Downstream transport of Colorado squawfish larvae in the Green River drainage: temporal and spatial variation in abundance and relationships with juvenile recruitment

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EXECUTIVE SUMMARY

This study was initiated in 1990 and was part of the Five-Year Flaming Gorge Flow Recommendations Investigations, 1992-1996. It was designed to assess aspects of reproduction, recruitment, and status of Colorado squawfish in the Green and Yampa rivers. Colorado squawfish reproduced in early to mid-summer in the Green River basin. Initiation of reproduction by Colorado squawfish each year was generally associated with increasing water temperature and diminishing spring runoff. Earlier spawning was associated with earlier occurrence of peak runoff and warmer water temperatures.

No single variable accurately predicted when Colorado squawfish first reproduce among sites or years. Water temperature at initiation of reproduction ranged from 16.0 to 22.3°C in the lower Yampa River and was 19.8 to 23.0°C in the lower Green River. In the lower Yampa River, Colorado squawfish generally initiated reproduction a few days prior to or within a few days after mean daily water temperature exceeded 18°C. In contrast, Colorado squawfish in the lower Green River initiated reproduction after mean daily temperature exceeded 18°C for 13 to 39 days. Time of year and accumulated degree days were also reasonable predictors of initiation of reproduction by Colorado squawfish. Initiation of reproduction was not closely associated with days post-peak discharge.

Abundance of larvae was generally higher in the Yampa River than in the lower Green River, and varied widely on diel, spatial, intra-annual and inter-annual scales. High transport abundance of larvae associated with increased turbidity, discharge, and darkness may be due to several factors including loss of orientation. High transport abundance under those conditions may also be a behavioral response to avoid sight-feeding predators. Increased transport abundance during turbidity events may have been caused by increased sediment deposition in interstitial spaces in the substrate, a stress which may have motivated larvae to emerge and drift. Differences in transport abundance of larvae across years and the patterns of abundance within a year may be due to several factors including timing of arrival, condition, and number of reproducing adults at the spawning areas.

Transport abundance appeared to be associated with discharge only during extreme years. High discharge was negatively associated with transport abundance in both the lower Yampa River and the lower Green River while low discharge was negatively associated with transport abundance only at the Yampa River station. Low abundance during either low or high discharge years could be a consequence of low abundance of adults and low production of larvae at spawning areas, high mortality of eggs or larvae at spawning areas or during downstream transport, sampling error, or other factors.

High intra-annual recruitment variation of juvenile Colorado squawfish in both the lower and middle Green River, 1990-1996 was not usually the result of inadequate numbers of larvae produced from spawning areas. Instead, high annual recruitment variation may be a consequence of factors that differentially affect growth and survival of early life stages. Colorado squawfish seem well-adapted to the fluctuating environmental conditions with which they have evolved. Thus, physical factors may regulate recruitment of age-0 Colorado squawfish only in relatively rare instances. Understanding the relative importance of mechanisms regulating recruitment of Colorado squawfish, including effects of discharge, habitat availability, and non-native fishes predators, is critical to management and recovery of this species.

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KEY WORDS

Colorado squawfish, reproduction, larvae, drift, diel and spatial variation, otolith aging, recruitment, recovery.

INTRODUCTION

Understanding the role of biotic and abiotic factors that affect timing and success of reproduction is central to ecology because abundance of young individuals often drives recruitment dynamics of subsequent life stages (Roughgarden et al. 1988). Mechanisms of recruitment variation in animals such as fishes with multi-phase life cycles are particularly difficult to assess because larvae typically disperse, sometimes long distances, away from juveniles and adults and individuals in each life history phase are constrained by different factors. Moreover, most aquatic organisms with early life stages that disperse have highly variable recruitment because their high fecundity, coupled with small variations in regulating processes, cause large differences in survival and recruitment of larvae (Hjort 1914, Thorson 1950, Fogarty et al. 1991). Thus, factors that regulate distribution, abundance, size-structure, and survival of early life history stages are integrated into processes that structure recruitment (Thorson 1950, Gaines et al. 1985, Houde 1987, Miller et al. 1988, Underwood and Fairweather 1989, Johnston et al. 1995).

Most populations of endangered Colorado squawfish *Ptychocheilus lucius* of the Colorado River basin may be recruitment limited (Tyus 1991). In the Green River, where the largest remaining population occurs, annual estimated density of juveniles in fall (recruits) ranged from near zero to 75 fish/100 m^2 in backwater habitat (Tyus and Haines 1991). However, the relative effects of discharge regime, habitat alterations, introduced fishes, and annual abundance of Colorado squawfish larvae on recruitment of juveniles remain poorly understood.

This study was initiated in 1990 and was part of the Five-Year Flaming Gorge Flow Recommendations Investigations (FGFRI); specifically Element 1 (Reproduction) of the Systematic Data Collection and Research (SDCR) program. The SDCR was composed of four interrelated elements and was intended to assess effects of water regulation by Flaming Gorge Dam on annual reproduction and long-term recruitment of fishes in the Green River system. The four elements included 1) reproduction, 2) age-0 survival to fall (age-0 recruitment), 3) over-winter survival of young fish (age-1 recruitment), and 4) links between recruitment of young fish and recruitment to adult stocks. This study addresses the first two elements. Integrated studies under FGFRI (i.e., SDCR studies and hypotheses-testing studies, which were intended to aid in interpretation of SDCR results by addressing specific questions) will facilitate determination of factors affecting annual reproduction, abundance, and recruitment of Colorado squawfish in the Green River basin.

Data from this study will be used as part of an annual assessment of reproduction and recruitment of Colorado squawfish so that various hypotheses regarding the affects of modified operation of Flaming Gorge Dam can be evaluated. Information will facilitate assessment of relationships between reproductive success and annual flow regimes, and provide a relative measure of input of fish larvae into downstream nursery habitats. Specific objectives of this research were to:

1) Document timing, duration, and intensity of reproduction by Colorado squawfish as measured by capture of larvae drifting from the lower Yampa River (Yampa Canyon) and the lower Green River (Grey Canyon) spawning areas,

2) Determine the relative abundance of Colorado squawfish larvae transported from spawning areas into downstream nursery habitats in the middle Green River (Jensen-Ouray reach) and the lower Green River (Stillwater and Labyrinth canyons) in relation to environmental variables, and
3) Determine if abundance of larvae produced from spawning areas was related to abundance of juveniles in the fall.

Colorado squawfish natural history.--Although most recruitment studies on animals with ecologically and morphologically distinct life stages have been in marine systems (Thorson 1950, Roughgarden et al. 1988, Cushing 1995), freshwater animals with analogous life-history strategies exist. Potadromous Colorado squawfish, a piscivorous cyprinid endemic to the Colorado River basin, is an example. Adult Colorado squawfish attain a maximum length of about 1 m and may exceed 25 years of age (Tyus 1991, Osmundson et al. 1997). In the Green River basin of Colorado and Utah, adult Colorado squawfish migrate to one of two known high-gradient canyon reaches in early summer for spawning (Tyus 1990, Irving and Modde 1994). Spawning begins four to six weeks after peak spring runoff, when water temperatures exceed 16 to 18°C, and extends up to six weeks (Nesler et al. 1988, Tyus and Haines 1991). Embryos are deposited over cobble bars and develop in interstitial spaces for four to six d at temperatures of 18 to 26°C (Hamman 1981, Bestgen and Williams 1994). Following incubation, larvae hatch and are transported by river currents 40 to 200 km or more downstream to low-gradient reaches where they occupy shallow low-velocity backwaters at the channel margin until fall (Haynes et al. 1984, Haines and Tyus 1990, Tyus and Haines 1991).

Reduced distribution and abundance of Colorado squawfish throughout the Colorado River basin is likely due to both disruption of physical habitat and negative interactions with non-native fishes (Vanicek and Kramer 1969, Holden 1979, Carlson and Muth 1989, Stevens et al. 1995). Mainstem dams block migration routes, inundate riverine habitat, and modify natural discharge patterns and water temperatures in downstream reaches. Over 40 fish species have been introduced in the upper Colorado River basin (Carlson and Muth 1989), many of which may compete with, or prey upon, early life stages of Colorado squawfish.

STUDY AREA

The Green River basin drains portions of southern Wyoming, eastern Utah, and northwestern Colorado (Fig. 1) and the Green River is the largest tributary of the Colorado River. Yampa Canyon in the lower Yampa River (river kilometer [RK] 0-74), Whirlpool and Split Mountain canyons (RK 555-515) in the upper Green River, and Desolation and Gray canyons (RK 340-211) in the middle Green River have high gradient and mixed cobble and sand substrate. A valley reach in the middle Green River (RK 515-340) and Stillwater and Labyrinth canyons in the lower Green River (RK 211-0) have lower gradient and substrate dominated by sand and silt with small amounts of cobble. Discharge in the mainstem Green River upstream of the Yampa River has been regulated since 1963 by Flaming Gorge Dam. During 1964-1996, releases typically ranged from 22.6-130 m^3/s, but were sometimes higher because of spillway releases in high-water years (e.g. 1983, Tyus and Haines 1991). During the same period, discharge in downstream reaches of the Green River in spring and early summer was high and originated mostly in the Yampa River. In contrast, Green River discharge in late summer, fall, and winter was lower and dominated by releases from Flaming Gorge dam. Discharge in the highly variable and unregulated Yampa River was occasionally 566 m^3/s in spring but sometimes declined to < 2 m^3/s in late summer (U. S. Geological Survey records, gage 09251000). As a result of an agreement between dam operators and the U. S. Fish and Wildlife Service, releases from Flaming Gorge Dam since 1985 have maintained discharge of the Green River near Jensen at a minimum of 51 m^3/s $\pm$25% from July through September to maximize backwater habitat for age-0 Colorado squawfish (Pucherelli et al. 1990). During 1979-1995, mean July-August discharge of the middle Green River at Jensen, Utah (gauge # 09261000), and the lower Green River at Green River, Utah (gauge # 09315000), was highly correlated ($r = 0.99$) and discharge was higher downstream (mean = 141 m^3/s, SD = 108 m^3/s) than upstream (mean = 100 m^3/s, SD = 73 m^3/s) mainly because of discharge from the White River.

METHODS

Field collections--The three sampling sites for Colorado squawfish larvae were the Yampa River just upstream (RK 1) of its confluence with the Green River in Echo Park within Dinosaur National Monument (1990-1996), the Green River near Jensen, Utah (1990, 1994, and 1995), and the Green River about 15 km upstream of Green River, Utah (1991-1996). Sampling started in late-June to early-July each year, two to six weeks after peak spring discharge when daytime water temperature exceeded about 16°C (Nesler et al. 1988, Tyus and Haines 1991). Sampling continued for four to nine weeks after the first Colorado squawfish larvae were captured and ended when none were captured for three to five consecutive days, usually by mid-August.

Colorado squawfish larvae were sampled daily at dawn (ca. 0600 hr) with conical drift nets (0.15 m^2 mouth diameter, 4 m long, 560 μm mesh) set nearshore in water 30 to 40 cm deep. Three nets were set on each sampling occasion for up to 2 hr, but sampling stopped if debris load exceeded 3.8 L/sample. Water depth at which a white object disappeared from sight was recorded as a measure of water turbidity. General Oceanics flow meters (model 2030) suspended in each net mouth recorded water velocity during the net-set.

To evaluate whether dawn-nearshore-samples represented the abundance, age, and size of larvae transported downstream past sampling sites, additional diel and cross-channel sampling was conducted. Diel and cross-channel sampling was conducted at the Yampa River collection site in 1992 (9, 10, 13, 15, 17, 18, 23, 24, 25, 27, and 29 July). This sampling consisted of standard dawn-nearshore-samples supplemented with three dawn-samples collected at each of midchannel-surface and midchannel-bottom locations. Samples were also collected at those same locations at noon (1200 to 1400 hr), dusk (1900 to 2100 hr) and midnight (0000 to 0200) and resulted in 36 samples/d (3 locations x 4 times x 3 replicate samples). Samples could not be collected at all positions during all periods on 15 and 23 July, 1992. In addition to 1992 diel and cross-channel sampling, diel-only sampling was conducted on at least four but up to 14 occasions annually from 1992-1996. Each diel sampling occasion consisted of nearshore-samples collected at each of the four time periods (12 samples/d).

Samples were fixed immediately in 100% ethanol and fish were removed from debris within 4 hr and preserved in 100% ethanol. Rapid sample processing prevented fish from being stained by debris pigments. This protocol recovered 100% of a known number of larvae (range 9-10) from five experimental samples.

Laboratory procedures.--Colorado squawfish larvae (< 20 mm TL) captured in drift nets were measured to the nearest 0.1 mm TL. Ages of selected specimens collected in 1990-1992 were estimated by counting daily increments in otoliths. Counts of otolith increments, which were first formed at hatching, were estimated two to four separate times in the left sagitta or lapillus and averaged (see Bestgen and Bundy [1998]), for details on aging techniques). Otoliths from all but 9 of 2537 fish sampled in 1991-1992 were readable. Laboratory studies showed that ages of Colorado squawfish reared in fluctuating temperatures of 18, 22 and 26°C for up to 165 d post hatching were estimated without bias (Bestgen and Bundy 1998). Therefore, age underestimation of wild fish was discounted as a source of error.

Initiation of reproduction was estimated by subtracting the average age of larvae at capture (6 d, Bestgen 1997) and average incubation time of fertilized eggs at 18°C (6 d, Bestgen and Williams 1994) from the date that larvae were first captured in drift nets set in the lower Yampa River and the lower Green River. Date of cessation of reproduction was similarly estimated by subtracting 12 d from the date that the last larvae were captured at each sampling site. The first peak in reproductive activity was qualitatively determined by subtracting 12 d from the first substantial increase in capture of larvae in drift nets. Most temperature data for the Yampa River from 1990-1996 were recorded just upstream of the Green River with a continuously recording thermograph (G. Smith, pers. comm., U. S. Fish and Wildlife Service, Denver, Colorado). Lower Yampa River data were estimated in 1993 and 1994 by adding 2.1°C to temperature measurements from an upstream gauge at Government Bridge upstream of Maybell, Colorado. That value was the average difference between the two stations in the month of June in 1991, 1992, 1995, and 1996. Degree-day accumulation in the lower Yampa River was estimated from temperature data collected near Jensen, Utah because this was the most geographically proximate gauge with a full year of records. Most lower Green River temperature data were estimated by adding 2.3°C to temperature measurements from an upstream gauge at the Ouray National Wildlife Refuge (G. Smith, pers. comm.). That value was the average difference between the two stations in the month of June in 1992. All 1991 and 1995 temperature data and degree-day accumulation data for all years were from instantaneous records collected by the U.S. Geological Survey near the town of Green River, Utah. In general, we avoided use of data collected instantaneously at U.S. Geological Survey stations because those records often did not accurately reflect the average river conditions. Temperature values at first reproduction and at the first peak of reproduction were the average of the 5 d-period centered on the estimated date of interest. The 5-d mean temperature likely better reflected the average water temperature at initiation and first peak of reproduction than would measurements taken on a single date because of single day climatic anomalies and because of uncertainty (± 2.5 d) in estimates of hatch dates of larvae that were aged with otoliths (Bestgen and Bundy 1998). Days post-peak discharge was the number of days between the highest recorded daily average discharge during spring runoff and first reproduction.

Diel and cross-channel abundance of larvae.--Sampling bias may explain differences in seasonal or annual abundance of larvae captured in drift nets during summer. Mean abundance of Colorado squawfish larvae in samples collected during combined diel and cross-channel (1992 only) and diel-only (1992-1996) sampling was analyzed by general linear models (PROC GENMOD, SAS Institute, Inc. 1993). This analysis calculated maximum likelihood estimates of model parameters and was used to evaluate sampling bias. The discrete nature of the data (counts of larvae) and high occurrence of zeros or low capture values suggested a Poisson model. Log transformation of the response variable (i.e., log-link) ensured that the mean number of larvae predicted by the fitted model was positive (SAS Institute, Inc. 1993).

The independent variables used in the analyses of the diel and cross-channel sampling data was sample date, net position, time, turbidity, and their interactions. Independent variables for the diel-only sampling data were year of sampling, sample time, turbidity, and their interactions. Turbidity was included as an analysis variable because levels may vary widely in the Yampa River during summer and affect abundance of larvae in the drift. Sediment mobilized by runoff from afternoon thunderstorms usually increased water turbidity in the Yampa River by noon the following day. Therefore, samples collected on days when turbidity had increased due to a storm event the previous day were classed as turbid; samples collected when turbidity levels were stable or declining were classed as clear. The natural logarithm of the volume of water filtered by each net (m^3) was also included as a covariate (offset) in models to account for differences in sampling effort. Volume of water filtered by each net was estimated by multiplying sampling time by flow rate by area of the net frame. Model selection was by Akaike's Information Criterion (AIC; Akaike 1981) adjusted for over-dispersed data (QAIC;

Anderson et al. 1994) with final model goodness-of-fit estimated by the scaled deviance. Abundance of Colorado squawfish larvae in dawn nearshore samples and in samples collected at other times and positions was compared by inspecting the mean and standard error (SE) of catch rates.

Position, time, and date effects on age and TL of larvae captured.--Dawn-nearshore-samples may detect only a subset of the age- or length-classes of larvae drifting at other times or locations across the channel. Therefore, differences in age (d) and TL (mm) of Colorado squawfish captured in the 1992 diel and cross-channel sampling were analyzed by least-squares GLM (SAS Proc GLM) which had sampling time, net position, and their interaction as covariates. Differences in age and TL of larvae on 30 June, and 4, 13, 15, 24, and 27 July when large numbers were captured were evaluated by analysis of variance (ANOVA). Age and TL response variables were normally distributed. Means and SE's of ages and lengths of larvae in these analyses were also inspected to determine if statistically significant differences were biologically important.

Annual transport abundance.--Previous studies calculated number of larvae/volume of water sampled to obtain a density index for Colorado squawfish abundance. Although this was adequate for comparing densities of larvae from samples collected at different positions in the stream or during times of a single day, comparisons of abundance of larvae produced and transported downstream past the sampling station among years or rivers would be flawed because the percentage of the river sampled by drift nets was inversely correlated with river discharge. Hypothetically, if an identical number of larvae was present in the river at both a high and low discharge, density/sample would be higher at low discharge and lower at high discharge but actual numbers transported past the station would be the same. Therefore, transport abundance was estimated by dividing the number of larvae captured in drift net samples adjusted to an hourly rate (dawn samples only) by the estimated percent of total discharge that was sampled. Discharge for Yampa River transport abundance calculations for a given day were those recorded from a station about 75 RK upstream. Discharge for lower Green River transport abundance calculations were from the gage at Green River, Utah (station # 09315000) the day of sampling. Summing transport abundance values for all sampling days within each year allowed an estimate of the abundance of larvae transported past each station during the sampling period.

Fall recruitment of juveniles.-- Fall abundance of juvenile Colorado squawfish from 1990-1996 was measured by other biologists using the *Interagency Standardized Monitoring Program* (ISMP) protocol (McAda et al. 1996) in which the first two backwaters $\geq$ 30 m^2 in area and $\geq$ 30 cm deep encountered in each 8 RK reach of the middle (322-515 RK) and lower (0-193 RK) Green River were sampled with two non-overlapping hauls with a 4.6 m long seine (3.2 mm mesh). Area seined and number and TL of Colorado squawfish captured were recorded. Densities of Colorado squawfish were calculated per backwater sampled by dividing number of Colorado squawfish caught by area sampled. Densities were transformed ($\log_e$ [density + 1]), averaged over the reach, and back transformed to yield a geometric mean abundance (McAda et al. 1996). Abundance of Colorado squawfish juveniles in the lower Green River and middle Green River was plotted as a function of the transport abundance of larvae for the lower Green River (1991-1996) and lower Yampa River (1990-1996) spawning areas, respectively, to determine if there was a relationship between the number of larvae transported to nursery areas and recruitment in fall.

RESULTS

Timing of reproduction.-- Based on capture of recently-hatched larvae in drift nets, Colorado squawfish initiated reproduction in the lower Yampa and lower Green rivers in June in most years (Table 1). Colorado squawfish larvae first appeared in dawn drift net samples collected at the Yampa River sampling station in late-June to mid-July (Fig. 2). Drift-net sampling at the middle Green River station in 1990 suggested that larvae reached that station within 2 d after larvae were collected at the Yampa River station (Fig. 3). However, in 1994 larvae were collected at the middle Green station 5 d before they were detected at the upstream Yampa River station; larvae were rare in all samples collected at both sites that year and a few early larvae were likely missed at the Yampa River sampling station. Absence of larvae in the middle Green River 1995 samples until well after larvae were detected upstream was also probably due to low abundance river wide and sampling error caused by high discharge. In the lower Green River, larvae were detected in drift-net sampling earlier than in the Yampa River in low or moderate discharge years (Fig. 4). Detection of larvae at the downstream lower Green River station in 1995 was later than at the upstream Yampa River station probably because discharge was much higher and the few early larvae produced were simply missed by sampling gear.

No single variable was a reliable predictor of initiation of reproduction by Colorado squawfish among sites or within a site among years. Dates of initiation of reproduction by Colorado squawfish were within a relatively narrow time window from 13 June to 1 July in the Yampa River and from 9 June to 24 June the lower Green River, when the high flow year 1995 deleted. Reproduction occurred 4 to 11 d earlier in the lower Green River than in the Yampa River. Mean daily water temperatures at initiation of reproduction in the Yampa River ranged from 16.4 to 18.6°C if the low flow year 1994 (23.1°C) was excluded. Mean daily water temperatures at initiation of reproduction were higher in the lower Green River and ranged from 19.8 to 23°C.

The only other environmental variable that had a relationship with initiation of reproduction was accumulated degree days. During 1992 to 1996, Colorado squawfish in the Yampa River initiated reproduction after 1414 to 1646 degree days had accumulated, but accumulated degree days in 1990 and 1991 were substantially lower (794 to 1263). If the mean daily temperature was 18°C, even that relatively narrow range represents a time window of almost 13 d (232 degrees/18°C = 12.9 d). In the lower Green River, the average number of degree days prior to initiation of reproduction was higher than that for the Yampa River, and with the exception of 1995, had a relatively narrow range of 1513 to 1704. If the mean daily temperature was 18°C, that range of degree days represented a range in the time window of about 11 d (191 degrees/18°C = 10.6 d). Date of initiation of reproduction in the lower Green River in 1995 may have been underestimated because high flows made detection of larvae difficult.

The number of days ≥ 18°C prior to first reproduction had a relatively small range in the Yampa River (0 to 10 d). In the three of seven years when water temperature had not achieved a mean daily average of 18°C by first reproduction it did so within 2 to 6 d. In contrast, Colorado squawfish in the lower Green River initiated reproduction after mean daily temperature exceeded 18°C for 13 to 39 days. Total days ≥ 18°C were greater in the lower Green River than in the lower Yampa River mainly because the Green River often warmed above 18°C prior to runoff. Days post-peak discharge had a wide range in the Yampa River (5 to 39 d), but was narrower in the lower Green River (12 to 35 d). If the low flow year 1994 was excluded from the lower Green River data, the range of days post-peak discharge was a relatively narrow 24 to 35 d.

The average reproductive season for Colorado squawfish lasted 34 d (24 to 46 d) in the Yampa River compared to 37 d (17 to 47 d) for squawfish in the lower Green River. Length of season was apparently not related to discharge level because the longest season recorded in the Yampa River (46 d) was in a high discharge year (1993) but the longest season recorded in the lower Green River (47 d) was in the lowest discharge year (1994).

The first peak in reproductive activity for Colorado squawfish in the Yampa River occurred an average of 5 d (range 3 to 8 d) after first reproduction was detected when mean daily water temperatures ranged from 16.3 to 23.1°C. Mean daily water temperature had generally exceeded 18°C for 2 to 15 d. The first peak in reproductive activity for Colorado squawfish in the lower Green River occurred an average of 6 d (range 0-9 d) after first reproduction was detected when mean daily water temperatures ranged from 19.9 to 20.6°C. Mean daily water temperature had generally exceeded 18°C for 22 to 45 d.

Inter- and intra-annual abundance patterns of larvae.--Colorado squawfish larvae were detected each year in drift-net samples from the lower Yampa River sampling station (1990-1996) and the middle (1990, 1994-1995) and lower Green River (1991-1996) sampling stations.

Abundance of larvae in samples at individual sites varied dramatically within and among years (Figs. 2-4). For example, at the Yampa River site, three peaks in drift abundance that exceeded 5,000 larvae/hr were documented in 1990, whereas only one was documented per year in 1991, 1992, and 1995, and none were detected in 1993 and 1994. The large peak in early 1992 was the single highest abundance of larvae found in any year.

Peaks in transport abundance were usually sporadic and, short in duration (increased to peak and declined within 2 d). For example, 62% (835 of 1338) of larvae captured at dawn during the high transport year of 1990 were from five sampling days. Exceptions to sporadic patterns of drift occurred in 1993 at both sampling stations and at the Yampa River station in 1996 when no large peaks in abundance of larvae were detected.

Peaks in transport abundance of larvae in the Yampa River were often associated with increased turbidity and discharge, as a consequence of thunderstorm activity and subsequent runoff of rainfall; this was especially true in 1991 and 1992. Peaks in abundance of larvae associated with increased turbidity, but not necessarily increased discharge, suggested that turbidity may be the most influential factor.

At the lower Green River sampling station, peaks in transport abundance were also episodic but were of lesser magnitude than in the Yampa River. For instance, two peaks that exceeded 2,000 larvae/hr were noted in 1991 and 1992, one was detected in 1996, and none were observed in years 1993-1995.

Diel and cross-channel patterns of abundance of larvae.--The GLM analysis of the 1992 Yampa River data demonstrated that day and time variables accounted for most of the variation in mean number of larvae captured (Table 2). However, the time•position variable and all interactions that included turbidity were also significant in this QAIC-selected model. Position was not a significant main effect ($P = 0.34$) but was included in interactions and all variation as a result of turbidity was accounted for by interactions so a main effect was not estimated. Higher-order GLM models that included at least one combination of day•position, time•day, and time•position•day variables did not converge because no larvae were captured on some days, times, or positions.

Abundance of Colorado squawfish larvae in dawn-nearshore samples (4.2 fish/1000 m^3, SD = 4.61, n = 42) was about half that of samples collected at other times and positions (8.7 fish/1000 m^3, SD = 12.40, n = 372). In general, mean abundance of Colorado squawfish larvae in 1992 was moderately high at dawn, highest at noon, and low at dusk and midnight (Fig. 5). Mean abundance of Colorado squawfish larvae in samples collected when water was turbid (10.0 fish/1000 m^3, SD = 29.3, n = 156) was nearly twice that of samples collected in clear water (6.6 fish/1000 m^3, SD = 22.1, n = 258) regardless of sampling time or position and was highest at noon in mid-channel-surface samples. Highest abundance of Colorado squawfish larvae in clear water samples was at noon in mid-channel-bottom samples. Mean abundance of Colorado squawfish larvae was highly variable in samples collected at all times and in all channel positions.

Slight over-dispersion of the GLM was suggested by a deviance/degrees of freedom value of 1.33; values < 1 indicate under-dispersion while values = 1 indicate the data do not contain extra-Poisson variation. Standard errors of model parameter estimates were multiplied by the square root of the deviance (1.153) to correct for over-dispersion. The scaled Pearson X^2 for the GLM model indicated slight lack of fit (436.6, 377 df, $P = 0.023$), which was due mainly to samples collected in clear ($P = 0.033$) rather than turbid ($P = 0.13$) water.

Slight lack of fit of the data to the GLM model was caused, in part, by the three non-estimable interaction terms. An exploratory GLM model using least squares estimation of model parameters and $\log_e$ transformed (catch + 1) data suggested that all parameters except position and its interactions, including ones not estimated by the maximum likelihood GLM, explained a statistically significant amount of the variation in abundance of larvae. This result was not surprising given the number of samples and consequently high power to detect relatively small effects. The GLM analysis corroborated the rank order and magnitude of *F*-values for time and sampling date produced by the maximum likelihood analysis. The exploratory model also verified the statistically significant, but relatively minor contribution of unestimated interactions.

The GLM analysis of diel-only data collected from 1992 to 1996 suggested that abundance of larvae in drift varied substantially among years and was also affected by turbidity and time of sampling especially through interactions of those variables (Table 3). Similar to the GLM analysis of the 1992 cross-channel and diel data, day of sampling accounted for a substantial amount of variation among years but was not included as an analysis variable because it obscured the year effect. The typical abundance pattern for larvae in a single day in most years was shown by the mean daily averages for combined turbid and clear samples (Fig. 6) and suggested that drift abundance was relatively low or moderate at dawn, higher at noon, low at dusk and low to high at midnight. The primary exception to this pattern was the low flow year 1994, when most Colorado squawfish larvae captured (101 out of 136) were from only five midnight sets. During that year, no turbidity event was recorded and thus, water clarity was very high throughout the season. Abundance of Colorado squawfish larvae in samples collected at midnight was much higher in 1993-1996 than in 1992 when diel and cross-channel sampling revealed lower abundance at midnight than during any other sampling time.

The influence of turbidity on abundance of larvae was important as a main effect and in interactions with year and time of sampling (Fig. 7). Differences in turbidity effects among years may be due to the number and magnitude of turbidity events in any given year. The importance of the time•turbidity interaction was due to the higher abundance of larvae drifting in turbid water at all times except midnight, a time when densities in clear water were higher.

Samples collected at dawn provided the most consistent estimates of abundance of Colorado squawfish larvae across all years compared to samples collected at noon, dusk, and midnight (Table 4). This was true because the CV of dawn samples was lowest when all years were considered compared to CV's for samples collected at noon, dusk, and midnight. When the anomalous low flow 1994 data were excluded, the CV for dawn samples was less than half of that for other sampling times.

Position, time, and date effects on age and TL of larvae captured.--Mean ages of Colorado squawfish larvae captured in nearshore, mid-channel surface, and mid-channel bottom nets were within 0.3 d of each other (Table 5). Likewise, mean ages of larvae captured at dawn, noon, dusk, and midnight were similar. These slight differences were not considered biologically significant. Large sample sizes and high statistical power to detect small differences resulted in significant differences in age of larvae among drift net positions ($P = 0.01$) and sampling times ($P < 0.0001$) in 1992 middle Green River samples; the position•time interaction was not significant ($P = 0.12$).

An identical analysis with TL as the response variable suggested that Colorado squawfish captured in nearshore, mid-channel surface, and mid-channel bottom nets were of similar size (Table 5), as were mean lengths of larvae captured at dawn, noon, dusk, and midnight. These small differences were also not considered biologically significant even though statistically significant effects of position ($P = 0.033$) and time ($P < 0.0001$) were detected; the position•time interaction was not significant ($P = 0.65$).

The ANOVA detected a significant effect of sampling day on age ($P < 0.0001$) and TL ($P < 0.0001$; Table 6). However, inspection of the means and SE's suggested that the only biologically important differences were on the 13 July sample date, when larvae averaged more than 1 d younger and were nearly 1 mm shorter than in other samples. Those smaller and younger larvae may have been entrained in the extremely turbid water that was caused by a thunderstorm the previous day.

Transport abundance related to discharge.--Annual transport abundance of Colorado squawfish larvae was variable at the Yampa River and lower Green River sampling stations and was relatively consistent at intermediate levels of peak annual discharge (Figs. 8, 9). The lowest transport abundance values at each sampling station were recorded in the low discharge year 1994 and in the high discharge year 1995. Transport abundance values for the lower Green River were surprisingly consistent among years with the exception of 1995. With the exception of 1994, transport abundance was lower in the lower Green River than for the Yampa River. Abundance of larvae transported from the lower Green River site in 1994 was similar to that measured in most other years. Few larvae were transported from the Yampa River sample site in 1994.

In 1990 when larvae were abundant and discharge was moderate, transport abundance at the Yampa River (49,714/hr) and middle Green River (57,407/hr) sampling stations were similar. In 1994 when few larvae were present and discharge was low, transport abundance was slightly lower at the Yampa sampling station (978/hr) than the middle Green (1,904/hr) sampling station. In 1995 when moderate numbers of larvae were present and discharge was high, transport abundance was low at the middle Green River station (2,687/hr) compared to the Yampa River (18,462) station. Comparison of patterns of transport abundance in 1990 suggested that major abundance-peaks of larvae transported downstream past the Yampa River station were also detected at the middle Green River station the same day or 1 d later (Fig. 10). If peaks in transport abundance detected at each station the same day or 1 d later represent the same pulse of larvae moving downstream, larvae at the upstream station should be on average 1 d or less younger than larvae captured at the downstream station. Otolith aging supported this hypothesis because larvae captured on 19 July at the Yampa River station averaged 7.4 d-old and were 8.1 d-old at the middle Green River station on 20 July. Larvae transported downriver at an average velocity of 0.5 m/sec, which approximated the minimum water velocity sampled by our nearshore drift nets in 1990, would travel 43 km. Thus, the distance between the two stations (40 km) could be traversed by larvae in about a day.

Fall recruitment of juveniles related to transport abundance.--Transport abundance of Colorado squawfish larvae, which was a measure of annual abundance of larvae produced from spawning areas, had little apparent relationship with abundance of juveniles present in autumn (Figs. 11, 12). Annual transport abundance of larvae from the Yampa River was highly variable among years, but similar levels of juveniles were found in autumn in the middle Green River. An exception was the low-discharge year 1994, when transport and juvenile abundance were low. In contrast, transport abundance estimates in the lower Green River were similar among years but recruitment of juveniles in the fall was variable. An exception was the high discharge year 1995, when transport and juvenile abundance was low.

DISCUSSION

Timing of reproduction.--Colorado squawfish reproduced in early to mid-summer in the Green River basin. Dates of initiation of reproduction were earlier, temperatures at first reproduction lower, and days post-peak runoff fewer than reported by other researchers (Hamman 1981, Haynes et al. 1984, Nesler et al. 1988, Tyus 1990, Tyus and Haines 1991). This was probably because capture and aging of larvae more accurately estimated timing of reproduction than presence of adults near spawning areas or regression back-calculation of hatching date from total lengths of larvae or juveniles.

No single variable accurately predicted date of initiation of spawning by Colorado squawfish. Water temperatures at the initiation of reproduction were more variable and lower at the Yampa River site than at the lower Green River site and were lower than those previously reported (Hamman 1981, Haynes et al. 1984, Tyus 1990, Tyus and Haines 1991). Those lower temperatures were somewhat surprising because it was generally believed that Colorado squawfish did not spawn until water temperatures exceeded 18°C (Hamman 1981, Tyus 1990, Tyus and Haines 1991), although reproduction at lower temperatures had been postulated (Nesler et al. 1988). In the lower Yampa River, Colorado squawfish reproduced just a few days prior to, or just a few days after, water temperature exceeded 18°C which is suggestive of a threshold effect. Water temperatures were closer to 20°C in the lower Green River when Colorado squawfish first reproduced.

Weak correlation between initiation of reproduction by Colorado squawfish and environmental variables such as water temperature and days post-peak discharge may be a consequence of other factors. Estimates of initiation of reproduction may be biased in low discharge years such as 1994 in the Yampa River because most larvae were captured in just a few midnight samples. Thus, unless diel samples were collected relatively early in the season, the normal dawn samples may not detect the first larvae that are transported downstream in a season. Sampling during high discharge, such as occurred in the lower Green in 1995, likely contributed to the low catches because such a small percentage of water was sampled. It was also possible that reproduction in Colorado squawfish was initiated by dramatic declines in discharge rather than a peak. If this was true, days post-peak discharge and associated water temperature variables would be influenced if multiple peaks of nearly the same magnitude were observed in a single year or if runoff was extended.

There was no clear relationship between water temperature and initiation of reproduction by Colorado squawfish even though temperature thresholds have been postulated in the past (Hamman 1981, Tyus 1990, Tyus and Haines 1991). It was possible that Colorado squawfish responded to thermal cues but perhaps only after peak runoff. However, number of days that exceeded 18°C following peak runoff (not reported) were nearly as variable as total days so that hypothesis was dismissed. Annual records for the lower Green River consistently had many days when water temperatures exceeded 18°C prior to runoff. These higher temperatures prior to runoff were the likely cause for consistently higher degree day accumulations in the lower Green compared to the Yampa River, where spring temperatures prior to runoff were cooler and rarely exceeded 18°C.

Our results and those of Nesler et al. (1988) confirm that cues for reproduction by Colorado squawfish in the variable and fluctuating environment of the Colorado River basin were complex and likely a mixture of factors interacting with or without flow spikes. During this study, Colorado squawfish initiated reproduction within a fairly restricted time frame in both the Yampa River (13 June-1 July) and the lower Green River (9 June-24 June; high flow year 1995 deleted) even when discharge and temperature regimes were highly variable. This suggests that a temporal factor such as photoperiod may also serve as a cue for reproduction, perhaps in conjunction with discharge regimes, water temperature, and other unmeasured factors, to initiate reproduction in Colorado squawfish.

Inter- and intra-annual abundance patterns of larvae.--Differences in transport abundance of larvae across years and the patterns of abundance within a year may be the result of a number of factors (e.g., timing of arrival, condition, and number of adult fish at the spawning areas). Even if these factors were relatively constant across years and seasons within a year, environmental conditions probably affect the survival of eggs and larvae at the spawning area. Because no data were collected that describe the abundance and condition of adults and their relative reproductive success within and among years, transport abundance as measured by density of drifting larvae was the best measure of reproductive success.

High transport abundance of larvae associated with increased turbidity and discharge has been described for other cypriniform fishes (Lindsey and Northcote 1963, Geen et al. 1966, Gale and Mohr 1978) and could be the result of several factors. Larvae may lose orientation in turbid water and subsequently become entrained in the river current and swept downstream. Similar loss of orientation in the dark may be the reason for high transport abundance of Colorado squawfish at midnight in most years except 1992. Transport under such conditions may also reduce susceptibility to predators that are sight feeders or which may be inactive at night (Armstrong and Brown 1983).

Elevated water turbidity may also cause increased sediment deposition in interstitial spaces of the substrate, an impetus which may motivate larvae to emerge and drift. If larvae were simply emerging and losing visual acuity or avoiding predators, more uniform patterns of drift throughout days of high turbidity would be expected. Our data do not support this scenario; drift peaked at dawn or more frequently, noon on most days with high water turbidity but declined dramatically by dusk and was very low by midnight and on the days following even though water remained turbid. This suggested that the larvae ready to emerge were entrained over a short time at the beginning of the event rather than slowly entering the drift over the entire period of elevated turbidity. The turbidity-stress hypothesis was supported by age and length data for larvae captured on six different sample dates throughout the 1992 sampling season; larvae captured during an extreme turbidity event were more than 1 d younger and 1 mm shorter than larvae captured on other dates when turbidity was lower. During that event, a settled volume of Yampa River water was about 50% sediment (pers. obs., KRB). The underdeveloped state of those larvae captured when sediment loads were very high but discharge increased only slightly, indicated that larvae prematurely emerge from the substrate and drift in order to avoid being buried in sediment. In the absence of turbidity events, larvae likely emerged from the substrate and entered the drift more uniformly and over a period of days or at times other than when they would be susceptible to sampling at dawn.

In 1994, when transport abundance was highest at midnight, the combined effects of low stream discharge and velocity and clear water likely reduced the tendency of larvae to get entrained except in the dark. Rarity of larvae in samples at the downstream Jensen sampling station also suggested that very few larvae were produced or transported downstream that year. The very low recruitment of juveniles observed in that Jensen-Ouray reach (McAda et al. 1996, Haines et al. 1998) supported the notion that few larvae arrived at the middle Green River nursery habitat reach.

Uncertainties remain regarding interpretation of patterns of drift of Colorado squawfish larvae in the Yampa River. For example, several hours may elapse between emergence of larvae from the substrate at the spawning area and their subsequent capture at the sampling station 25 km or more downstream. This spatial and temporal separation may confound interpretation diel drift patterns. Examination of temporal patterns of drift revealed a relationship between turbidity events and seasonal peaks in drift of larvae, but the explanation for large abundance peaks observed in clear water remains elusive. Although it is reasonable to assume that such clear-water peaks may reflect high levels of adult spawning activity and subsequent emergence of larvae, other unmeasured factors may also be involved.

Unlike Nesler et al. (1988), we did not detect peaks in reproductive activity associated with increases in discharge above baseflow, or “flow spikes”, in the Yampa or the Green rivers. In their study, larvae captured in drift nets and seines in the lower Yampa River were aged using a polynomial regression equation with TL as the dependent variable, and were assigned a deposition (egg fertilization) date. Modes in the histogram of ages of larvae, which represented modes for reproduction by adults, co-occurred in five instances over the period 1983-1986 with thunderstorm-induced flow spikes of 27-71 m^3/s in the Yampa River.

We indirectly assessed the association of reproduction and flow spikes for our data by subtracting 12 d from the modes in our catch data (Figs. 2-4) to account for average age of the larvae (6 d) and incubation time (6 d). Close association of modes of reproduction with notable increases in discharge were generally not observed in this study and may occur only under specific discharge conditions or in certain years when the correct combination of environmental factors were present. For example, flow spikes $> 27\ m^3/sec$ concurrent with the reproductive season occurred only once during this study in each of the Yampa (1991) and Green (1992) rivers. It may be that large discharge spikes in the Yampa River were important reproductive cues in those relatively high discharge years (1983-1986, Nesler et al. 1988) when flows on 30 June, a convenient benchmark of time, ranged from about 100-350 m^3/sec. During this study, Yampa River discharge on 30 June was in that range only in 1993 and 1995 but no flow spikes were observed. In the remaining years of this study (1990-1992, 1994, and 1996), which had discharge levels on 30 June that ranged from 18-85 m^3/sec, Colorado squawfish in the Yampa and lower Green rivers may have used other reproductive cues because even the small increases in discharge observed were not associated with reproduction. It is also possible that flow spikes are a surrogate expression for an associated but unmeasured environmental cue for reproduction (Nesler et al. 1988). This may explain reproduction when flow spikes are absent.

The polynomial regression equation used by Nesler et al. (1988) to indirectly estimate ages of Colorado squawfish may bias the relationship between flow spikes and reproductive activity. They captured 9.0 mm TL larvae in drift nets in the Yampa River that were aged at 11.3 d by polynomial regression but similar-sized larvae captured in this study that were otolith-aged averaged 6.5 (6 to 7) d. Laboratory studies confirmed that aging Colorado squawfish larvae with otoliths was accurate (Bestgen and Bundy 1998). Endogenously feeding larvae reared to 7 d post-hatch in water temperatures from 18 to 26°C averaged 9.0 to 10.0 mm TL in separate experiments (Bestgen and Williams 1994, Bestgen and Bundy 1998) compared to 7-d post-hatch larvae reared by Hamman (1981) that were only about 8 mm TL. Those slow-growing larvae biased the polynomial regression of Nesler et al. (1988), which suggested an age of 11.3 d for 9.0 mm TL larvae and 14.7 d for a 10 mm TL larvae. Age of 9-mm-TL larvae captured by Nesler et al. (1988) were overestimated by about 5 d (11.3 d - 6.5 d = 4.7 d), based on comparisons with otolith-aged larvae and laboratory experiments.

Regression age overestimation may be related to the data used to calculate the relationship. Growth of cultured larvae may have been slower than for wild larvae due to occasional additions of cold water to culture systems (Hamman 1981), inadequate food of appropriate size, or genetic factors. Another likely source of error in regression age estimation may have been the estimated length at hatching, 6.7 mm TL, which may be too large; Bestgen and Williams (1994) reported 5.5 mm TL at hatch. The larger length at hatching likely resulted in over-leveraging the initial slope and as a consequence, equation solutions for ages were biased high.

Regardless of the source of the age overestimation for early larvae, the association of flow spikes and reproductive activity noted by Nesler et al. (1988) in years 1983-1986 are still valid. Age-overestimation by several days would simply move the modes of reproduction that many days later than the flow spike rather than coincident with or in some cases slightly before the spike. The scenario of a slight lag between the cue and actual reproduction was probably more biologically reasonable than reproduction that was tightly linked with a cue. Fishes that use stochastic environmental events, such as flow spikes, as cues may require a short lag prior to reproduction to ensure that reproductive products are adequately developed and that a suitable number of mates are available. A lag between reproduction and a flow spike may also enhance reproductive success because embryos deposited in the gravel would not be suffocated by the high silt loads that typically accompany summer thunderstorm runoff in the Yampa River.

Diel and cross-channel patterns of abundance of larvae.-- Previous research showed that Colorado squawfish larvae in the Yampa River were generally most abundant in dawn drift-net samples and were distributed equally across the channel (Haynes et al. 1985, Nesler 1986; 1987). In contrast, mean abundance of Colorado squawfish larvae in dawn-nearshore samples in 1992 was only about half that for other times and positions and data collected in 1992-1996 suggested that squawfish larvae were most abundant in samples collected at noon or midnight. Diel and spatial abundance patterns may vary by year, depending on timing of emergence of larvae, the frequency of turbidity events that were associated with increased catch rates of Colorado squawfish larvae, and many other factors. Different annual discharge levels will also affect rates of transport of larvae from spawning areas to fixed sampling stations. Discrepancy between our patterns and those suggested by Nesler (1986, 1987) may be a result of low fish abundance in 1985 and 1986 and environmental conditions may also have been different. Relatively high abundance of Colorado squawfish larvae at midnight was similar to patterns observed for drifting larvae in other studies (Gale and Mohr 1978, Armstrong and Brown 1983, Muth and Schmulbach 1984, Corbett and Powles 1986, Harvey 1991, Johnston et al. 1995).

Transport abundance related to discharge.--Low annual transport abundance that followed extreme discharge events could be a consequence of a number of factors. In 1994, in the Yampa River, low transport-abundance could be the result of low production of larvae, low survival of eggs and post-hatching larvae, or both. These hypotheses were difficult to evaluate because reproductive effort and abundance of spawning adults was unknown. It seems reasonable that larvae may have been retained in Yampa Canyon in that low flow year instead of being advected downstream. Typical of other years however, low abundance of Colorado squawfish in a backwater near the Yampa drift net station (unpublished data, KRB) suggested that retention of larvae and recruitment of juveniles was low in the Yampa River in 1994.

The transport-abundance levels recorded at the middle Green River and the Yampa River stations were high and concordant in 1990 and low but reasonably similar in 1994. Similarities in transport abundance among stations in those years suggested that sampling error did not affect estimates of transport abundance in moderate-low discharge years. Similarities in transport abundance also suggest negligible reproduction by Colorado squawfish in intervening river reaches such as Split Mountain Canyon. The low transport abundance at the middle Green River station compared to the Yampa River station in 1995 was likely due to sampling error in that high flow year. Nearly half the larvae collected at the Yampa River station were from a short-duration peak on a single day which may have been missed downstream in the larger Green River. Fast water may also inflict higher mortality on larvae due to abrasions and the higher energetic cost of swimming and may account for the lower transport-abundance estimates at Jensen in 1995.

Slightly offset peaks in transport-abundance between the Yampa River and middle Green River sampling stations in 1990 suggested relatively fast movement of larvae in that relatively low discharge year. A single, large peak of larvae was detected at each station a day apart during 19-20 July 1990. These larvae averaged slightly less than 1 d younger in upstream than downstream samples, suggesting that larvae from the same peak were sampled at stations 40 km apart within a day. These travel rates were also consistent with water velocities near the sampling station.

Transport-abundance calculated from density estimates of larvae captured in drift nets has been shown to under-estimate actual abundance; differences in abundance across the stream channel or at different times of the day may be the source of error (Franzin and Harbicht 1992, Johnston et al. 1995). Those sources of error were confirmed in this study because patterns of transport abundance varied with time and sampling position and across years. However, sampling date was the single largest source of variation in the GLM models that predicted mean abundance of Colorado squawfish larvae. Daily sampling ensured that the high amplitude but short duration (most < 2 d) peaks of larvae transported downstream were sampled which reduced the effects of sampling error. Dawn sampling reliably estimated the relative abundance of larvae transported downstream, compared to estimates obtained during other sampling times. Thus, even though actual abundance of larvae estimated by our sampling protocol may be biased low, the patterns suggested by the data probably reflect actual abundance patterns on intra- and interannual scales.

Previously, the relative size and importance of the spawning population of Colorado squawfish in the lower Green River have been questioned as well as whether most lower Green River larvae originated from the Yampa River population. The 1994 data presented an opportunity to test this hypothesis because if the Yampa River supplied the lower Green River, the few larvae transported from the Yampa River should have resulted in low abundance in both the middle and lower Green River. Transport-abundance of larvae in the lower Green River in 1994 was average compared to other years, suggesting the presence of a distinct and relatively large spawning population of Colorado squawfish in the lower Green River. Although the lower Green River does not appear to produce as many larvae, on average, as the Yampa River, both reaches deserve equal management consideration because each spawning population supplies separate areas that are important for rearing and recruitment of juveniles.

Fall recruitment related to transport abundance.-- Lack of concurrence of transport abundance estimates and juvenile recruitment in the fall, except at low levels, and highly variable recruitment levels within a reasonably narrow range of transport abundance values, suggested that after a minimum threshold of larvae was produced, biotic and abiotic conditions in nursery habitat reaches were responsible for regulating juvenile recruitment in most years. That thesis was consistent with the findings of Bestgen (1997) and Bestgen et al. (1997), who suggested that a biotic factor, predation, interacted with growth mediated by an abiotic factor (water temperature), to affect recruitment. Specifically, predation by non-native fishes, such as red shiners *Cyprinella lutrensis,* may have influenced intra-annual recruitment of Colorado squawfish because larvae that hatched early and grew slowly were more susceptible to predation than those that hatched late and grew rapidly.

Taken together, these finding suggest that juvenile recruitment may be regulated in most years by factors other than abundance of larvae. Exceptions to this were extreme high and low discharge years when either very few larvae were produced or when very little low velocity habitat was present (Tyus and Haines 1991). Differential recruitment in other years may be a result of interacting effects of environmental factors that affect abundance of predators and influence growing conditions for young Colorado squawfish in low-velocity channel-margin habitats.

Analysis of recruitment data illuminated a potential conservation issue; a declining abundance of juveniles in the fall, especially in the lower Green River since about 1990 (in part Bestgen 1997; Figs. 10, 11). Relatively high recruitment in the middle and lower Green River was noted in the periods 1979-1982, followed by low recruitment in high discharge years 1983-1984 and again high recruitment from 1986-1989 (Tyus and Haines 1991). Recruitment since

1990 has been below the average of 1979-1989, with the exception of 1991 in the middle Green River and 1993 in the lower Green River (data in McAda et al. 1996). This declining trend for juveniles in the Green River population of Colorado squawfish is opposite that for adults, which appear to be increasing in abundance since ISMP sampling began in 1986 (McAda et al. 1996). Recruitment dynamics of this species need to be better understood before assessments of the status of this population can be made with certainty.

Monitoring of long-lived and rare species such as Colorado squawfish should include all life stages because presence of even large numbers of adults does not ensure that adequate reproduction and recruitment is occurring to sustain populations. Annual monitoring of abundance of larvae would allow: 1) assessment of the presence, timing, duration, and intensity of reproduction by Colorado squawfish; 2) determination of the relationship between relative abundance of Colorado squawfish larvae transported from spawning areas into downstream nursery habitats and environmental variables; and 3) determination of the relationship between abundance of larvae produced and abundance of juveniles in the fall. In the Green River drainage, such monitoring should be conducted annually downstream of both the Yampa River and lower Green River spawning areas. Daily sampling that encompasses the reproductive season is necessary to ensure that sporadic, but short duration, peaks in transport-abundance are measured (Nesler 1987). Time of sampling depends upon the objectives of the investigator but should minimally include the dawn period because sampling then provides the most reliable abundance estimates across years. Survey-type studies designed to assess presence of reproducing Colorado squawfish may require sampling at additional times.

Conclusions.--Transport-abundance appeared to be affected by discharge only during extreme years. High discharge was negatively associated with transport-abundance at both the Yampa River and lower Green River stations while low discharge was negatively associated with transport-abundance only at the Yampa River station. Low abundance during either low or high discharge years could be due to low abundance of adults and low production of larvae at spawning areas, high mortality of eggs or larvae at spawning areas or during downstream transport, sampling error, or other factors. Hypotheses about variation in transport-abundance would be easier to evaluate if abundance of spawning adults was known and if drift net sampling incorporated capture-recapture sampling of marked larvae (Nesler 1987, Muth and Bestgen 1991).

Effects of regulation of the Green River by Flaming Gorge Dam on reproduction and drift of Colorado squawfish were difficult to assess because one spawning area was in a tributary, the Yampa River, and one was far downstream in the mainstem where effects may be ameliorated. Maintenance of those spawning populations may be dependent on retaining the relatively natural discharge and temperature regimes in those river reaches, in particular, the Yampa River. Reproduction by Colorado squawfish in highly regulated stream reaches may be limited until more natural discharge and temperature regimes are restored. The effects of cooler water temperatures on growth and survival of Colorado squawfish larvae drifting from the Yampa River into the Green River are unknown.

High intra-annual recruitment variation of Colorado squawfish in both the lower and middle Green River, 1990-1996 was generally not the result of inadequate numbers of larvae produced from spawning areas. High recruitment variation may be due to differential effects of factors among years that affect growth and survival of early life stages. It has been previously shown that discharge levels during summer in the middle and lower Green River does not affect juvenile recruitment in the fall except at relatively high levels (Bestgen 1997). Discharge regimes that are not restricted to a particular level in summer may also allow managers more operational flexibility in order to fulfill requirements of other endangered species in the Green River such as razorback sucker *Xyrauchen texanus*. It has also been shown that early life stages of Colorado squawfish can grow and survive under a variety of environmental conditions and that the incidence of starvation in the wild is likely low (Tyus and Haines 1991, Bestgen and Williams 1994, Bestgen 1996, 1997). Because Colorado squawfish are well-adapted to the fluctuating environmental conditions with which they have evolved, physical factors may regulate recruitment of age-0 Colorado squawfish only in relatively rare instances.

There is a growing body of evidence that non-native fishes may play a much greater role in structuring recruitment patterns of native fishes in the Colorado River basin than was previously recognized (Haines and Tyus 1990, Muth and Nesler 1993, Stanford 1994, Gido et al. 1997, Bestgen 1997, Bestgen et al. 1997). However, past management strategies de-emphasized importance of effects of introduced fishes because of research emphasis on native fishes, perceived lack of options to control non-native fish abundance, and the poorly understood effects of river regulating structures like Flaming Gorge Dam. A better understanding of the relative importance of mechanisms regulating recruitment of Colorado squawfish and other native biota may suggest increased importance of management strategies that reduce effects of non-native fishes.

RECOMMENDATIONS

1). Continue drift sampling in the lower Yampa and Green rivers to monitor the abundance of Colorado squawfish larvae transported downstream from spawning areas. Monitoring the abundance of drifting larvae is a proven method for documenting reproduction and measuring relative reproductive success of Colorado squawfish. Data gathered is useful to evaluate the effects of recovery actions such as management of releases from Flaming Gorge Dam and non-native fish control.

2). Evaluate accuracy and precision of data collected by autumn *ISMP* sampling for estimating abundance of juvenile Colorado squawfish in backwaters. Acquisition of such data will ensure valid comparisons between abundance of larvae and recruitment of juveniles.

3). Evaluate importance of abiotic and biotic factors that influence intra- and interannual distribution, growth, and survival of early life stages of Colorado squawfish. Collection of such data will facilitate efforts to model population dynamics and long-term viability of Colorado squawfish.

4). Collect reliable, long-term water temperature data year-round at several locations in the basin with continuously recording thermographs. Instantaneous water temperature data collected at U.S. Geological Survey stations was not reliable. Suggested locations include the upper Green River at Flaming Gorge dam and in Browns Park, the middle Green River near Jensen, Utah, the lower Green River near Green River, Utah, and the upper (Maybell) and lower (Echo Park) Yampa River. Other locations may be needed to collect adequate data for researchers interested in other species or habitats.

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Table 1.--Estimated time of first and last reproduction and associated degree-day accumulation and days post peak runoff for the Yampa River and lower Green River spawning areas. Time of first and last reproduction, and time of first peak in reproduction was estimated by subtracting the average age of larvae at capture (6 d) and average incubation time of fertilized eggs at 18°C (6 d) from the date that larvae were first captured in drift nets set in the lower Yampa River and the lower Green River. The first peak of reproduction was qualitatively determined as the first substantial increase in abundance of captured larvae. Temperature data for the Yampa River were collected by a continuously recording thermograph placed at the mouth of the Yampa River. Data was not collected there in 1993 and 1994 so values were estimated by adding 2.1°C to mean daily values from an upstream gauge near Maybell, Colorado. Most lower Green River temperature data (1992-1994, 1996) were estimated by adding 2.3°C to mean daily values collected upstream at the Ouray National Wildlife Refuge; 1991 and 1995 data were from the U.S. Geological Survey gauge near Green River, Utah. Values are the mean of a five d-period centered on the date of interest. Days > 18°C is the number of days to first reproduction when average water temperature met or exceeded that value. Days post-peak discharge is the number of days between the highest recorded daily average discharge recorded during spring runoff and first reproduction.

		First reproduction					First peak of reproduction		
Site	Year	Reproductive period	Temperature (°C)	Days >18°C	Days post peak	Degree-days	Date	Temperature (°C)	Days >18°C
Yampa	1990	18 June - 16 July (29 d)	16.4	0	5	794	25 June	20.8	5
"	1991	25 June - 18 July (24 d)	17.8	5	33	1263	28 June	17.8	7
"	1992	13 June - 20 July (38 d)	18.6	5	16	1482	17 June	17.6	7
"	1993	30 June - 14 August (46 d)	17.4	0	39	1414	4 July	16.3	0
"	1994	20 June - 21 July (32 d)	22.3	10	37	1646	25 June	23.1	15
"	1995	1 July - 31 July (31 d)	16.0	1	24	1462	9 July	19.1	3
"	1996	26 June - 1 August (37 d)	17.2	0	41	1539	29 June	18.4	2
Lower Green	1991	21 June - 23 July (33 d)	22.0	24	28	1608	21 June	22.0	28
"	1992	9 June - 17 July (38 d)	20.6	38	26	1704	16 June	19.9	45
"	1993	24 June - 6 August (44 d)	20.6	36	24	1701	24 June	20.6	36
"	1994	9 June - 25 July (47 d)	19.8	9	12	1650	15 June	19.3	33
"	1995	20 July - 5 August (17 d)	23.0	39	32	2395	21 July	23.0	40
"	1996	15 June - 26 July (41 d)	20.0	13	25	1513	24 June	20.2	22

Table 2.--Type III likelihood ratio *F*-statistics for significant effects in the Poisson general linear model analysis of abundance of Colorado squawfish larvae in diel and cross-channel samples collected from the Yampa River in summer 1992.

Effect	Numerator df	Denominator df	*F*	$P > F$
Time	3	377	41.15	0.0001
Day	13	377	39.46	0.0001
Time x position	6	377	5.07	0.0001
Position x turbidity	2	377	8.44	0.0003
Time x turbidity	3	377	4.11	0.0069
Time x position x turbidity	6	377	2.54	0.0200

Table 3.--Type III likelihood ratio *F*-statistics for significant effects in the Poisson general linear model analysis of abundance of Colorado squawfish larvae in diel only samples collected from the Yampa River in summer 1992-1996.

Effect	Numerator df	Denominator df	*F*	$P > F$
Year	4	376	9.82	0.0001
Turbidity	1	376	21.10	0.0001
Time x year	12	376	5.53	0.0001
Year x turbidity	2	376	7.32	0.0007
Time x turbidity	3	376	13.88	0.0001

Table 4.--Percent of larvae captured in dawn, noon, dusk, and midnight samples (N) in 24-hr periods (3 samples/period) in the Yampa River in summer 1992-1996. Samples are a composite of those collected from clear and turbid water. The 1994 data contain no samples collected in turbid water. Abundance in different time periods was from density estimates (number/1000 m^3 water sampled) corrected for differences in the volume of water sampled and discharge during sampling periods so abundances are directly comparable within and among years. The coefficient of cariation (CV; standard deviation/mean density * 100) reflects the relative variation in densities of larvae at different sample times across years and is calculated with all years and with the anomalous low discharge 1994 excluded.

	Percent abundance of larvae per year					CV	
Time	1992	1993	1994	1995	1996	All years	All but 1994
Dawn	15.5	16.7	1.5	11.6	15.4	51.5	15.0
	(39)	(18)	(15)	(12)	(15)		
Noon	51.2	24.3	0.8	38.7	33.4	63.5	30.5
	(42)	(18)	(15)	(12)	(18)		
Dusk	20.9	15.0	0.9	17.3	8.9	62.4	32.5
	(42)	(18)	(12)	(12)	(18)		
Midnight	12.3	44.0	96.8	32.4	42.3	68.7	44.5
	(39)	(18)	(12)	(12)	(15)		

Table 5.--Mean age (SE, n) and total length (TL; SE, n) of Colorado squawfish larvae captured in drift-net samples collected at three cross channel positions and four diel periods in the Yampa River, 1992.

	Position			Diel period			
Response	Nearshore	Mid-channel surface	Mid-channel bottom	Dawn	Noon	Dusk	Midnight
Age (d)	6.4	6.3	6.1	6.5	6.1	6.3	6.5
	(0.047, 467)	(0.071, 218)	(0.043, 269)	(0.045, 426)	(0.042, 392)	(0.107, 84)	(0.203, 52)
TL (mm)	9.0	9.0	8.8	9.0	8.8	9.0	9.1
	(0.030, 463)	(0.032, 218)	(0.025, 267)	(0.026, 425)	(0.023, 387)	(0.060, 82)	(0.140, 54)

Table 6.--Mean age (SE, n) and total length (TL; SE, n) of Colorado squawfish larvae captured in drift-net samples collected over the sampling season in the Yampa River, 1992.

	Collection date					
Response	30 June	4 July	13 July	15 July	24 July	27 July
Age (d)	6.8	6.4	4.7	6.3	6.4	5.9
	(0.067, 106)	(0.093, 47)	(0.010, 49)	(0.060, 155)	(0.056, 141)	(0.040, 120)
TL (mm TL)	9.0	9.1	8.2	8.9	8.9	8.9
	(0.044, 106)	(0.060, 44)	(0.064, 49)	(0.029, 154)	(0.050, 140)	(0.034, 120)

Fig. 1. The Green River study area. Primary spawning areas for Colorado squawfish are in the lower Yampa River in Yampa Canyon and in Gray Canyon downstream of RK 251. Primary nursery habitat for age-0 squawfish was the middle (RK 515-340) and lower (RK 211-RK 0) Green River. Filled circles depict towns.

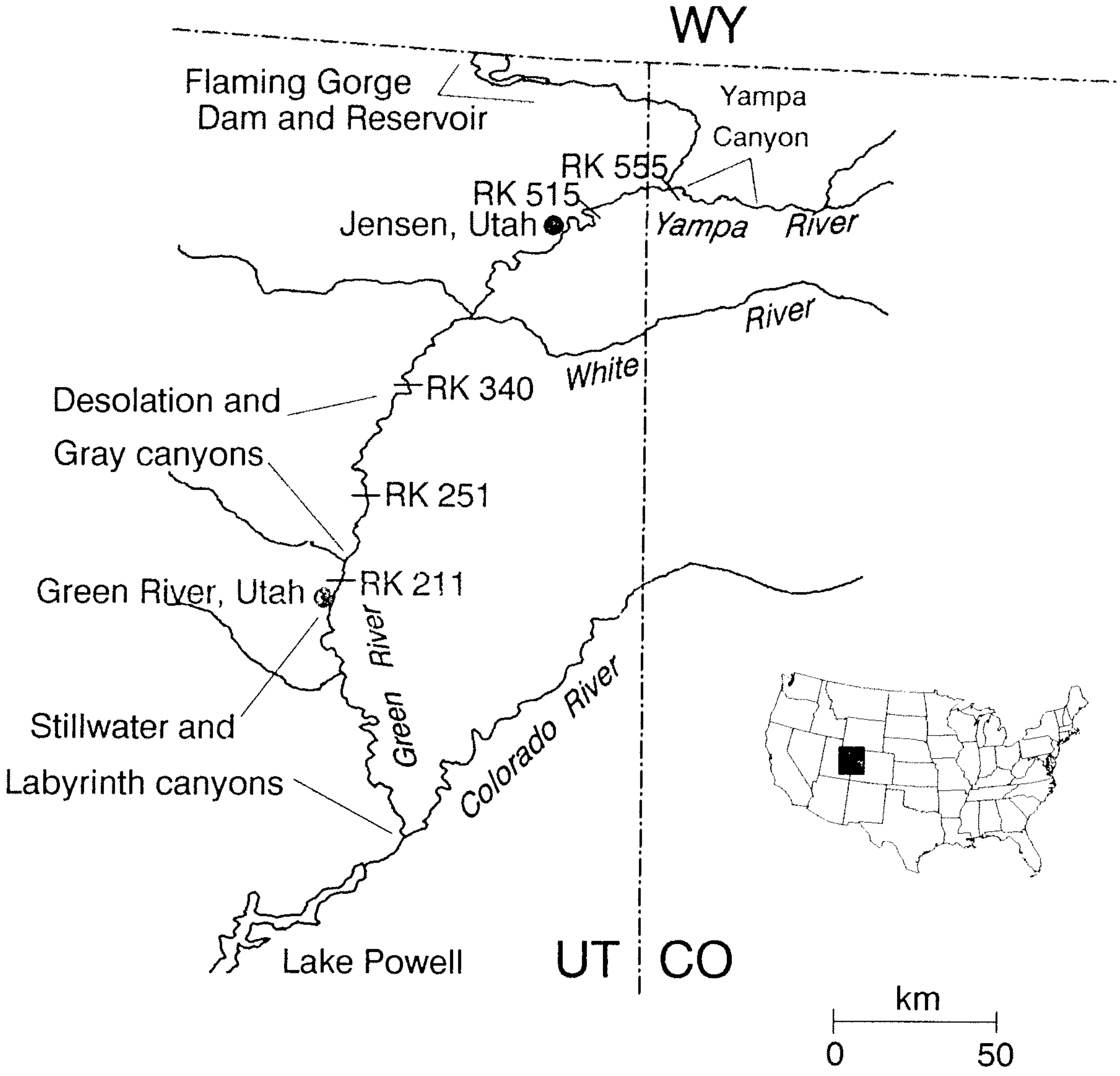

WY
Flaming Gorge Dam and Reservoir
Yampa Canyon
RK 555
RK 515
Jensen, Utah
Yampa River
White River
RK 340
Desolation and Gray canyons
RK 251
Green River, Utah
RK 211
Green River
Stillwater and Labyrinth canyons
Colorado River
Lake Powell
UT
CO
km
0
50

Fig. 2. Abundance of Colorado squawfish larvae transported downstream past the lower Yampa River sampling station (RK 0.8) in summers 1990-1996. Transport abundance was estimated by dividing the number of larvae captured (n = total in season) in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled.

Yampa River

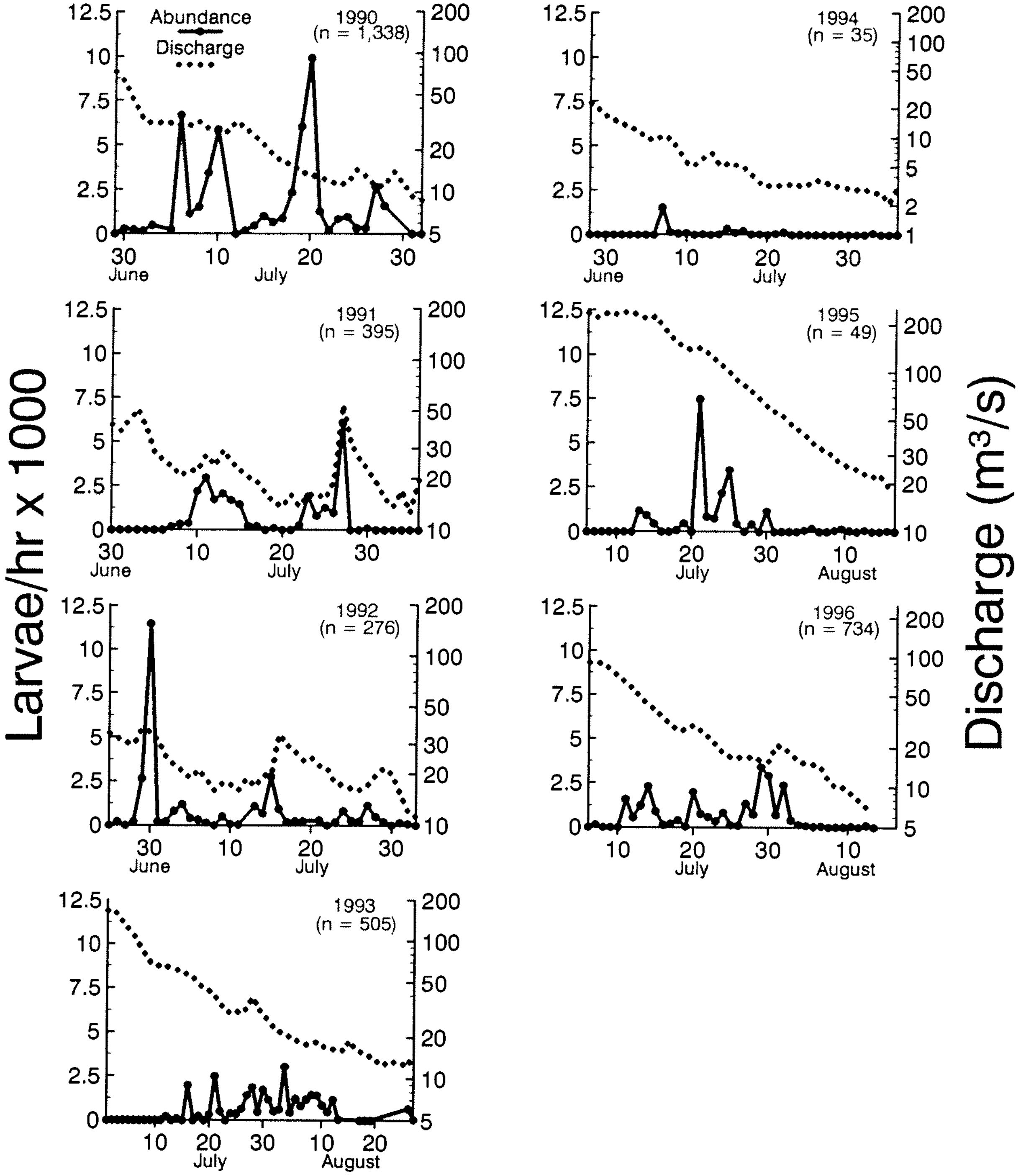

Larvae/hr x 1000
Discharge (m³/s)
Abundance
Discharge
1990
(n = 1,338)
1991
(n = 395)
1992
(n = 276)
1993
(n = 505)
1994
(n = 35)
1995
(n = 49)
1996
(n = 734)
12.5
10
7.5
5
2.5
0
200
100
50
30
20
10
5
2
1
June
July
August
30
10
20
30

Fig. 3. Abundance of Colorado squawfish larvae transported downstream past the middle Green River sampling station near Jensen, Utah in summers 1990, 1994, and 1995. Transport abundance was estimated by dividing the number of larvae captured (n = total in season) in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled.

Middle Green River

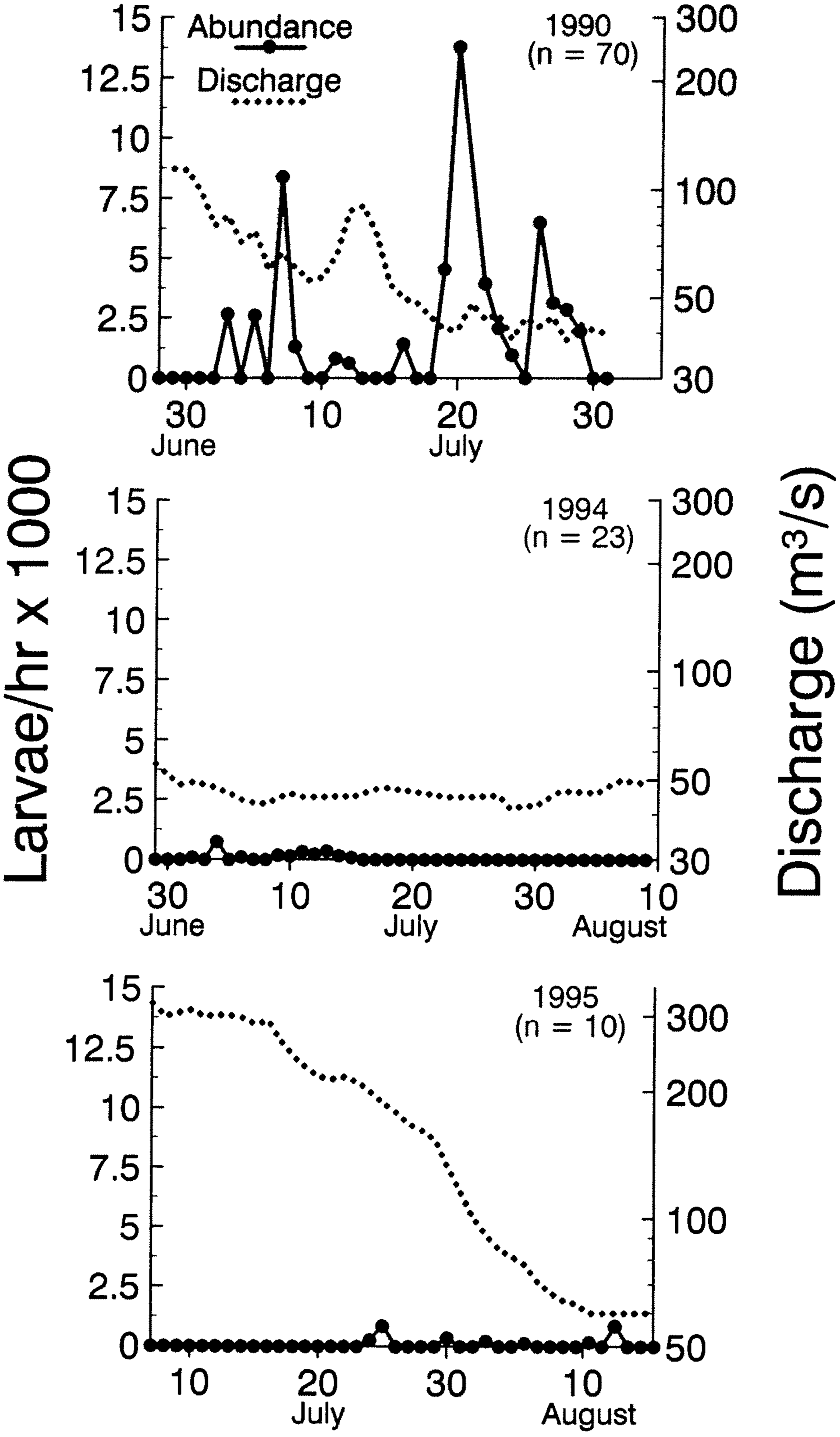


Fig. 4. Abundance of Colorado squawfish larvae transported downstream past the lower Green River sampling station near Green River, Utah in summers 1991-1996. Transport abundance was estimated by dividing the number of larvae captured (n = total in season) in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled.

Lower Green River

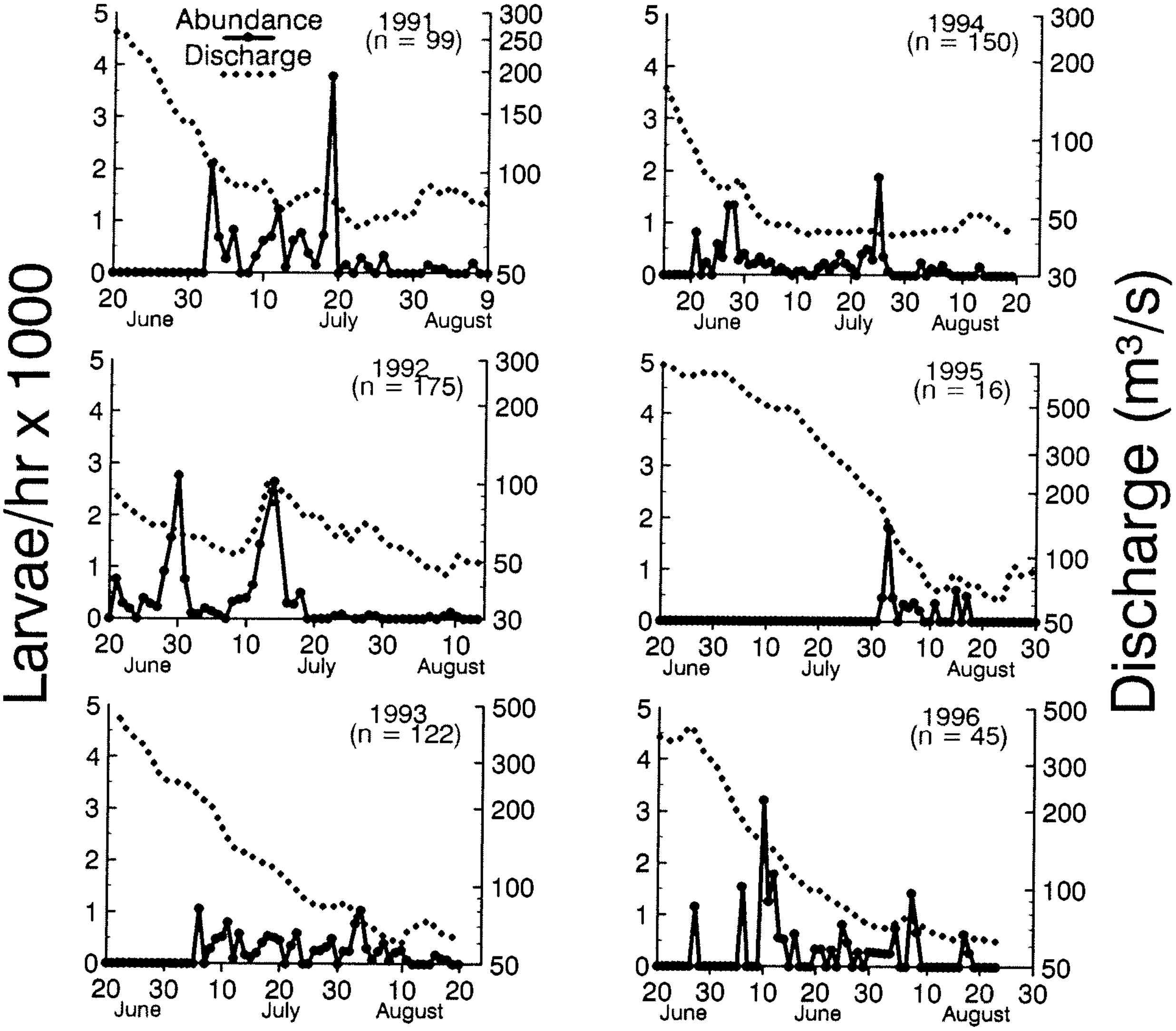


Fig. 5. Mean abundance of Colorado squawfish larvae collected in drift net samples at four times and in three different channel positions in the Yampa River in summer 1992 as predicted by a Poisson general linear model. Vertical lines through symbols represent ± 1 SD.

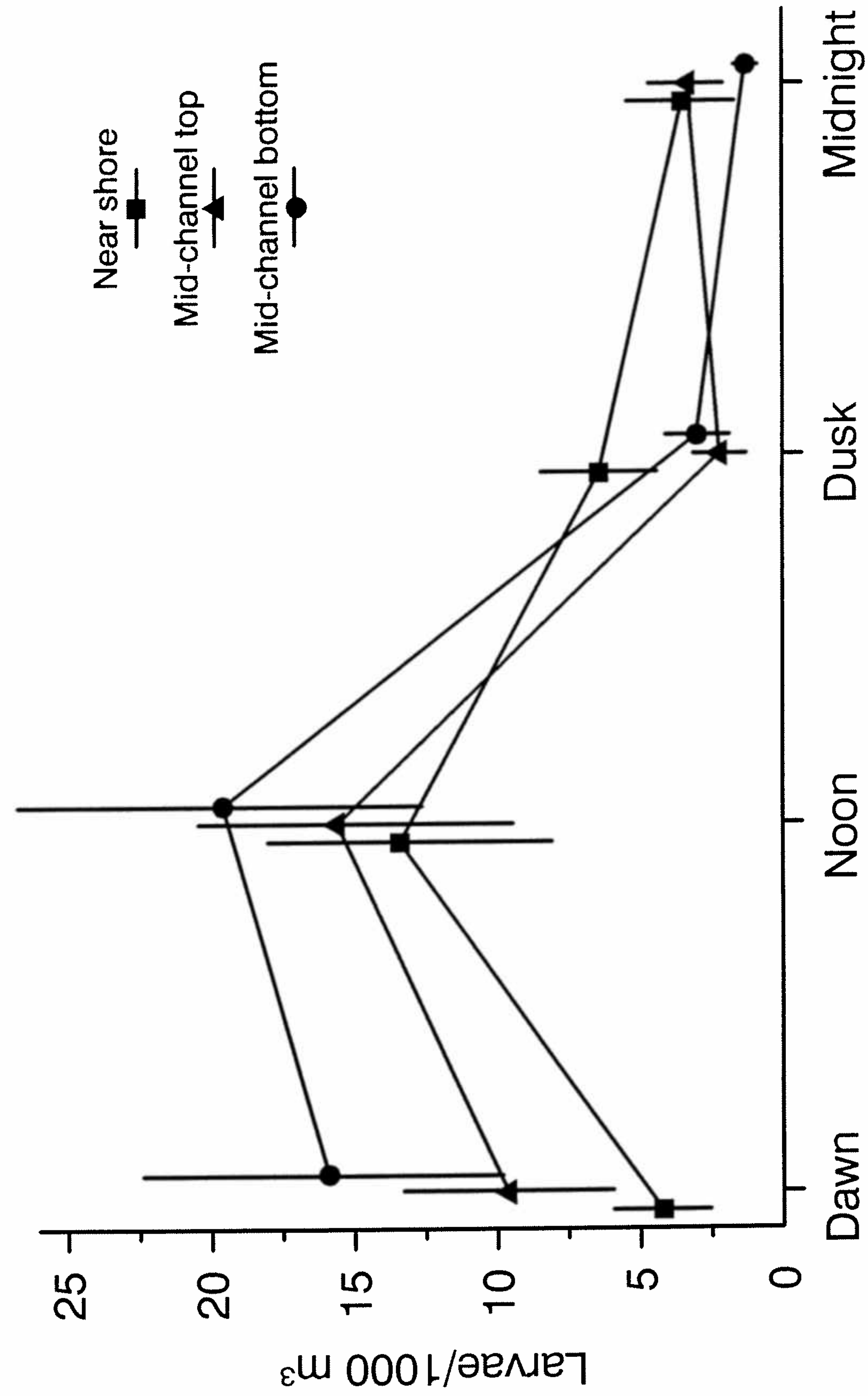

Near shore
Mid-channel top
Mid-channel bottom
Larvae/1000 m^3
0
5
10
15
20
25
Dawn
Noon
Dusk
Midnight

Fig. 6. Annual variation in mean abundance of Colorado squawfish larvae collected in summer drift net samples at dawn, noon, dusk, midnight in the lower Yampa River, 1992-1996 as predicted by a Poisson general linear model. Samples collected in clear and turbid water were pooled. To account for different discharge conditions in each year and make abundances directly comparable, densities of larvae were adjusted by the percentage of the river sampled each year.

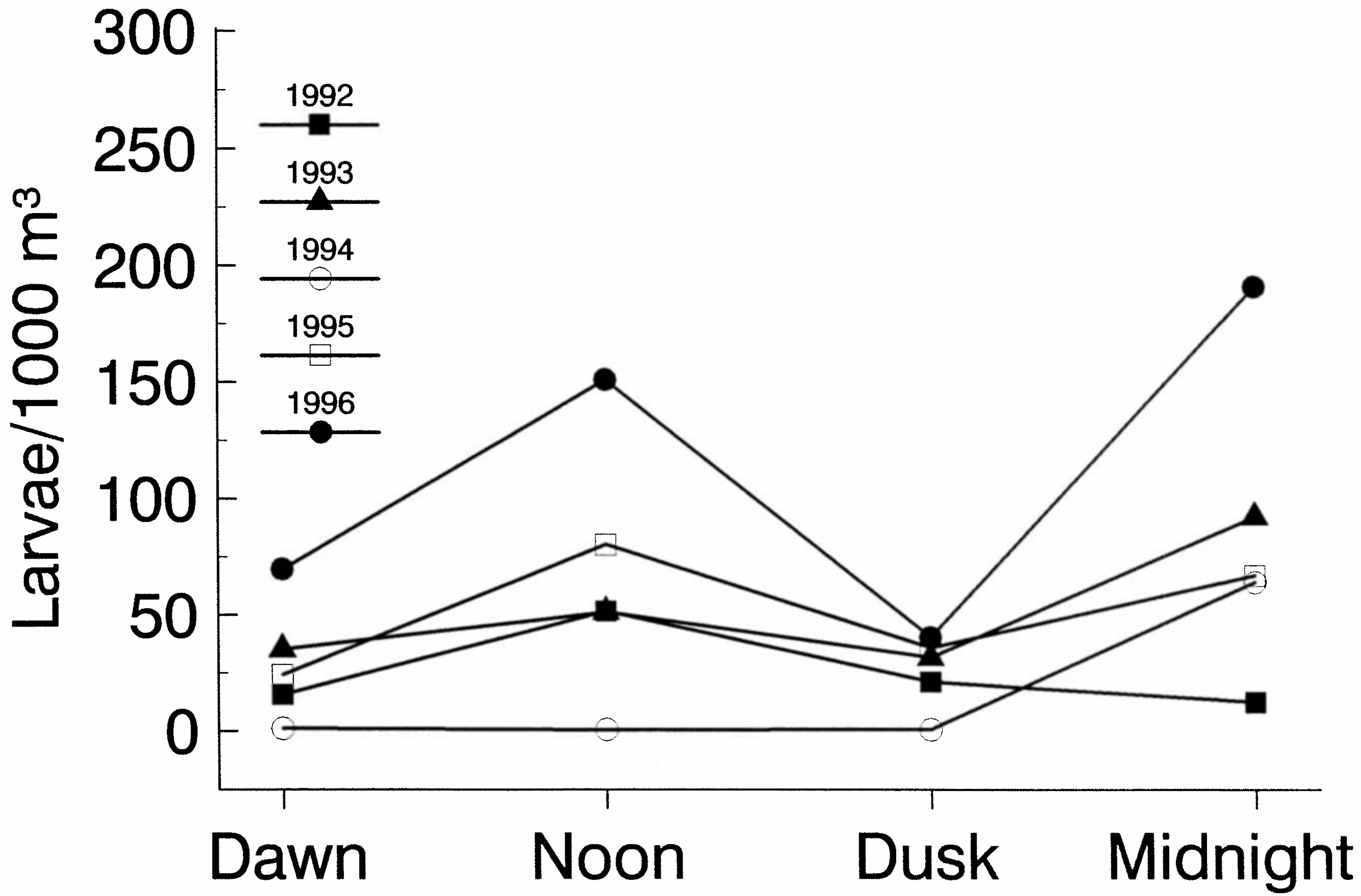

300
250
200
150
100
50
0
Larvae/1000 m3
1992
1993
1994
1995
1996
Dawn
Noon
Dusk
Midnight

Fig. 7. Mean abundance of Colorado squawfish larvae collected in dawn, noon, dusk, and midnight samples in turbid and clear conditions in the lower Yampa River, 1992-1996 as predicted by a Poisson general linear model. To account for different discharge conditions, abundance was adjusted by the percentage of the river that was sampled. Vertical lines through symbols represent ± 1 SE, some of which are obliterated by symbols.

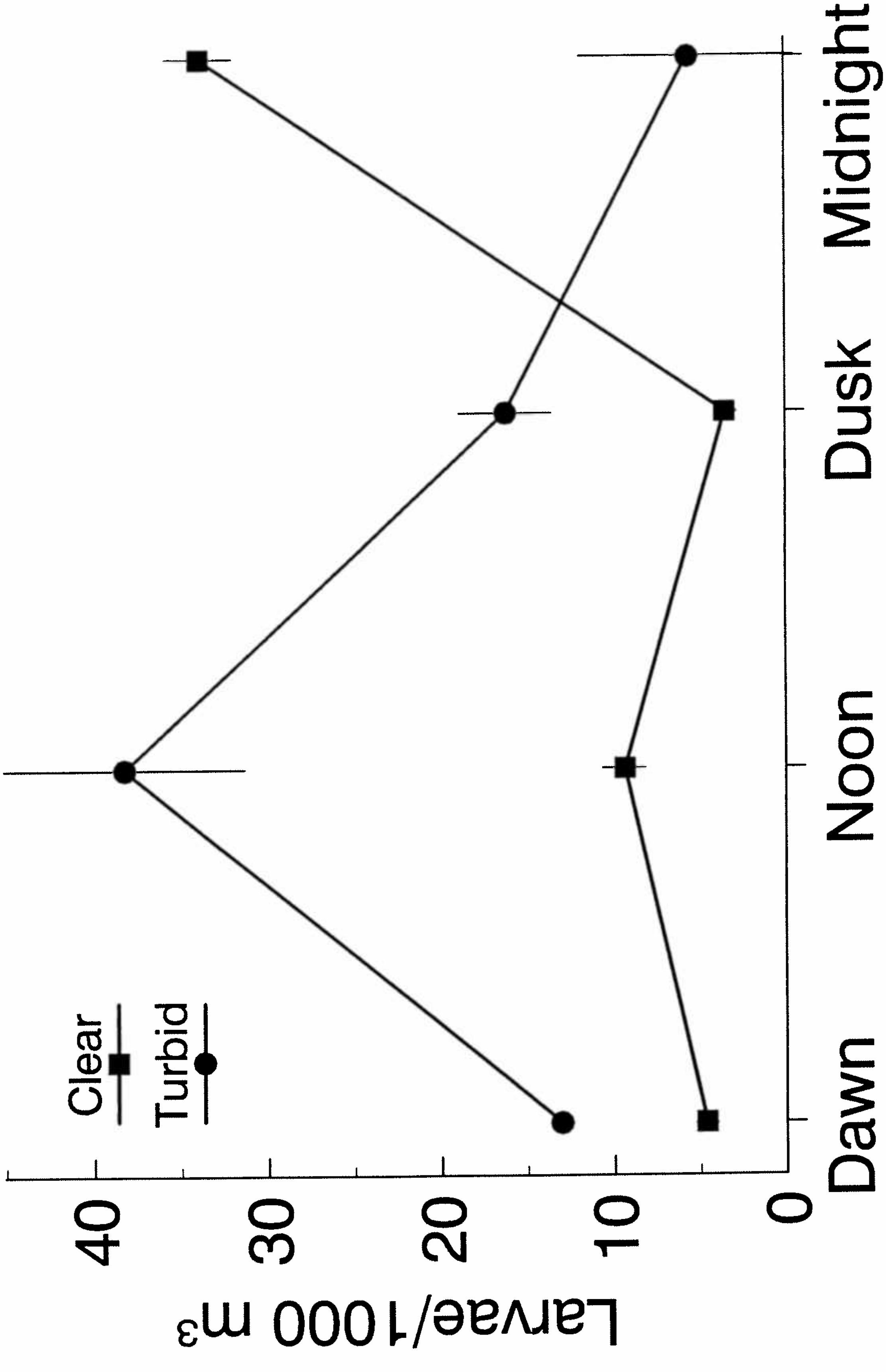

Larvae/1000 m3
0
10
20
30
40
Dawn
Noon
Dusk
Midnight
Clear
Turbid

Fig. 8. Annual abundance of Colorado squawfish larvae transported downstream past the middle Green River sampling station in summer 1990-1996, as a function of maximum average daily discharge in the Yampa River in spring. Numbers next to symbols denote years (e.g., 94 = 1994). Transport abundance was estimated by dividing the number of larvae captured each day in dawn nearshore drift net samples (n = 3), which was adjusted to an hourly rate and by the estimated proportion of total discharge that was sampled, and summing over all sampling days in the season. Discharge values are from the Deerlodge gauge (# 09260050) or the combined values of the Maybell (# 09251000) and Little Snake River (# 09260000) gauges.

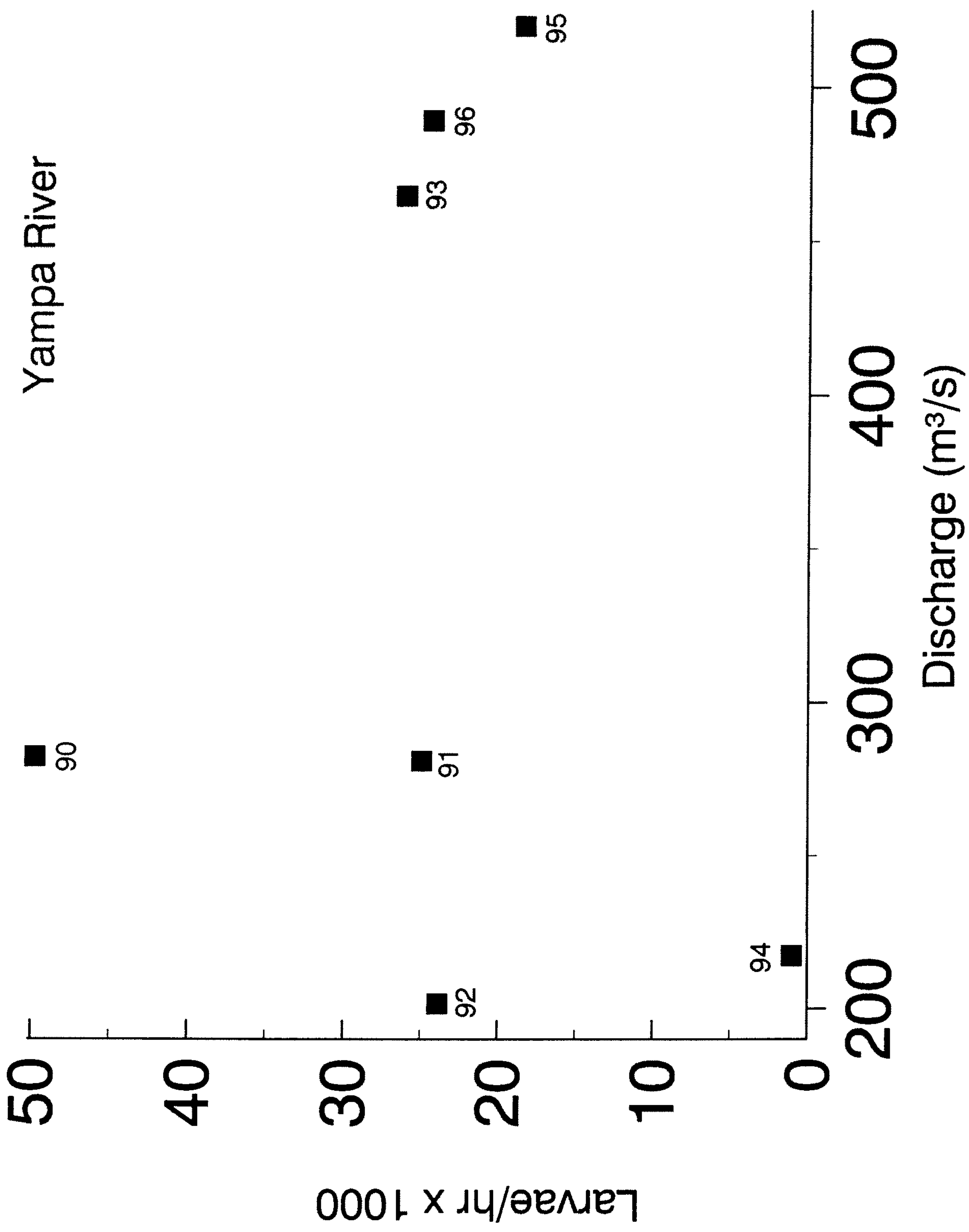

Yampa River
Larvae/hr x 1000
0
10
20
30
40
50
Discharge (m³/s)
200
300
400
500
90
91
92
93
94
95
96

Fig. 9. Annual abundance of Colorado squawfish larvae transported downstream past the lower Green River sampling station in summer 1991-1996, as a function of maximum average daily discharge in the Green River in spring. Numbers next to symbols denote years (e.g., 94 = 1994). Transport abundance was estimated by dividing the number of larvae captured each day in dawn nearshore drift net samples (n = 3), which was adjusted to an hourly rate and by the estimated proportion of total discharge that was sampled, and summing over all sampling days in the season. Discharge values are from the Green River at Green River gauge (# 09315000).

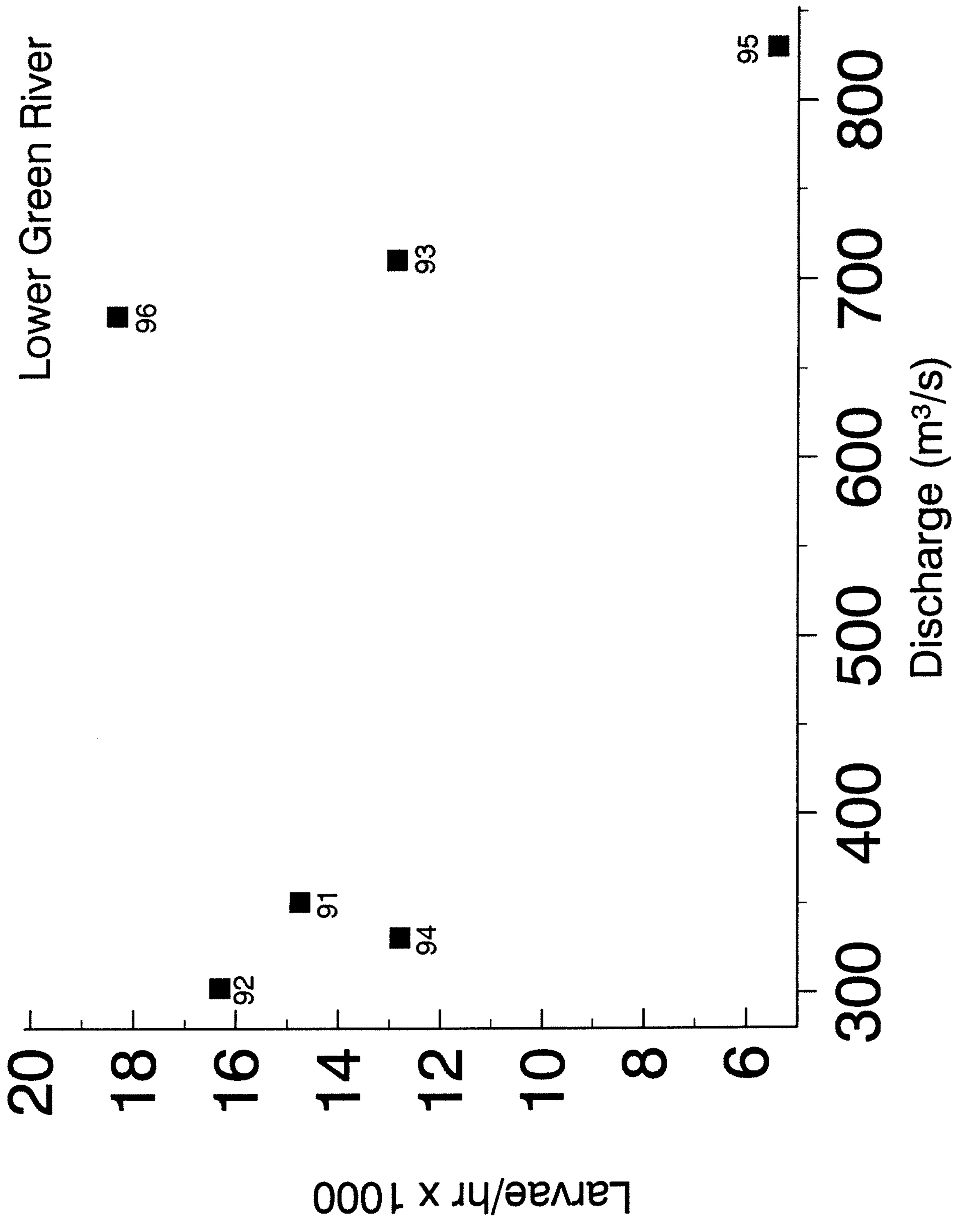

Lower Green River
Larvae/hr x 1000
20
18
16
14
12
10
8
6
Discharge (m³/s)
300
400
500
600
700
800
92
94
91
96
93
95

Fig. 10. Comparison of abundance of Colorado squawfish larvae transported downstream past the lower Yampa River sampling station and the middle Green River sampling station near Jensen, Utah, in summer 1990. Transport abundance was estimated by dividing the number of larvae captured in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled.

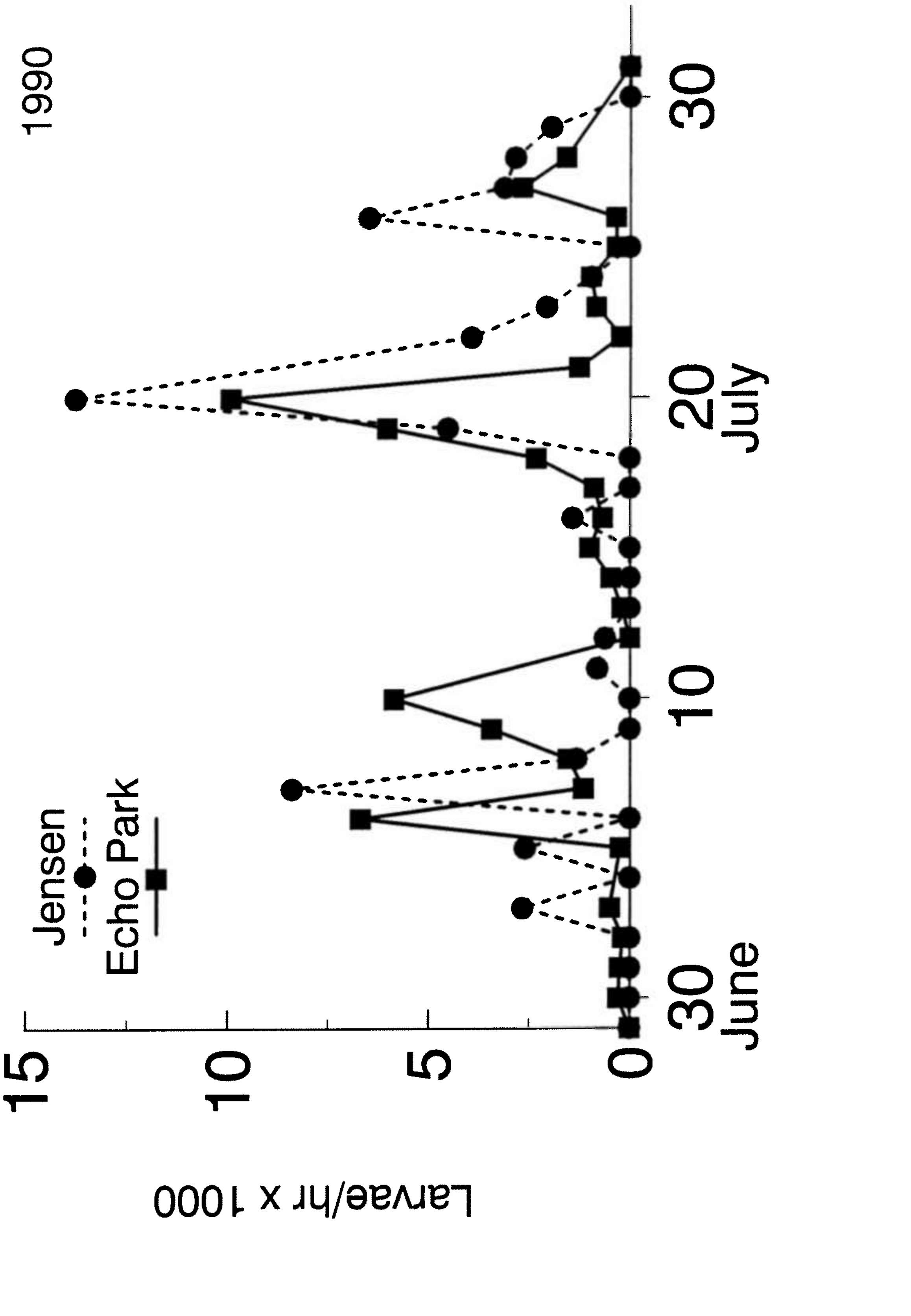

1990
Jensen
Echo Park
Larvae/hr x 1000
0
5
10
15
30
June
10
20
July
30

Fig. 11. Geometric mean abundance of juvenile Colorado squawfish in backwaters in the fall estimated by a standardized monitoring program in the middle Green River as a function of abundance of larvae transported downstream past the Yampa River sampling station in summer, 1990-1996. Numbers next to symbols denote years (e.g., 94 = 1994). Transport abundance of larvae was estimated by dividing the number captured each day in dawn nearshore drift net samples (n = 3), which was adjusted to an hourly rate and by the estimated proportion of total discharge that was sampled, and summing over all sampling days in the season.

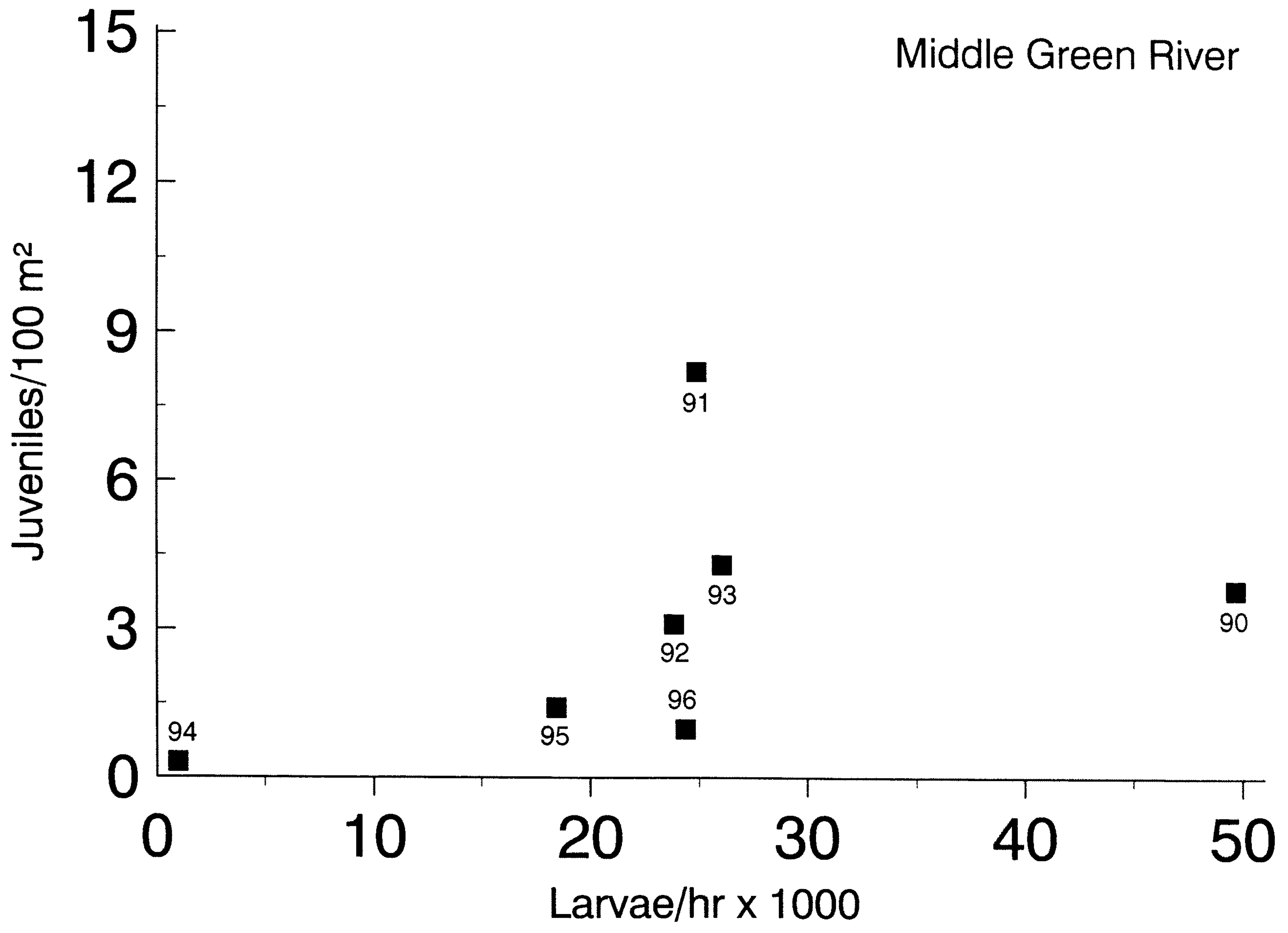
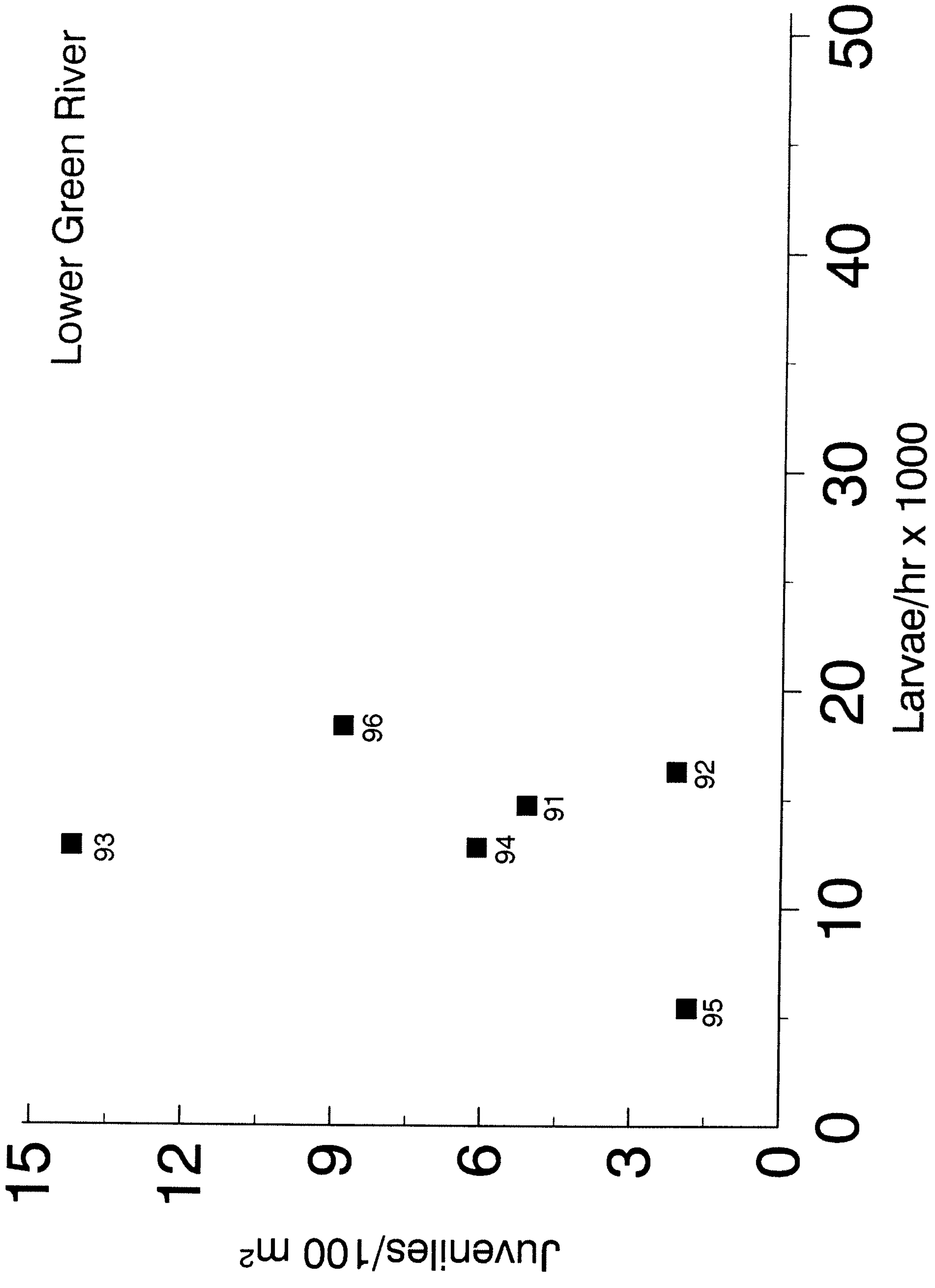

Middle Green River
Juveniles/100 m²
Larvae/hr x 1000
0
3
6
9
12
15
0
10
20
30
40
50
94
95
96
92
93
91
90

Fig. 12. Geometric mean abundance of juvenile Colorado squawfish in backwaters in the fall estimated by a standardized monitoring program in the lower Green River as a function of abundance of larvae transported downstream past the lower Green River sampling station in summer 1991-1996. Numbers next to symbols denote years (e.g., 94 = 1994). Transport abundance of larvae was estimated by dividing the number captured each day in dawn nearshore drift net samples (n = 3), which was adjusted to an hourly rate and by the estimated proportion of total discharge that was sampled, and summing over all sampling days in the season.


Lower Green River
Juveniles/100 m²
15
12
9
6
3
0
0
10
20
30
40
50
Larvae/hr x 1000
93
96
94
91
92
95