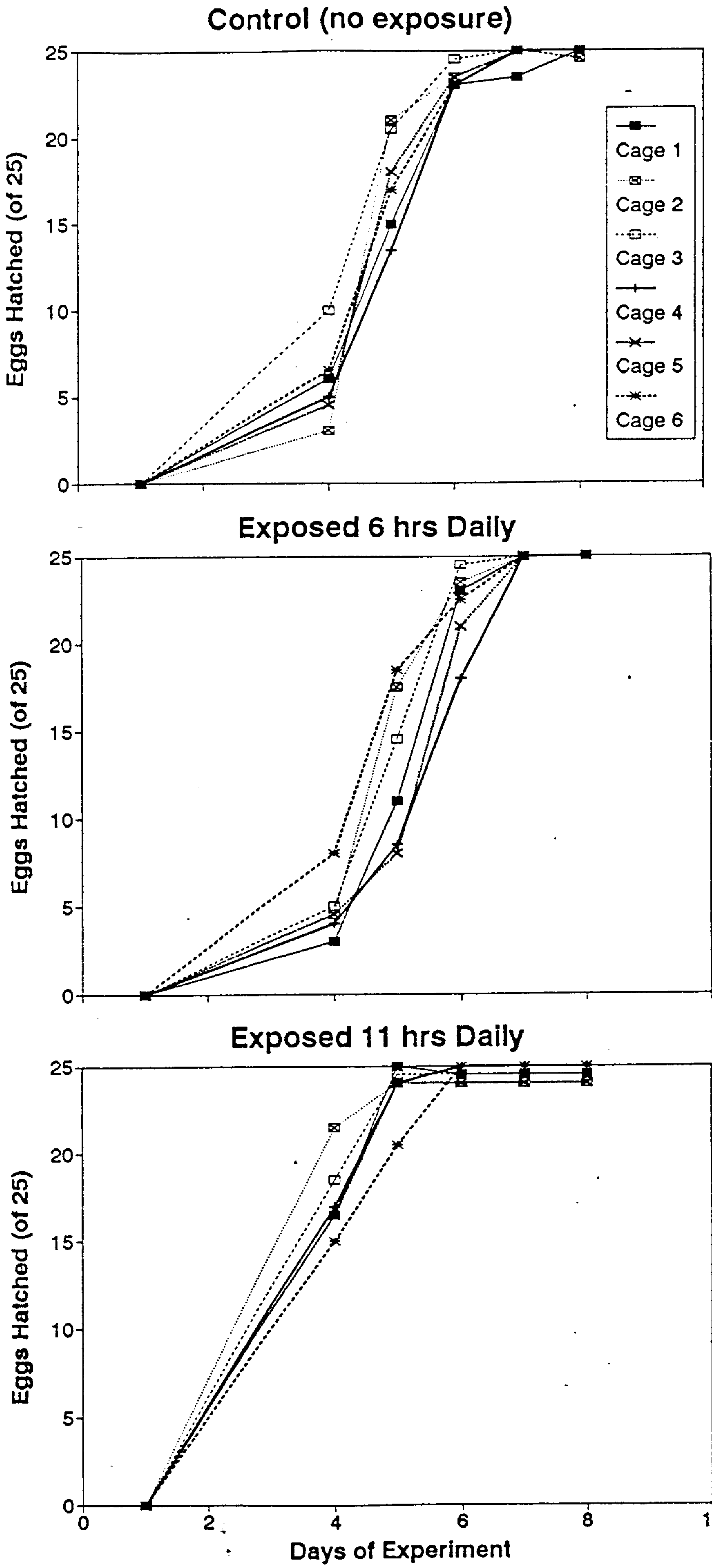
In Experiment II, fiberglass screen glued to the interior walls of the Whitlock-Vibert boxes eliminated escapism. Exposures were for 11, 6 and 0 hrs daily for 18 days.

Maximum hatching success was estimated as the number of eggs hatched by Days 8 (Redds 1 and 3) or 10 (Redds 2 and 4; Figure 7, Table 12). No additional hatching occurred after these days. Analysis of Variance found no effect on hatching of Cage ($F = 0.83$, 5 df, $p = 0.54$), Exposure ($F = 2.103$, 2 df, $p = 0.13$) or Redd nested within Exposure ($F = 0.965$, 9 df, $p = 0.48$). As in Experiment I, hatching was earlier in eggs exposed for 11 hours that in those exposed for 0 or 6 hours (Figure 7; ANOVA on data from Days 4-5, Exposure effect: $F = 52.84$, 2 df, $p < 0.0001$).

Table 12. Hatching success during laboratory Experiment II. Data are the average number of eggs that had hatched, out of 25 initially placed in the Whitlock-Vibert boxes, on Day 8 (Redds 1 and 3 checked) or Day 10 (Redds 2 and 4 checked). No additional hatching occurred after Days 8 or 10. Cages 1-3 and Cages 4-6 were in separate tanks, and Cages 1 and 4 were at the upstream end of their respective tanks, Cages 3 and 6 at the downstream end. There were no significant differences among means for any combination of cage or exposure.

Exposure	Cage 1	Cage 2	Cage 3	Cage 4	Cage 5	Cage 6
11 hrs						
mean	24.67	24.75	24.75	25.00	24.50	25.00
sd	0.58	0.50	0.50	0	1.00	0
n	3	4	4	4	4	4
6 hrs						
mean	25.00	25.00	25.00	25.00	25.00	25.00
sd	0	0	0	0	0	0
n	4	4	4	4	4	4
0 hrs						
mean	24.33	24.667	24.75	25.00	25.00	25.00
sd	1.15	0.58	0.50	0	0	0
n	3	3	4	4	4	4

Figure 7. Hatching success of rainbow trout eggs during Laboratory Experiment II. See Figure 6 for explanation.


Control (no exposure)
Eggs Hatched (of 25)
Cage 1
Cage 2
Cage 3
Cage 4
Cage 5
Cage 6
Exposed 6 hrs Daily
Eggs Hatched (of 25)
Exposed 11 hrs Daily
Eggs Hatched (of 25)
0
5
10
15
20
25
0
2
4
6
8
10
Days of Experiment

Exposure exerted a strong effect on sac fry during Experiment II (Figure 8). Controls (no exposure) experienced little mortality of sac fry over the 10-11 days of the experiment following attainment of maximum hatch on Days 7-8. Redds exposed for 6 hours per day also attained near-maximal hatching, but mortality began to increase by Days 10-12 and by Day 18 less than ~ 60% of the sac fry remained alive. In eggs exposed for 11 hours per day, mortality was initially variable in onset and magnitude, began prior to or at the time of maximal hatch, and resulted in death of all sac fry on or before Days 16-17.

Experiment III

Eggs for Experiment III were acquired at an earlier stage of development than those for the previous experiments, so hatching did not begin until after Day 10. Eggs and sac fry were exposed for 0, 3 and 15 hours in an experiment that lasted 28 days. As with Experiment II, fiberglass screen was glued to the inside of Whitlock-Vibert boxes to prevent escape of sac fry.

Hatching in Experiment III differed from the previous experiments in that maximum hatch was slightly lower (ca. 80-95%), at least for the two shorter periods of exposure, and almost no eggs hatched when exposed for 15 hours per day (Table 13, Figure 9). Analysis of Variance recognized the clear exposure effect ($F = 2542,78$, 2 df, $p < 0.0001$), with 15 hours exposure distinguished from 0 and 3 hours (Tukey test, $p < 0.0001$), but detected no effect of Cage ($F = 1.26$, 5 df, $p = 0.30$) or of Redd nested within Exposure ($F = 0.964$, 9 df, $p = 0.481$). As before, hatching began earlier, on Day 8, in eggs exposed for 15 hours per day, than in eggs exposed for 0 or 3 hours (first hatch recorded on Day 12).

Figure 8. Total and live sac fry recorded in Laboratory Experiment II for exposures of 0, 6 and 11 hours daily. As for plots of hatching success, each point represents the mean of two boxes and only 2 of 4 boxes were scored on a given day for each Cage and Exposure.

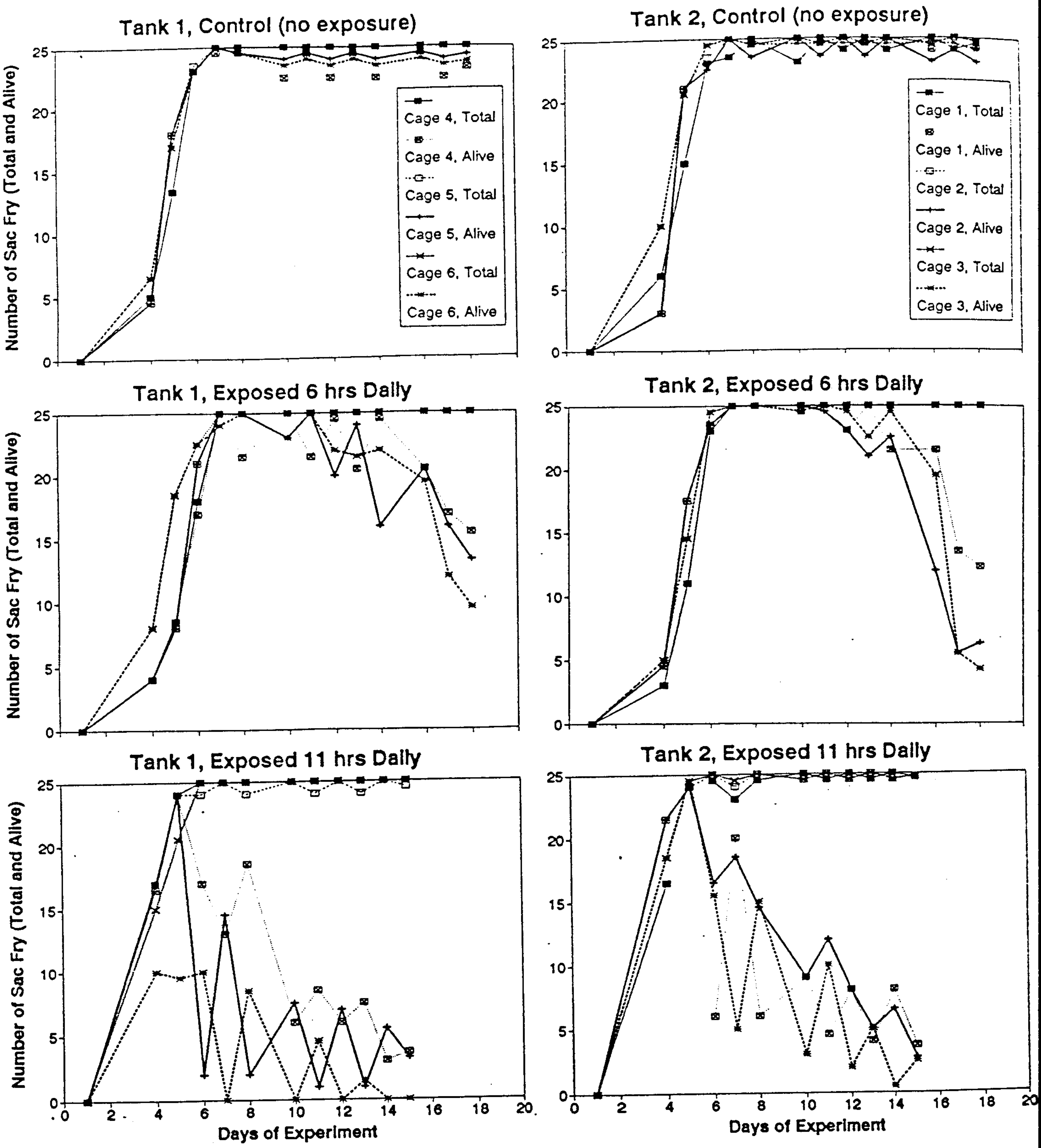
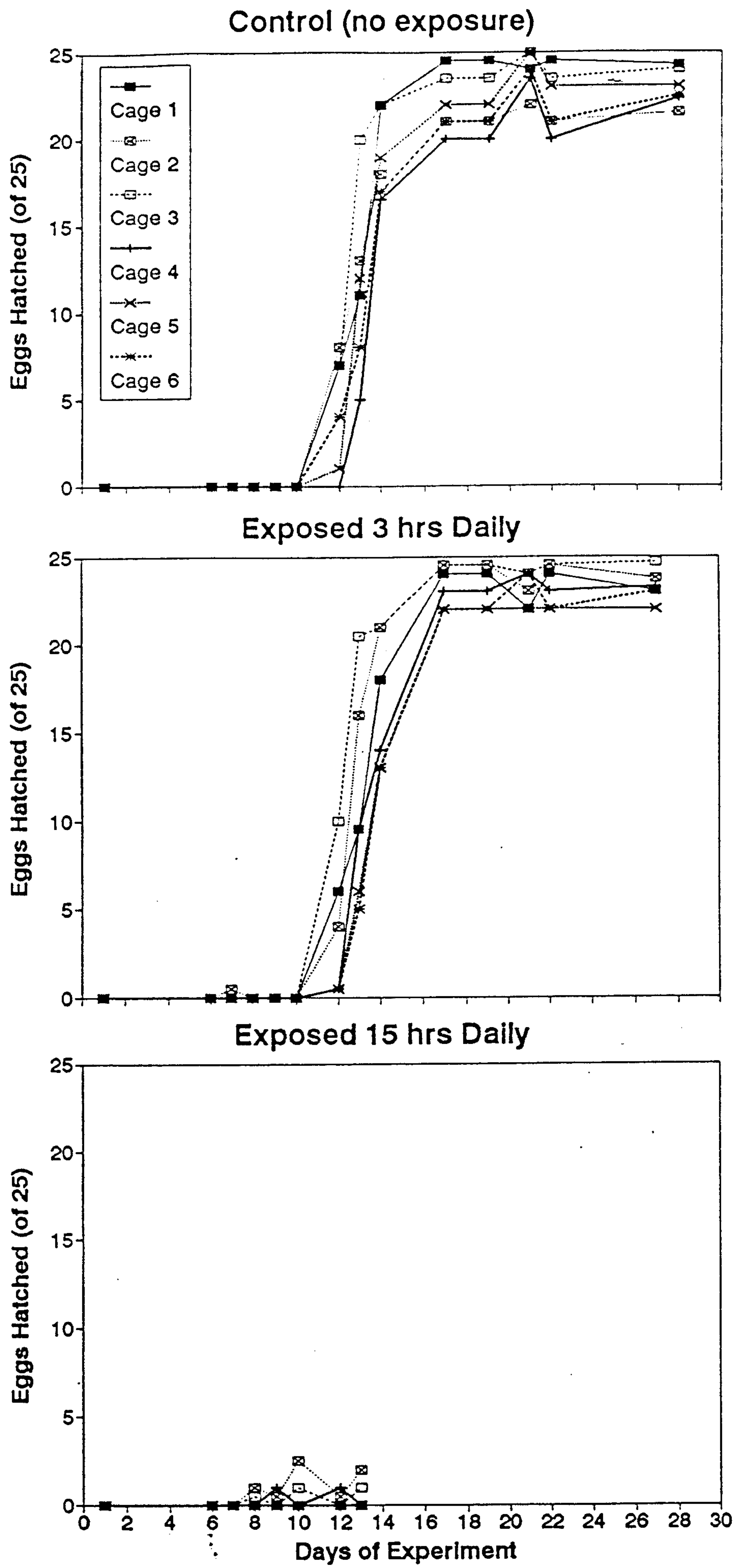

Tank 1, Control (no exposure)
Tank 2, Control (no exposure)
Cage 4, Total
Cage 4, Alive
Cage 5, Total
Cage 5, Alive
Cage 6, Total
Cage 6, Alive
Cage 1, Total
Cage 1, Alive
Cage 2, Total
Cage 2, Alive
Cage 3, Total
Cage 3, Alive
Tank 1, Exposed 6 hrs Daily
Tank 2, Exposed 6 hrs Daily
Tank 1, Exposed 11 hrs Daily
Tank 2, Exposed 11 hrs Daily
Number of Sac Fry (Total and Alive)
Days of Experiment
0
5
10
15
20
25
0
2
4
6
8
10
12
14
16
18
20

Table 13. Hatching success during laboratory Experiment III. Data are the average number of eggs that had hatched, out of 25 initially placed in the Whitlock-Vibert boxes, on Day 19 (Redds 1 and 3 checked) or Day 21 (Redds 2 and 4 checked) for exposures of 0 and 3 hours per day, or on Day 9 (Redds 2 and 4 checked) or Day 10 (Redds 1 and 3 checked) for an exposure of 15 hours per day. No additional hatching occurred after these particular days. Cages 1-3 and Cages 4-6 were in separate tanks, and Cages 1 and 4 were at the upstream end of their respective tanks, Cages 3 and 6 at the downstream end.

Exposure	Cage 1	Cage 2	Cage 3	Cage 4	Cage 5	Cage 6
15 hrs						
mean	0	1.50	0.50	0.50	0	0
sd	0	1.29	1.00	1.00	0	0
n	4	4	4	4	4	4
3 hrs						
mean	23.00	23.75	24.33	23.50	22.00	23.00
sd	1.41	1.26	0.58	1.00	1.00	1.41
n	4	4	3	4	3	4
0 hrs						
mean	24.25	21.50	24.00	22.33	23.00	22.50
sd	0.50	0.71	1.00	2.08	2.00	2.12
n	4	2	3	3	3	2

There was virtually no mortality of sac fry under exposure regimes of 0 and 3 hours per day (Figure 10). The exceptions to this were the three cages in Tank 2. During the last few days of the experiment, the aerator and cooling unit on Tank 2 malfunctioned, allowing temperatures to rise above the 11 C chosen for all experiments. This appears to have generated mortality only in the fry exposed for 3 hours per day, with no effect on the Control fry (all eggs and fry exposed for 15 hours were dead by this time), suggesting that fry exposed for even a short time were susceptible to any additional stress. The few fry that hatched under 15 hours of exposure per day were dead by Days 14-17.

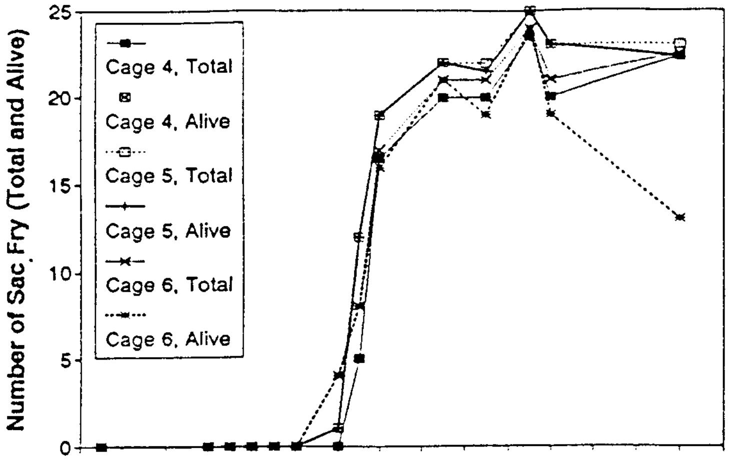
Figure 9. Hatching success of rainbow trout eggs during Laboratory Experiment III. All hatching that occurred during this experiment under 15 hours of exposure had been completed by Days 12-13. No viable eggs remained on subsequent days. See Figure 6 for additional explanation.



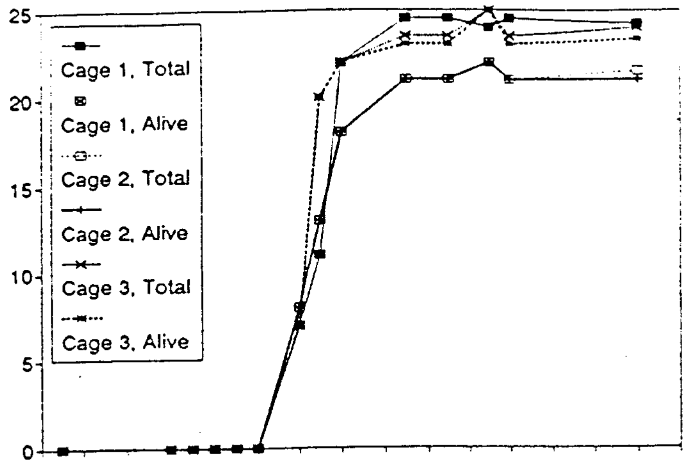
Control (no exposure)
Cage 1
Cage 2
Cage 3
Cage 4
Cage 5
Cage 6
Eggs Hatched (of 25)
Exposed 3 hrs Daily
Eggs Hatched (of 25)
Exposed 15 hrs Daily
Eggs Hatched (of 25)
Days of Experiment

Figure 10. Total and live sac fry recorded in Laboratory Experiment III for exposures of 0, 3 and 15 hours daily. Under 15 hours daily exposure, all sac fry were dead by Day 16. See Figure 8 for additional explanation.

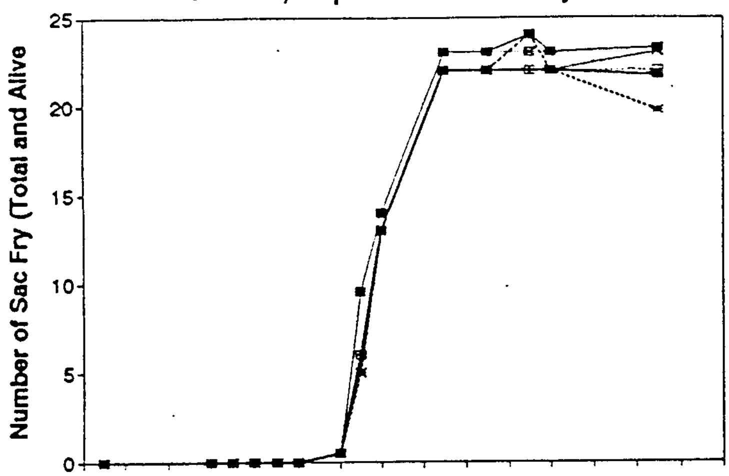
Tank 1, Control (no exposure)



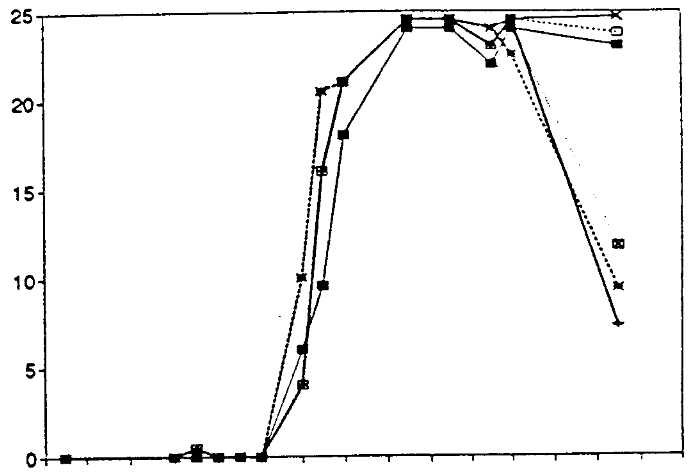
Tank 2, Control (no exposure)



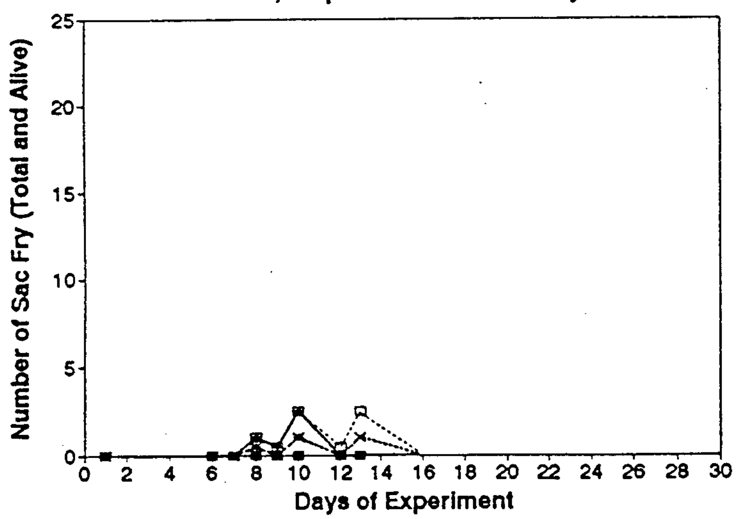
Tank 1, Exposed 3 hrs Daily



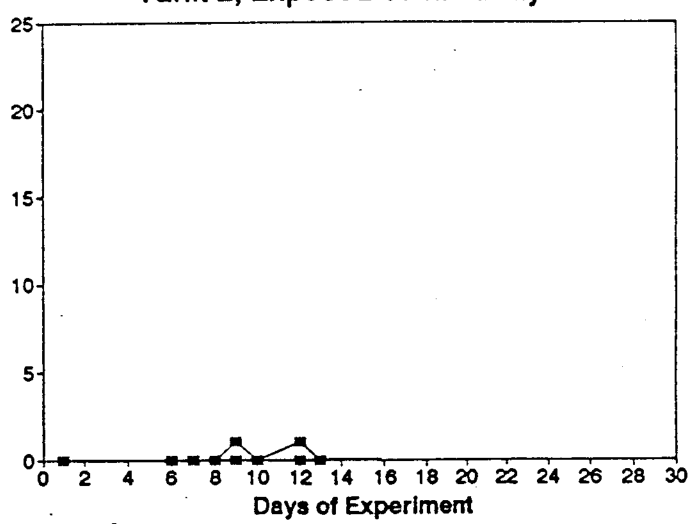
Tank 2, Exposed 3 hrs Daily



Tank 1, Exposed 15 hrs Daily



Tank 2, Exposed 15 hrs Daily



TOLERANCE TO EXPOSURE: FIELD EXPERIMENTS

At both sites, hatching began on or slightly before Day 13 (Figure 11) and was maximal by Day 22 (no eggs remained viable on Day 22; Table 14). With the exception of a low average for hatching (54.4%) on the 10,000 cfs water line at the 13.5 mile site, hatching success was high at both the 9 mile ($\geq$ 70%) and 13.5 mile ($\geq$ 86.0%) sites.

Analyses of Variance were performed on data for Day 22 at both sites (Table 14), using Flow, Hole and Box nested within Hole as factors. Although the ANOVA detected significant differences among flows ($F = 4.05$, 3 df, $p = 0.03$), a posthoc Tukey test found no significant differences. Neither Hole ($F = 0.23$, 2 df, $p = 0.80$) nor Box ($F = 0.76$, df 3, $p = 0.53$) exhibited an effect. A similar ANOVA for 13.5 mile data detected no significant effects of Flow ($F = 2.97$, 3 df, $p = 0.07$), Hole ($F = 1.69$, 2 df, $p = 0.22$) or Box ($F = 0.22$, 3 df, $p = 0.88$).

The low value for hatching at the 13.5 mile site was due to unusually low hatching (0 and 3 eggs of 25) in 2 of the 5 boxes; hatching was high in the other boxes (21, 22 and 22 of 25). The boxes exhibiting low hatch were both from the same hole. If these two boxes were excluded from calculations of hatching success, 13.5 mile hatching success would meet or exceed 84%.

Given the lack of a Box and Hole effect in previous ANOVA's, we pooled these data for a third ANOVA using Bar (9 and 13.5 Mile) and Flow as factors (Table 14). There were no effects of either Bar ($F = 0.05$, 1 df, $p = 0.82$) or Flow ($F = 1.208$, 3 df, $p = 0.32$) on hatching success.

There was also no evidence that exposure for extended periods accelerated hatching (Figure 11). Only the 1000 cfs (control, no exposure) samples at the 9 mile site had higher hatching by Day 13.

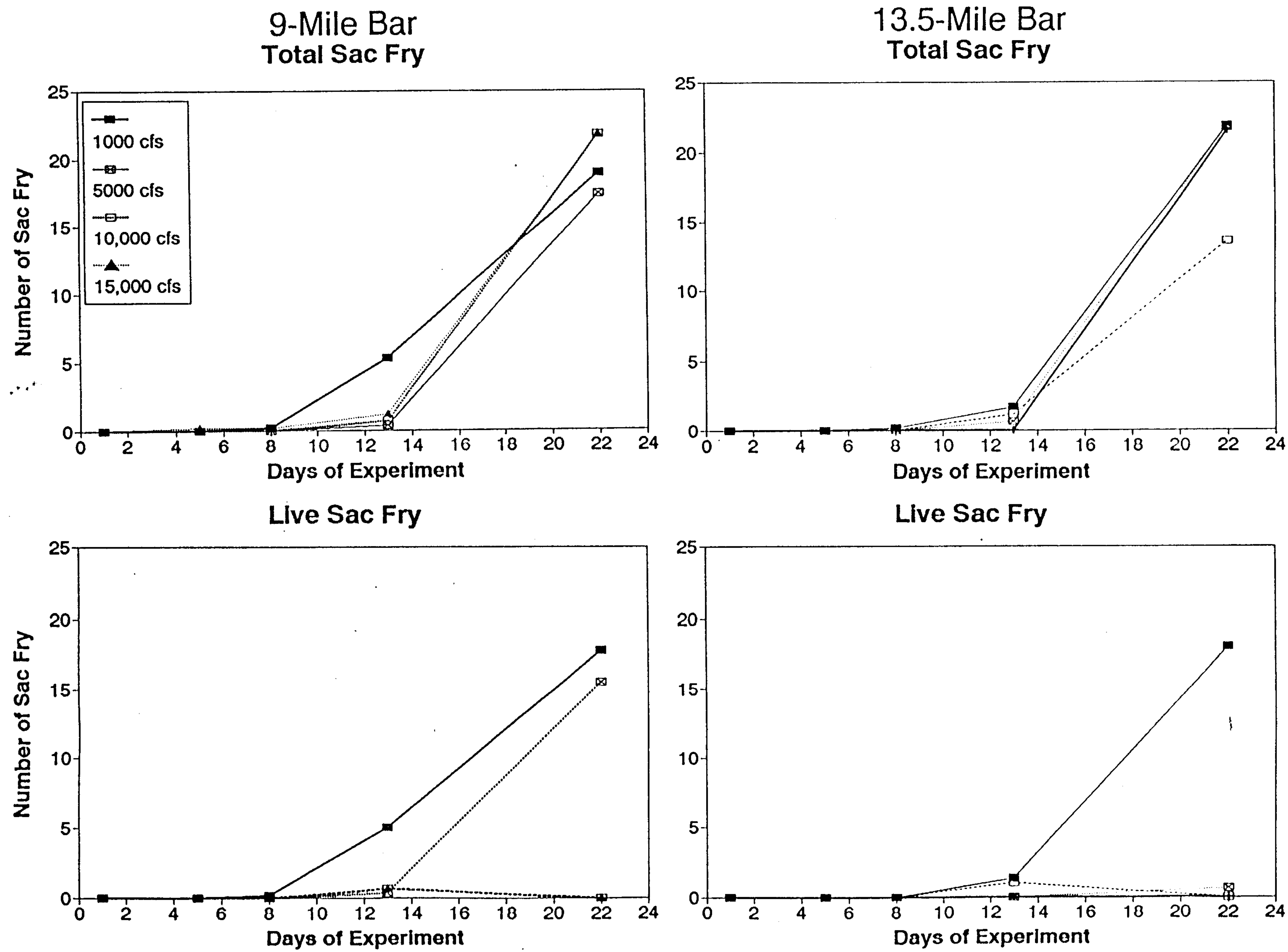
Table 14. Results of field experiments on hatching of eggs and survival of alevins. All data are for the final day (Day 22) of the experiment, and are the means number of dead eggs, total fry to hatch (hatching success), and number of surviving fry out of a total of 25 possible.

Water Line		9-Mile Site Dead Eggs	Total Fry	Live Fry	13.5 Mile Site Dead Eggs	Total Fry	Live Fry
15.000	x	3.17	21.8	0	3.5	21.5	0
	sd	0.8	0.8	0	0.6	0.6	0
	n	6	6	6	6	6	6
10,000	x	3.2	21.8	0	11.4	13.6	0
	sd	1.5	1.5	0	11.1	11.1	0
	n	6	6	6	5	5	5
5000	x	7.5	17.5	15.5	3.2	21.8	0.7
	sd	3.5	3.5	3.3	1.2	1.2	0.8
	n	6	6	6	6	6	6
1000	x	5.25	19.0	17.8	3.2	21.8	18.0
	sd	3.2	3.2	3.0	2.0	2.0	2.8
	n	4	4	4	6	6	6

		Both Sites Dead Eggs	Total Fry	Live Fry
15.000	x	3.3	21.7	0
	sd	0.7	0.7	0
10,000	x	6.9	18.1	0
	sd	8.3	8.3	0
5000	x	5.3	19.7	8.1
	sd	3.4	3.4	8.1
1000	x	4.0	20.7	17.9
	sd	2.6	2.8	2.7

Unlike the weak or absent effects of exposure on hatching of eggs, exposure exerted a strong effect on survival of sac fry (Figure 11; Table 14). At the 9 mile site, survival was high along both the 1000 cfs and 5000 cfs water lines, consistent with

Figure 11. Hatching success (total number of sac fry recorded) and mortality of sac fry during field experiments at 9- and 13.5-mile research sites, Lees Ferry, 16 March-7 April 1990. Approximate hours of exposure for each water line were: 0 hrs @ 1000 cfs; 6 hrs @ 5000 cfs; 10 hrs @ 10,000 cfs; $\geq$ 15 hrs @ 15,000 cfs.



9-Mile Bar
Total Sac Fry
13.5-Mile Bar
Total Sac Fry
Live Sac Fry
Live Sac Fry
Number of Sac Fry
Days of Experiment
1000 cfs
5000 cfs
10,000 cfs
15,000 cfs
0
2
4
6
8
10
12
14
16
18
20
22
24
0
5
10
15
20
25

experimental findings that exposures of $\leq$ 6 hrs per day had little effect on survival if additional stress were not imposed. Extended exposure (10,000 cfs ~ 10 hrs per day, 15,000 cfs ~ 15 hrs per day) produced total mortality by Day 22. An ANOVA similar to that described above detected no effect of Hole ($F = 0.41$, 2 df, $p = 0.67$) or Box nested within Hole ($F = 0.24$, 3 df, $p = 0.87$), but there was a strong effect of Flow ($F = 85.5$, 3 df, $p < 0.001$) and a posthoc Tukey test distinguished 1000-5000 cfs data from 10,000-15,000 data at the $p < 0.001$ level.

The pattern differed somewhat at the 13.5 mile site. There, all exposures produced virtually complete mortality by Day 22 (Figure 11; Table 14). Again, no effects of Hole ($F = 1.14$, 2 df, $p = 0.35$) or Box nested within Hole ($F = 1.04$, 3 df, $p = 0.41$) were evident, but there was a strong effect of Flow ($F = 210.61$, 3 df, $p << 0.001$). A posthoc Tukey test distinguished Control (1000 cfs) data from all exposures $p < 0.05$).

As with hatching data, Boxes and Holes were pooled for an ANOVA examining effects of Bar and Flow. Both Bar ($F = 11.346$, 1 df, $p = 0.002$) and Flow ($F = 52.26$, 3 df, $p << 0.001$) exerted strong effects. A Tukey test distinguished 3 groups based on Flow: 1000 cfs, 5000 cfs, and 10,000-15,000 cfs.

HABITAT AVAILABLE TO FRY

Gravel and cobble dominated substrata 1-5 m from the 5000 water line at both the 9 and 13.5 mile sites, consistent with these locations being swept by strong currents at high discharge. Along the 20,000 cfs water line at the 13.5 mile site, gravel and cobble again prevailed. In contrast, sandy sediments with rooted macrophytes characterized the substrata 0-5 m from the 20,000 cfs water line at the 9 mile site.

With one exception (13.5 mile, Transect C, 5000 cfs), depth and slope were less at the 9 mile site than at the 13.5 mile site (Figure 12). In general, recently emerged salmonid fry tend to occupy depths <25-30 cm, although they have been reported from water up to at least 85 cm in depth. At the 9 mile site, water < ~ 30 cm in depth was available 0-3 m from shore at high water (20,000 cfs) and 0-5 m at low water. Again with one exception (13.5 mile, Transect C, 5000 cfs), at 13.5 mile water < ~ 30 cm did not occur beyond 3 m from shore.

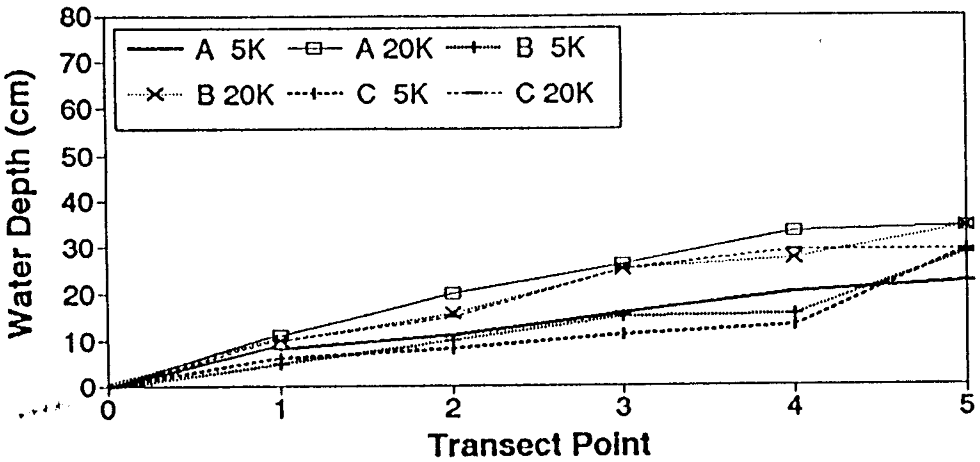
The 9 mile and 13.5 mile sites differed greatly in measured current velocities. At the 9 mile site, currents rarely exceeded 0 $cm \cdot sec^{-1}$, regardless of river discharge. In fact, no currents >0 $cm \cdot sec^{-1}$ were ever recorded along the bottom (n = 60: 2 sampling periods x 2 discharges x 3 transects x 5 sampling points), and in 13 of 60 samples where measurable current was detected, the current never exceeded 10 $cm \cdot sec^{-1}$.

Current velocities from the 13.5 mile site (Table 15) were higher than those at the 9 mile site and exhibited several distinct patterns. First, at virtually all sampling points, velocities declined from surface to bottom. Second, velocities increased from shore toward the center of the river. Third, tolerable velocities (we consider velocities < 25 $cm \cdot sec^{-1}$ to be the maximum tolerable for recently emerged fry; see literature review) extend farther from shore during periods of low discharge (5000 cfs) than periods of high discharge. Fourth, and corollary to the first pattern, tolerable velocities extended farthest from shore near the bottom and the least distance from shore at the surface.

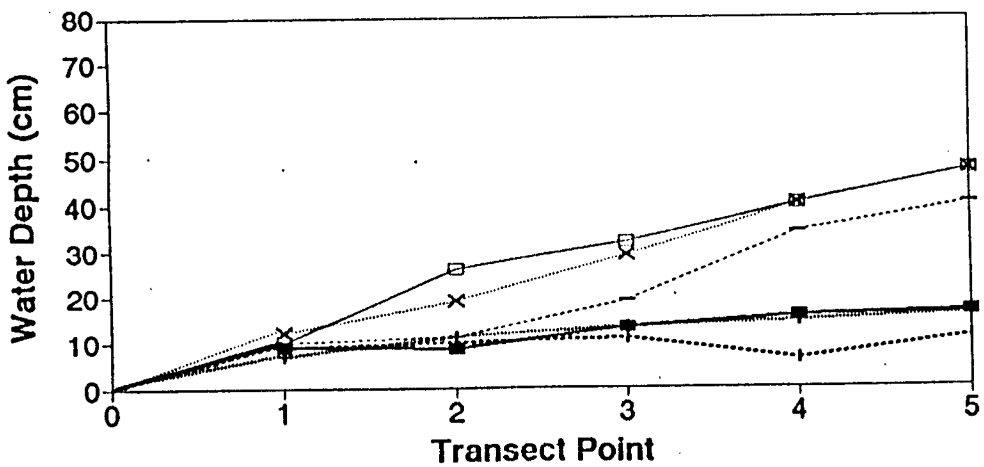
Figure 12. Depth profiles for transects at 5000 and 20,000 cfs water lines, 9- and 13.5-mile research sites, November 1991 and January 1992. Bold lines represent the 5000 cfs data in all plots. Water line was at Transect Point 0, with Points 1-5 at 1 m intervals toward the center of the river.

9 Mile Site

November 1991

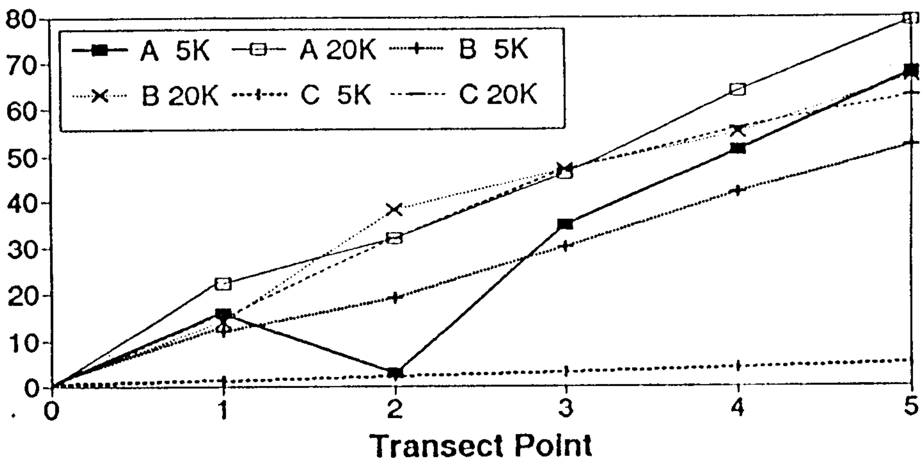


January 1992



13.5 Mile Site

November 1991



January 1992

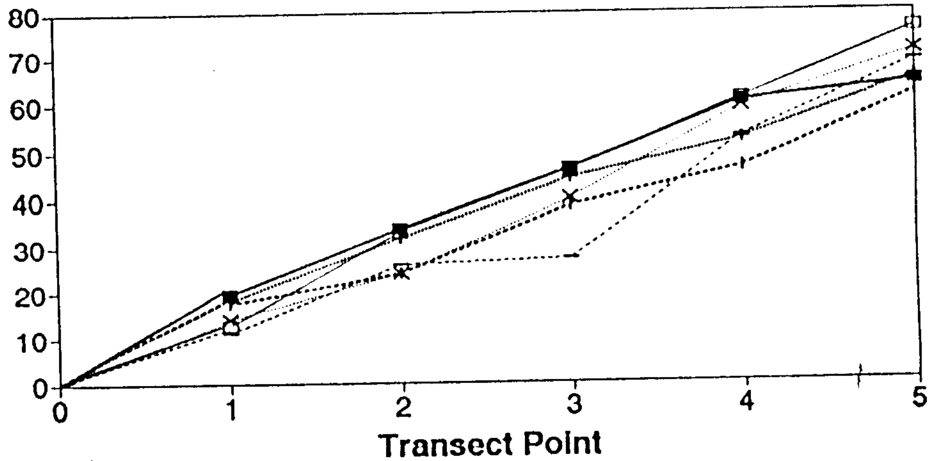


Table 15. Water velocities at surface, midpoint and bottom of water column at points along three transects from 5000 cfs and 20,000 cfs water lines, 13.5 mile site, during November 1991 and January 1992. Points were at 1 m intervals along a line perpendicular to the water's edge. Transects and sampling points are identical to those for which depth data are plotted in Figure 12. N = 3 for all means and standard deviations. **BOLD** type indicates velocities <25 cm•sec^{-1}, the velocity we consider to be the maximum tolerable for recently emerged fry (see Review of Literature).

NOVEMBER 1991

VELOCITY (cm per second)

5000 CFS						
Surface	x	**2.7**	**16.3**	**19.0**	27.3	33.7
	sd	2.5	7.6	4.2	5.9	2.9
	range	0-5	11-25	16-27	23-34	32-37
Midpoint	x	**2.3**	**9.0**	**19.3**	**23.7**	29.7
	sd	2.1	2.6	1.5	5.0	2.1
	range	0-4	6-11	18-21	19-29	28-32
Bottom	x	**0.3**	**4.3**	**13.3**	**11.3**	**13.0**
	sd	0.6	2.1	4.5	4.6	7.0
	range	0-1	2-6	9-18	6-14	5-18
20,000 CFS						
Surface	x	**12.7**	34.3	39.5	50.7	55.3
	sd	6.7	10.0	3.5	4.0	4.5
	range	7-20	24-44	37-42	47-55	51-60
Midpoint	x	**11.3**	27.7	40.3	47.0	50.0
	sd	4.5	5.7	6.0	2.6	7.0
	range	7-16	23-34	34-46	45-50	45-58
Bottom	x	**11.0**	**19.3**	30.7	27.0	32.3
	sd	4.0	3.5	4.0	10.6	8.0
	range	7-15	16-23	29-35	15-35	24-40

Table 15. (continued)

JANUARY 1992

VELOCITY (cm per second)

5000 CFS

Surface	x	<u>8.0</u>	26.3	28.5	38.3	45.7
	sd	3.6	6.7	4.9	4.2	4.0
	range	4-11	22-34	25-32	35-43	42-50
Midpoint	x	<u>6.7</u>	<u>22.3</u>	<u>23.7</u>	35.3	40.7
	sd	3.2	3.8	4.0	3.8	3.8
	range	3-9	18-25	20-28	31-38	38-45
Bottom	x	<u>4.3</u>	<u>9.3</u>	<u>13.3</u>	<u>19.0</u>	<u>19.0</u>
	sd	3.1	4.7	5.5	1.0	6.1
	range	1-7	4-13	8-19	18-20	15-26

20,000 CFS

Surface	x	<u>6.0</u>	27.3	33.0	50.0	59.0
	sd	3.6	11.4	1.4	4.0	3.5
	range	2-9	18-40	32-34	46-54	57-63
Midpoint	x	<u>6.0</u>	<u>18.0</u>	30.3	45.7	50.0
	sd	3.6	4.4	0.6	2.5	4.0
	range	2-9	15-23	30-31	43-48	46-54
Bottom	x	<u>6.0</u>	<u>12.3</u>	<u>17.0</u>	26.3	29.0
	sd	3.6	5.1	5.6	2.1	7.5
	range	2-9	8-18	11-22	24-28	21-36

ABILITY OF YOUNG FISH TO HOLD POSITION

Initial collecting efforts sampled sandy substrata with submerged vegetation and woody debris, and produced 33 marked fry and 1 naturally spawned fry. Many additional marked fry were also observed adjacent to partially submerged vegetation several meters offshore of the water line, but were out of reach of the sampling gear. Seine hauls upstream and downstream of the release site produced 1 marked fish downstream.

The morning collections at low flow (5000-7000 cfs) were over cobble-gravel habitat. No released fry were captured in seine hauls, but electroshocking (194 seconds) produced 2 marked fry and 2 natural fry. Several other fry were observed but not captured, and no large groups of fry similar to those observed the previous evening were observed.

Seine hauls repeated at 1300 hrs (discharge ~ 20,000 cfs) captured no released or naturally spawned fry.

DISCUSSION

POTENTIAL SPAWNING GRAVELS

According to Crisp and Carling (1989) and Kondolf et al. (1989), the gravel sizes found at both study sites fall into the suitable/used category for spawning by rainbow trout. The large contribution of fine particles (particularly <0.63 cm) would be reduced significantly by the actions of females as they dig redds (see review), and should result in improved water flow through the redds.

Due to their strong prevalence in sediment samples and the fact that smaller sediment categories would be washed out to varying degrees as females prepared redds, we selected the 2.75-4.85 particle size for all subsequent laboratory and field experiments. This insured both consistency among experimental treatments and the best possible match of conditions in redds at Lees Ferry.

MOISTURE CONTENT OF SEDIMENTS

The 9% moisture content determined in our study exceeds the 4% suggested by Reiser and White (1983) as minimal for normal hatching. Our estimates should be viewed as likely underestimates, since samples were air dried in shaded conditions and with only gently circulating air. Paradoxically, sediments lost additional moisture after already being exposed for many hours in the field. This is almost certainly due to release of moisture from sediments previously below the surface, and suggests that drying of subsurface materials would take a much longer time than periods of exposure normally encountered due to fluctuating water levels at Lees Ferry.

Laboratory experiments bear this out. First, maximal water loss was experienced in only 3-6 hours, suggesting that even short exposure will lead to drying of surface sediments. Second, in mixed or small-medium sized sediments (<2.8 cm), losses never reached those seen in field collected samples spread to air dry in a shaded room. Retention in the cloth bags and higher ambient humidity may have reduced rates of water loss and amounts lost. Nonetheless, we believe that the failure of recently-wetted mixed sediments, similar to those found at Lees Ferry, to lose the quantities of water expected is due to the buffering effects of drying surface sediments on loss from subsurface materials. We have, therefore, no information to suggest that subsurface moisture is insufficient to allow hatching of eggs.

We also cannot evaluate the direct effects on alevin survival of reduced moisture content during exposure. Alevins differ in that they have a much greater surface/volume ratio and more delicate surface covering than do eggs.

SEDIMENT TEMPERATURES

Air and sediment temperatures exhibited similar patterns in daily change, but even relatively short exposure (~ 6 hrs) caused considerable increases in both range and variation of temperature in sediments. As expected, daily fluctuations were slightest where immersion was essentially continuous, and the range in temperature at 3000 cfs for the study period (5.4 to 10.5 C) was well within tolerance limits for normal development of trout eggs and alevins.

Average rates of change in temperature were much higher for intermittently exposed sites than at 3000 cfs. Although we cannot evaluate the potential stress on developing fish that such rates of change might cause, these rates of change (0.38-0.56 C degrees$\cdot$hr^{-1}) are far less than those suggested for thermal tolerance studies (0.3-1.0 C degrees$\cdot$hr^{-1}; Wedemeyer et al. 1990).

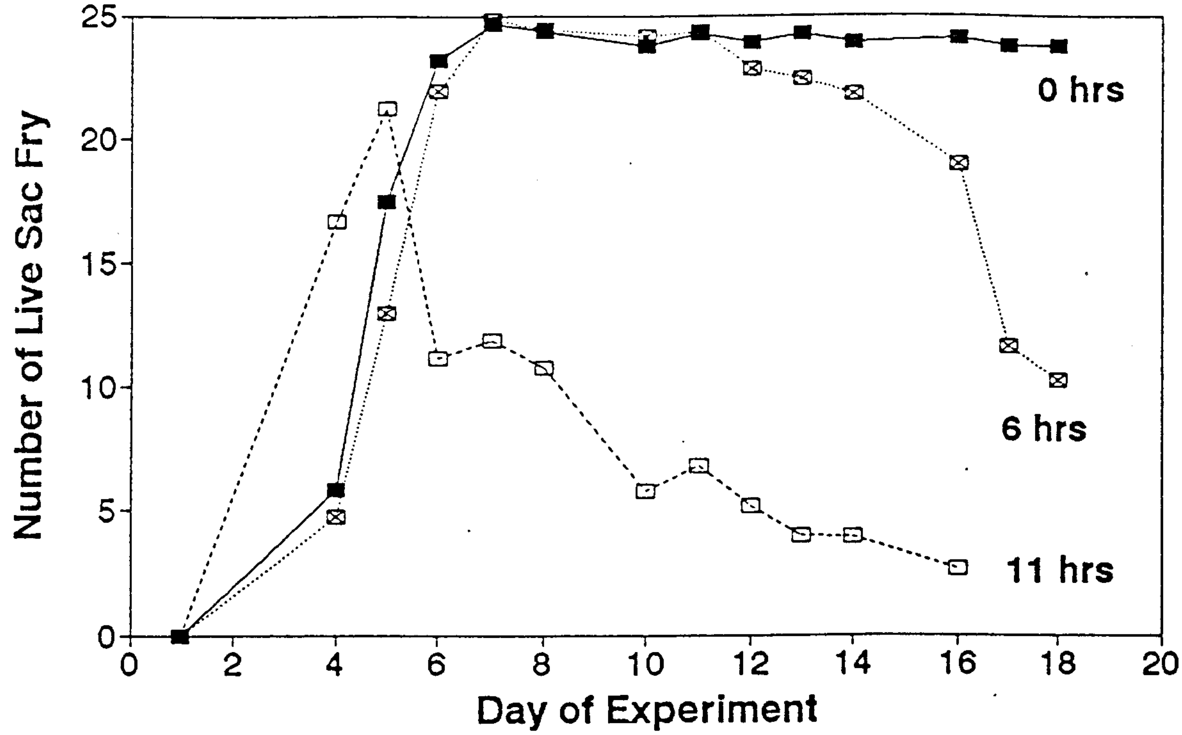
Conditions over the course of the study may reflect greater cause for alarm than do analyses of fluctuations within days. Minimum daily temperatures recorded during the study period were within the range known to support normal development. In contrast, on 3-4 occasions, maximum daily temperatures reached or exceeded the 12-15 C level that reduces hatching success or increases mortality in various salmonids. Accompanying these high temperatures were very high ranges in daily temperature, and both high maximum temperature and high temperature range in sediments correlated with periods of high air temperature. Thus, regular or extended exposure of sediments when daytime temperatures are high may increase the likelihood of damage to eggs buried well below the surface. At least at Lees Ferry during the study period, low temperatures did not pose a problem.

TOLERANCE TO EXPOSURE: LABORATORY EXPERIMENTS

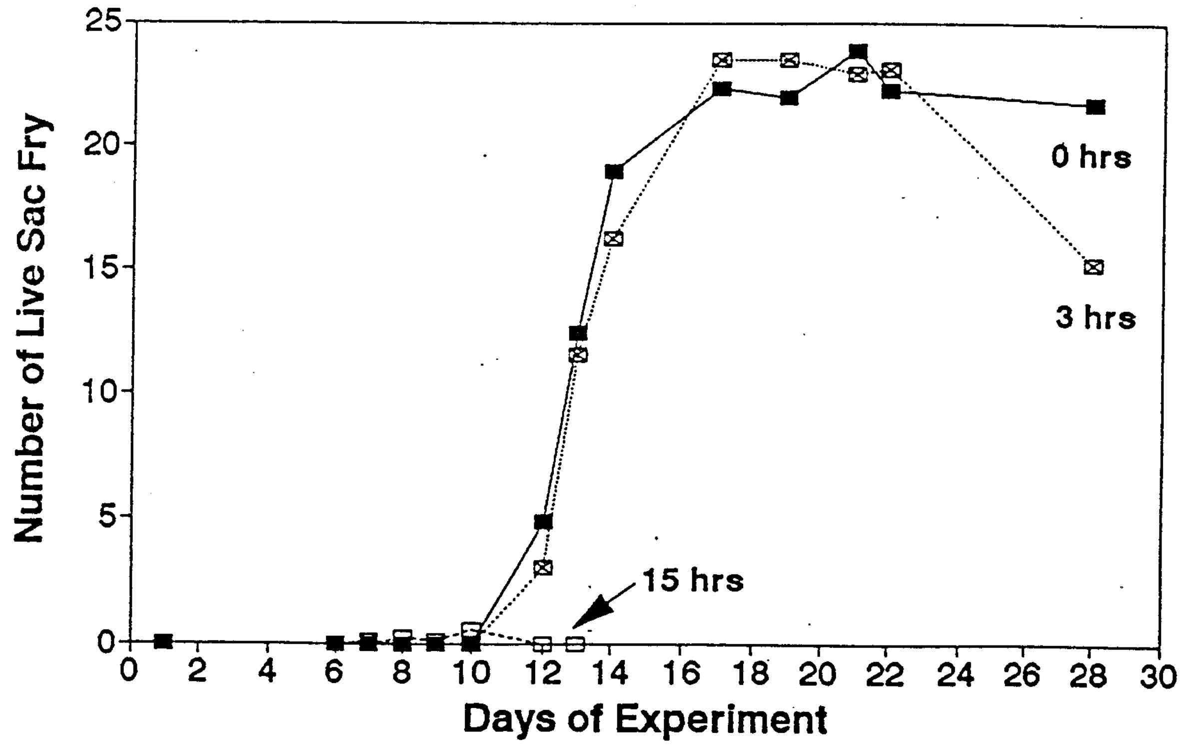
Under the rather moderate conditions of our laboratory experiments, exposures of $\leq$ 12 hours had little effect on hatching of eggs (Figure 13). Exposure of 15 hours per day, however, killed virtually all eggs. Reiser and White's (1981, 1983) findings that eggs suffered little mortality with continuous exposure for several weeks appears to contrast with our results. The difference is probably due to our technique of raising experimental

Figure 13. Summary of sac fry mortality under all exposures, showing graded levels of mortality relative to duration of daily exposure and tendency for long exposure (12, 15 hours) to accelerate onset of mortality. Based on Laboratory Experiments II and III.

Experiment II - Living Sac Fry
Means of All Cages and Redds



Experiment III - Living Sac Fry
Means of All Cages and Redds



redds out of the water, unlike the approach of Reiser and White (1983) that involved dropping water levels to ~ 10 cm below the egg pockets. We suspect that moisture levels in our gravels were probably below those of Reiser and White (1983).

Extended exposure (12, 11 and 15 hours per day in Experiments I, II and III, respectively) also accelerated the time of hatching by ~ 2-4 days. This could have been due to an increase in developmental rate correlated with an increase in egg temperature (redd temperatures were not monitored), in turn due to longer exposure to the slightly higher room temperature (13-18 C), or to other physiological and behavioral responses caused by the additional stress.

Exposure generally increased mortality of sac fry. At 3 hours of exposure per day, fry survived for extended periods, generally paralleling the response of control fry. The accidental imposition of temperature stress in one tank late in the experiment immediately increased mortality in the 3-hr group but had no effect on the control group that was immersed in the same water. This is strong evidence that fry subject to even short exposures suffer physiological stress and increased sensitization to additional stressors. Proper evaluation of this phenomenon will require focussed study of fry mortality, development, growth, and performance at swim-up under conditions of short daily exposure combined with additional stressors.

Extent and rates of mortality increased with increases in exposure from 6 to 11 and 15 hours per day. Both Experiments II and III continued for approximately 2 weeks after maximal hatching; the time required for rainbow trout to develop from hatching to the free-swimming stage is approximately 3 weeks (P. Wheeler, Washington State University, personal communication) at our experimental temperature. At 11 and 15 hours of exposure, all fry were killed within the experimental period, indicating that these periods of exposure, even under mild environmental conditions, would destroy all fry. At 6 hours exposure per day (Experiment II), approximately 40% of the fry hatched and alive on Days 7-8 lived the additional 10 days to Day 18. Emergence as free-swimming fry could be expected by about Days 25-30. The slope of a regression line through mean daily counts of surviving sac fry (survivors = 48.06 - 2.02• [day of experiment]; Figure 13) from Day 10 (the last day when mortality was nil) to the end of the experiment, indicates that approximately 2 fry (8% of initial 25 fry) would die per day. Thus, if this rate of mortality continued, all fry exposed for 6 hours per day should die by Day 23, well before the time of expected free-swimming.

In addition to acceleration of hatching, extended exposure (11 and 15 hours per day) reduced the time between hatch and the onset of mortality. At moderate exposure (6 hours per day), maximal hatching was attained and fry survived for several days before they began to die. At 11 and 15 hours of exposure, fry began dying shortly after hatching.

TOLERANCE TO EXPOSURE: FIELD EXPERIMENTS

Hatching success in field experiments was similar to that observed in laboratory experiments. In the laboratory, daily exposures of up to 12 hours did not suppress hatching significantly. Hatching was similarly high in field tests at 1000 cfs (no exposure), 5000 cfs (~ 5 hours exposure per day), and 10,000 cfs (~ 10 hours). Exposure for 15 hours daily in the laboratory suppressed hatching greatly, however, in strong contrast to the lack of effect on hatching seen in field studies. This suggests that the laboratory tests were more stressful than field tests during March-April.

We suspect that the differences are due to higher temperatures experienced by eggs both when immersed and when exposed during laboratory studies. In the laboratory, eggs were immersed at 11 C and exposed to 13-18 C in air. Although detailed temperature records are lacking for conditions at Lees Ferry in 1990, temperature data exactly one year later (see section above) indicate that gravel temperatures at the 15,000 cfs level probably ranged 2-10 C. Cooler intragravel temperatures in the field were also probably responsible for the unexpected delays in hatching for eggs in the field.

There was also generally good agreement between expectations based on laboratory assessments of sac fry mortality and observed mortality in the field. Mortality was very low in Control (1000 cfs) Boxes, and was virtually complete in the field at those exposures where we had near complete mortality in the laboratory (10,000-15,000 cfs and 12-15 hrs per day, respectively).

Predictions and results were not entirely consistent for the 5000 cfs exposure in the field, however. At the 9 mile site, survival of sac fry along the 5000 cfs water line was consistently high, while mortality was virtually complete at the same Flow at the 13.5 mile site. The explanation for this difference may reside with the physical conditions at the two sites. The 9 mile site is relatively flat, while the 13.5 mile site has a much steeper slope (see following sections). We suspect that draining of water from sediments on the steeper slope is more rapid than on the slight slope, so that true exposure was probably much shorter at the 9 mile than at 13.5 mile site.

HABITAT AVAILABLE TO FRY

At steady river discharge of either 5000 or 20,000 cfs, depths and currents tolerable for newly emerged fry are available adjacent to shore. The extent of these tolerable conditions probably correlate with the number of fry that could be maintained in a particular area, as fry tend to be territorial.

Several factors suggest that positive statements about the availability of fry habitat must be tempered with caution. First, as noted above, characteristic depths and currents for areas where eggs are laid exceed those tolerable by fry, so that emerging fry encounter currents that almost certainly sweep them downstream from sites of their redds.

Second, fluctuating flows require that fry, if they are to remain in tolerable conditions, follow the water line closely. It is clear, however (see depth profiles in Figure 12), that slope along river shores is not constant and that localized and possibly short-term changes in flow will occur as water levels rise or fall. These changes may lead to compression of fish into reduced available space and social interactions that increase stress or drive some fish into intolerable habitat, flushing of fish downstream when highly localized intolerable currents are encountered, stranding in pools left in small channels cut off from flow, etc.

Third, tolerable habitat near the bottom may be insufficient if fry encounter intolerable currents as they swim to the surface to gulf air to fill their air bladders (see literature review).

Fourth, of our four sample sites (9 and 13.5 mile, each at 2 discharges), only the 9 mile site at 20,000 cfs discharge provided cover (in this case, rooted vegetation). All other sites were essentially clean, gravel-and-cobble substrata devoid of woody debris or vegetation. As recognized by others (Bjornn and Reiser 1991), cover and benefits of cover are difficult to quantify, but the amount of cover correlates positively with fish abundance in streams, avoidance of predators, and food availability.

Finally, our studies dealt with two rather expansive bars in a river where low-slope environments are quite limited. At this point, we have no estimates of the likelihood that small fish swept off these bars may regain shallow habitats with slow currents.

ABILITY OF YOUNG FISH TO HOLD POSITION

Fry appeared able to hold position under slightly rising and steady high flow conditions. However, fry were rare following a period of drastic reduction in discharge, and were completely absent from the release site following a complete cycle of fall and rise to discharge similar to release discharge.

Casual observations of recently emerged (naturally spawned, ~ 25 mm in length) fry at the release site in the early morning indicated that they remained within 1 m of the water's edge both at steady flow and as the water began to rise. Similar observations were made at other bars downstream of the release site.

On 17 July 1990, during a period of constant 5000 cfs flows, hundreds of fry gathered at the edges of beaches along gravel bars at 4 mile and 5 mile. These same sites were surveyed for fry 3 days later, after the water had risen and undergone normal fluctuations for a 24 hour period. Fewer than 6 fry were observed in the same areas following these fluctuations.

MANAGEMENT RECOMMENDATIONS

POTENTIAL SPAWNING GRAVELS

No recommendations.

MOISTURE CONTENT OF SEDIMENTS

Although moisture content appears sufficient to maintain eggs and support normal hatching, we cannot assess the impact of drying on sac fry. Under our experimental conditions, maximal drying occurred within 2-5 hrs of exposure. Loss of moisture from sediments in the field would be slower, but until data are available on this subject, we recommend that areas with large numbers of redds should be exposed < 3-5 hrs at a time.

SEDIMENT TEMPERATURES

During some months when rainbow trout characteristically spawn at Lees Ferry, there appears to be the potential for exceeding tolerable temperatures for normal development. This potential could be reduced by maintaining high flows to cover redds during midday to late afternoon or reducing fluctuations so that spawning sites are exposed for only short periods. Similar practices during extremely cold periods could reduce the chance that eggs and sac fry would be harmed by freezing.

TOLERANCE TO EXPOSURE

Reduced fluctuations in river discharge during periods of peak spawning activity could potentially have two positive effects. First, reduced fluctuations, particularly at relatively low discharge, could concentrate spawning activity in bands of potential spawning habitat that would be exposed for only short periods when larger fluctuations occurred. Second, reduced fluctuations should reduce time of exposure for all redds.

Mortality of alevins was virtually complete in both laboratory and field experiments at exposures of >10 hours daily. Mortality at $\sim$ 6 hours daily was high in laboratory experiments, but the impact of a similar period of exposure in the field appeared to depend on the physical structure of the gravel bars.

HABITAT AVAILABLE TO FRY; RETENTION OF FRY

Salmonid fry typically emerge from redds at night (Burgner 1991, and references therein). At Lees Ferry, habitat tolerable by fry is restricted to a narrow band of shallow, slow water along the shore; sparse but more extensive backwaters also occur in a few areas. Successful movement by fry from redds to shoreline would probably be enhanced by stabilization of discharge at night, and at levels necessary to cover most redds, during periods of emergence.

Although our data are no conclusive in this regard, stable flows at all times would probably enhance survival of fry that reached tolerable habitat along shore or in backwaters. Fluctuations increase the likelihood that fry are swept out of tolerable habitat or stranded.

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Appendix. List of common and scientific names of fishes referred to in this report.

Oncorhynchus mykiss	rainbow trout, steelhead
O. gorbuscha	pink salmon
O. keta	chum salmon
O. kisutch	coho salmon
O. nerka	sockeye salmon
O. tschawytscha	chinook salmon
Salmo salar	Atlantic salmon
S. trutta	brown trout
Salvelinus alpinus	Arctic charr
S. fontinalis	brook trout, brook charr
S. namaycush	lake trout