BIOLOGICALLY DEFENSIBLE FLOW RECOMMENDATIONS FOR THE MAINTENANCE AND ENHANCEMENT OF COLORADO SQUAWFISH HABITAT IN THE '15-MILE' REACH OF THE UPPER COLORADO RIVER DURING JULY, AUGUST AND SEPTEMBER

FINAL REPORT

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Introduction

The 15-mile reach of the Colorado River between Palisade, Colorado (River Mile 185), and the confluence of the Colorado and Gunnison rivers at Grand Junction (RM 170) is habitat for the endangered Colorado squawfish (*Ptychocheilus lucius*) and the very rare razorback sucker (*Xyrauchen texanus*). The general physical characteristics of the 15-mile reach as well as its use by these rare fishes were described in a report by Osmundson and Kaeding (Appendix A). That report concludes that the 15-mile reach is of primary importance as habitat for adults of these rare fishes, though some spawning of Colorado squawfish and razorback sucker may sometimes occur there under present conditions. In that report, the probable factors limiting the Colorado squawfish and razorback sucker populations in the 15-mile reach were identified.

In the present report, we outline a strategy for developing biologically defensible flow recommendations for the maintenance and enhancement of habitat for Colorado squawfish in the 15-mile reach. As part of that process, we identify logical objectives for flow-habitat management efforts in the 15-mile reach, investigate approaches to achieving these objectives, and we make preliminary flow recommendations intended to meet these objectives during July, August and September. We also suggest a general river-management scenario that may be one means of achieving these objectives and we discuss the development of flow recommendations for the remaining October-June period.

The ultimate goal of which this effort is a part, as directed by the Recovery Implementation Program (USFWS 1987), is the recovery and delisting of the Colorado squawfish. Although the razorback sucker is not addressed in the present report, it is believed that the preliminary flow recommendations that we propose will also benefit the recovery of this rare species. Comments received on drafts of this document, and our subsequent responses, have been incorporated into the text. Appendix E provides a list of persons who commented on drafts of this report.

A Strategy for Determining the Flow-habitat Requirements of the Endangered Fishes

The fundamental and obvious component of the aquatic ecosystem and of the habitats of fishes is water. However, quantifying the amount of water needed to sustain a fish population of a particular size is not an easy task. In an effort to understand the important factors that control the size of fish populations, numerous studies have attempted to relate population size to river discharge and other variables of the aquatic environment. Results of these studies have most often been less than definitive, with few important correlations being found between presumed important environmental variables and the size of the populations themselves (see for example Orth 1987). These and other studies have clearly shown that a complex array of interacting variables affects the size of fish populations, and that the relative importance of these variables may change over time and space. Thus, there can be no simple, universal formula to describe the relation between discharge or any other environmental variable and fish population size (also see Orth 1987). But the general lack of correlation with discharge should not be taken to mean that discharge has no important effect on the size of fish populations. In many instances, the carrying capacity of a river for a particular fish species may be less than that allowed by the volume of water alone--the actual physical space available to the fish. This is because other environmental variables--the availability of food or of hiding places away from predators, for example--become limiting factors on the fish population before the population reaches a size that is limited by the availability of physical space. However, if the volume of physical space is reduced because of reduction in river flow, there will be a point reached where the available habitat volume is effectively filled by the fish, food availability becomes inadequate or other structural or functional aspects of the habitat become limiting factors and further reductions in volume therefore will have a direct, negative effect on fish population size.

But how might flow recommendations to maintain or enhance important fish populations be developed despite the prevailing scarcity of empirical relations between discharge and the populations themselves? To begin, two critical concerns must be addressed. First, an understanding of the important factors limiting the fish population must be developed. If the important factors are related to flow, either directly or indirectly, then the factor vs. flow relation would provide a good basis for developing a flow recommendation. If the important limiting factors are not related to flow, there remains a need to identify flow values required to sustain some level of population because, as discussed earlier, as flow decreases there will be a point reached where further flow reduction will reduce the carrying capacity of the river and thereby reduce the maximum attainable population size. An extreme example of this might be a river flowing at 10 ft^3/sec but otherwise having suitable conditions for Colorado squawfish. Such a river will not sustain a population of 100, 10-pound adult squawfish per mile, although this might be an established population goal considered important to recovery.

Thus, the second critical concern that must be addressed is the level of population established as a recovery goal for the species. In its most simple form, this goal consists of a desired number of animals in the entire river or in a specified river reach. Establishment of such goals would require an objective assessment of the factors having important limiting effects on the population, and of the management options available to reduce or eliminate these effects.

A strategy for determining the flow-habitat requirements for the recovery of the endangered fishes has both short- and long-term components and may be portrayed diagrammatically as follows:

Implement Flow Recommendations

Short-term	Long-term
1. Identify probable limiting factors	1. Monitor populations, flows and habitats
2. Establish recovery goals (numerical population objectives)	2. Test and refine hypotheses
3. Develop provisional flow recommendations based on probable limiting-factor vs. flow relations	3. Refine recovery goals as needed
4. Develop testable hypotheses based on predicted population responses to implementation of provisional recommendations	4. Refine flow recommendations as needed

The short-term effort should be accomplished within two years, after adequate baseline data on the fish populations and their habitats has been collected. Assuming that the flow recommendations that result from the short-term effort are implemented, the long-term monitoring, hypothesis-testing and hypothesis-refinement effort will require many years. Moreover, preliminary results of this long-term effort may necessitate refinement of flow recommendations, recovery goals and hypotheses to be tested. The outcome of the long-term effort, however, should be a good understanding of the interactions of the fish population and the important environmental variables that affect it, including river discharge.

Assessment of flow recommendations, the long-term process

Flow recommendations need to be assessed in terms of the actual flows that are provided after implementation of the recommendation, the resulting availability (in terms of quantity and quality) of the habitat, and the subsequent response of the fish population to the anticipated habitat changes. Thus monitoring of flows, habitats and fishes is essential to this assessment. Moreover, as additional data are collected and further understanding of important factors affecting the fish population is gained, it may be necessary to adjust flow recommendations or recovery objectives. Of course, the most important concern in any assessment is the response of the fish population to implementation of the flow recommendation. Such responses will determine whether the population is increasing toward the recovery goals necessary for delisting of the species.

Assessment of the flow recommendation thus becomes a matter of determining whether the predicted responses occur in both the habitat and the population of the endangered species. Responses of the fish population to implementation of the recommended flows may include changes in fish growth, movement, spawning time, population size, etc. It must be clearly recognized, however, that adequate flows by themselves may not bring about the recovery of the fish. Such flows must be viewed as only one, albeit major, step in the recovery process. Failure of the population to increase after implementation of flow recommendations would not necessarily mean the flow regime is inadequate. Rather, it might indicate that the anticipated population response was too small to be detected or that our management efforts must be directed toward additional important factors controlling the population. Moreover, because Colorado squawfish apparently exhibit both long-term as well as short-term (migrational) movements throughout their life history, such management efforts may need to include other river reaches.

The objectives for recovery and delisting of the Colorado squawfish will probably include the maintenance of certain numerical levels of self-sustaining adult fish in specified river reaches. Thus the size of the adult population will be tracked as part of a monitoring program. Ultimately, however, the success of this and other recovery efforts under the Recovery Implementation Program needs to be based on achieving and maintaining a self-sustaining adult population size (number of animals) considered necessary for species recovery and delisting. This requires that numerical population targets or recovery goals be established for specific river reaches. These targets could be actual population sizes or catch-rate statistics, direct indicators of population size.

Flow-habitat Management Objectives for the 15-mile Reach

Osmundson and Kaeding (Appendix A) presented data on the use of the 15-mile reach by the endangered fishes and summarized information on several environmental variables that might now be limiting the populations of those fishes or might become important limiting factors as we endeavor to create conditions important to the recovery of the Colorado squawfish. In this report section, we briefly review those environmental variables, discuss their importance to the recovery of Colorado squawfish, and establish flow-habitat management objectives for each of the limiting factors that have been identified in the 15-mile reach. Those flow-habitat management objectives are based on the habitat requirements that we believe are important to the recovery of Colorado squawfish in the upper Colorado River, as directed by the Recovery Implementation Program.

Physical habitat

The 15-mile reach is occupied habitat for Colorado squawfish and razorback sucker, species that cannot be recovered and delisted if such habitats are not maintained and improved. In their earlier report, Osmundson and Kaeding presented data that indicated Colorado squawfish extensively use deep runs and pools in the 15-mile reach during July, August and September (see, for example, Figure 22, Appendix A). Although the present availability of such habitat may not now limit the size of the adult Colorado squawfish population of the 15-mile reach, such availability nonetheless might prevent an increase in the population toward the recovery goals that need to be established. Because the numerical recovery objectives for the self-sustaining adult Colorado squawfish populations have yet to be established and the relation between the size of such populations and habitat quantity has yet to be determined, it is prudent to seek a near-maximum quantity of habitat for the adult fish and thereby eliminate the availability of such physical habitat as an impediment to the achievement of recovery goals.

The argument that maintenance of a high availability of habitat for adult Colorado squawfish is important to recovery is not entirely speculative. There are data that suggest the availability of habitat for adult fish could have an important effect on the size of the adult population. That argument is based on the observation that Colorado squawfish can make extensive spawning movements and, more important, return to their former home range subsequent to spawning (e.g., Miller et al. 1983). The return of Colorado squawfish to feeding/wintering areas occupied during the non-spawning season is remarkable because during its accomplishment the fish pass through river reaches that contain suitable feeding/wintering habitat--habitats so used, in fact, by other Colorado squawfish. Because such migrations require the fish to expend considerable energy, one must ask why the adult squawfish simply do not remain in the adult feeding/wintering habitats nearer their spawning area. This presumably would conserve energy and thus would be advantageous to the survival of the individual fish. But the adults return to their former feeding/wintering areas after spawning. The most dramatic example of this homing behavior is the return of adult Colorado squawfish to the upper White River, after they have traveled more than 150 miles to spawning sites on the lower Yampa River (Miller et al. 1983). Numerous other, less dramatic examples have been recorded throughout the upper basin.

A possible explanation for this major expenditure of energy to return to former feeding/wintering areas is that it represents a needed disbursal of the adult population throughout the range of the species. Without such disbursal, negative interactions--

agonistic behavior or competition for food, space or other limited resources--might occur among adults or perhaps between adult Colorado squawfish and other fish species. It might therefore be hypothesized that the energy cost involved in returning to former feeding/wintering areas is ultimately less than that which the fish would experience if it attempted to reside in a new feeding/wintering area subsequent to spawning. As Olson et al. (1978) suggested for walleye (Stizostedion vitreum), Colorado squawfish might seek suitable adult habitats as they mature and establish residency in areas where habitat not occupied by other squawfish is available. A knowledge of the location and characteristics of the particular feeding/wintering area that it selects is then retained by the fish. Such memory thus allows the fish to return to this area after spawning elsewhere. If this hypothesis is correct, the loss of a river reach that includes feeding/winter habitat for adult Colorado squawfish, the 15-mile reach for example, could result in a real reduction in the adult squawfish population or--of equal or greater importance--in the potential size of the population that may be achieved as a result of recovery efforts.

Our flow-habitat management objective for July, August and September is to maintain a near-maximum amount (95% or more) of the aggregate run, pool and riffle habitat in the 15-mile reach. In so doing, we believe each of these three important habitat types will occur in sufficient quantity to assure that their availability will not prevent the achievement of recovery goals for Colorado squawfish.

Temperature

Kaeding and Osmundson (Appendices A & B) developed the hypothesis that the relative scarcity of temperatures near the physiological optimum of Colorado squawfish (25 C) is an important limiting factor in the 15-mile reach, as well as elsewhere in the upper Colorado River. Cool water temperatures reduce the growth rate of Colorado squawfish and cause squawfish spawning to occur relatively late in the year. This results in age-0 Colorado squawfish that are small when they enter their first winter. Based on studies of other fish species, the rate of over-winter survival of such small age-0 fish is low. Moreover, the slow growth of Colorado squawfish in the 15-mile reach and elsewhere in the upper Colorado River lengthens the period when the young squawfish are vulnerable to predators and other sources of mortality. Such slow growth thus reduces the likelihood that the fish will survive to maturity. A detailed account of the development of the hypothesis that temperature-mediated slow-growth is an important limiting factor for Colorado squawfish in the upper Colorado River is provided by Kaeding and Osmundson (Appendix B). Our flow-habitat management objective for temperature in the 15-mile reach is to increase the length of the growing season for Colorado squawfish and to advance their time of spawning, with the ultimate goal being larger age-0 Colorado squawfish in the Grand Valley at the end of their first growing season. Age-0 squawfish as long as the ones commonly found in the Green River in late fall of most years (50+ mm TL) would be desirable.

The scarcity of temperatures near the physiological optimum (25 C) of Colorado squawfish is not the only significant factor affecting the reproduction and early-life history and survival of this species in the 15-mile reach or elsewhere in the upper

Colorado River. The decline of Colorado squawfish in the upper Colorado is attributable to the interaction of these and other negative effects (Appendix B). Only in relatively few river reaches can the decline be attributed to a single adverse factor, such as the appreciable modification of the natural temperature regime immediately downstream from some reservoirs.

Introduced fishes

Introduced fishes no doubt have a negative effect on the endangered fishes in the 15-mile reach and elsewhere in the upper Colorado River. This may be especially true for the introduced predator species, whose negative effects on the Colorado squawfish may be enhanced by the slow early-life growth of squawfish (Appendix B). Moreover, some introduced species may successfully compete with Colorado squawfish for limited resources, thereby lowering the carrying capacity of the stream for squawfish. The flow-habitat management objective for introduced fishes is to reduce the negative influence of the introduced fishes on the Colorado squawfish to the maximum extent possible.

Water clarity

Osmundson and Kaeding (Appendix A) provided data that suggested the periodic high clarity of the water in the 15-mile reach may limit the use of shallow waters by adult Colorado squawfish. The fish were more likely to use shallow waters when the water was turbid than they were when the water was clear. Our flow-habitat management objective is to increase turbidity (decrease clarity) in the 15-mile reach.

Agricultural pesticides

Agricultural pesticides were identified as a possible limiting factor for the endangered fishes in the 15-mile reach (Appendix A). Our management objective is to (a) determine the pesticides that present important problems for Colorado squawfish and (b) reduce the levels of these pesticides in the river to the maximum extent possible.

Angling mortality

Fishing is a popular recreational use of the upper Colorado River, including the 15-mile reach. Most angling on the Colorado in the Grand Valley is for channel catfish (Ictalurus punctatus). Catfish fishermen sometimes catch and kill adult-size Colorado squawfish (U. S. Fish and Wildlife Service, unpublished data). The degree that such angling mortality affects the maintenance of the Colorado squawfish population in the Grand Valley and elsewhere is unknown. Our management objective is to minimize angling-related mortality of Colorado squawfish to the maximum extent possible.

Approaches for Achieving Flow-habitat Management Objectives for the 15-mile Reach

In this section, we identify ways to achieve the flow-habitat management objectives that we have described for each of the important limiting factors discussed above.

Physical habitat

The Physical Habitat Simulation method (PHABSIM) uses data on the habitat use of Colorado squawfish to predict how the availability of such habitat will be affected by changes in flow. An important component of the PHABSIM model is the habitat suitability index (HSI) curve. Hann and Rose (Appendix C) used data collected from radio-tagged adult Colorado squawfish in run, pool and riffle habitats in the 15-mile reach during July, August and September to create HSI curves for water depth and velocity, as well as for the substrates used by squawfish. Smoothed curves were fitted to the empirical data for depth and velocity in two ways. In the first (Set A), the smoothed curve was closely fitted to the raw-data histogram and its peak (suitability value of one) was made to correspond with the modal group of data. In the second (Set B), both the mean of the empirical data and the modal group in the raw-data histogram were given a suitability value of one.

The approach used to create curve Set B was justified because each of our sampling gears, including radiotelemetry, works more efficiently in shallow (often low-velocity) habitats. For example, after the seasonal high flows began to recede in 1988 and continuing through the summer, field crews reported that radio-tagged Colorado squawfish had begun the extensive use of deepwater habitat and that radio contact with these fish often could be established only when the boat passed nearly over them. Thus the likelihood that such fish could be missed was significant. We believe the curves fitted to the empirical data such that the mean value is also given a suitability of one (Set B) may more accurately represent the actual habitat use of Colorado squawfish than do the empirical data alone because they compensate for some of the effect of this sampling bias.

Colorado squawfish, like all animals, need to conserve energy in order to survive. Because maintaining position in a current requires the expenditure of energy for swimming, Colorado squawfish and other riverine fishes most often occupy microhabitats with little or no current velocity. Viewed in isolation, data collected from such areas would suggest that habitats with little or no current velocity are all that Colorado squawfish require. This would be a grave misconception, however. An important element of the complete habitat of squawfish is the nearby habitats that often have greater current velocities than do the habitats actually occupied by the squawfish. These higher-velocity habitats can be important to the production and transport of food organisms, they may be used by important forage-fish species, they could include the areas of cobble substrate considered necessary for squawfish spawning, they may be important to nutrient and oxygen transport and general aeration of the river, and so on. These adjacent habitats are important components of the habitat mosaic that constitutes the complete habitat of Colorado squawfish. If only the low-velocity areas often occupied by squawfish are used in the PHABSIM process, the important higher-velocity, surrounding habitats will not be represented. Our approach to developing the smoothed HSI curve for velocity--wherein both the modal data group and the overall mean are given a suitability index value of one (Set B)--helps to assure that those adjacent, higher-velocity habitats are represented in the PHABSIM model.

There was no important difference between the habitat vs. discharge relations that resulted from application of HSI curve Sets A and B (Table 1). With both curves, the maximum aggregate amount of run, pool and riffle habitat for adult Colorado squawfish occurred at 900-1100 ft^3/sec. Ninety-five percent or more of this maximum, as determined by interpolation, occurred between 712 and 1177 ft^3/sec when the Set A HSI curves were used, and between 675 and 1177 ft^3 with Set B.

Table 1. Habitat (ft^2/1000 linear ft of stream) vs. discharge (ft^3/sec) relations at the Palisade PHABSIM site for July, August and September, based on two sets of habitat suitability index (HSI) curves. (Taken from Hann and Rose, Appendix C.)

	HSI Curve			
	Set A		Set B	
Discharge	Habitat	(% max.)	Habitat	(% max.)
300	56,028	(69)	57,592	(69)
450	67,297	(83)	72,157	(87)
600	73,952	(92)	78,080	(94)
750	77,237	(96)	79,808	(96)
900	80,319	(100)	83,254	(100)
1100	80,701	(100)	83,059	(100)
1300	70,046	(87)	72,721	(87)
1500	64,367	(80)	66,760	(80)

Temperature

In exploring the means to increase water temperatures during July, August and September in the 15-mile reach, we studied the general relation between mean-monthly discharge and mean-monthly temperature for each of these months over a 23-year period (1959-81). Those data were available from the U. S. Geological Survey gage at Cameo, about nine miles upstream from the 15-mile reach. Results showed a strong, negative relation (r = -.93) between flow and temperature in July (Figure 1), with each 1,500 ft^3/sec reduction in flow resulting in an approximate 1 C increase in temperature. Similar trends occurred in August and September, though the statistical relations for these months were appreciably weaker than they were for July. These analyses strongly suggested that one way to increase water temperature in the 15-mile reach in July would be to reduce flows. July is typically the last month of seasonal runoff in the upper Colorado and flows are relatively high.

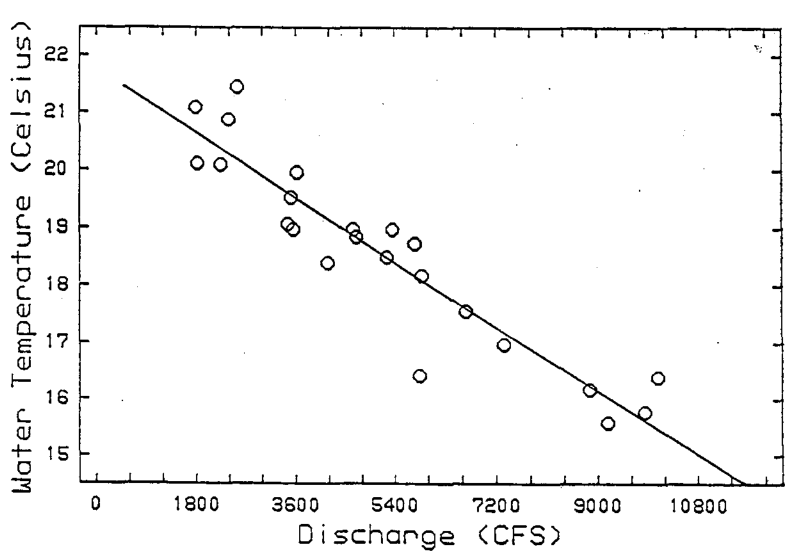

Figure 1. Relation between mean-monthly discharge and mean-monthly temperature of the upper Colorado River in July at Cameo, Colorado.

Introduced fishes

Introduced fishes probably have important negative effects on the endangered fishes in the 15-mile reach and elsewhere in the Colorado River. Because many of the introduced species are best adapted for life in lakes and ponds, they are most often found in backwaters in the Colorado River. High flows during spring runoff may help reduce the populations of these introduced fishes in the river, or perhaps prevent them from becoming established there. Native southwestern fishes--unlike most non-native fishes--are believed to be adapted to the large seasonal floods that characterize many rivers of the southwestern United States (Minckley and Meffe 1987).

Opportunities for flow-mediated management of undesirable introduced fishes might occur during the high-flow period of May and June, but apparently not during the July-September period that is the focus of the present effort. McAda and Kaeding (1989a) recently drafted a report describing the relations between maximum-annual river discharge and the relative abundance of age-0 Colorado squawfish and other fish species in the upper Colorado River. Their preliminary results indicate possible important relations between peak annual discharge and the relative abundance of age-0 Colorado squawfish and several other fish species. In another report, however, McAda and Kaeding (1989b) analyzed the habitat use of age-0 Colorado squawfish and compared it to those of several other native and non-native fishes also collected by seines. They found that some differences in habitat use occurred between squawfish and the sympatric native fishes but generally not between squawfish and the non-native fishes. Because the non-native fishes are believed to be those most likely to have significant negative effects on age-0 Colorado squawfish, results of McAda and Kaeding's (1989b) analyses indicate that it may not be possible to create habitat conditions both suitable for young squawfish and unsuitable for these non-native species. Which of the non-native species present important problems for Colorado squawfish is not yet known, however. Such necessary information will begin to be collected as part of laboratory studies that we will initiate this year.

Water clarity

No technically feasible or institutionally acceptable means of augmenting turbidity (reducing water clarity) in the 15-mile reach was found. River turbidity is largely dependent upon the erodibility of the soils and the extent of the erosional forces acting in the drainage basin. Although turbidity therefore could be increased by encouraging poor land-use practices that lead to increased soil erosion, obviously such options cannot be seriously considered. However, the data provided by Osmundson and Kaeding (Appendix A) suggest the possible negative effects of high water clarity on the habitat use of Colorado squawfish can be at least partly offset by the provision of deepwater habitats.

Agricultural pesticides

Definitive conclusions regarding the possible importance of agricultural pesticides as a limiting factor for Colorado squawfish in the 15-mile reach are not yet possible. Surveys of pesticides that occur in the upper Colorado River need to be made, and the literature on the effects of these pesticides on fishes needs to be closely reviewed. If pesticides are found in the river and their negative effect on Colorado squawfish and other species is suspected, regulatory agencies should institute appropriate corrective measures. In addition, if pesticides are important, it seems their effects on squawfish--either directly or indirectly as the result of biomagnification of toxins as they move up the trophic pyramid--would be most significant during periods of extremely low flow, when pesticides would be most concentrated in the river. Thus, augmentation of flows during such periods should serve to reduce whatever risk agricultural pesticides may now pose to the endangered fishes.

Angling mortality

The 15-mile reach should be made part of an Information and Education effort directed particularly toward fisherman who might inadvertently capture Colorado squawfish or other endangered fishes. Elements of such a program should include appropriate signage at fisherman access points, education programs for presentation before various citizen groups, and informational brochures and related materials. Such an I & E effort is being planned for the entire upper basin as part of the Recovery Implementation Program.

Flow-management Recommendation for the 15-mile Reach

Our development of biologically defensible flow recommendations for the maintenance and enhancement of Colorado squawfish habitat during July, August and September is based on the attainment of three important objectives. In keeping with the directives of the Recovery Implementation Program, these objectives are considered important components of the effort to recover the Colorado squawfish in the upper Colorado River basin. The objectives are:

1. to provide a near-maximum (95% or more) aggregate amount of run, pool and riffle habitat for adult Colorado squawfish, and
2. to enhance the first-year growth of age-0 Colorado squawfish in the Grand Valley area by increasing water temperatures in the 15-mile reach.
3. While achieving 1 and 2 above, do not compromise our ability to meet other flow-habitat requirements that need to be determined for the remainder of the year.

A flow "window" of 700-1200 ft^3/sec during July, August and September will meet the objectives outlined above. During the relatively infrequent dry years (80% exceedence in total July-September discharge) when this flow recommendation will be more difficult to meet, 600 ft^3/sec (92-94% of the maximum aggregate amount of run, pool and riffle habitat; Table 1) is considered an adequate lower limit for this flow window. As opposed to a single-value flow recommendation, the flow window that results from application of our 95% criterion (objective 1, above) provides necessary flexibility for the process of meeting flow needs. This flow recommendation is targeted at the PHABSIM site in the 15-mile reach (RM 181.4) near Palisade, Colorado, with the assumption that the provision of adequate flows at that location will also result in adequate flows in the remainder of the 15-mile reach.

Importance to Colorado squawfish of implementing the flow recommendation

Implementation of the flow recommendation will benefit the recovery of the Colorado squawfish population in two important ways. First, the recommended flows will provide a near-maximum aggregate amount of run and pool habitat for adult Colorado squawfish, habitats whose availability may importantly affect the recovery potential of the species. The size of the adult squawfish population will be an important measure of the success of recovery efforts. Implementation of this recommendation will assure that the growth of the adult population will not be constrained by the availability of habitat for adult Colorado squawfish.

Secondly, July water temperatures in the 15-mile reach warmer than those that occurred historically should result in earlier spawning of Colorado squawfish in the Grand Valley, a longer first-year growing season for the resulting young, and larger age-0 squawfish at the end of their first growing season. These larger age-0 fish should result in greater recruitment to the adult population (Appendix B). Recruitment that may now occur to the adult Colorado squawfish population in the 15-mile reach is likely the result of spawning in river areas downstream from the 15-mile reach. Our flow recommendation for July will improve conditions for early-life growth of Colorado squawfish not only in the 15-mile reach but in these areas downstream as well. The magnitude of the temperature increase that would result from implementation of the flow recommendation is demonstrated by application of the Service's temperature model. Model output showed that a flow of 700 ft^3/sec in July would result in an average increase of 2.41 C during the first half of the month and of 1.51 C during the last half. Because the Service temperature model was recently recalibrated, the extent of this temperature increase is less than that reported in drafts of this report (Mike Brewer, U. S. Fish and Wildlife Service, personal communication). Temperature augmentation in July also occurred at 1200 ft^3/sec, and to a lesser degree in August with a discharge of 700 ft^3/sec. In September, though flows would often be increased with implementation of our recommendation, average temperatures would decline less than one degree (Table 2; Figure 2).

The dry-year recommendation of 600 cfs would reduce the amount of adult habitat somewhat (Table 1); however, because of the low frequency of this event (one year in five) we do not believe it will have a significant negative effect on the Colorado squawfish population. A flow of 600 ft^3/sec increases river temperatures slightly above those that would occur with a river discharge of 700 ft^3/sec (Table 2).

Table 2. Comparison of mean historic temperatures for semi-monthly periods with temperatures that would have occurred in the 15-mile reach under flows of 1,200, 700 and 600 ft^3/sec.

	JULY 1-15			JULY 16-31			AUGUST 1-15			AUGUST 16-31			SEPTEMBER 1-15			SEPTEMBER 16-30		
YEAR	1200	HIS	DIFF	1200	HIS	DIFF	1200	HIS	DIFF	1200	HIS	DIFF	1200	HIS	DIFF	1200	HIS	DIFF
1978	19.84	19.29	0.55	21.36	21.90	-0.54	20.33	23.96	-3.63	18.66	20.63	-1.97	18.80	19.69	-0.89	17.16	16.55	0.61
1979	19.31	17.65	1.66	20.52	20.60	-0.08	19.90	20.91	-1.01	17.87	18.58	-0.71	18.29	19.13	-0.84	17.56	17.30	0.26
1980	20.63	19.36	1.27	21.56	22.40	-0.84	21.54	25.07	-3.53	19.32	21.87	-2.55	17.81	21.25	-3.44	16.95	18.87	-1.92
1981	21.14	22.75	-1.61	20.99	24.69	-3.70	20.14	21.50	-1.36	20.74	21.70	-0.96	18.93	20.76	-1.83	17.76	18.51	-0.75
1982	19.89	18.35	1.54	22.18	21.49	0.69	21.32	20.41	0.91	20.88	19.80	1.08	17.65	16.81	0.84	17.19	15.78	1.41
1983	16.92	15.60	1.32	21.27	18.06	3.21	22.65	19.73	2.92	21.82	20.59	1.23	20.74	20.24	0.50	16.67	18.48	-1.81
1984	20.55	16.23	4.32	22.59	18.52	4.07	23.06	20.51	2.55	22.40	20.44	1.96	21.55	20.69	0.86	18.91	19.61	-0.70
1985	22.54	19.91	2.63	21.95	19.84	2.11	23.30	23.01	0.29	22.06	22.26	-0.20	20.02	22.51	-2.49	18.22	21.81	-3.59
1986	19.25	17.90	1.35	20.22	19.81	0.41	21.54	21.42	0.12	21.14	20.49	0.65	18.78	19.98	-1.20	15.75	18.09	-2.34
Sum:			13.03			5.33			-2.74			-1.47			-8.49			-8.83
Mean Diff:			1.45			0.59			-0.30			-0.16			-0.94			-0.98

	JULY 1-15			JULY 16-31			AUGUST 1-15			AUGUST 16-31			SEPTEMBER 1-15			SEPTEMBER 16-30		
YEAR	700	HIS	DIFF	700	HIS	DIFF	700	HIS	DIFF	700	HIS	DIFF	700	HIS	DIFF	700	HIS	DIFF
1978	21.00	19.29	1.71	22.36	21.90	0.46	21.23	23.96	-2.73	19.34	20.63	-1.29	19.21	19.69	-0.48	17.08	16.55	0.53
1979	20.34	17.65	2.69	21.50	20.60	0.90	20.78	20.91	-0.13	18.43	18.58	-0.15	18.90	19.13	-0.23	17.91	17.30	0.61
1980	21.58	19.36	2.22	22.63	22.40	0.23	22.47	25.07	-2.60	19.81	21.87	-2.06	18.30	21.25	-2.95	17.18	18.87	-1.69
1981	22.26	22.75	-0.49	22.02	24.69	-2.67	21.02	21.50	-0.48	21.44	21.70	-0.26	19.30	20.76	-1.46	18.03	18.51	-0.48
1982	20.72	18.35	2.37	23.06	21.49	1.57	22.02	20.41	1.61	21.48	19.80	1.68	17.98	16.81	1.17	17.34	15.78	1.56
1983	18.08	15.60	2.48	22.26	18.06	4.20	23.59	19.73	3.86	22.36	20.59	1.77	21.14	20.24	0.90	16.95	18.48	-1.53
1984	21.30	16.23	5.07	23.26	18.52	4.74	23.75	20.51	3.24	23.19	20.44	2.75	22.35	20.69	1.66	19.68	19.61	0.07
1985	23.36	19.91	3.45	22.61	19.84	2.77	24.18	23.01	1.17	22.48	22.26	0.22	20.77	22.51	-1.74	19.47	21.81	-2.34
1986	20.08	17.90	2.18	21.22	19.81	1.41	22.24	21.42	0.82	21.51	20.49	1.02	19.63	19.98	-0.35	16.89	18.09	-1.20
Sum:			21.68			13.61			4.76			3.68			-3.48			-4.47
Mean Diff:			2.41			1.51			0.53			0.41			-0.39			-0.50

	JULY 1-15			JULY 16-31			AUGUST 1-15			AUGUST 16-31			SEPTEMBER 1-15			SEPTEMBER 16-30		
YEAR	600	HIS	DIFF	600	HIS	DIFF	600	HIS	DIFF	600	HIS	DIFF	600	HIS	DIFF	600	HIS	DIFF
1978	21.36	19.29	2.07	22.70	21.90	0.80	21.54	23.96	-2.42	19.58	20.63	-1.05	19.41	19.69	-0.28	17.17	16.55	0.62
1979	20.66	17.65	3.01	21.83	20.60	1.23	21.08	20.91	0.17	18.65	18.58	0.07	19.13	19.13	0.00	18.07	17.30	0.77
1980	21.90	19.36	2.54	22.98	22.40	0.58	22.80	25.07	-2.27	20.03	21.87	-1.84	18.51	21.25	-2.74	17.33	18.87	-1.54
1981	22.61	22.75	-0.14	22.36	24.69	-2.33	21.33	21.50	-0.17	21.71	21.70	0.01	19.49	20.76	-1.27	18.19	18.51	-0.32
1982	21.01	18.35	2.66	23.38	21.49	1.89	22.29	20.41	1.88	21.73	19.80	1.93	18.14	16.81	1.33	17.46	15.78	1.68
1983	18.46	15.60	2.86	22.59	18.06	4.53	23.94	19.73	4.21	22.63	20.59	2.04	21.36	20.24	1.12	17.11	18.48	-1.37
1984	21.55	16.23	5.32	23.52	18.52	5.00	24.03	20.51	3.52	23.49	20.44	3.05	22.64	20.69	1.95	19.94	19.61	0.33
1985	23.64	19.91	3.73	22.87	19.84	3.03	24.50	23.01	1.49	22.70	22.26	0.44	21.04	22.51	-1.47	19.82	21.81	-1.99
1986	20.36	17.90	2.46	21.55	19.81	1.74	22.53	21.42	1.11	21.73	20.49	1.24	19.92	19.98	-0.06	17.20	18.09	-0.89
Sum:			24.51			16.47			7.52			5.89			-1.42			-2.71
Mean Diff:			2.72			1.83			0.84			0.65			-0.16			-0.30

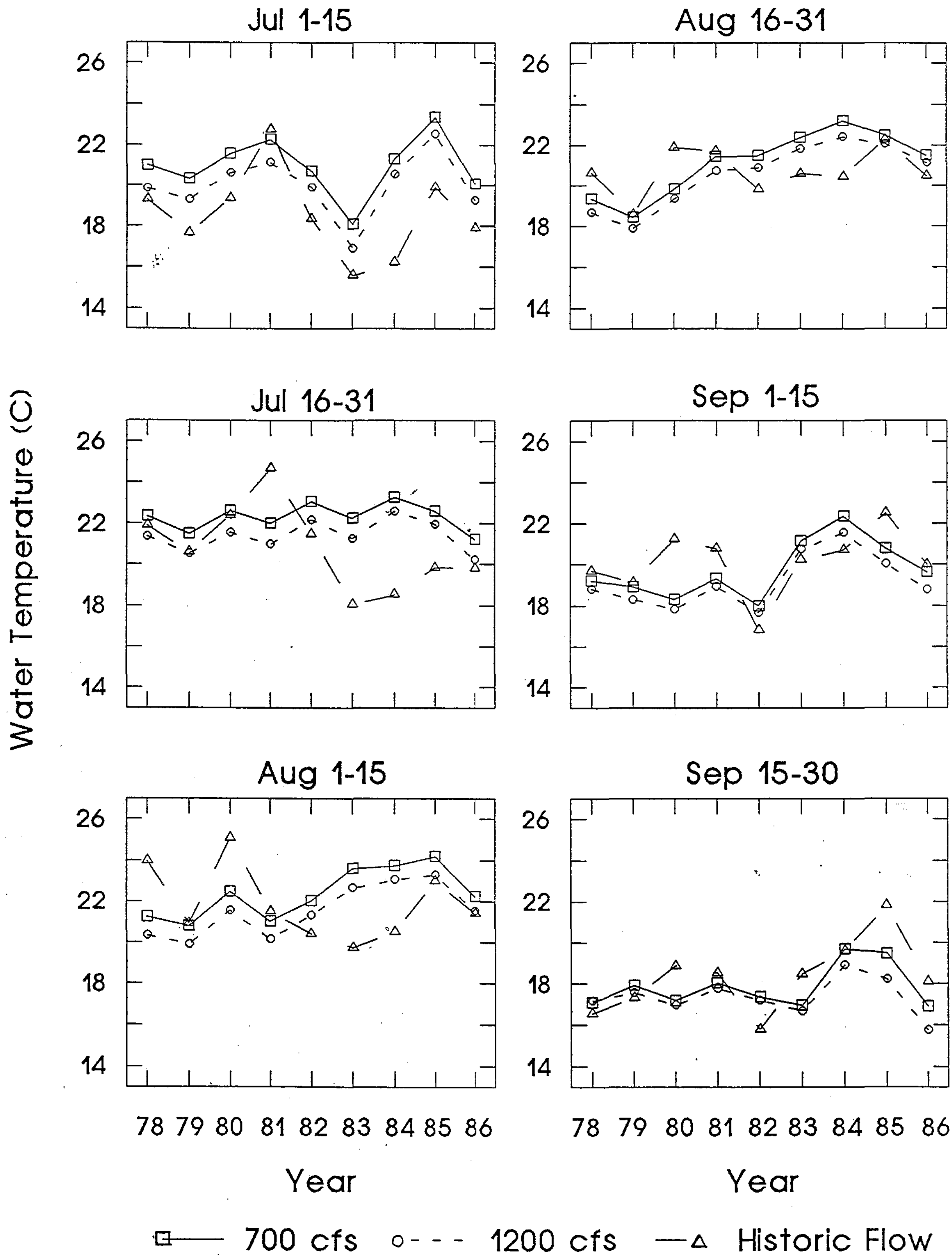

Figure 2. Comparison of mean historic temperatures for semi-monthly periods with temperatures that would have occurred in the 15-mile reach under flows of 1,200 and 700 ft^3/sec.

Comparison of the flow recommendation to historic flows

We compared our flow recommendation to the mean-monthly discharges that would have occurred in the 15-mile reach during the period 1952-82 under the level of upstream water-project operation that occurs today. Results showed that during the 31-year period of record, the minimum for July was exceeded in all but 3 years, those for August were exceeded in 45% of the years, and those for September were exceeded in 16% of the years. Table 3 provides the delivery requirements that would be necessary to meet the minimum flows specified for each of these months, as well as for the total July-September period. Those data show that, for example, delivery of 10,000 AF per year during the July-September period would have substantially increased, from 5 (16%) to 14 (45%), the number of years during which the minimum requirements were met.

Although this analysis is useful, it is important to recognize that it is based on estimates of mean-monthly discharge. Instantaneous discharge can vary markedly from mean-monthly values within months. The frequency of extremely low flows, which can have important limiting effects on both habitat availability and fish populations, is not evident when such mean data are used. Moreover, the effect of flows that greatly exceed the flow recommendation can be as undesirable as that of flows that are too low. This is the case for July flows that much exceed the recommended flow window and thereby inhibit the early seasonal warming of the waters that we seek.

Table 3. Delivery requirements (acre feet) to provide flows of 600 or 700 ft^3/sec in the 15-mile reach. Years are ranked from wettest to driest, according to the total delivery requirement for July-September.

	JULY		AUGUST		SEPTEMBER		TOTAL	
YEAR	600	700	600	700	600	700	600	700
52	0	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0
69	0	0	0	0	0	1666	0	1666
73	0	0	0	0	0	2558	0	2558
75	0	0	0	0	0	2558	0	2558
70	0	0	0	2583	0	0	0	2583
76	0	0	0	2583	0	2558	0	5141
67	0	0	0	2583	0	2618	0	5201
79	0	0	0	0	0	5236	0	5236
68	0	0	0	0	536	6486	536	6486
72	0	0	2276	8426	0	0	2276	8426
62	0	0	0	0	13447	19397	13447	19397
80	0	0	0	2583	13447	19397	13447	21980
61	0	2583	14206	20356	0	0	14206	22939
64	0	0	0	0	20111	26061	20111	26061
74	0	0	0	2583	25823	31773	25823	34356
78	0	0	6888	13038	20290	26240	27178	39278
53	0	0	0	0	33558	39508	33558	39508
55	0	0	0	0	33736	39686	33736	39686
66	0	0	15436	21586	13090	19040	28526	40626
59	0	0	2768	8918	28322	34272	31090	43190
63	6826	12976	11316	17466	10710	16660	28852	47102
81	0	0	27675	33825	14578	20528	42253	54353
60	0	0	12608	18758	33618	39568	46226	58326
56	0	0	19803	25953	34034	39984	53837	65937
58	0	0	23800	29950	33142	39092	56942	69042
54	0	0	34748	40898	29631	35581	64379	76479
77	24784	30934	31119	37269	19873	25823	75776	94026

Comparison of the flow recommendation to natural flows

Hann and Rose (Appendix C) compared our flow recommendation to "natural" flows for the 15-mile reach, flows that the Colorado Water Resource and Power Authority estimates would have occurred there without any water development upstream. Those data proved to be particularly interesting in that, contrary to an earlier and perhaps prevailing belief, water development has reduced rather than increased July-September flows in the reach (Figure 3). According to the PHABSIM analyses performed by Hann and Rose (Appendix C), however, such reduced flows during summer have resulted in a general increase in the aggregate amount of run, pool and riffle habitat for adult squawfish (compare Figure 3 to habitat vs. discharge relation described in Table 1).

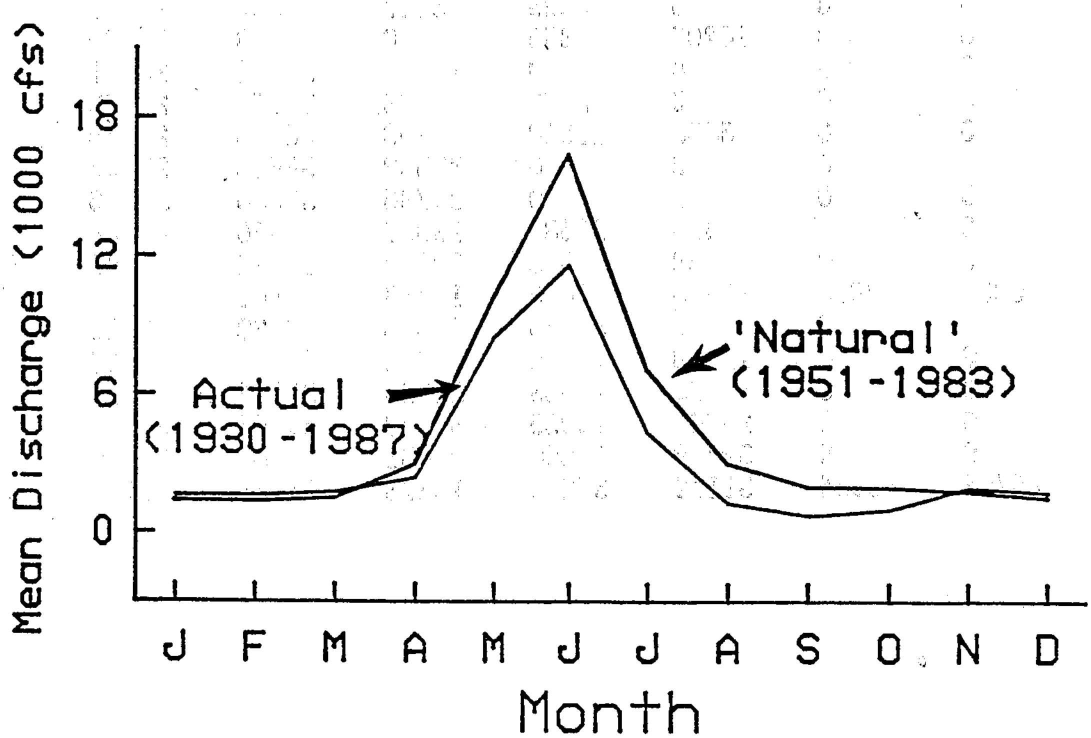

Figure 3. Comparison of "natural" and actual flows in the 15-mile reach, showing the general effect of water development on flow regime.

Hypotheses to be tested as part of the long-term assessment effort

Our most important hypothesized response of the Colorado squawfish population to implementation of the flow recommendation is earlier spawning and increased first-year growth of Colorado squawfish in the Colorado River of the Grand Valley. In turn, this could increase recruitment to the adult population, including that which uses the 15-mile reach. It should be recognized, however, that this response is anticipated only if our 700-1200 ft^3/sec recommendation for July, which would appreciably reduce current average flow, can be met.

Such recruitment of wild fish to the adult stock may not be sufficient to effect an important increase in adult numbers, however. Control of undesirable fish species and other measures to increase Colorado squawfish recruitment may be necessary. Supplemental stocking of Colorado squawfish, as part of an experimental augmentation program, could bring about a rapid increase in the adult population and also allow us to perform yet another important test: determination of the degree that physical habitat availability might limit the adult Colorado squawfish population. Because stocked experimental fish would be uniquely marked, the relative contribution of experimental vs. wild fish to the adult stock could be measured. We would like to begin the experimental augmentation program in 1990.

Problems with Developing and Implementing the Flow Recommendation

Water storage on the descending limit of the hydrograph

Our flow recommendation for July, August and September encourages the storage of water on the descending limb of the hydrograph, rather than during the traditional ascending and peak parts. An assessment of the problems associated with implementation of such a water-storage scenario is provided in Appendix D. Perhaps the greatest of these problems involves the administration of water rights. In addition, water storage during the descending limb of the hydrograph would probably require that predictive techniques used for seasonal-discharge and yield estimates be refined so that necessary annual storage of water is achieved. Although such modification of storage procedures would not be without problems, water-storage procedures that provide for human needs and also aid the recovery of the endangered fishes must be recognized as an important component of the recovery process. Additional water needed to meet the flow recommendation might be made available from reservoirs upstream, through the purchase of water rights, as a result of conservation efforts on irrigated lands, or by other means.

Flow recommendations that differ from "natural" conditions

Our flow recommendations acknowledge that natural, predevelopment conditions, including discharge and temperature regimes, are not necessarily "optimal" or "ideal" for

Colorado squawfish. This fact becomes clear when one recognizes that, over the range of any species, environmental conditions for the species become less optimal as one moves away from the center of population toward the limits of the species' range. Just beyond the limits of range, conditions are less than optimal to such a degree that the species can no longer persist there. Thus in regions near the upstream limits of a species' range, such as the 15-mile reach for Colorado squawfish, flow-habitat management recommendations should be directed toward the enhancement of habitat conditions for the species over those that probably occurred there historically.

Concern for other important habitats

Runs, pools and riffles are not the only habitats of importance in the 15-mile reach. Backwaters, for example, are important habitats as well, though our earlier investigations have demonstrated that the quantity of backwaters alone is not now a limiting factor for Colorado squawfish in the upper Colorado River (Archer et al. 1985). Based on our experience and observations in the 15-mile reach, the recommended flow window will provide adequate backwater habitat for young Colorado squawfish. However, as specified earlier, if our flow recommendation is implemented it will be necessary for us to monitor the availability of important habitats, including backwaters. This important monitoring procedure constitutes, in part, the validation process described in the strategy presented at the beginning of this document.

Habitats in other river reaches downstream from the 15-mile reach are of course also of importance to the recovery of the endangered Colorado River fishes. The habitat characteristics of these important downstream reaches will be investigated, in light of the outcome of our flow recommendations for the 15-mile reach, during the consultation process for the Aspinal Unit. That process is scheduled to begin sometime after completion of the ongoing Flaming Gorge consultation. The Aspinal Unit consultation process will be extensive and will include additional field studies, especially of the endangered humpback chub (Gila cypha), and thorough analyses of existing data for all species.

Development of Flow Recommendations for the Remaining Months

Our flow recommendation for July, August and September should not be viewed without regard for the remaining months, when flows will also be required to maintain and enhance Colorado squawfish habitat as part of the recovery effort. It is therefore important that we discuss, in a general way, our plans for the development of flow recommendations for the remainder of the year in the 15-mile reach.

During May and June, two months of high runoff flows in the Colorado, recommended flows will probably be based on the control of undesirable introduced fishes and on the maintenance of channel morphology and desirable substrate characteristics in the 15-mile reach and in reaches downstream. We are currently analyzing data on larval and "young-of-the-year" fishes collected from throughout the upper Colorado River during 1982-88. Preliminary results indicate significant correlations between maximum spring discharge and the subsequent relative abundance of several species, including Colorado squawfish (McAda and Kaeding 1989a). Those correlations differ among species and are both positive and negative with regard to discharge. We envision that our May-June discharge recommendations will be based in part on these relations and on our desire to reduce the relative abundance of undesirable species while increasing that of age-0 Colorado squawfish.

Our second concern with regard to the development of May-June flow recommendations is for the maintenance of gross channel geomorphology and important substrate characteristics. Channel maintenance and sediment dynamics are important concerns in all river reaches inhabited by the rare fishes, not just the 15-mile reach. It may be necessary to conduct a study to determine the relation between peak discharge and the sediment dynamics of the upper Colorado.

With regard to the fall and winter months (October-April), we have begun to analyze existing data using the techniques employed for July-September (Appendix C). Adult Colorado squawfish habitat-use data collected during the October-April periods of the past two years suggested that appreciable habitat for adult Colorado squawfish occurs at discharges much lower than those that occur under both present (actual) and "natural" flow conditions (Appendix C). We are recommending a study to develop other means to substantiate these preliminary observations, as well as to provide additional information on habitat versus discharge relations for other habitats not modeled by PHABSIM. For example, backwaters are important habitats for age-0 squawfish and many other fish species during October and November and perhaps during the December-April period as well, but backwaters are not usefully modeled by our current PHABSIM techniques. The backwater-availability versus flow relation is unknown for the 15-mile reach. Mapping based on aerial photographs or related techniques may be needed to quantify how flows affect backwater quantity.

Winter recommendations will also need to take into account the potential for river icing, a factor believed important to the habitat use of adult Colorado squawfish and razorback sucker in the upper Green River (Richard Valdez, Bio/West, Inc., personal communication). Perhaps the temperature model will be of value in this assessment. Details of the proposed study will be provided in a statement of work for this effort, which will be developed during 1989. We recommend that the proposed study begin in 1990, after important results of related efforts in the Green River basin are available in final report form.

Summary

The intent of the Recovery Implementation Program is to bring about the recovery and delisting of the endangered fishes while allowing Colorado and the other upper-basin states to develop their entitled water under the Colorado River Compact. An important component of the Recovery Implementation Program is the determination of flows needed for recovery of the fishes. The 15-mile reach of the Colorado River between Palisade, Colorado (River Mile 185), and the confluence of the Colorado and Gunnison rivers at Grand Junction (RM 170) is important habitat for the endangered Colorado squawfish and the very rare razorback sucker. We outlined a strategy for developing biologically defensible flow recommendations for the maintenance and enhancement of habitat for Colorado squawfish in the 15-mile reach. An important component of this strategy is the identification of limiting factors affecting the Colorado squawfish population, or that may affect the population as its numbers increase toward the levels established for recovery of the species. In addition, we identified logical objectives for flow-habitat management efforts in the 15-mile reach, investigated approaches to achieving these objectives, and made preliminary flow recommendations intended to meet these objectives during July, August and September.

Our recommendation is for a 700-1200 ft^3/sec flow "window" during July, August and September. During the relatively infrequent dry years (80% exceedence in total July-September discharge) when this flow recommendation will be more difficult to meet, 600 ft^3/sec is an acceptable lower limit for this window. We compared our flow recommendations to the mean-monthly discharges that would have occurred in the 15-mile reach during the period 1952-82 under the level of upstream water-project operation that occurs today. Results showed that delivery of 10,000 AF per year, generally during the August-September period, would have substantially increased, from 5 (16%) to 14 (45%), the number of years during which the minimum requirements were met. Additional water needed to meet the flow recommendation might be made available from reservoirs upstream, through the purchase of water rights, as a result of conservation efforts on irrigated lands, or by other means. Our flow recommendation is based on the best information and knowledge currently available, and, is subject to modification based on the results of future investigations and data analyses.

Recovery of Colorado squawfish in the upper Colorado River will require that habitat conditions there be made as nearly optimal for squawfish as possible. The recommended flows will provide a near-maximum aggregate amount of run and pool habitat for adult Colorado squawfish, habitats whose availability may importantly affect the recovery potential of the species. Implementation of this recommendation will assure that the growth of the adult population will not be constrained by the availability of habitat for adult Colorado squawfish. Our flow recommendation for July encourages the storage of water on the descending limb of the hydrograph, rather than during the traditional ascending and peak parts. Water storage upstream during July will result in water temperatures in the 15-mile reach warmer than those that occurred there historically and should result in earlier spawning of Colorado squawfish in the Grand Valley, a longer first-year growing season for the resulting young, and larger age-0 squawfish at the end of their first growing season. These larger age-0 fish should lead to greater recruitment to the adult population.

The enhancement of habitat for Colorado squawfish will require the provision of flows that differ from those that occur there presently or even historically. <u>However, the provision of such flows alone will not bring about the recovery of the Colorado squawfish in the upper Colorado River.</u> Such flows must be viewed as only one, albeit major, step in the recovery process. Failure of the population to increase after implementation of flow recommendations would not necessarily mean the flow regime is inadequate. Rather, it might indicate that the anticipated population response was too small to be detected or that our management efforts must be directed toward additional important factors controlling the population. Such additional management actions might include the control of undesirable fish species and the experimental augmentation of the Colorado squawfish stock, an action that we believe is imperative in view of the low numbers of both adults and young of this species in the upper Colorado River. Our goal of enhancing the habitat for Colorado squawfish in the 15-mile reach is an important step in the recovery process that may differ from those that pertain to other river reaches elsewhere in the upper Colorado River basin. In the Yampa River, for example, where a viable Colorado squawfish population occurs and where the most abundant spawning of this species in the basin may take place, the goal for the development of flow recommendations is to maintain current habitat conditions for the species (Tyus and Karp 1988).

The razorback sucker was not included in our analyses because we have too few habitat-use data available for this very rare species in the 15-mile reach. Nonetheless, based on the observations that we have made on razorback sucker, we feel confident that its habitat requirements for July, August and September will be met if those for Colorado squawfish are provided through proper flow management.

Acknowledgments

We thank the many people who contributed importantly to the development of this report. George Smith and Mike Brewer, U. S. Fish and Wildlife Service Division of Water Resources, ran the hydrology and temperature models; Chuck McAda provided considerable computing assistance; Cheryl Harris typed the many drafts of the report. The reviewers identified in Appendix E provided many useful suggestions.

REFERENCES

Archer, D. L., L. R. Kaeding, B. D. Burdick and C. W. McAda 1985. A study of the endangered fishes of the upper Colorado River. Final Report. U. S. Fish and Wildlife Service, Colorado River Fishery Project. Grand Junction, Colorado. 134 pp.

McAda, C. W., and L. R. Kaeding, 1989a. Relations between maximum-annual river discharge and the relative abundance of age-0 Colorado squawfish and other fishes in the upper Colorado River. Unpublished draft final report. U. S. Fish and Wildlife Service, Colorado River Fishery Project. Grand Junction, Colorado. 25 pp.

McAda, C. W., and L. R. Kaeding. 1989b. Relations between the habitat use of age-0 Colorado squawfish and those of other sympatric fishes in the upper Colorado River basin. Unpublished draft report. U. S. Fish and Wildlife Service, Colorado River Fishery Project.. Grand Junction, Colorado. 41 pp.

Miller, W. H., H. M. Tyus and C. W. McAda. 1983. Movement, migration and habitat preference of radiotelemetered Colorado squawfish; Green, White and Yampa rivers, Colorado and Utah. U. S. Fish and Wildlife Service, Colorado River Fishery Project. Salt Lake City, Utah. 33 pp.

Minckley, W. L., and G. K. Meffe 1987. Differential selection by flooding in stream-fish communities of the arid American Southwest. Pages 93-104 <u>in</u> W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Olson, D. E., D. H. Schupp and V. Macins. 1978. An hypothesis of homing behavior of walleyes as related to observed patterns of passive and active movement. American Fisheries Society Special Publication 11:52-57.

Orth, D. J. 1987. Ecological considerations in the development and application of instream flow-habitat models. Regulated Rivers: Research and Management 1:171-181.

Tyus, H. M., and C. A. Karp. 1988. Habitat use and stream-flow needs of rare and endangered fishes, Yampa River, Colorado. Preliminary final report. U. S. Fish and Wildlife Service, Colorado River Fishery Project. Vernal, Utah. 65 pp.

U. S. Fish and Wildlife Service. 1987. Recovery implementation program for endangered fish species in the upper Colorado River basin. Final report, USFWS Region 6, Denver.

APPENDIX A

STUDIES OF COLORADO SQUAWFISH AND RAZORBACK SUCKER USE OF THE '15-MILE REACH' OF THE UPPER COLORADO RIVER AS PART OF CONSERVATION MEASURES FOR THE GREEN MOUNTAIN AND RUEDI RESERVOIR WATER SALES

Final Report

May 1988

Submitted in accordance with provisions of Agreement No. 7-AA-60-00410 between the U.S. Fish and Wildlife Service and the U.S. Bureau of Reclamation

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INTRODUCTION

Background

The range of the Colorado squawfish (*Ptychocheilus lucius*) and razorback sucker (*Xyrauchen texanus*) has been reduced by about 75% since the turn of the century (Seethaler 1978, McAda and Wydoski 1980). Although both fish are rare in their remaining habitat, only the Colorado squawfish is federally listed as 'endangered', despite the fact that the razorback is considerably more rare than the squawfish and may be near extirpation in nature (Tyus 1987). The razorback sucker is protected by the states of Utah, Colorado, Arizona, Nevada and California.

Colorado squawfish are restricted to the upper basin of the Colorado River system above Glen Canyon Dam, inhabiting the Colorado and Green rivers and various large tributaries. The razorback sucker is also largely restricted to the upper basin, though a remnant population of old adults persists in Lake Mohave, a lower basin reservoir.

Loss of habitat for these rare fishes has occurred over many years. Construction of dams and diversions has had a major impact by altering natural flow and temperature regimes. Habitat in the lower basin has been altered to such an extent that it no longer supports self-sustaining populations of Colorado squawfish or razorback sucker (Minckley 1973, 1983). Although the upper basin supports populations of the endangered fishes, their continued existence there is far from assured. Because demands for municipal and agricultural water continue to increase, the accompanying loss of suitable habitat for these fishes in the upper basin may be paralleling that which occurred in the lower basin. In the upper basin, major tributaries that formerly provided a variety of habitats to which these fishes had unrestricted access have been partitioned by Flaming Gorge, Taylor Draw, Redlands Diversion, and Price Stub Diversion dams. In addition, operation of these and other dams and diversions further upstream has altered flow regimes in the downstream habitats of the rare fish. The cumulative negative effects of such projects, in conjunction with other man-caused changes in the river environment, may ultimately lead to the extirpation of these endemic species.

The 15-Mile Reach

The upstream range of the Colorado squawfish and razorback sucker in the Colorado River is delimited by the Price Stub diversion dam near Palisade, Colorado (Fig. 1). The Redlands Diversion on the Gunnison River, 2.2 miles upstream from the confluence with the Colorado River, blocks upstream movement of fishes in that tributary. A small, disjunct population of adult Colorado squawfish still persists in the reach above the Redlands dam, however. The stretch of the Colorado River between the Grand Valley Diversion (River Mile 185.1) and the confluence with the Gunnison River (RM 171.0), hereinafter referred to as the '15-mile reach,' experiences man-caused alteration of its natural flow regime throughout the year. Perhaps most important to the habitat of the endangered fishes is the additional reduction in flow caused by irrigation withdrawals during August-October, when natural flows typically are already low. Because the 15-mile reach is used by the Colorado squawfish and razorback sucker, there is concern that additional flow-regime alteration may further

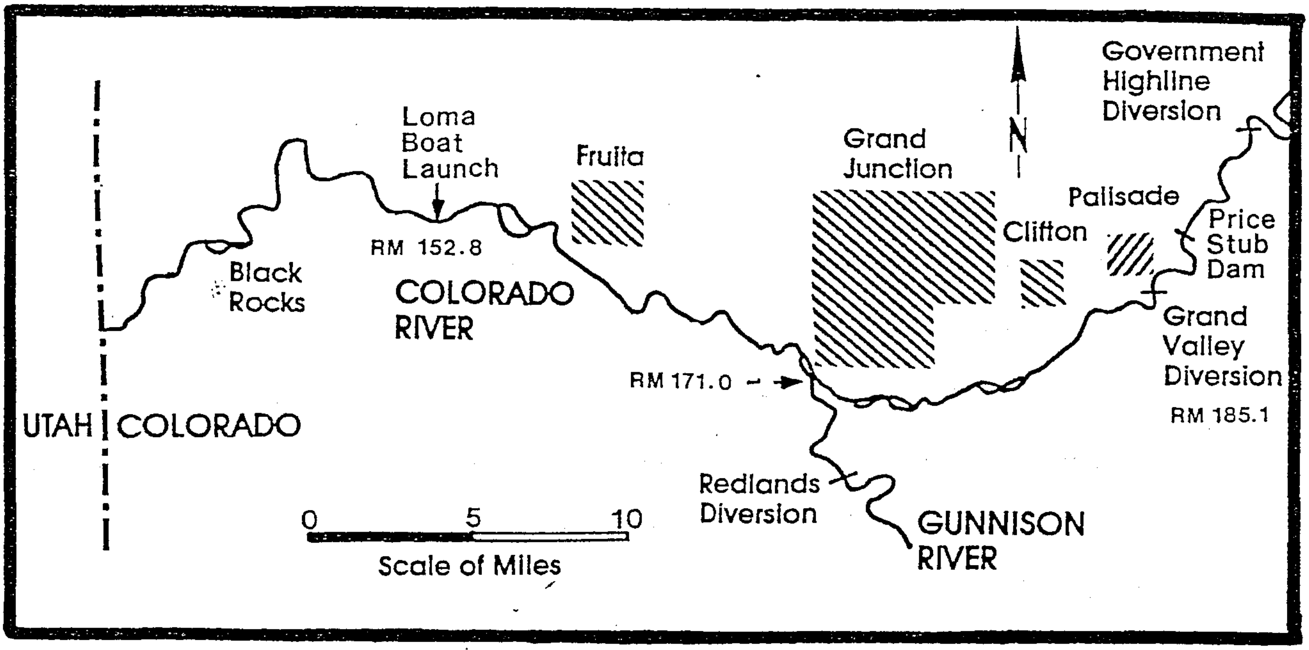


Figure 1. Map of the general study area.

degrade the habitat there, perhaps to the extent that the reach will become uninhabitable to the endangered fishes.

This report summarizes available biological information on use of the 15-mile reach by Colorado squawfish and razorback sucker, describes the relative importance of the reach to these species, and identifies possible important limiting factors affecting their populations. The report will focus on the findings of a recently completed study designed to evaluate the relative abundance, movement and habitat use of Colorado squawfish and razorback sucker in the 15-mile and adjacent reaches throughout the year. Data collection for this study was conducted from May 1986 through December 1988. Data collected during previous studies by Valdez et al. (1982) and Archer et al. (1985) were employed where appropriate.

METHODS

Relative abundance of adult Colorado squawfish and razorback sucker (as described by the catch of fish per unit of sampling effort) was estimated using electro-fishing. Timers on electrofishing units recorded actual shocking time (seconds) during each sampling effort. The number of Colorado squawfish or razorback sucker captured (or seen but not captured) per hour of shocking was used as the standard unit of relative abundance. All areas within a reach did not receive equal shocking effort; thus, electofishing searches should not be considered systematic. Although both shorelines and all large backwaters of each reach were sampled, those areas where squawfish or razorback suckers were found were subsequently searched more intensively.

Radiotelemetry was used to follow movement of adult Colorado squawfish and razorback sucker, as well as to identify the microhabitats used by these fish. Electrofishing and trammel nets were used to capture fish. Fish longer than 550 mm total length (TL) and captured from within the 15-mile reach were surgically implanted with radio transmitters following procedures outlined by Tyus (1982). Various sizes of transmitters were used depending on fish size. Battery life of the smallest transmitter was estimated as 150-245 days; the largest, 547-940 days. All captured rare fish were measured to total length, weighed, and had a numbered Carlin tag attached to them. Fish were released at their location of capture 1-2 hr after implantation. The river was searched for radio-tagged fish on a weekly basis. The area routinely searched included the 32.4 miles of the Colorado River between the Grand Valley Diversion and the Loma Boat

Launch, and the lower 2.2 miles of the Gunnison River (the reach downstream from the Redlands Diversion Dam). The search area was expanded upstream to the Price Stub Dam and downstream to the Utah state line when some fish could not be located in the immediate study area (Fig. 1). Radio-tracking was conducted from boats; however, immediately below the Price Stub Dam, searches from shore were necessary because of inaccessibility by boat. Locations of fish in the Colorado River were specified as river mile (RM) distance from the confluence with the Green River, and in the Gunnison River as distance from the confluence with the Colorado River.

There is some confusion regarding river-milage at the Gunnison confluence; thus, a brief explanation of the circumstances there is warranted. Prior to this study, the Gunnison confluence (Gunnison RM 0.0) was considered to be at the site where the Gunnison first met the Colorado main channel at RM 170.2; the distance from there to the Grand Valley Diversion (CO RM 185.2) was therefore approximately 15 miles (thus the term '15-mile reach'). However, waters of the Gunnison actually first mix with those of the Colorado in a side channel at CO RM 171.0. Subsequent to the floods of 1983 and 1984, this Colorado side channel became the new main channel. The designated 'confluence' therefore shifted 0.8 miles upstream from the former site. The Gunnison mouth now occurs at CO RM 171.0 and the lower 0.8 miles of the Gunnison, as previously mapped, became part of the Colorado River. For the sake of consistency, however, we retained the original river-mile designations (Fig. 1). Thus, the Gunnison river now ends at GU RM 0.8 and not GU RM 0.0, and there are 2.2 miles of river between the confluence and the Redlands Diversion at GU RM 3.0. In addition, the '15-mile reach' is now 14.2 miles long.

Distribution of larval fishes was determined by seining river backwaters from mid-July through the end of August. The river was subdivided into 2-mile reaches; once weekly, backwater, embayment or shoreline habitat from each reach was sampled using 0.5-mm-mesh hand seines. Captured fish were preserved in 10% formalin and identified by the Colorado State University Larval Fish Laboratory. Sampling effort was not constant among samples within a given year, but average effort per sample was similar among years. The area sampled included the aforementioned 15-mile-reach, the adjacent 18-mile segment of Colorado River immediately downstream, and the lower 2.2 miles of the Gunnison River between the Redlands Diversion Dam and the confluence.

Distribution and relative abundance of young-of-the-year (YOY) Colorado squawfish were estimated by seining backwaters with 3-mm-mesh beach seines. Each year, two samples were collected from each of two backwaters in each 5-mile reach. The 1986 effort was conducted on 22 September and 1 October; in 1987, on 22 and 23 September; the 1988 effort, on 20 and 22 September. Collected fish were preserved in 10% formalin in the field and identified in the laboratory. To determine relative abundance of squawfish and other species, the surface area seined was measured and the number of individuals of each species collected per 100 square meters was calculated. The study area sampled for YOY included the 15-mile reach and the adjacent 18-mile segment of the Colorado River immediately downstream.

Habitat use by adult Colorado squawfish and razorback sucker was estimated by visually categorizing the habitat type at the locations of radio-tagged fish (e.g. pool, eddy, riffle, etc.). We divided riverine habitat used by adults into eight major categories, the definitions of which are given in the appendix (Table 2). Placing the site of a fish location into a particular category was unambiguous in some cases but not in others. The limits of precision in locating radio-tagged fish created some problem when habitat types were closely juxtaposed such as at shear zones between runs and eddies. Also, the lack of a clear demarcation between some habitat types, such as runs and pools, is a problem inherent in any such categorization. The categorization of a particular site was, therefore, somewhat subjective and relied on the best judgment of the field crew leader.

Microhabitat use was characterized by measuring depth, velocity, substrate and temperature at fish locations. Velocity was measured at a depth 60% of the water column (measured from the bottom) at sites $\leq$ 3.0 ft deep; at sites > 3.0 ft deep, velocity was averaged from two measurements taken at 20 and 80% of the water column. In addition to temperature measurements made at the fish location, temperature was also measured at a nearby location in the main channel. In 1987 and 1988, water clarity at a location (RM 174.4-175.2) in the 15-mile reach was routinely monitored using a standard Secchi disk.

Possible spawning sites were identified by the aggregation of ripe adults during the spawning season and, for squawfish, by the subsequent collection of larvae. Unfortunately, techniques for identifying razorback sucker larvae have not yet been developed. Post-hatching ages of collected squawfish larvae were calculated using total lengths of individual larvae in age-length equations developed by Haynes and Muth (1985). Spawning date was then estimated by subtracting four days from the estimated hatching date. Four days was considered the mean embryo incubation time, based on the 3.8-5.0-day range reported by Hamman (1981) for fertilized eggs of hatchery-reared squawfish incubated at 20-24 C.

RESULTS

Adult Relative Abundance

The Colorado River Fishery Project (CRFP), U.S. Fish and Wildlife Service, has conducted studies on the rare fishes of the upper Colorado River since 1979. From 1979 to 1985, studies encompassed the length of river from the upper end of Lake Powell, Utah, to Rifle, Colorado, including the 15-mile reach. As part of the standardized surveys of the Colorado River upstream from Lake Powell conducted between 1979 and 1981, the river was divided into 11 reaches, each from 13 to 50 miles long (Valdez et al. 1982). Each reach was extensively sampled annually during pre-runoff, runoff and post-runoff periods. Results showed captures of adult Colorado squawfish (> 450 mm TL) were fairly evenly distributed among the seven reaches that occur between the Colorado River confluence with the Green River and Palisade, Colorado. The mean number of adults captured per reach was 3.1 (SD = 1.3) and the mean number of fish caught per mile per reach was 0.12 (SD = 0.04). Three adult Colorado squawfish, or 0.10 per mile, were captured from the Grand Valley area, the reach between the towns of Palisade and Loma, Colorado. Thus relative abundance of Colorado squawfish in the Grand Valley was about average that of the seven Colorado River reaches where adult squawfish were captured (Table 1). Length of the Grand Valley reach is about 16% of the total length of these seven reaches.

Table 1. Numbers of adult Colorado squawfish caught from the upper Colorado River during standardized surveys, 1979-81. Fish were caught from seven of eleven reaches sampled between Lake Powell, Utah, and Rifle, Colorado, during pre-runoff, runoff and post-runoff periods.

Reach	Miles		Number caught	No./mile
	Number	Percent		
Spanish Bottom - Potash	50	26.6	4	0.08
Potash - Big Bend	24	12.8	3	0.13
Big Bend - Onion Creek	15	8.0	2	0.13
Onion Creek - Agate Wash	25	13.3	5	0.20
Agate Wash - Westwater	14	7.4	1	0.07
Westwater - Loma	29	15.4	4	0.14
Loma - Palisade	31	16.5	3	0.10
Total	188	100.0	22	
Mean			3.1	0.12
SD			1.3	0.04

Although razorback sucker are very rare in the upper Colorado River, most of those captured in recent years were found in the Grand Valley area. During 1979-85, river-wide surveys conducted by CRFP yielded 70 different individuals; 53 (76%) of these were captured from the Grand Valley area.

Within the Grand Valley, endangered fish utilize three adjacent river reaches: the 15-mile reach, the 18-mile reach of the Colorado immediately downstream, and the lower 2.2 miles of the Gunnison River between the Redlands Diversion dam and the confluence with the Colorado (Fig. 1).

Results of electrofishing surveys conducted during May and June of 1986-1988 indicate that certain areas in the 15-mile reach may be concentration points for many Colorado squawfish and razorback sucker of the Grand Valley during spring runoff. During this time in 1986, the number of squawfish caught or seen per hour of shocking in the 15-mile reach was approximately 3.2 times that caught or seen in the adjacent 18-mile reach of river immediately downstream; in 1987, there was approximately 6.1 times as many caught or seen per hour. In 1988, however, 1.5 times as many squawfish were caught or seen per hour in the 18-mile reach as were in the 15-mile reach. Thus, in two of three years the electrofishing success rate was higher in the 15-mile reach. The combined data indicated relative abundance during spring runoff was about 2.0 times higher in the 15-mile reach than the adjacent lower reach (Fig. 2).

The number of razorback suckers shocked in the 15-mile reach during the three years was about 5.9 times larger than in the lower 18-mile reach (Fig. 2).

Although relatively little sampling effort was expended in the Gunnison River below the Redlands Diversion in spring 1987 and 1988 (no effort in 1986), there were three Colorado squawfish caught or seen during 3.8 hr of shocking; this rate was considerably higher than that for the other two adjacent Colorado River reaches (Fig. 2). During our July and August electrofishing efforts in the lower Gunnison in 1987, Colorado squawfish were either caught or seen at rates of 2.00 and 2.23 fish per hour (Table 2). Almost all of these captures or observations were made in the plunge pool of the Redlands Diversion Dam, the use of which by squawfish dropped off entirely in September. Many squawfish seem attracted to a 1.3-mile

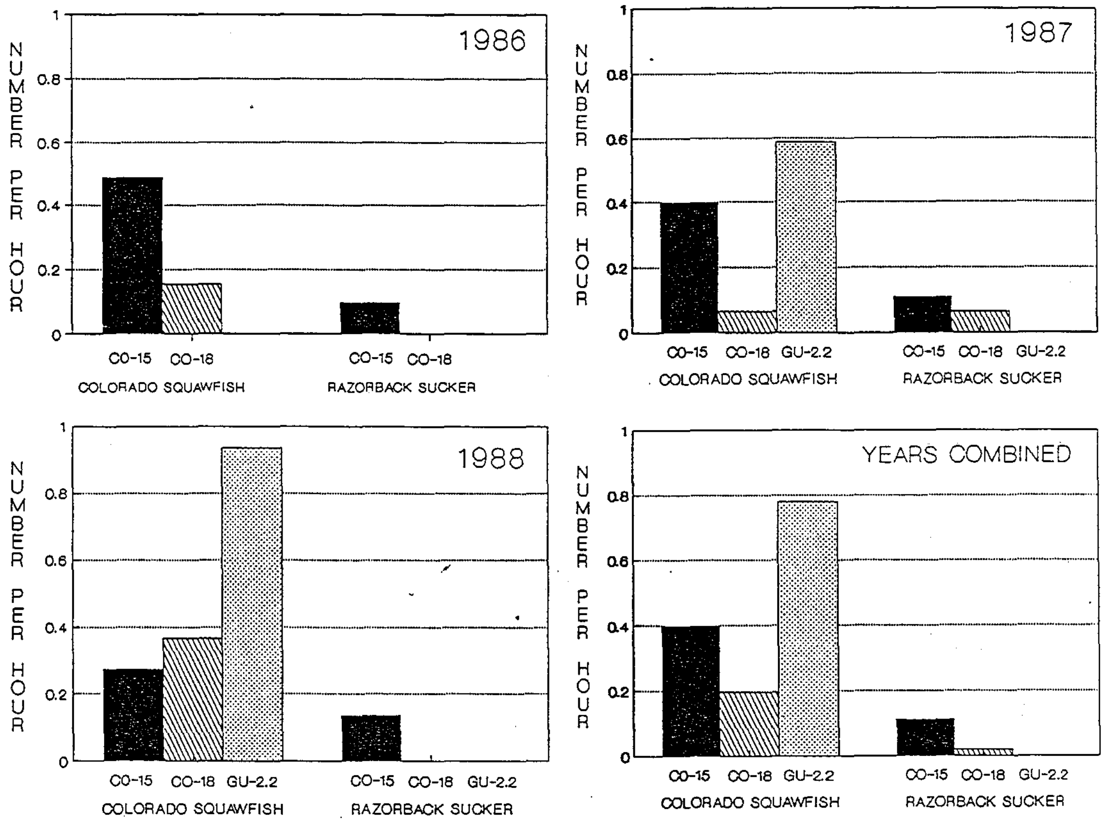


Figure 2. Electrofishing catch per effort for Colorado squawfish and razorback sucker in three contiguous river reaches during spring, 1986, 1987 and 1988. River reach codes: CO-15 = Colorado River 15-mile reach (RM 171-185); CO-18 = Colorado River 18-mile reach (RM 153-171); GU-2.2 = Gunnison River 2.2-mile reach (RM 0.8-3.0). Note: the Gunnison River was not sampled in 1986.

section (RM 174.4-175.7) of the 15-mile reach during spring and to the plunge pool of the Gunnison River during summer. Radio-tracking data on the movement of adult Colorado squawfish, reported below, also support this conclusion. In 1988, however, extremely low flows in the lower Gunnison apparently precluded use of this reach by Colorado squawfish: extensive electrofishing (as well as radiotelemetry) effort failed to reveal the presence of any individuals there during July-October. No razorbacks were seen in the lower Gunnison during our sampling efforts in either year.

Table 2. Electrofishing catch per effort for Colorado squawfish in the lower 2.2-mile reach of the Gunnison River, 1987 and 1988.

		MAY	JUN	JUL	AUG	SEP	OCT
Shocking effort (hr)	1987	1.70	-	1.50	3.59	2.46	-
	1988	2.14	2.90	0.68	0.46	-	0.82
No. caught	1987	0	-	2	7	0	-
	1988	1	0	0	0	-	0
No. seen but not caught	1987	1	-	1	1	0	-
	1988	1	1	0	0	-	0
No. caught/hr	1987	0.00	-	1.33	1.95	0.00	-
	1988	0.47	0.00	0.00	0.00	-	0.00
No. caught + seen but not caught/hr	1987	0.59	-	2.00	2.23	0.00	-
	1988	0.94	0.35	0.00	0.00	-	0.00

Movement of Radio-Tagged Adult Fish

Colorado squawfish

Movement of adult Colorado squawfish in the 15-mile reach and adjacent areas has been monitored in recent years using radiotelemetry. During 1982-85 fish were radio-tagged in May and June and tracked through fall (Archer et al. 1985). During 1986-88, extended-life radio tags were used and the radio-tagged fish were monitored through the winter months, into the following year.

During the 1982-85 studies, 15 of 34 squawfish (44%) captured and radio-tagged in the Colorado River upstream from Black Rocks (RM 136, Fig. 1) occupied the 15-mile reach at one time or another during the May-October period.

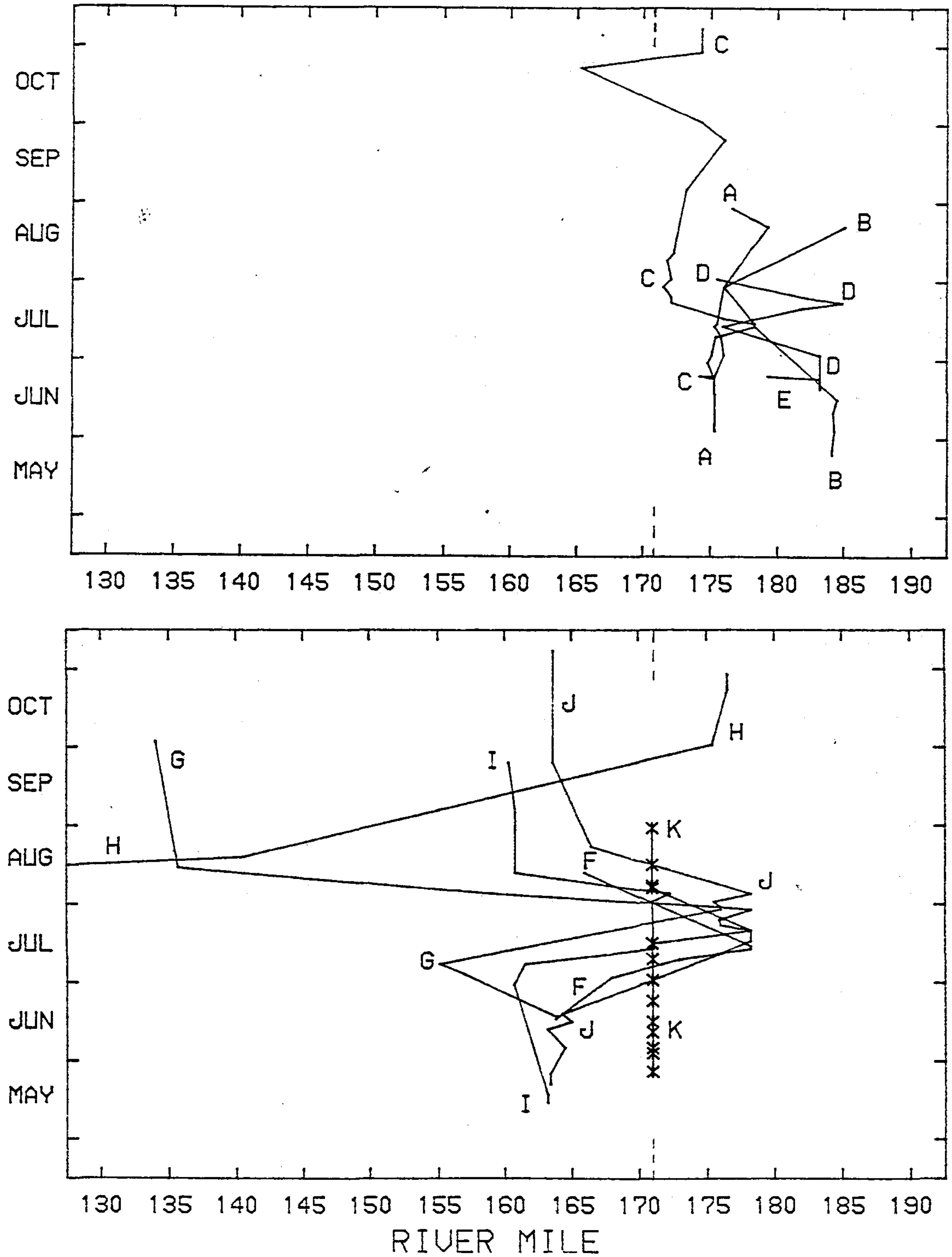


Figure 3. Movement of 11 radio-tagged Colorado squawfish (fish A-K) during 1982. Top diagram shows movement of five squawfish that were tagged within the 15-mile reach; bottom diagram shows movement of six squawfish tagged elsewhere that moved into the 15-mile reach (others that were tagged elsewhere that did not move into the reach are not shown). Dotted lines mark downstream end of 15-mile reach (RM 171); crosses along vertical line at RM 171 represent times when fish were located in the lower 2.2 miles of the Gunnison River.

In 1982, five squawfish were tagged and released within the 15-mile reach (Fig. 3). One fish (designated E on Fig. 3) disappeared shortly after release, one (D) stayed within the reach through July, and two others (A and B) stayed through August. Another (C) remained in the reach from June through September, then moved a few miles downstream from the reach in October. Six fish (F, G, H, I, J and K) tagged elsewhere moved into the 15-mile reach for at least a brief period. One of these fish (H) had been tagged in upper Lake Powell in April; it moved 198 miles to the 15-mile reach by late September, where it remained at least through October.

In 1983, one squawfish tagged at Black Rocks the previous fall moved 47 miles upstream to a site within the reach at the end of July (Fig. 4); however, contact was lost one week later.

Four squawfish tagged in lower reaches during 1985 subsequently moved into the 15-mile reach (Fig. 5). One fish (A) moved there from RM 58.3 to RM 178.3 during July and August, a distance of 120 river miles. The remaining fish (B, C and D) were tagged 7-10 miles below the reach in May. One of these (D) moved in and out of the lower Gunnison River on three separate occasions. All four fish moved back out of the reach between late July and early September.

In 1986, six squawfish and two razorback suckers from the 15-mile reach were radio-tagged. Contact was lost with one squawfish and one razorback almost immediately. Two squawfish moved into the Gunnison River during June (Fig. 6). One of these (A) later lost its tag and the other (F) returned to the area of release in late July, where it remained until at least May of the following year. This fish (F) was next located near the Walker Wildlife Area (WWA, RM 163.7) of the downstream 18-mile reach on 25

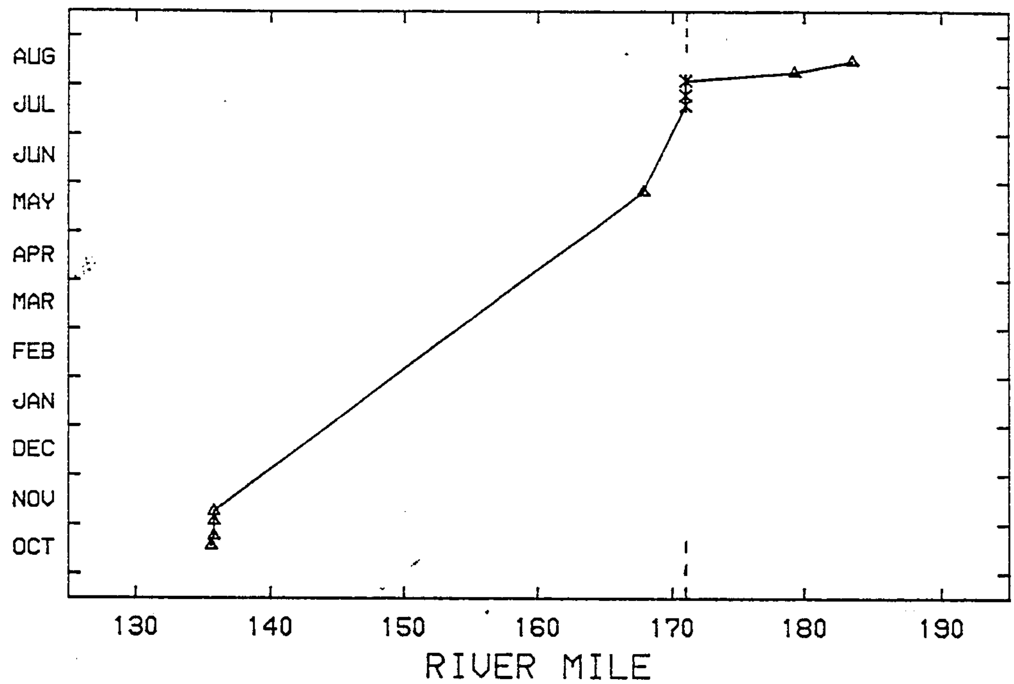


Figure 4. Movement of one radio-tagged Colorado squawfish during 1983. Dotted lines mark downstream end of 15-mile reach (RM 171); crosses on vertical line at RM 171 represent times when the fish was located in the lower 2.2 miles of the Gunnison River.

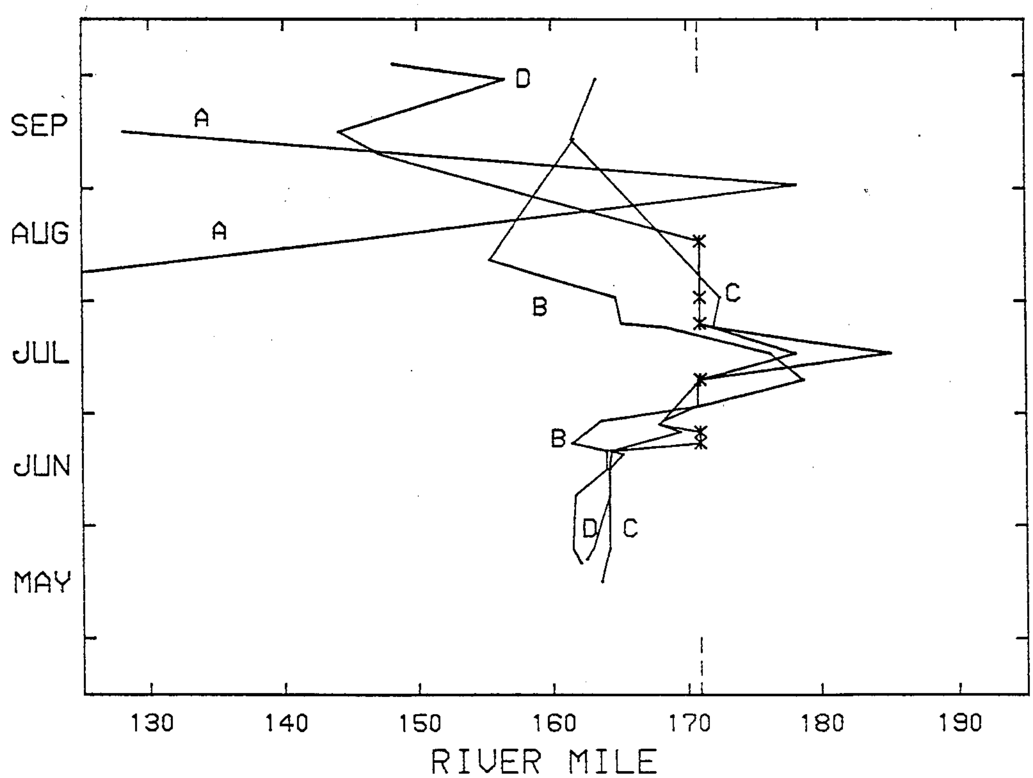


Figure 5. Movement of four radio-tagged Colorado squawfish during 1985. Only squawfish that moved into the 15-mile reach are shown. Dotted lines mark downstream end of 15-mile reach (RM 171); crosses along vertical line at RM 171 represent times when fish were located in the lower 2.2 miles of the Gunnison River.

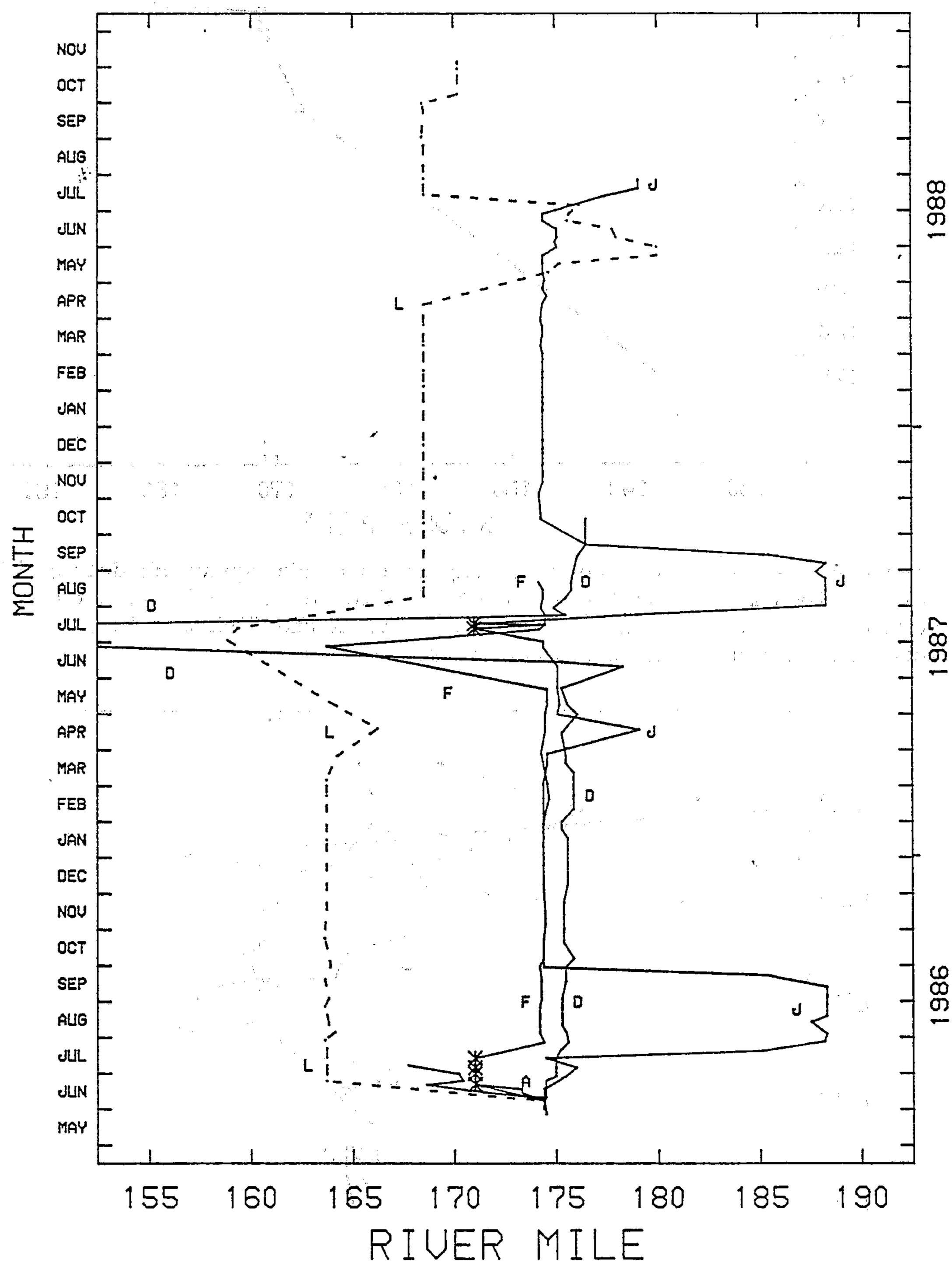


Figure 6. Movement of five Colorado squawfish (fish A, C, D, F and J) and one razorback sucker (fish L) radio tagged in 1986. Crosses along vertical line at RM 171 represent times when fish were located in the lower 2.2 miles of the Gunnison River.

June 1987, but returned to the original release location in the 15-mile reach by 9 July where it remained through mid August when contact was lost (presumably tag failure). Another squawfish (D) stayed near the point of release until at least mid June of the following year. On 7 July 1987 it was located 45 miles downstream near the Utah border. By 21 July, it had returned to the original release location in the 15-mile reach. Another squawfish (J) moved upstream in mid July 1986, over the Grand Valley Diversion dam, to the plunge pool of the Price Stub Dam. It remained there until the end of September when it returned downstream. Between early October and the end of March, the fish (J) remained near its initial point of release. In July 1987, it made two brief forays to the base of the Redlands Diversion Dam on the Gunnison River, each time returning to the 15-mile reach after a day or two. In late July 1987, it returned to the plunge pool of the Price Stub Dam and remained there until mid September, when it again made its way downstream. From early October through mid May, it stayed within 0.2 miles of its point of release. In mid July 1988, it was again moving upstream for the third year in a row when tag failure occurred.

In 1987, four squawfish from the 15-mile reach were equipped with radio transmitters (Fig. 7). One of these (B) remained near the center of the reach through the end of the study, making local movements no more than a few miles from the capture site. Another (G) stayed in the reach during June and most of July, then moved seven miles downstream. It expelled its tag while in a deep pool 2.5 miles below the reach. This fish was again captured in the 15-mile reach at RM 180.5 on 12 May of the following year. Two other tagged fish (H and I) remained in the reach until late July,

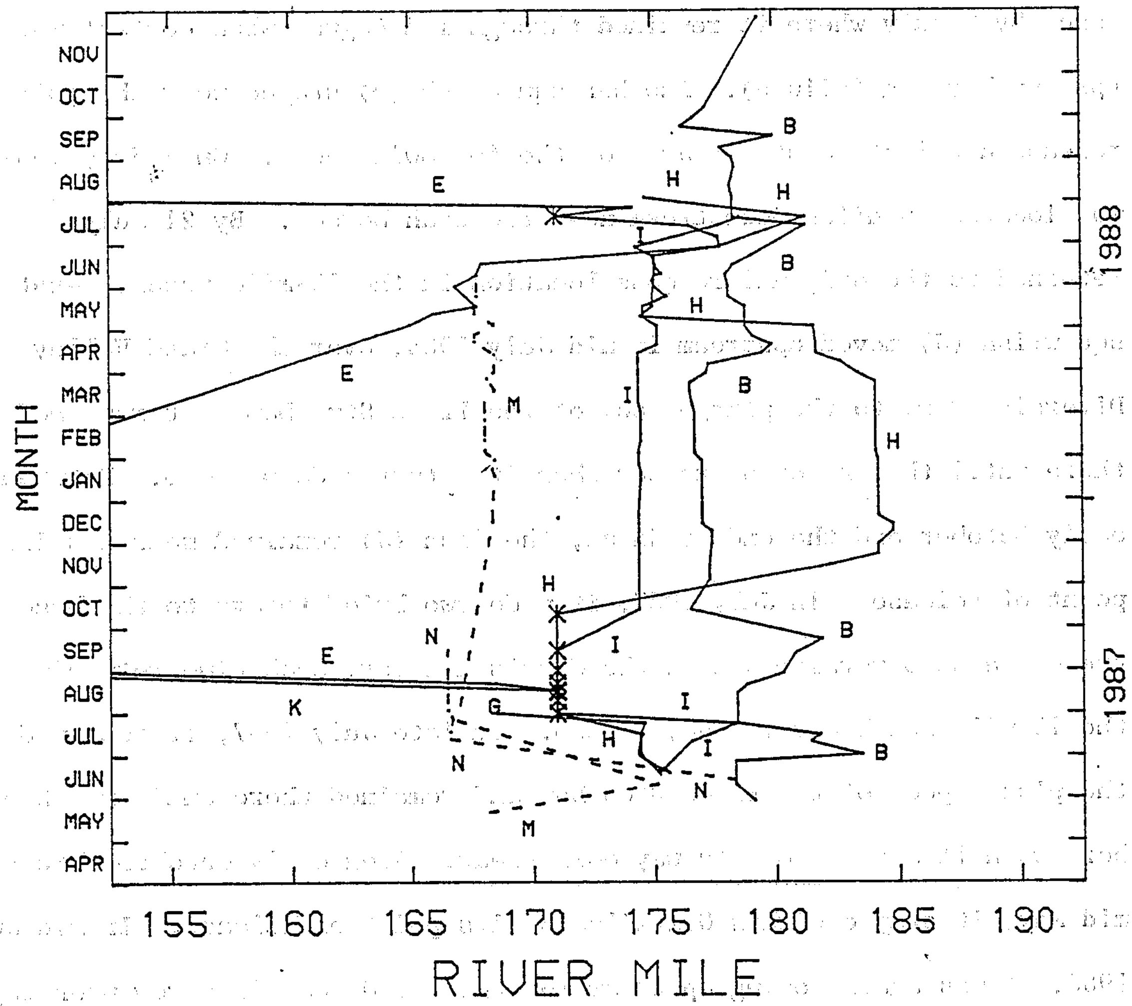


Figure 7. Movement of six Colorado squawfish (fish B, E, G, H, I and K) and two razorback suckers (fish M and N) radio tagged in 1987. Crosses along vertical line at RM 171 represent times when fish were located in the lower 2.2 miles of the Gunnison River.

then moved to the Redlands Diversion plunge pool on the Gunnison River. In late September or early October, one of these (I) returned to within one mile of its release site in the 15-mile reach and remained in that vicinity through June of the following year. It then moved about four miles upstream in early July 1988. We presume that this fish was then killed by a fisherman because its naked transmitter was found on a bank above the river, in a location where fishermen had been previously observed. The other fish that had been in the Gunnison similarly returned to the 15-mile reach in late October or early November and overwintered near RM 184.1. In mid March 1988 it began making local movements and appeared to stay within the reach until the tag failed in late July. Three squawfish were captured from the Gunnison River and radio-tagged in mid August 1987; contact was lost with one of the fish immediately and then with another a month later after it had moved 34 miles downstream. The third fish moved downstream about 38 miles during the following month and stayed in the Black Rocks area until at least mid-November. We regained contact with this fish the following April when it moved back into the Grand Valley. It remained in the lower 18-mile reach until mid-June 1988 when it then moved up into the 15-mile reach. In early July it traveled downstream to the mouth of the Gunnison River, which at that time had extremely low flow because of low runoff and heavy irrigation demand; the fish then briefly returned to the 15-mile reach in mid-July before moving back downstream to the Black Rocks area. After some local movement in that area, it remained at Black Rocks from mid-September through at least the end of October.

In 1988, eight squawfish from the 15-mile reach, one from the 18-mile reach and one from the lower Gunnison River were equipped with radio transmitters. Contact was lost almost immediately with one fish; another moved from the 15-mile reach downstream to the Walker Wildlife Area (RM 164.0) at the end of June and either died or lost its transmitter there. Another fish (T) moved downstream and either died or lost its tag at RM 167.0 after only one month (Fig. 8). One (U) tagged at RM 175.4 on June 1 was located a mile up the Gunnison River the following week; a week later

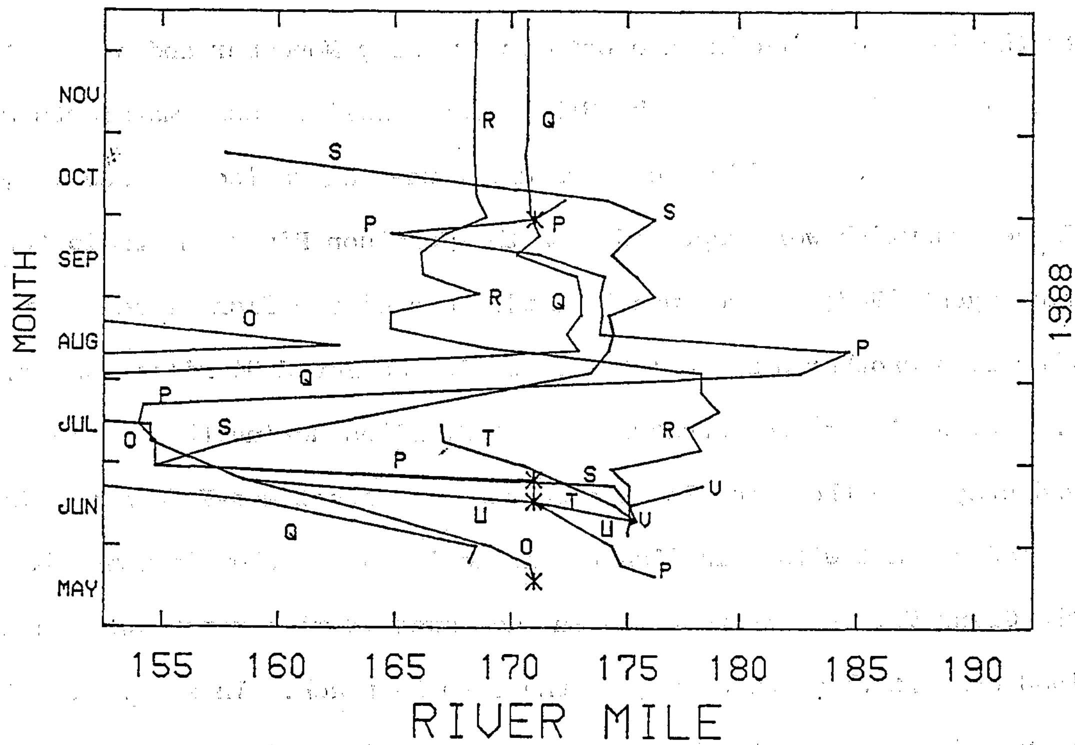


Figure 8. Movement of eight Colorado squawfish (fish O, P, Q, R, S, T, U and V) radio tagged in 1988. Crosses along vertical line at RM 171 represent times when fish were located in the lower 2.2 miles of the Gunnison River.

on June 16, it was located for the last time downriver at RM 158.5. Contact was lost with a fifth fish (V) after it had moved upstream three miles, two weeks after being tagged.

We maintained contact with the other five fish through at least September. One of these (P) moved from the 15-mile reach to RM 2.6 on the Gunnison River in early June. During five days in late June it moved 18 miles downstream to RM 154.7, where it remained through July 13. Two weeks later it was found near the top end of the 15-mile reach. It subsequently moved to the lower end of the reach where it remained through August. In mid-September it moved 6.4 miles out of the reach, moved back up to the lower mile of the Gunnison and then returned to the lower end of the 15-mile reach before contact was lost in late September. Another fish (S) tagged in late May at RM 175.0 remained in that vicinity until the last half of June when it traveled 20 miles downstream to the lower end of the 18-mile reach (RM 154.7). By late July it had returned to the 15-mile reach near the point of capture and remained there through September. In mid-October it was last located downstream at RM 157.7. Another fish (R) tagged at RM 175.0 in late May moved 4.1 miles upstream in late June and early July and then moved down to the 18-mile reach in late July or early August. It made local movements within that reach until late September, when it moved to a deep pool at RM 168.5; it remained there through at least early December. The fish (O) captured and tagged at the plunge pool of the Redlands Diversion Dam moved out of that river in mid-May, was located at progressively downstream sites within the 18-mile reach and spent the end of June near two other radio-tagged fish at RM 154.5. In mid-July it moved to Black Rocks and then to a site near the Utah border at RM 129.8. It then moved upstream at least as far as RM 162.6 in the Grand Valley in early August but then moved back downstream and was last contacted at Black Rocks in late October. The one fish tagged in the 18-mile reach (RM 168.2) moved downstream and spent early July near the Utah border at RM 130.2. In late July it moved back upstream 43 miles to the lower end of the 15-mile reach. From early September through at least early December it remained near the mouth of the Gunnison River.

Based on observations made during our recent studies, as well as during earlier efforts, it appears that individual squawfish have a relatively limited range during much of the fall-spring period. Many squawfish were found concentrated in a few localities during spring runoff in the 15-mile reach; they would then disperse throughout the Grand Valley. Much of the movement between late June and late August may represent migrations to and from spawning areas, or movements in search of such habitats. The range of one fish extended as far upstream as the Price Stub Dam, while several others spent part of the year in the Gunnison River; a few moved out of the Grand Valley and traveled downstream as far as RM 130 (Fig. 9). Some of these movements were no doubt related to spawning activity; however, movement after the spawning period may serve to disperse individuals, thereby minimizing intraspecific competition. Thus the 15-mile reach is used by some adult squawfish year round; by others, most of the year except during the spawning period. Some use it as a wintering area only; others move there prior to spring runoff and apparently then take advantage of the flooded gravel pits and large backwaters during the high-flow period. It is also periodically used during the spawning season by some adults from downstream reaches.

Razorback Sucker

In 1986, the single razorback sucker that was tracked left the 15-mile reach within one week after release and spent the remainder of the year in a side channel near WWA (Fig. 6). Contact with this razorback was lost during May and June, 1987, when the fish may have moved to a spawning site. It was later located downstream (RM 158.8), but then moved up to a deep pool at RM 168.5 where it remained until at least the beginning of April 1988. It was next located in the 15-mile reach near the 1986 point of capture. However, in mid May it moved upstream to RM 180.0. In late May it moved downstream but stayed within the 15-mile reach through the

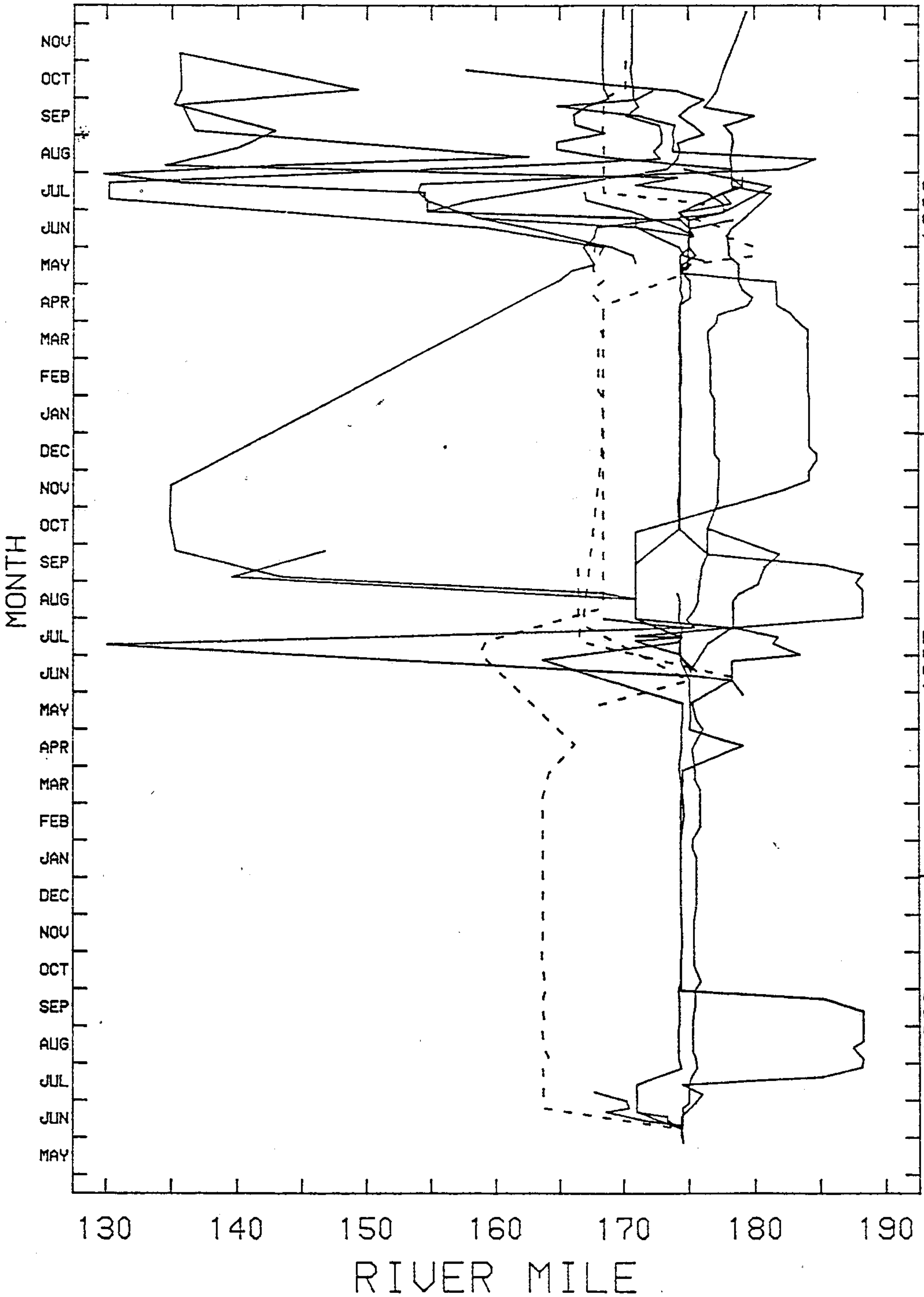


Figure 9. Movement of 19 Colorado squawfish and three razorback suckers radio tagged at various times during 1986, 1987 and 1988.

end of June. On 7 July it was back in the deep pool at RM 168.5 in the 18-mile reach. It stayed in this pool until the end of September when it moved a few miles upstream; it remained there through the end of October when the tag failed. Another razorback, captured from the 15-mile reach (RM 178.3) and tagged in early June 1987, was located in early July downstream at RM 166.6, where it remained through September of that year (Fig. 7). A third razorback, tagged 2.8 miles downstream from the 15-mile reach on 19 May 1987, was located in the 15-mile reach (RM 175.1) on 8 June. This fish was later found downstream stranded in an isolated pond near the point of release. We captured the fish and returned it to the river. It remained within half a mile of the release site from then until the tag failed at the end of May 1988.

Larval and Young-of-the-Year Collections

Colorado Squawfish

1986

No Colorado squawfish larvae were found within the 15-mile reach in 1986. Eight squawfish larvae were collected from the downstream 18-mile reach; five were from a backwater near WWA (RM 158.1) and three were from a backwater near the Fruita Bridge, 5.6 miles downstream (Fig. 10). In addition, one squawfish larva was found in shoreline habitat in the Gunnison River, 0.4 miles below the Redlands Diversion Dam. The average number of squawfish larvae per sample for the 18-mile reach was 0.14; for the lower Gunnison, 0.13 (Fig. 11). Estimated spawning dates calculated from these larvae were between 26 July and 5 August (Appendix; Table 5). Maximum-daily, main-channel temperatures at this time were 19-21 C; mini-

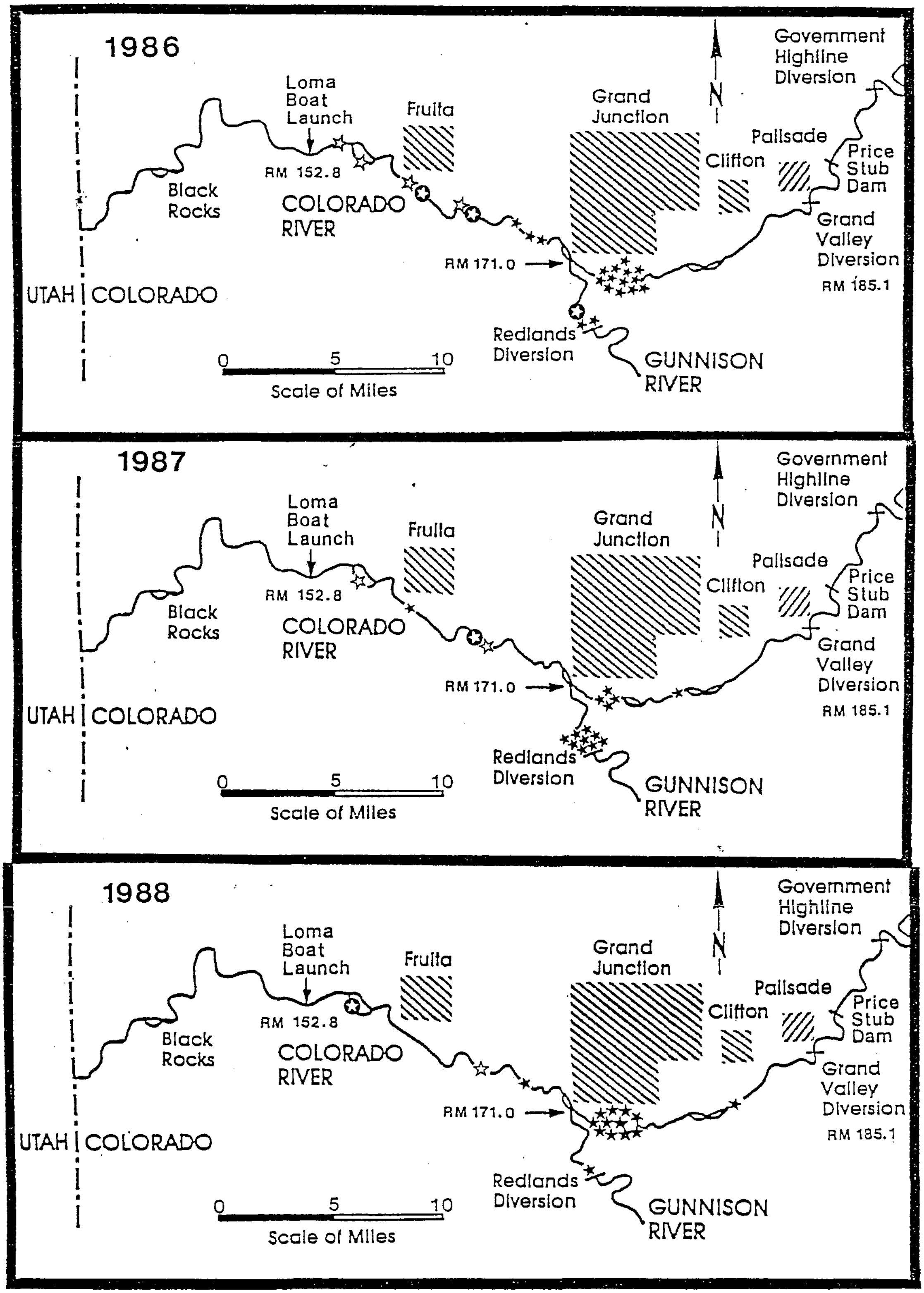


Figure 10. Capture sites of adult (dark stars), larval (enclosed stars) and young-of-year (white stars) Colorado squawfish during 1986, 1987 and 1988. Each dark star represents an individual adult squawfish; white and enclosed stars represent sites where one or more larval or young-of-year squawfish were captured.

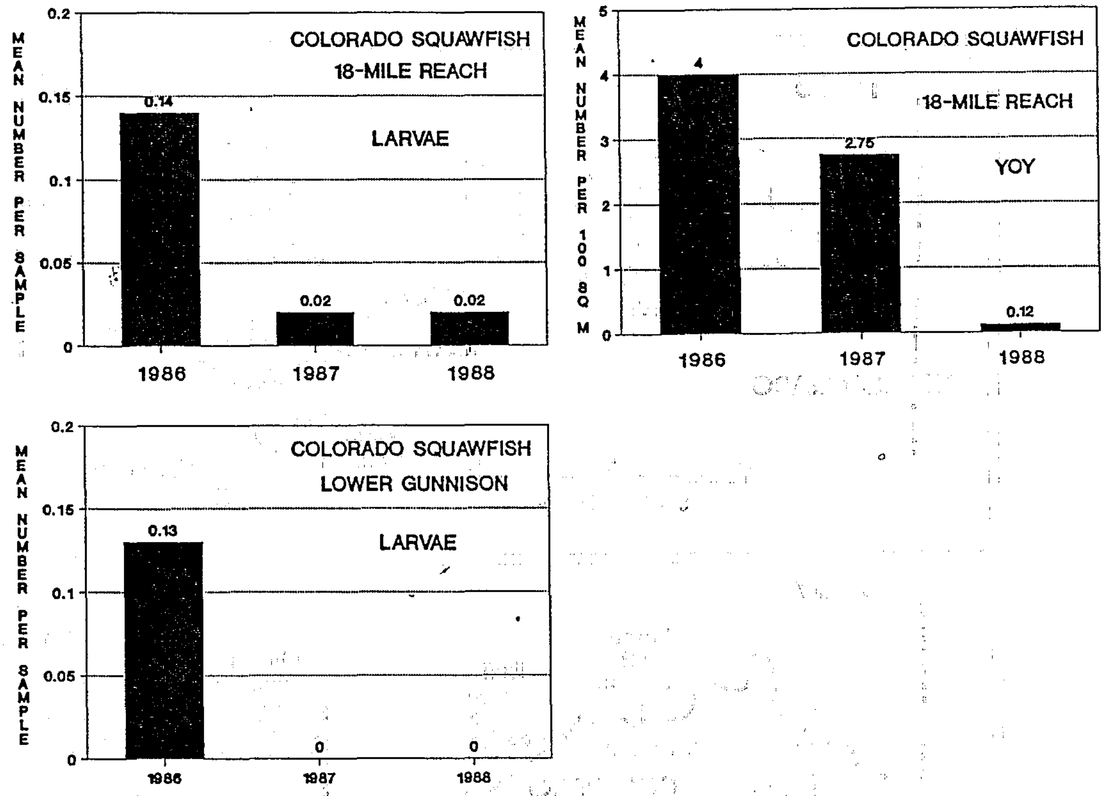


Figure 11. Catch rates of larval Colorado squawfish for the 18-mile and lower-Gunnison reaches, and young-of-the-year (YOY) for the 18-mile reach during 1986, 1987 and 1988.

mum-daily, 17-18 C. Though river temperatures at Palisade (15-mile reach) were slightly less than at WWA (lower 18-mile reach) during June and part of July, mean-daily temperatures at the two sites were very similar during the estimated spawning period and for the remainder of the season (Fig. 12). Thus temperatures suitable for spawning of Colorado squawfish occurred in the 15-mile reach during 1986.

No YOY Colorado squawfish were collected from the 15-mile reach in late September. However, one 105-mm-long (yearling-size) squawfish was seined from the 15-mile reach, from a backwater at RM 174.5; this is the same area where adult squawfish were most frequently found. A total of 29 YOY squawfish was collected from the adjacent 18-mile reach. These were

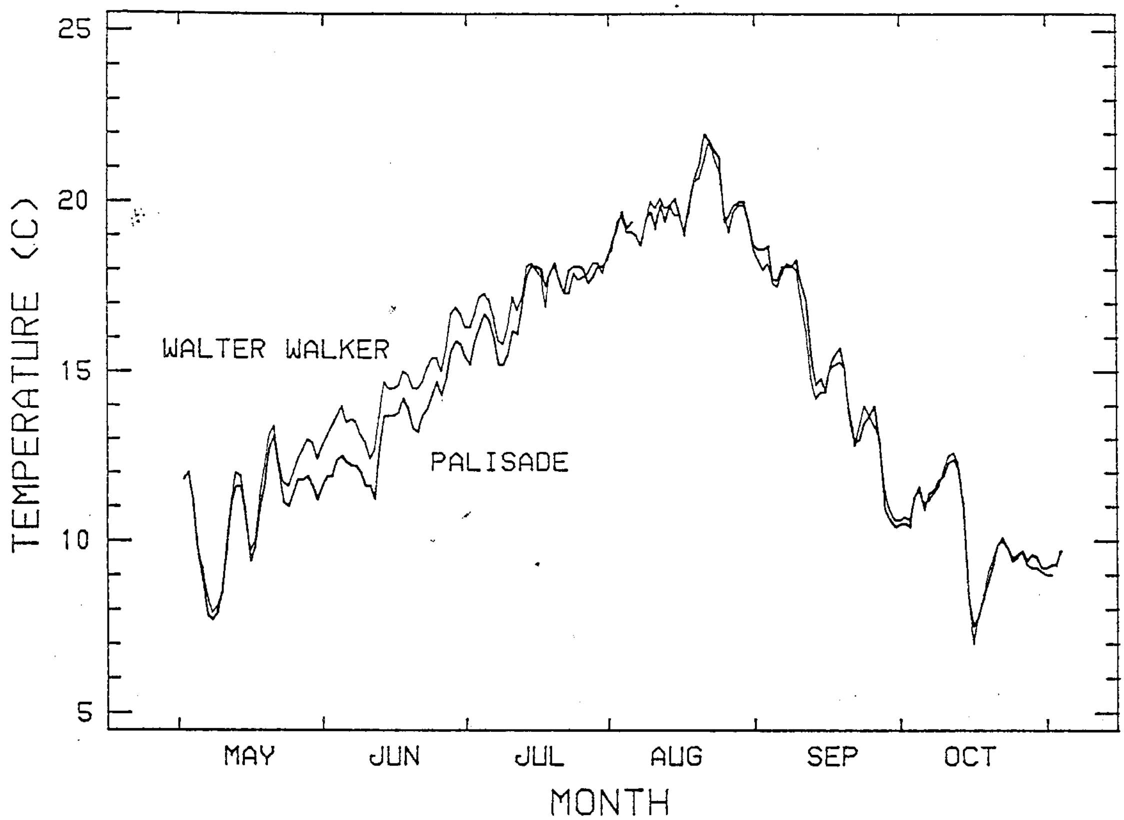


Figure 12. Main-channel temperatures at Palisade (RM 183.2) and Walker Wildlife Area (RM 164.8) on the Colorado River, 2 May - 30 October 1986. Daily-mean temperatures given for each site are mean values for data recorded by two Peabody Ryan thermographs at each site. Data from six daily readings were first averaged for each thermograph for a daily mean, and the daily means for the two thermographs were then averaged.

distributed among four of seven backwaters sampled; all four were downstream from the most upstream collection site for larval Colorado squawfish (RM 163.7; Fig. 10). Mean catch per effort of Colorado squawfish YOY within the 18-mile reach was 4.02/100 m^2 (SD = 7.87; Fig. 11 and Appendix; Table 6). Mean total length of these fish was 24.7 mm (SD = 3.14); range in length was 19-33 mm (Appendix; Table 7). Assuming they hatched at approximately the same time as the previously collected larvae, age at time of collection was 53-63 days.

1987

No squawfish larvae were found within the 15-mile reach in 1987, nor were any collected from the lower Gunnison River. Only one larval squawfish was collected, and this was from the lower 18-mile reach, from a shoreline habitat one mile downstream from WWA (RM 162.7; Fig. 10). The mean number of squawfish larvae per sample from the 18-mile reach was 0.02 (Fig. 11). Spawning date, estimated from this one larva, was 4 July, about one month earlier than the estimated spawning dates for 1986 (Appendix; Table 5). Main-channel temperatures warmed earlier in 1987 (Fig. 13), and were similar to those during the estimated spawning period in 1986; the minimum and maximum temperatures on 4 July were 17 and 21 C, respectively.

No YOY squawfish were collected from the 15-mile reach in 1987. However, a total of 13 YOY was collected from two of eight backwaters sampled in the lower 18-mile reach. The more upstream of the two backwaters that yielded YOY was 0.5 miles downstream from the collection site of the larva found in August (Fig. 10). Mean catch per effort of YOY squawfish for the reach was 2.75/100 m^2 (SD = 9.34; Fig. 11 and Appendix; Table 8). Mean total length of these fish was 27.0 mm (SD = 5.9); range in length was 20-39 mm (Appendix; Table 7).

1988

No larval squawfish were found in the 15-mile reach or lower Gunnison River during 1988. One specimen collected from the 18-mile reach was tentatively identified as a Colorado squawfish by the Larval Fish Laboratory. It was collected from a shoreline habitat at RM 158.2 (Fig. 10). The mean number of squawfish larvae per sample for the 18-mile reach was 0.02 (Fig. 11). Estimated spawning date, based on this one larva, was 4

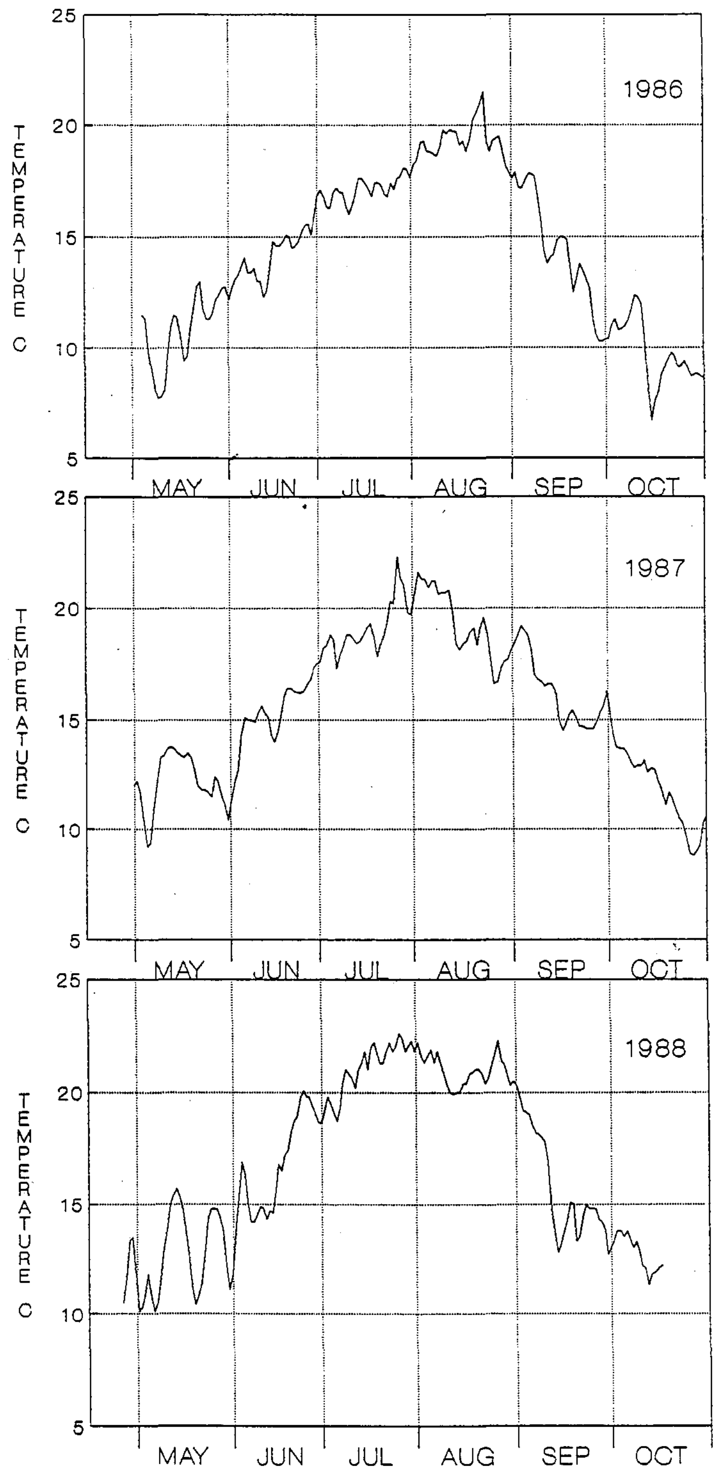


Figure 13. Mean-daily, main-channel temperatures at Walker Wildlife Area (RM 164.8) during 1986, 1987 and 1988. Means are from six daily temperature readings recorded by Peabody Ryan thermographs.

July (Appendix; Table 5). The minimum and maximum temperatures on 4 July were 18.5 and 20.5 C, respectively.

Only one YOY Colorado squawfish was collected during late September 1988. This was from the 18-mile reach at RM 162.8 (Fig. 10); total length was 32 mm. Mean catch per effort for the 18-mile reach was 0.12/100 m^2 (SD = 0.45; Fig. 11 and Appendix; Table 9).

Razorback Sucker

Because identification techniques have not yet been developed, no larval or YOY razorback suckers have been identified in samples collected from the 15-mile reach during this study. However, the Larval Fish Laboratory at Colorado State University is currently developing techniques to distinguish between the early life stages of sucker species found in the upper Colorado River. Our samples await development of these techniques.

Other Species

General

At least 16 other fish species inhabitat the rearing areas of larval and YOY Colorado squawfish in the Grand Valley. Little is known regarding the positive or negative effects these fish may have on the early life stages of Colorado squawfish. However, for young squawfish, the interactions among the fishes of this diverse fish community, of which they are a part, no doubt greatly influences their survival during the critical first year of life.

Because of the variable nature of Colorado River flows within and among years, the fish communities of backwaters are not stable over time (Fig.

14). Each species has its own specific set of conditions, both physical and biotic, which are optimal for growth and survival. Some years afford conditions which are well suited for some species, but not for others. Also, within a given year, a species may do better in one reach than in another because of differences in physical or hydrological characterisics between the two reaches. In addition, a species may do poorly during a year of otherwise good physical-habitat conditions if it is negatively affected by another species that is particularly abundant.

Six species comprised the majority of fish collected from habitats sampled for young squawfish (Fig. 14 and Appendix: Tables 6, 8, 9 and 10). Three were native species: roundtail chub (*Gila robusta*), bluehead sucker (*Catostomus discobolus*) and speckled dace (*Rhynichthys osculus*); three were introduced species: fathead minnow (*Pimephales promelas*), sand shiner (*Notropis stramineus*) and red shiner (*N. lutrensis*). Without speculating on the causal factors involved, we report here the changes in abundance of these six species during the three years of study.

Roundtail chub, bluehead sucker and speckled dace occupy backwater and other low-velocity, shallow habitats during their early life stages, but as adults they largely occupy main-channel habitats, much like Colorado squawfish. However, several other Colorado River fishes, common in the main channel as adults, apparently do not rely extensively on backwater habitats for the rearing of young, as relatively few are detected during larval or YOY sampling. These species include flannelmouth sucker (*Catostomus latipinis*), common carp (*Cyprinus carpio*) and channel catfish (*Ictaluras punctatus*). The three abundant introduced species, fathead

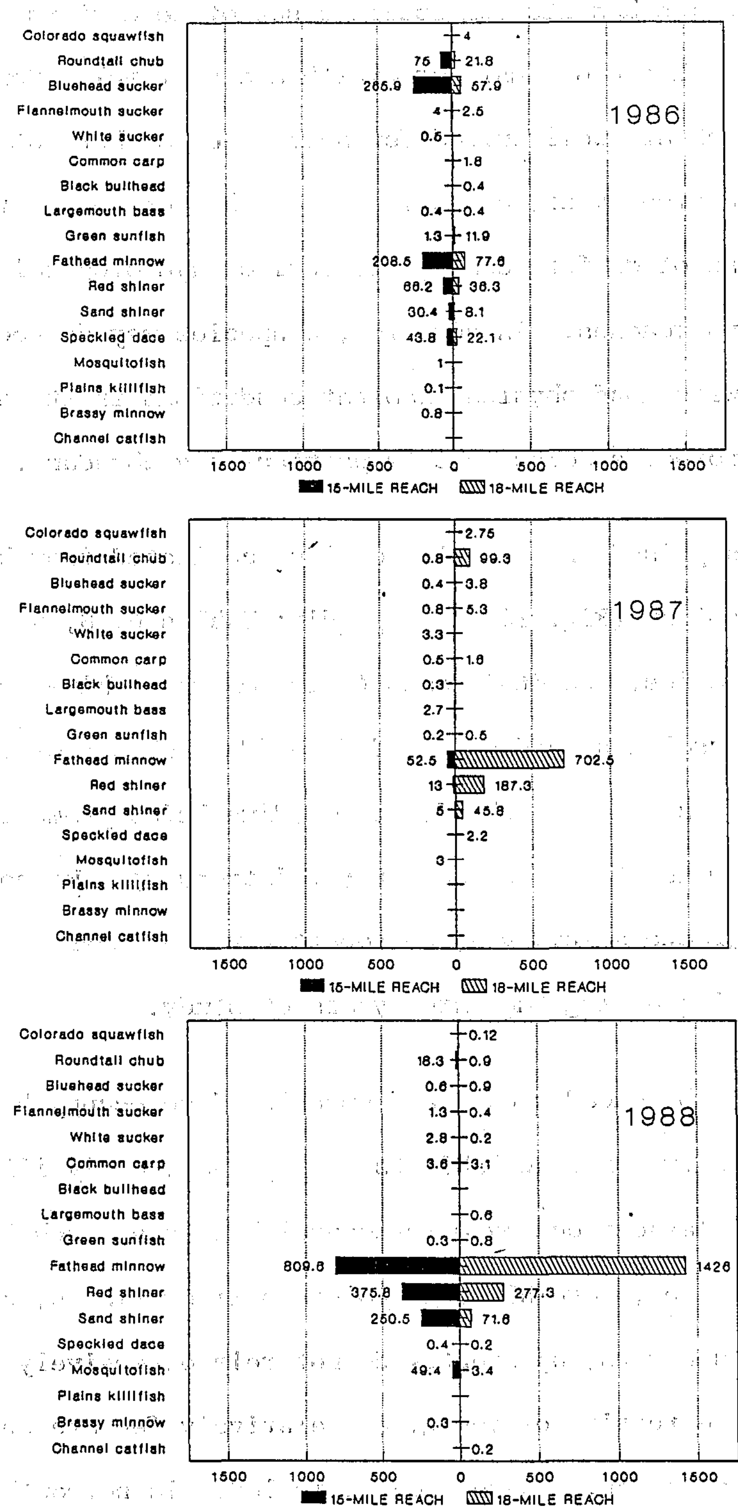


Figure 14. Catch rates (mean no. fish/100 m^2) of fish species collected during young-of-the-year sampling in two adjacent Colorado River reaches, 1986, 1987 and 1988.

minnow, sand shiner and red shiner, however, occur in backwaters as both young and adults.

Native fishes

Young of two of the three common native species declined in numbers over the three years of study; young roundtail chub were the exception. Larvae of roundtail chub were more abundant in all reaches during 1987 than in 1986 or 1988 (Fig. 15). Roundtail chub larvae were particularly abundant in the lower Gunnison reach during 1987. However, catch rates for YOY in late September, though high in the 18-mile reach, were low in the 15-mile reach that year. In 1988, we saw the opposite trend: compared to the 15-mile reach, almost no YOY roundtail chub were collected in the 18-mile reach.

Young of bluehead sucker declined from 1986 to 1988 (Fig. 16). There were more larvae and YOY captured in all three reaches during 1986 than during 1987 or 1988. YOY were particularly abundant during 1986 in the 15-mile reach. The very low number of larvae collected from the lower Gunnison in 1988 might have resulted from the extremely low flows in the reach during July and August of that year. Though numbers of larvae collected from the 15-mile and 18-mile reaches were somewhat lower during 1987 and 1988 than during 1986, YOY were dramatically lower. This suggests that reproductive success, as measured by larval abundance, cannot be used to predict later abundance of YOY. Survival from the larval stage in July to the YOY stage in late September may be extremely limited during some years. Alternatively, these data might indicate that these young fish disperse into the main channel earlier in some years, before fall sampling occurs.

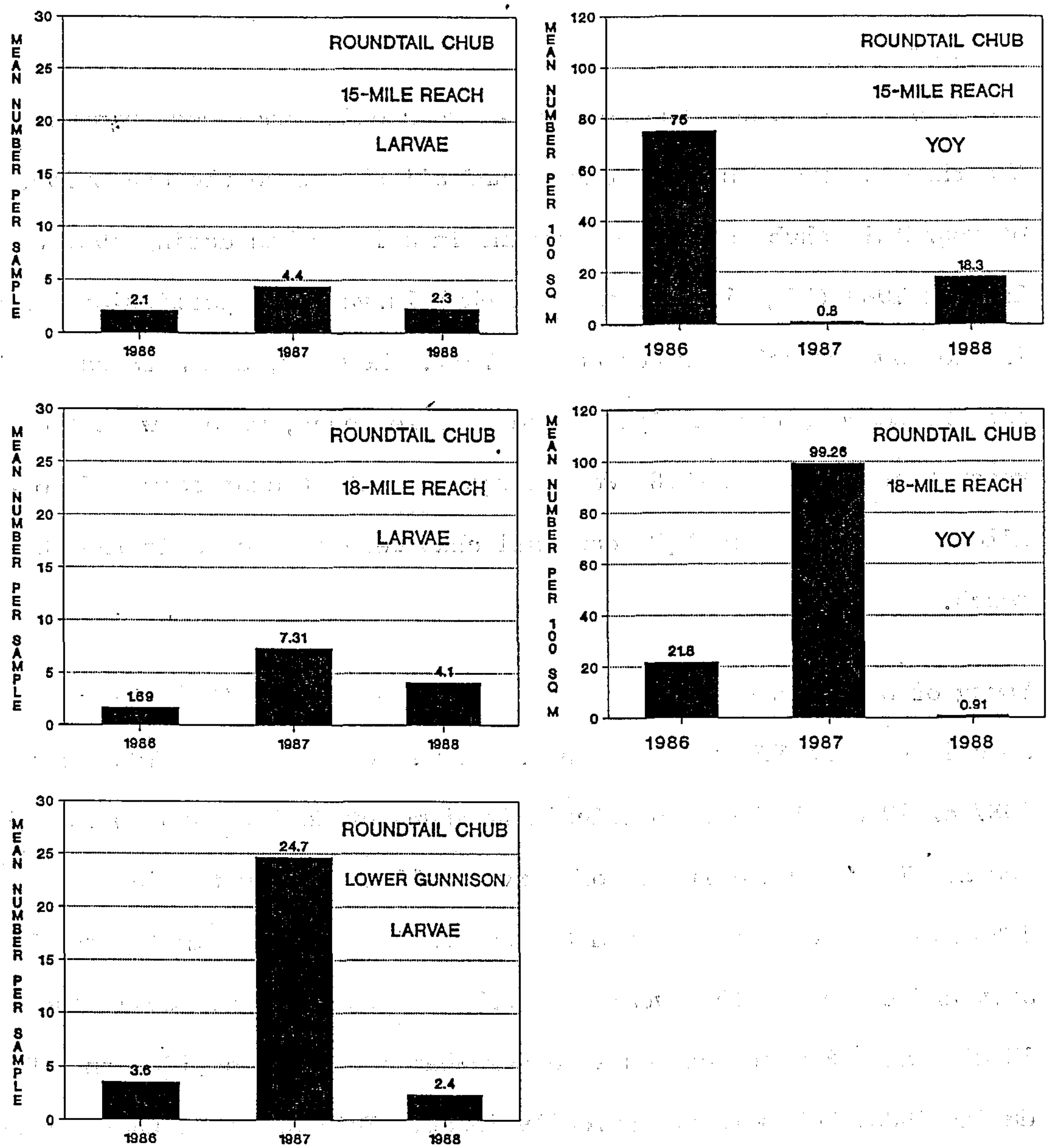


Figure 15. Catch rates of larval and young-of-the-year (YOY) roundtail chub in the 15-mile, 18-mile and lower-Gunnison reaches during 1986, 1987 and 1988.

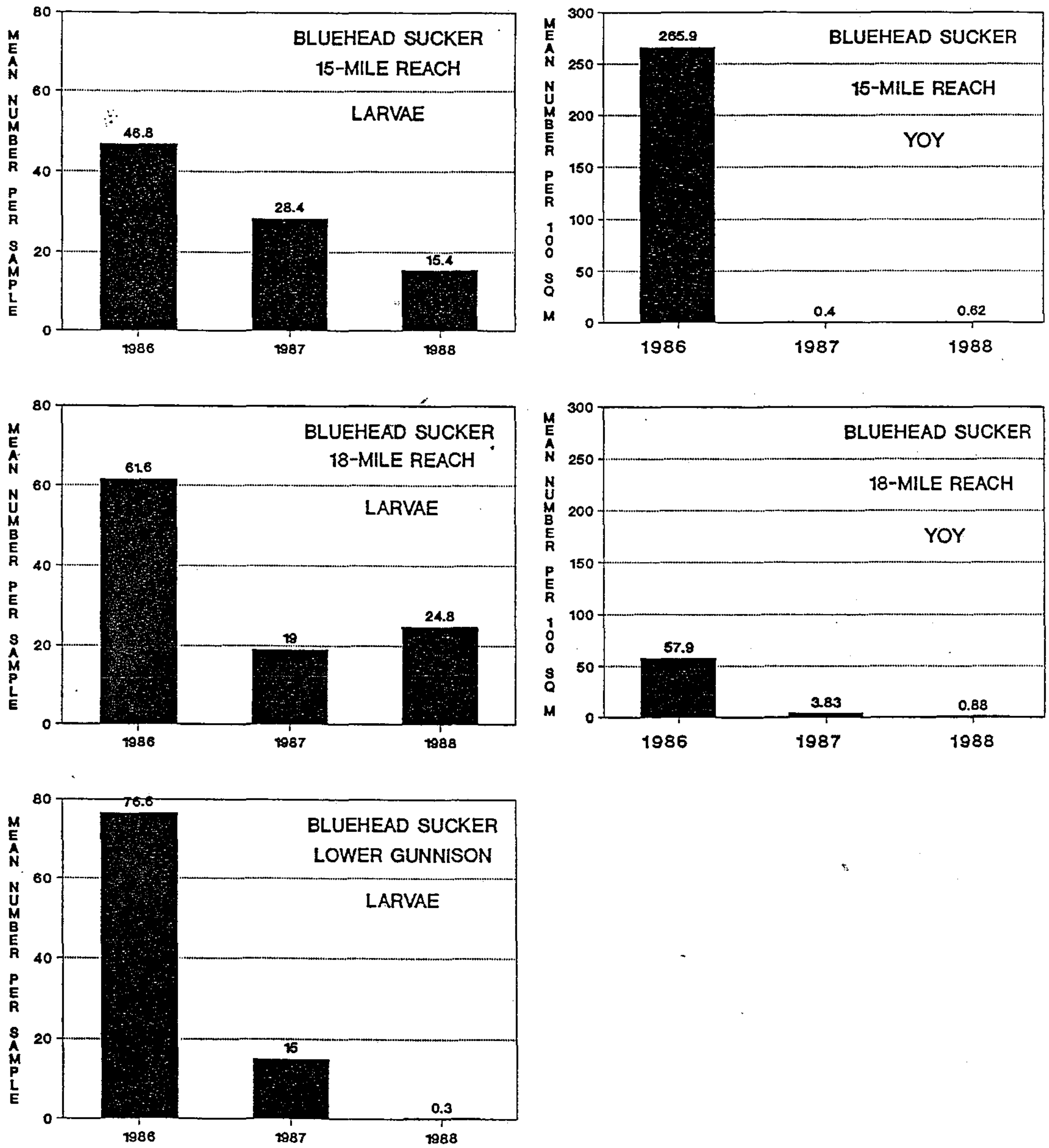


Figure 16. Catch rates of larval and young-of-the-year (YOY) bluehead sucker in the 15-mile, 18-mile and lower Gunnison reaches during 1986, 1987 and 1988.

Speckled dace numbers declined over the three years of study (Fig. 17). There were slight declines in larval abundance in the 15-mile and 18-mile reaches, and a large decline in 1988 in the lower Gunnison. Declines in YOY abundance were much more pronounced, however; densities measured during 1987 and 1988 were appreciably less than they were in 1986. No YOY speckled dace were detected in backwaters of the 15-mile reach during 1987, and almost none were found in both the 15-mile and 18-mile reaches in 1988.

Introduced Fishes

In general, the three common introduced species increased in abundance over the three-year period of study, particularly in the 18-mile reach. The increase in all reaches in 1988 was dramatic (Fig. 14). Also, for a given species, trends in YOY abundance of the introduced species more nearly reflected trends of larval abundance than they did for the three native species discussed above.

Numbers of larval sand shiners increased steadily over the three years and were particularly high in all three reaches in 1988 (Fig. 18). Unlike larval bluehead sucker and speckled dace, which became scarce during the period of extremely low flow in the lower Gunnison in 1988, larval sand shiners apparently did quite well. Though there was a decline in YOY abundance from 1986 to 1987 in the 15-mile reach, their numbers greatly increased there in 1988.

Of all the species, fathead minnows displayed the most dramatic increase in numbers (Fig. 14). They increased in all reaches over the 3-yr period, with the exception of a decrease in YOY in the 15-mile reach from 1986 to 1987, much like sand shiners (Fig. 19). In all years, larvae were most

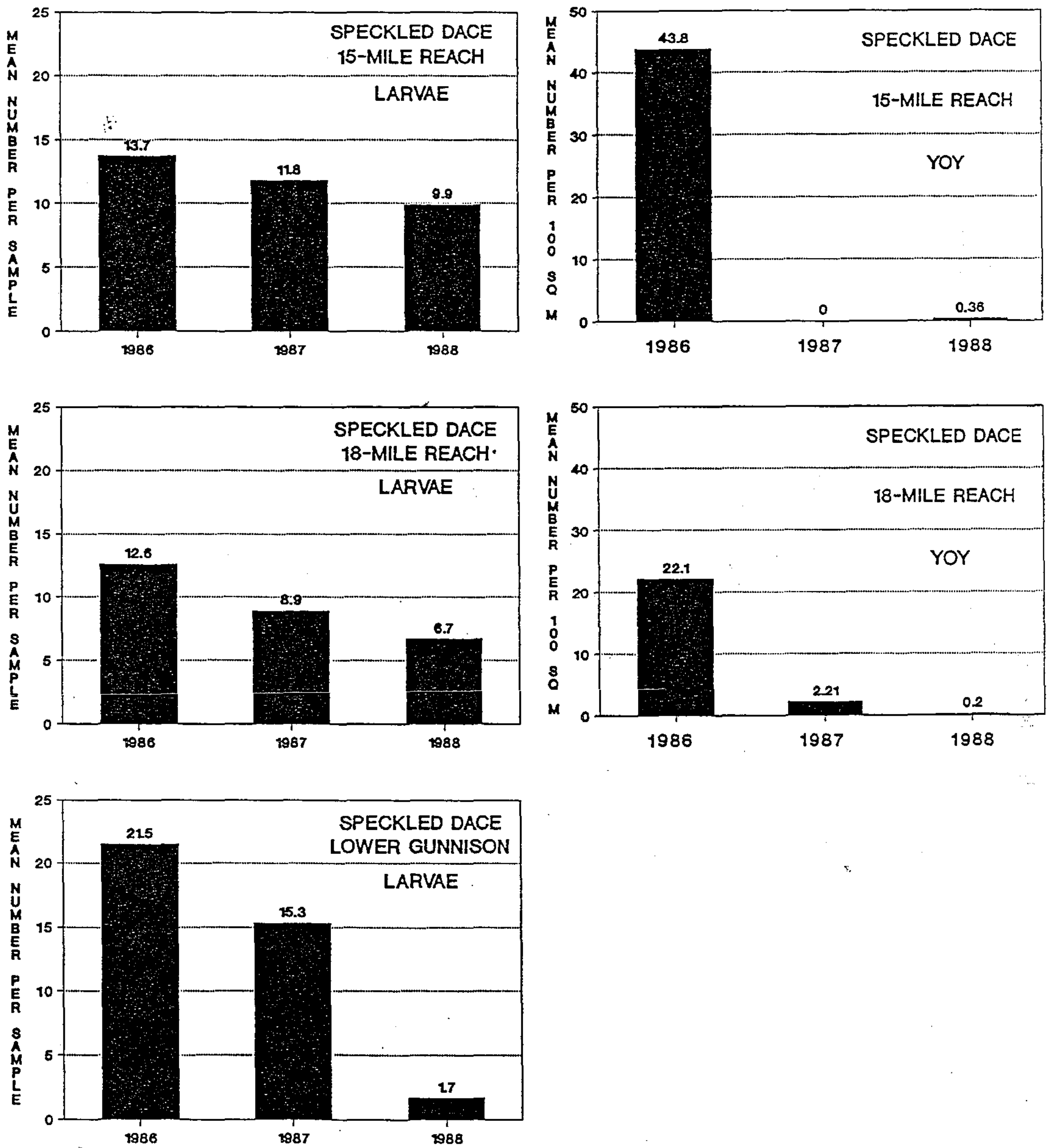


Figure 17. Catch rates of larval and young-of-the-year (YOY) speckled dace in the 15-mile, 18-mile and lower Gunnison reaches during 1986, 1987 and 1988.

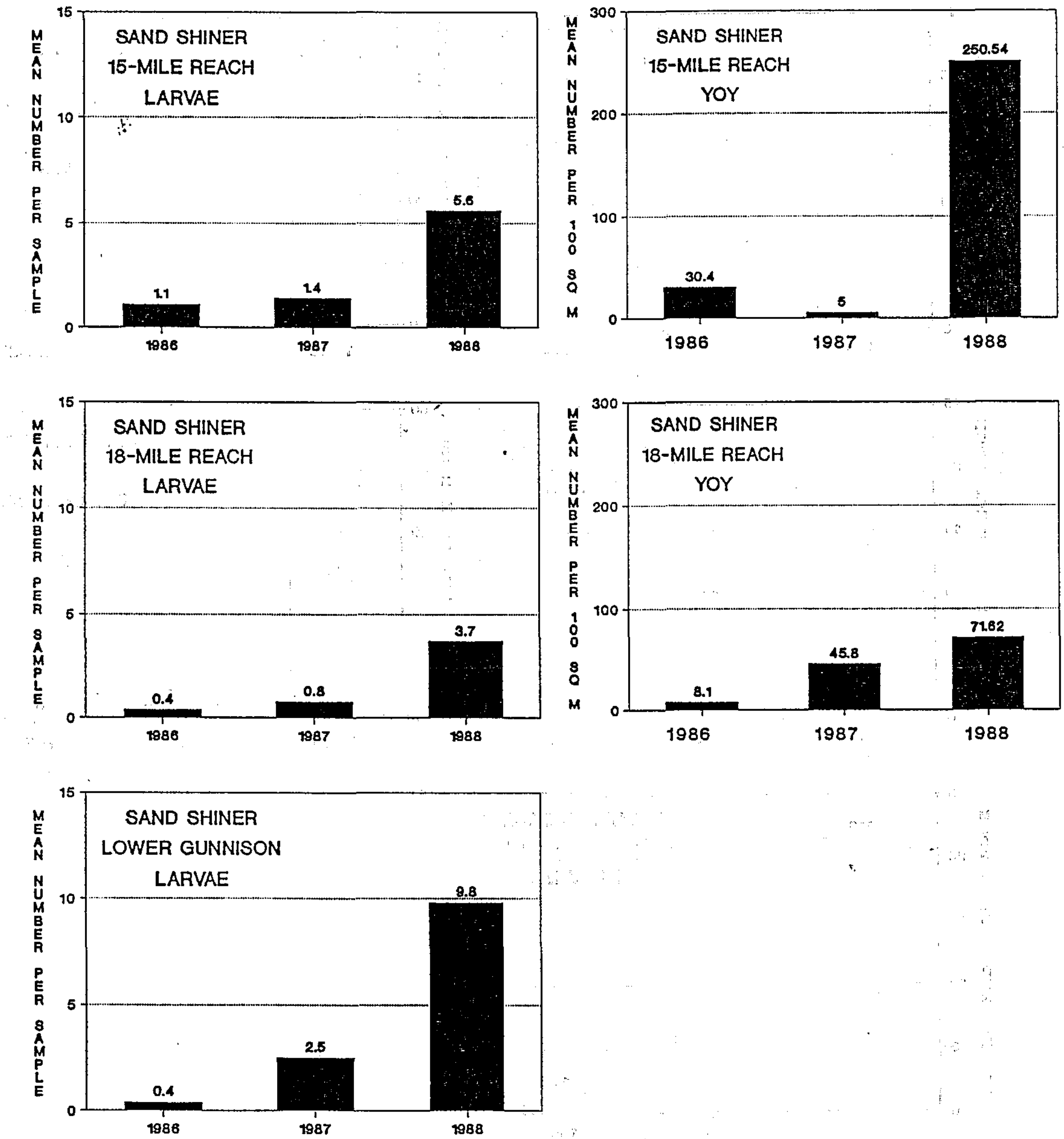


Figure 18. Catch rates of larval and young-of-the-year (YOY) sand shiners in the 15-mile, 18-mile and lower Gunnison reaches during 1986, 1987 and 1988.

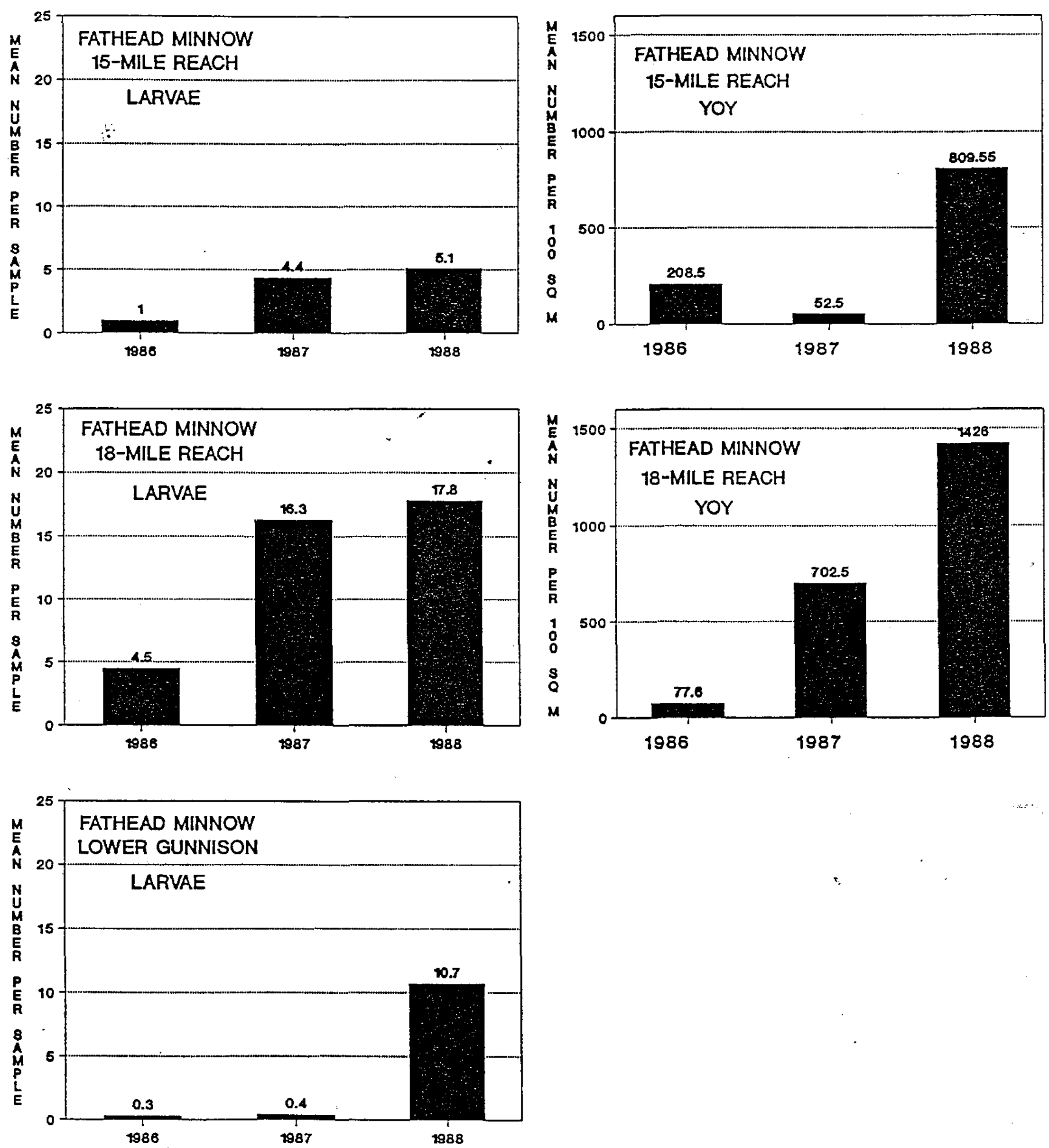


Figure 19. Catch rates of larval and young-of-the-year (YOY) fathead minnows in the 15-mile, 18-mile and lower Gunnison reaches during 1986, 1987 and 1988.

abundant in the 18-mile reach. Though catch rates varied between reaches, the relative increases in larvae over the three years were similar between the 15-mile and 18-mile reaches. Numbers of larval fathead minnows, like sand shiners, increased substantially in the lower Gunnison in 1988. Increases in YOY were particularly pronounced in the 15-mile and 18-mile reaches in 1988.

Red shiners also displayed a general increase in abundance over the three years of study (Fig. 20). Larvae were relatively scarce in all reaches during 1986, but in 1987 and 1988, numbers were substantially higher. The most pronounced increase in numbers of larvae was in 1988 in the 18-mile reach. Though larvae increased in abundance in the 15-mile reach from 1986 to 1987, YOY declined, a trend very similar to that of sand shiners and fathead minnows. In 1988, however, persistence to late September (YOY abundance) was high. YOY in the 18-mile reach showed a steady increase over the three years, much as larvae did.

The abundance of early life stages of most of the native and introduced fishes discussed above, including Colorado squawfish, showed either a positive or negative trend during the three-year period of study. In general, native species decreased in abundance while introduced species increased. We do not know whether this alarming trend will continue or whether these changes are short-term and related to the flow conditions of these particular years. Peak spring flows and summer flows progressively decreased between 1986 and 1988: 1986 was a relatively wet year, 1987 was an average-flow year and 1988 was a low-flow year. Additional analyses and additional data will be required before the relationship between flows and abundance of young in backwaters is understood.

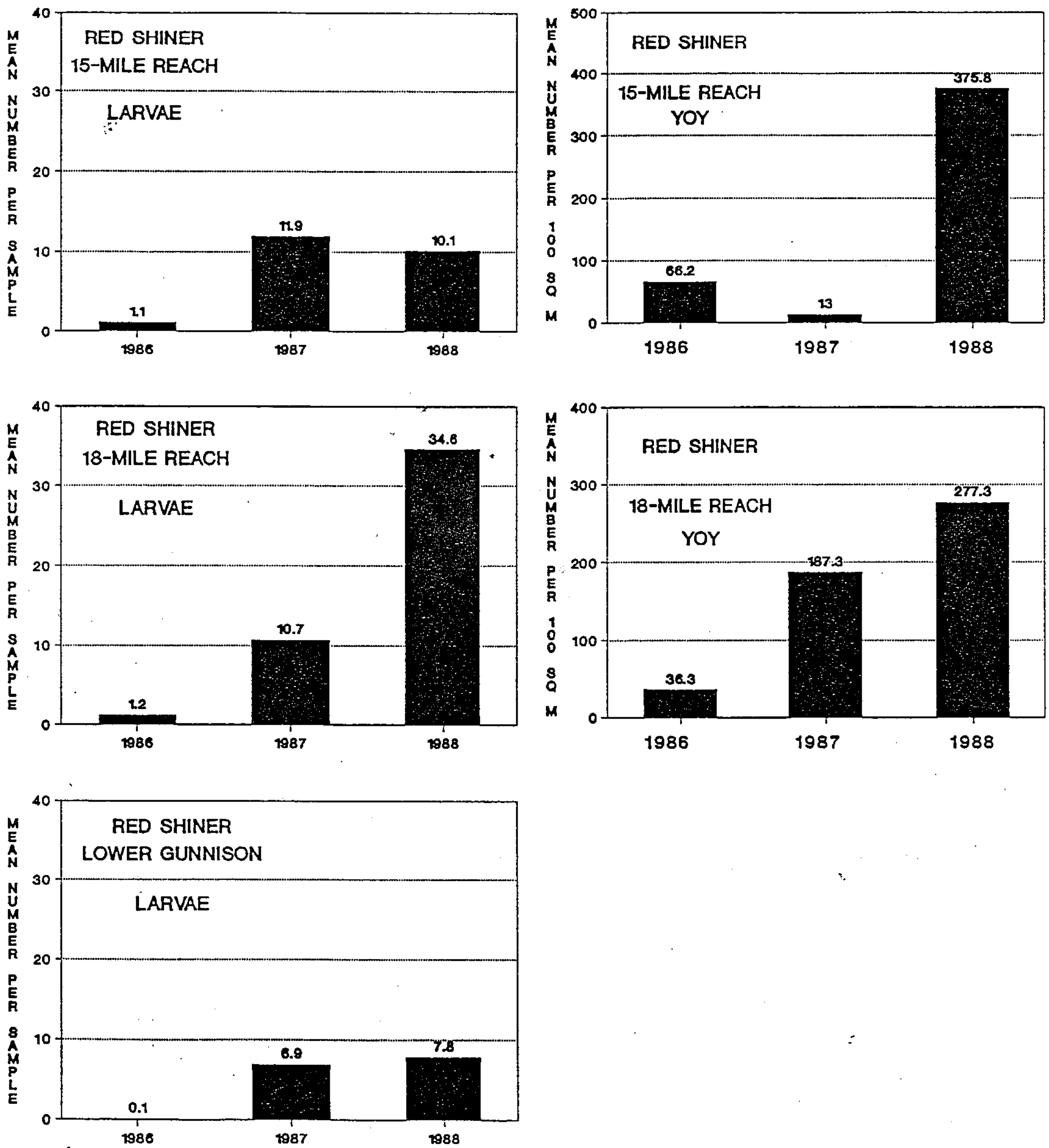


Figure 20. Catch rates of larval and young-of-the-year (YOY) red shiners in the 15-mile, 18-mile and lower Gunnison reaches during 1986, 1987 and 1988.

Spawning of Endangered Fishes

Colorado Squawfish

When spring flood waters subside and the water warms, squawfish begin to exhibit their most extensive movements. Much of the movement exhibited between late June and late August may represent migrations to and from spawning areas, or movements in search of such habitats.

In 1982, 1983, 1984, 1985 and 1988, one or more squawfish, tagged elsewhere, moved into the 15-mile reach during the spawning season and subsequently departed the area. In 1982, five radio-tagged Colorado squawfish were located in a pool in the 15-mile reach at RM 178.3 during 12-19 July. Sampling of this pool with nets yielded nine adult squawfish in or near spawning condition. Although subsequent floods (1983 and 1984) appreciably changed the habitat there, three other radio-tagged squawfish were located very near that same site on 21 July 1987. However, only one of these three fish remained in the reach during the entire spawning period.

The estimated ages of larvae collected in fall enable us to estimate the dates of spawning activity for each year. In turn, interpretation of radio-telemetry data is aided by our knowing when spawning occurred; this allows us to distinguish which movements were most likely migrations to and from spawning sites.

In 1986, spawning in the Grand Valley was estimated, based on the length of the larval fishes collected, to have occurred between 26 July and 5 August. Only one larva was collected in 1987 and one in 1988; in both cases spawning was estimated to have occurred on 4 July. A 20-day period encompassing this date (24 June to 14 July) is assumed to be a reasonable estimate of the spawning period in the Grand Valley during these two years. Movements related to spawning were distinguished based on a careful examination of fish locations prior to, during, and subsequent to the estimated spawning periods.

One of five squawfish radio-tagged in 1986 apparently stayed within the 15-mile reach during the estimated spawning period, and another moved above the reach to the base of the Price Stub Dam. Three others had moved downstream from the reach prior to the period: two to the Gunnison River, and a third to the Walker area.

In 1987, three of seven radio-tagged squawfish apparently stayed within the reach during the entire spawning period. Three tagged fish moved downstream and out of the reach during or just prior to the spawning period and were located outside the reach during the spawning period; a fourth fish may have moved to the Gunnison during the end of the period but was not found there until after the estimated period was over. If all of these fish spawned, four of them probably did so inside the reach, two outside; the seventh fish, having moved in and out on two separate occasions during the estimated spawning period, may have spawned either in or out of the reach. Interestingly, both of the fish that stayed within or moved above the reach during the spawning season in 1986 moved downstream and out of the reach during the 1987 spawning period. One was located at the base of the Redlands Diversion Dam (GU RM 3.0), and the other near the Utah state line (CO RM 130.1). Both of these fish returned to the 15-mile reach during or shortly after the estimated spawning period. Another 1986-tagged squawfish that had moved to and returned from the Gunnison

River in 1986, moved instead, in 1987, to the Walker area (RM 163.7) during the spawning period and returned shortly thereafter.

In 1988, five of nine squawfish present in the 15-mile reach during spring definitely moved out prior to or during the estimated spawning period, and were located in downstream reaches. The other four were missing for 1-3 weeks during this period, though were not located elsewhere. Of three fish outside the reach in spring, one moved in and stayed there through most of the spawning period (though it did make one brief foray to the lower end of the Gunnison during this time); the other two moved downstream rather than into the 15-mile reach.

Despite the presence of adult squawfish in the 15-mile reach during the spawning seasons of 1986, 1987 and 1988, successful reproduction may have not occurred there then. No larvae were collected there during our intensive sampling program. Only two larval (< 25 mm TL) and no young-of-year-size (25-60 mm TL) squawfish have been collected from the reach since 1982. Larval Colorado squawfish were collected only during 1982, the year when the aggregation of adult squawfish occurred in mid-July at RM 178.3 in the 15-mile reach. However, in 1986 a 105-mm-long (yearling size) squawfish was seined from a backwater at RM 174.5. Colorado squawfish larvae and YOY were collected 6-8 miles downstream from the 15-mile reach (in the lower 18-mile study reach) in 1986 and 1987, as well as in 1983, 1984 and 1985. In these years, some (1-23) larvae were collected between RM 162.7 and 164.8 (Walker Wildlife Area), as well as from other sites downstream. In 1988, one larva was collected from the lower 18-mile reach but downstream of the Walker Area. Although it is possible that these larvae drifted down from the 15-mile reach, it seems unusual that none was collected from the 15-mile reach itself. This might imply that downstream movement of larval Colorado squawfish from the 15-mile reach, if it occurs, is accomplished rapidly and essentially simultaneously by all larvae. Interestingly, the only year when larvae were collected from the 15-mile reach (1982) was also the only year they were not collected from the lower 18-mile reach. Perhaps the best explanation is that detectable spawning activity in the 15-mile reach occurs only during infrequent years; limited spawning activity may occur more frequently but the resulting larvae are so few that they are not detected by our sampling efforts.

In 1986, the first year that we sampled the lower Gunnison for larval fishes, one larval Colorado squawfish was found immediately downstream from the Redlands Diversion plunge pool (Fig. 10), suggesting that spawning may occur there. It is possible, however, that this larva drifted downstream from the reach of the Gunnison above the dam, where adult squawfish also occur. The movement of radio-tagged Colorado squawfish to the Redlands Diversion plunge pool described earlier may be associated with spawning in this Gunnison reach, or perhaps with attempts to reach spawning areas above the diversion dam. Alternatively, movements of some fish to this pool and to the pool below the Price Stub dam, especially movements well after the spawning period, may indicate that dam plunge pools are good feeding and resting habitat sought by Colorado squawfish during low summer flows. No larvae were found in the lower Gunnison in 1987 or 1988. If spawning occurs in the lower Gunnison, it may, as may be the case in the 15-mile reach, occur in detectable levels only during infrequent years. It may be that Colorado squawfish spawn at various sites within the Grand Valley; the sites selected might depend on conditions that vary from year to year. Perhaps individuals return to areas where they spawned before, and, if conditions are no longer suitable, the fish seek alternate sites.

Catch rates of larval Colorado squawfish indicate that 1986 was a considerably better year for squawfish reproduction in the Grand Valley than was 1987 or 1988 (Fig. 11).

Razorback Sucker

Because razorback sucker are so rare and our data on radio-tagged razorbacks is relatively limited, it is difficult to draw definitive conclusions about their movement patterns. Razorbacks spawn in the Grand Valley area in May and June, the precise period being determined by water temperature, and perhaps photoperiod or other environmental variables. A ripe razorback captured within the 15-mile reach on 3 June 1986 and given a radio tag at that time spent the remainder of the year at a location 10.7 miles downstream. Another razorback captured in the 15-mile reach on 11 June 1987 similarly spent the remainder of the year at a location 12 miles downstream (RM 166.5). A third razorback tagged on 19 May at RM 168.2 (2.8 miles below the 15-mile reach) was located on 8 June in the 15-mile reach, seven miles upstream from its point of release. The fish subsequently returned to the vicinity of its release site. However, the following year, it apparently did not move to the 15-mile reach during the suspected spawning season as it did in 1987. These results suggest that razorback suckers may sometimes move to areas within the 15-mile reach to spawn, then return to feeding and resting areas of relatively small size for the remainder of the year.

The two razorback suckers captured from the 15-mile reach in spring 1986 were in spawning condition when caught. One was a female captured on 3 June; she had very ripe eggs that could be expressed when slight external pressure was applied. The other was a male captured eight days later, about 30 m from the site of the female; he had thin milt expressable with slight pressure.

No young or juvenile razorback sucker has been collected from the Grand Valley area during our investigations. However, as mentioned before, larval razorbacks are difficult to distinguish from the larvae of the other sucker species of the upper Colorado River and it is possible that some may have been collected but not identified as such. Two long-time residents who live along the 15-mile reach near Clifton report that "humpback" (razorback) suckers were plentiful there through at least the early 1940's (Glen Humphreys and Raymond Lurvey, personal communication). They report that during spring runoff periods in the 1930's and early 1940's, several thousand razorbacks used a flooded pasture near their homes at RM 175.6, ostensibly to spawn. Thus, a sizable population of adult razorbacks formerly existed in the area and the 15-mile reach may have included important spawning habitat. In 1945, the pasture that had been used by razorbacks was diked, filled in, and converted to an orchard. Whether this particular site was unique to the area or was one of many such habitats is unknown.

During the 1979-88 studies, 50 of the 57 razorbacks (88%) captured in the Grand Valley were caught from flooded gravel-pit ponds: Walker Wildlife Area (RM 163.6), Connected Lakes (RM 167.8) and Clifton Pond (RM 177.8). McAda (1977) captured 43 razorbacks from the Walker Wildlife Area during

1974-1976 and he believed razorbacks spawned there in 1975. We captured a ripe female from WWA on 16 June 1982. Eighteen razorbacks have been captured from Clifton Pond, a gravel-pit pond connected to the river in the 15-mile reach. One of these fish was a ripe male captured on 9 June 1982. Spring floods of 1983 and 1984 dramatically altered the Colorado River channel in many areas of the Grand Valley. The three gravel-pit ponds from which razorbacks had been routinely caught were washed out, or made inaccessible to fish from the river because of sediment deposition or subsequent diking. The two ripe razorbacks radio-tagged in the 15-mile reach (RM 174.4) during 1986 were captured from a small gravel-pit pond. Both had been caught previously; the female, from Clifton Pond in June 1980; the male, from a gravel pit at RM 175.3 in June 1981.

Habitat Use

Adult Colorado Squawfish

Habitat Type

Although a variety of habitat types is used during each month, some seasonal trends in habitat use are apparent. Extensive use of runs, the most common riverine habitat type, occurs throughout the year, but run use increases and decreases as other habitat types become seasonally important (Figs. 21 and 22). A relatively constant pattern of habitat use occurs during the winter months of November-February (Fig. 21). In November, water temperature drops dramatically; at the same time, flows increase as the irrigation season ends. During winter, fish movement is restricted to localized areas. Pool habitat is most frequently used, followed by low-velocity runs. During January, ice forms over the low-velocity areas, and

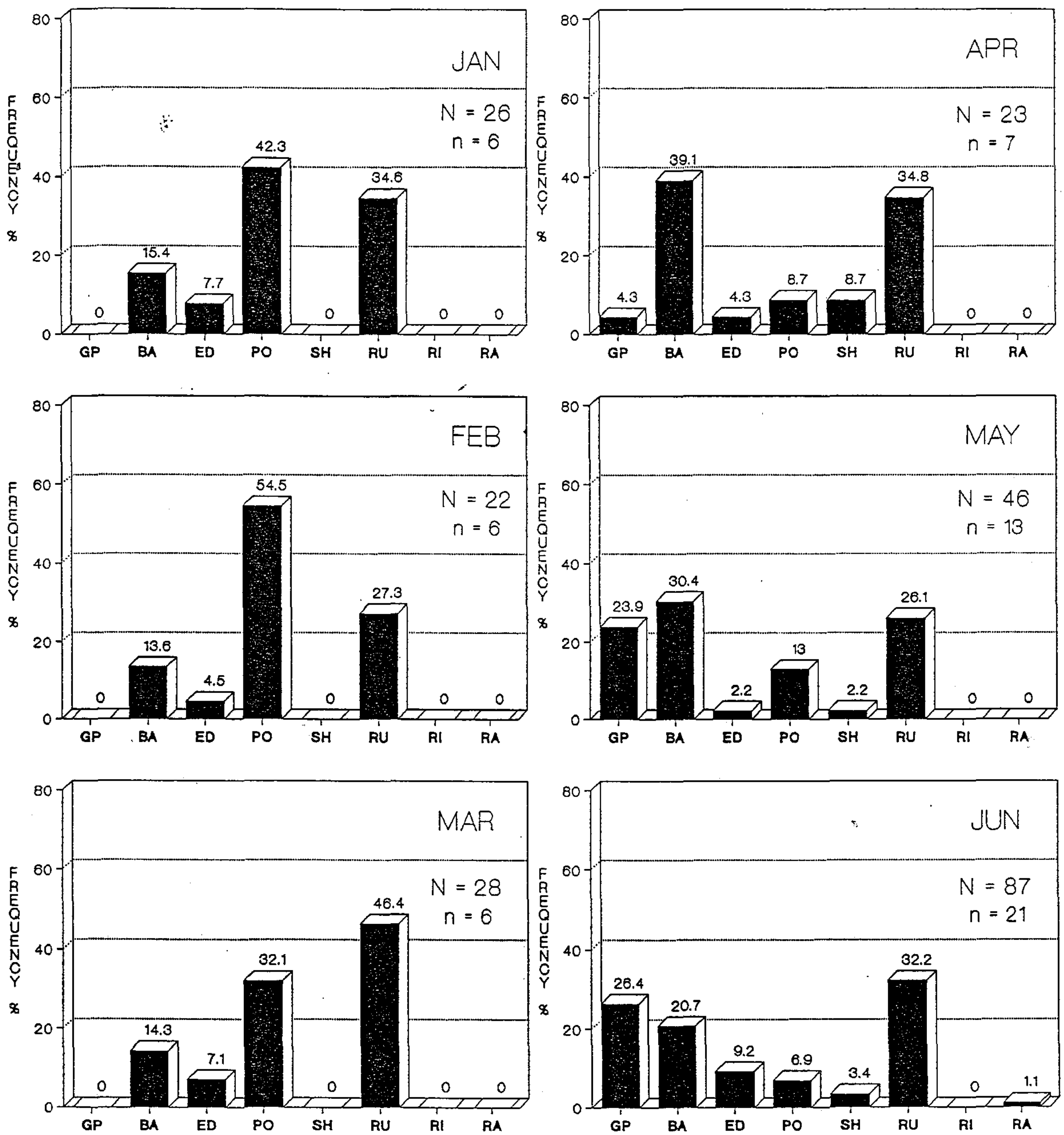
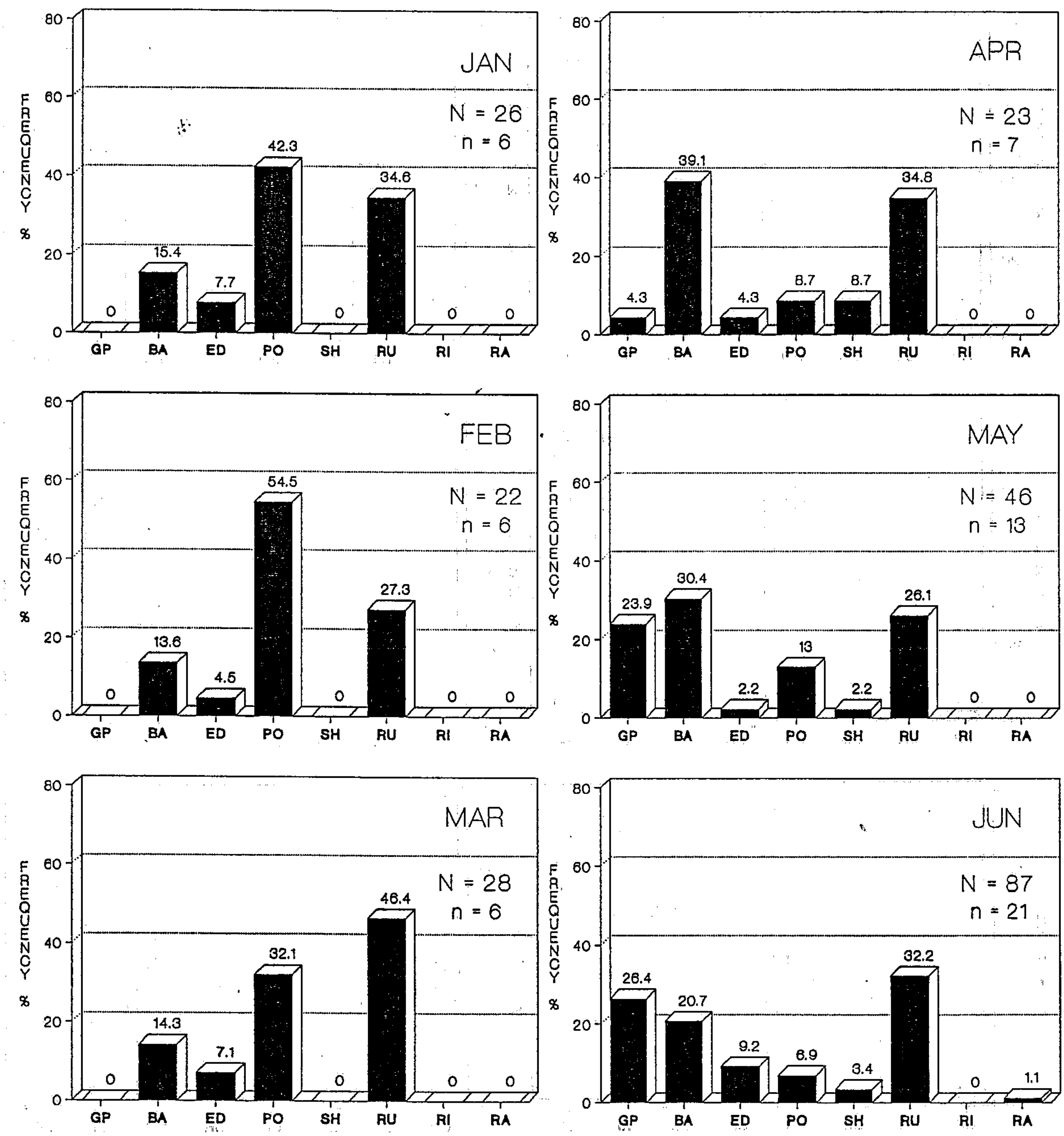


Figure 21. Frequency of habitat type at locations of radio-tagged Colorado squawfish, by month. Data were collected during 1986, 1987 and 1988 in the Grand Valley, Colorado. N = number of observations; n = number of different squawfish. Habitat codes: GP = gravel pit; BA = backwater; ED = eddy; PO = pool; SH = shoreline; RU = run; RI = riffle; RA = rapid.



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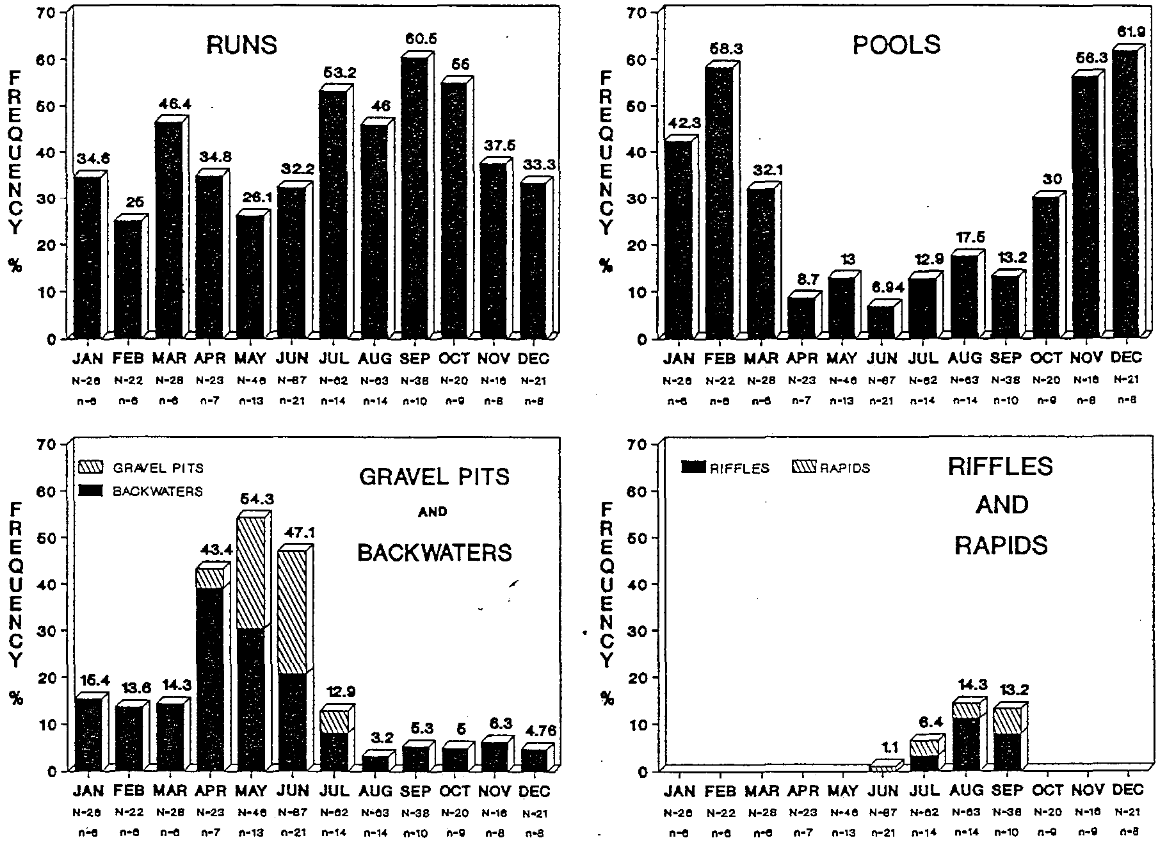

Figure 22. Frequency of Colorado squawfish use of selected habitat types, by month. Data were collected in the Grand Valley, Colorado during 1986, 1987 and 1988. N = number of observations; n = number of different squawfish.

squawfish are often located under the ice. Ice-out is usually in early February. March is a transition month between winter and spring habitat-use patterns. Water begins to warm, but flows have not yet increased; the use of pools begins to drop and the use of runs increases. Flows are reduced in early April when the irrigation season begins. During late April to early May a spring-runoff period begins and lasts through early July. As flows increase in late April, there is a substantial increase in the use of backwaters. In May and June, flows increase dramatically and riverside gravel pits become flooded; many squawfish then move into these protected off-channel habitats. The yearly use of gravel pits and backwaters reaches a peak at this time (Fig. 22). A pattern of summer habitat use occurs from July through September. Flows decrease and can become quite low, particularly in the 15-mile reach. Water is warm during this period and fish metabolism is therefore at its peak. Runs are predominately used and some use of riffles and rapids occurs (Fig. 22). October is a transition period between summer and winter; flows are still low and water temperatures drop. Though fish predominately use runs, the use of pools increases (Fig. 21).

Depth

Depths at locations of radio-tagged squawfish varied seasonally. Shallow sites (< 3 ft deep) were used in all months except November and December; the highest frequency of shallow-water use was during April, May and August (Fig. 23). Use of deep water (≥ 4.5 ft) was greatest during winter from November to January. Deep water began to decrease in use in February and was little used during April and May. Though flows decreased from July through October, use of deep water increased. Mean depth perhaps best illustrates the seasonal trend (see Fig. 24).

Velocity

Mean water-column velocity measured at sites of radio-telemetered squawfish was low (< 0.35 ft/sec) over 50% of the time during all months except for the July-October period (Fig. 25). This reflects the high use of zero- to low-velocity pools during November-February, and the high use of zero-velocity backwaters and gravel pits during the April-June period. Conversely, use of relatively swift-water areas (> 1.0 ft/sec) was at its peak during July-September, reflecting the high use of runs, riffles and rapids during this time. Elevated fish metabolism due to warm water

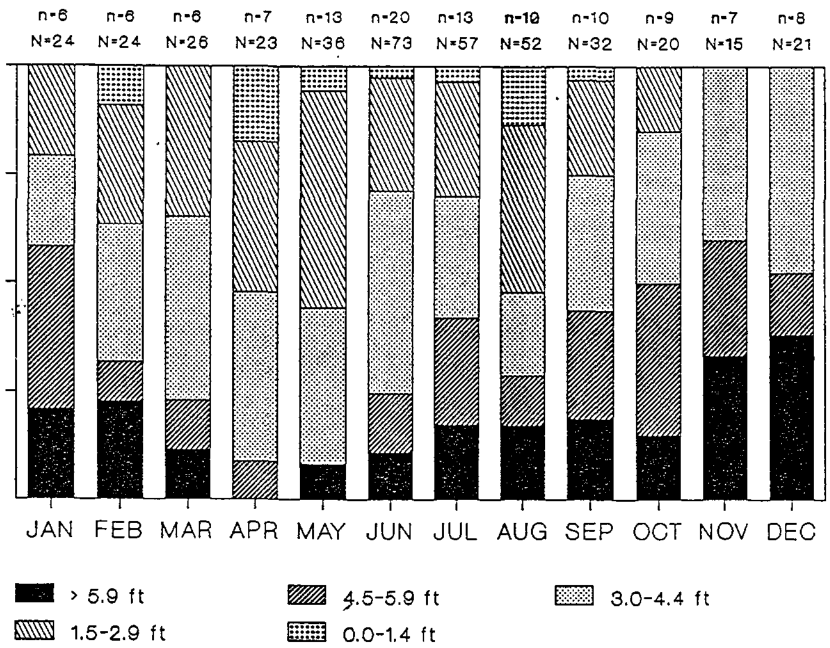

Figure 23. Frequency of depths at locations of radio-tagged Colorado squawfish, by month. Data were collected during 1986, 1987 and 1988 in the Grand Valley, Colorado and pooled by one of five depth categories. N = number of observations; n = number of different squawfish.

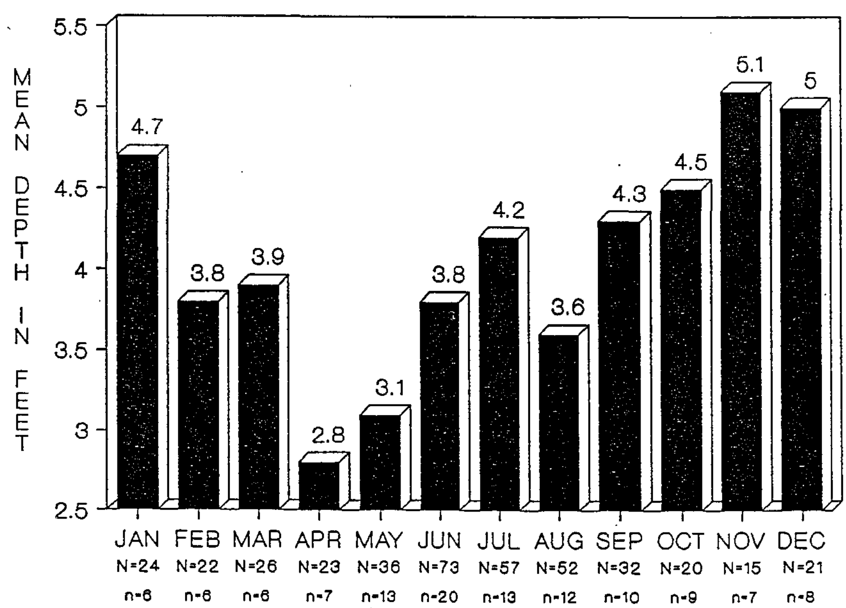

Figure 24. Mean depth at locations of radio-tagged Colorado squawfish, by month. Data were collected during 1986, 1987 and 1988 in the Grand Valley, Colorado. N = number of observations; n = number of different squawfish.

temperatures allows greater use of high-velocity areas. However, we were surprised by the high frequency of use of relatively fast water areas, especially during the colder months; consequently, in September 1988 we began measuring the bottom velocity (0.1 ft from the bottom) in addition to the mean column velocity. We found that in all cases, bottom velocity was less than mean column velocity--in most cases, substantially so. Because we did not know the position in the water column that a radiotelemetered fish actually occupied, currents that the fish maintained itself in might have been considerably less strong than indicated by mean column velocity, especially if the fish was at or near the bottom. From September through December 1988, velocities at the bottom were ≤ 0.35 ft/sec 77% of the time and ≤ 0.5 ft/sec 94% of the time (n = 35 locations).

Substrate

Substrate type is closely correlated with water velocity. Where water is swift, sediments are carried away leaving larger substrate particles behind. In swift-water areas, rubble, boulder or bedrock are the likely substrate types. At low-velocity sites, deposition occurs, leaving a sand or silt substrate. Thus, the frequency distribution for substrate type at squawfish locations resembles the seasonal trend for velocity in these areas (Figs. 25 and 26). It is unclear whether substrate is a key factor in site selection by Colorado squawfish or a relatively unimportant variable affected by the velocity at the site. In some cases, large stones such as those in rubble or boulder substrates may allow use of an otherwise swift portion of river by slowing velocity along the bottom and creating sheltered microhabitats.

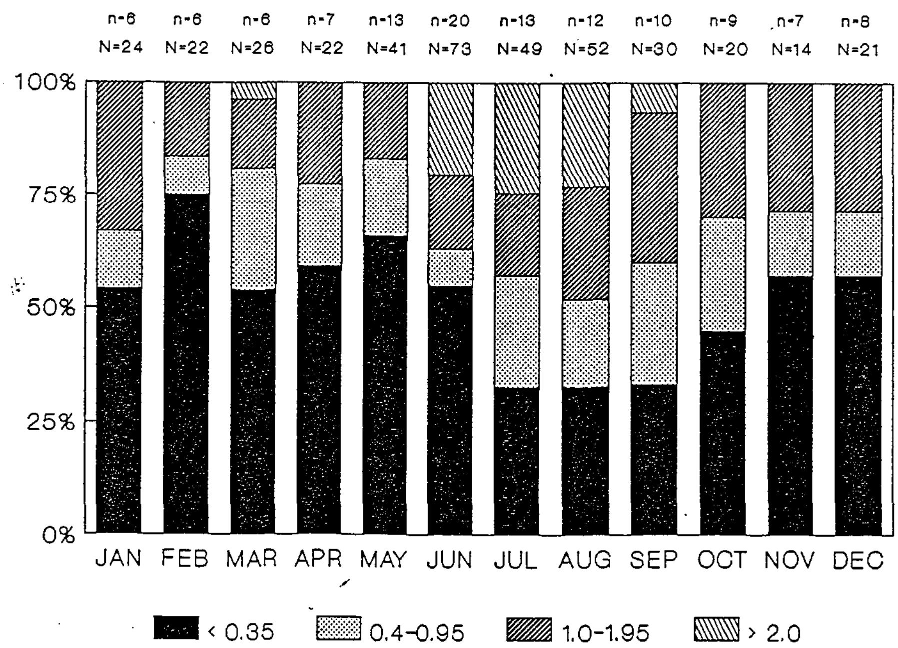

Figure 25. Frequency of mean column velocity (in cubic feet per second) at locations of radio-tagged Colorado squawfish, by month. Data were collected during 1986, 1987 and 1988 in the Grand Valley, Colorado and pooled by one of four velocity categories. N = number of observations; n = number of different squawfish.

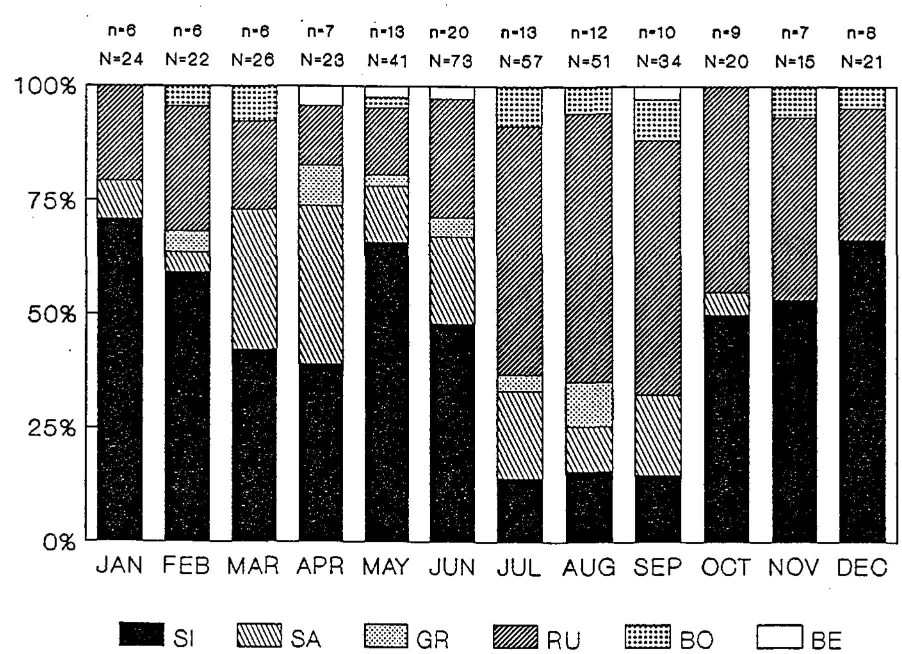

Figure 26. Frequency of substrate type at locations of radio-tagged Colorado squawfish, by month. Data were collected during 1986, 1987 and 1988 in the Grand Valley, Colorado. Substrate type codes: SI = silt; SA = sand; GR = gravel; RU = rubble; BO = boulder; BE = bedrock. N = number of observations; n = number of different squawfish.

A better knowledge of the feeding activity of squawfish is needed before the factors involved in site selection can be sorted out. It is not known how squawfish divide their time between resting and pursuing prey, or whether they do both simultaneously (ambush strategy). One hypothesis for the occurrence of various substrate types at squawfish locations might be that during colder months, metabolic demands and feeding are reduced and more time is spent in low-velocity areas to rest--areas where silt tends to deposit. During warmer months, feeding activity increases causing squawfish to spend a large proportion of their time in rocky areas where prey fish like bluehead sucker are in greatest abundance. The unseasonably high occurrence of silt substrate in May and June is explained by the overriding attraction of warm backwaters and flooded gravel pits during this time (Fig. 22 and 26).

Adult Razorback Sucker

General

We collected data from four radio-tagged razorback suckers during 1986-1988. One fish was tracked through all three years and provided 68-71% of the habitat-use data. From one to four different fish provided a total of three to 15 observations per month. Unfortunately, more observations per month from more individuals are needed before we can draw conclusions about habitat-use patterns with any degree of confidence. Judging from our frequency-of-use data for Colorado squawfish, at least 15-20 observations are needed per month to produce relatively stable frequency values.

Habitat Type

Despite the limitations of our data, use of various habitat types by razorbacks displayed some seasonal patterns (Fig. 27). Pools and low-velocity eddies, often associated with pools, were extensively used from November through April. In April or May, razorbacks begin to move in search of spawning sites. In May, habitats used were primarily runs and backwaters. In June, most use was of backwaters and flooded gravel pits; no use of runs was detected. In July, as spring flows declined, razorbacks moved out of flooded gravel pits (one became stranded) and the use of runs again increased. During the August-October period, runs and pools were primarily used.

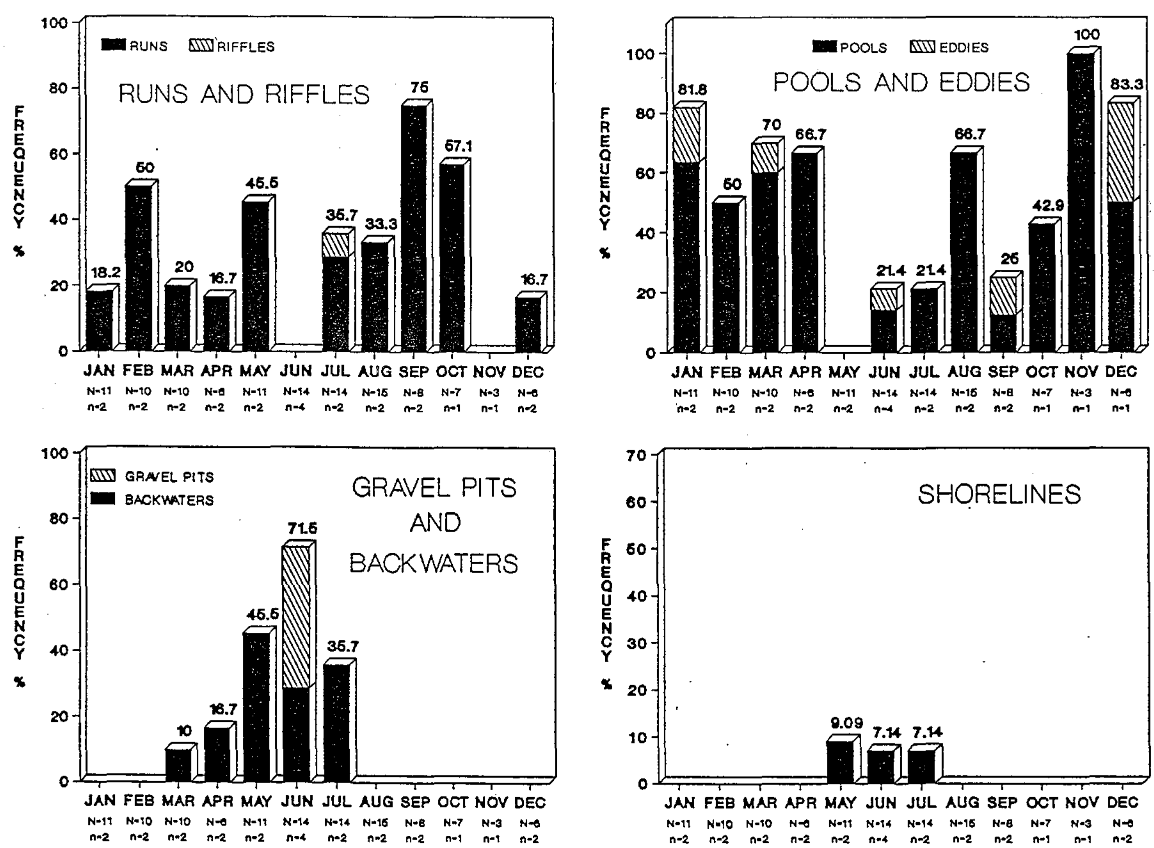

Figure 27. Frequency of razorback sucker use of selected habitat types, by month. Data were collected in the Grand Valley, Colorado during 1986, 1987 and 1988. N = number of observations; n = number of different razorback suckers.

Depth

Depth at locations of radiotelemetered razorbacks varied seasonally in a pattern similar to that of Colorado squawfish (Figs. 23 and 28). However, razorbacks displayed a much stronger preference than squawfish for deep-water sites, particularly for sites $\geq$ 6.0 ft deep. Mean depth at sites was $\geq$ 6.0 ft from November through April. Unlike squawfish, which began to use more shallow sites in April, razorbacks did not increase their use of shallow sites until May. Mean depth at razorback locations was lowest during May-July (Fig. 29).

Velocity

No strong seasonal pattern was evident in velocities at the locations of razorbacks (Fig. 30). However, as previously discussed regarding sites of radiotelemetered squawfish, velocity near the bottom, where suckers are likely to be, was probably considerably less than the mean-column velocities that we measured.

Substrate

Substrate may be a very important habitat variable for suckers, and may be a better indicator of bottom velocity than is mean-column velocity. Substrates where razorback suckers were located during November through April were always silt and/or sand, indicative of low-velocity habitat (Fig. 31). Metabolism increases during the warmer months and abundance of various food types are apt to change seasonally. This may explain the increased frequency of rubble and boulder substrates at sites used by razorbacks during the May-October period. The high use of flooded backwaters and gravel pits during June explains the high frequency of silt substrate at that time.

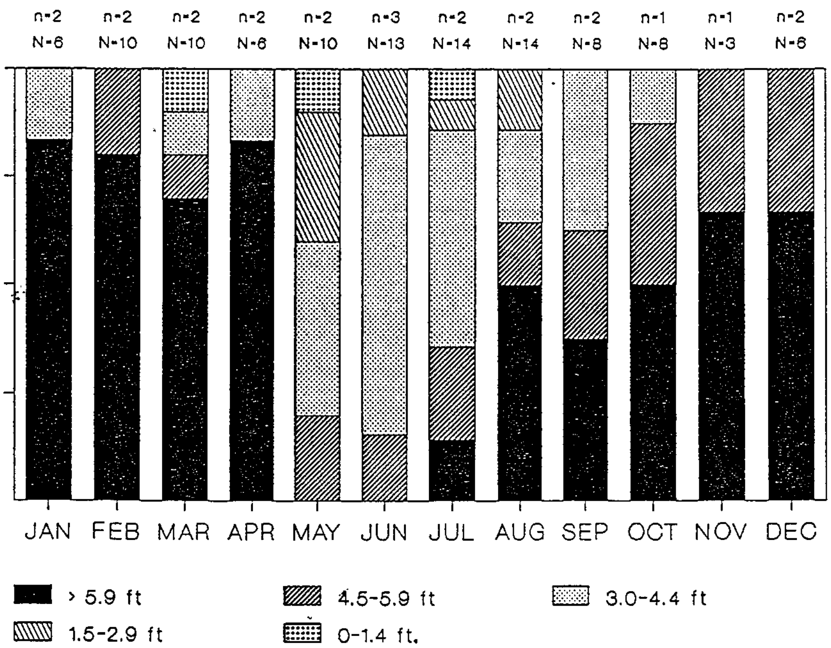

Figure 28. Frequency of depths at locations of radio-tagged razorback suckers, by month. Data were collected during 1986, 1987 and 1988 in the Grand Valley, Colorado and pooled by one of five depth categories. N = number of observations; n = number of different razorback suckers.

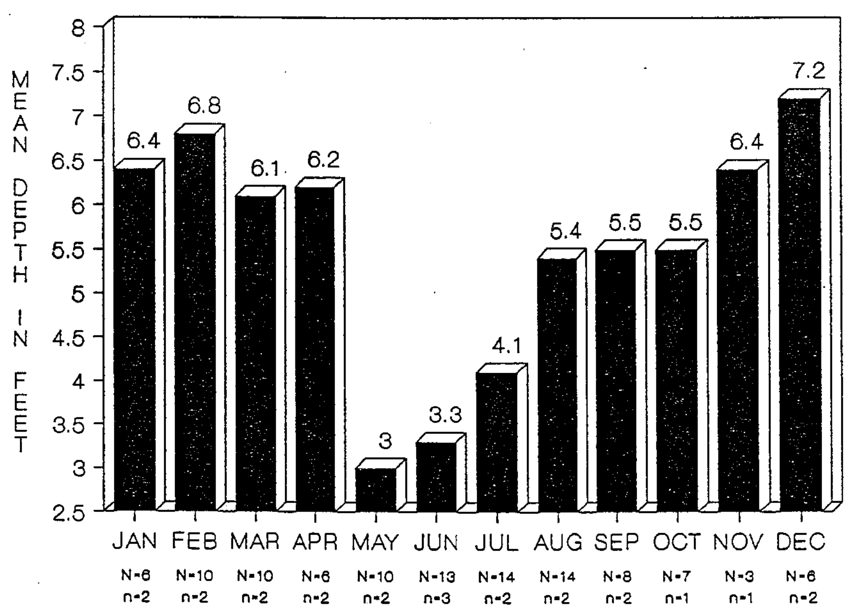

Figure 29. Mean depth at locations of radio-tagged razorback suckers, by month. Data were collected during 1986, 1987 and 1988 in the Grand Valley, Colorado. N = number of observations; n = number of different razorback suckers.

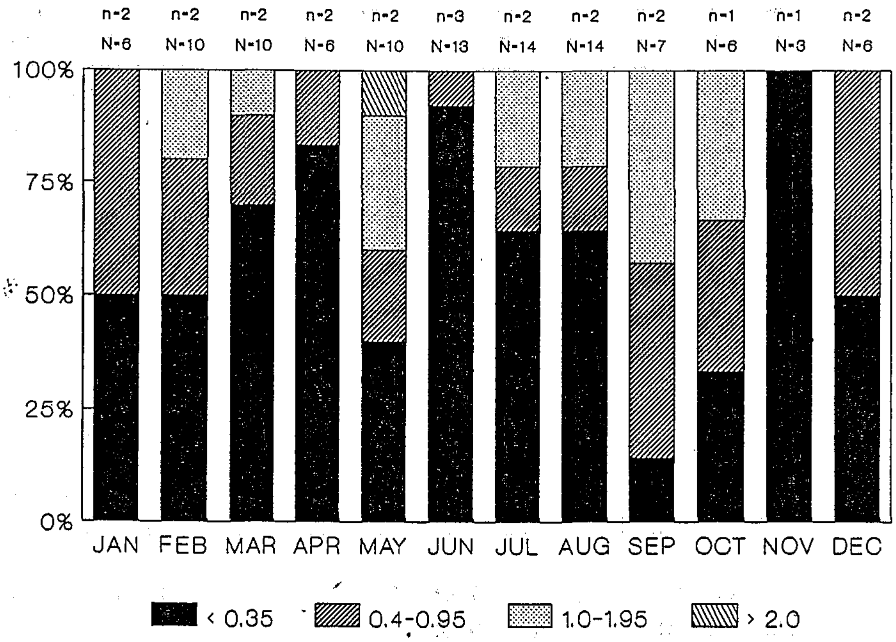

Figure 30. Frequency of mean column velocity (in cubic feet per second) at locations of radio-tagged razorback suckers, by month. Data were collected during 1986, 1987 and 1988 in the Grand Valley, Colorado and pooled by one of four velocity categories. N = number of observations; n = number of razorback suckers.

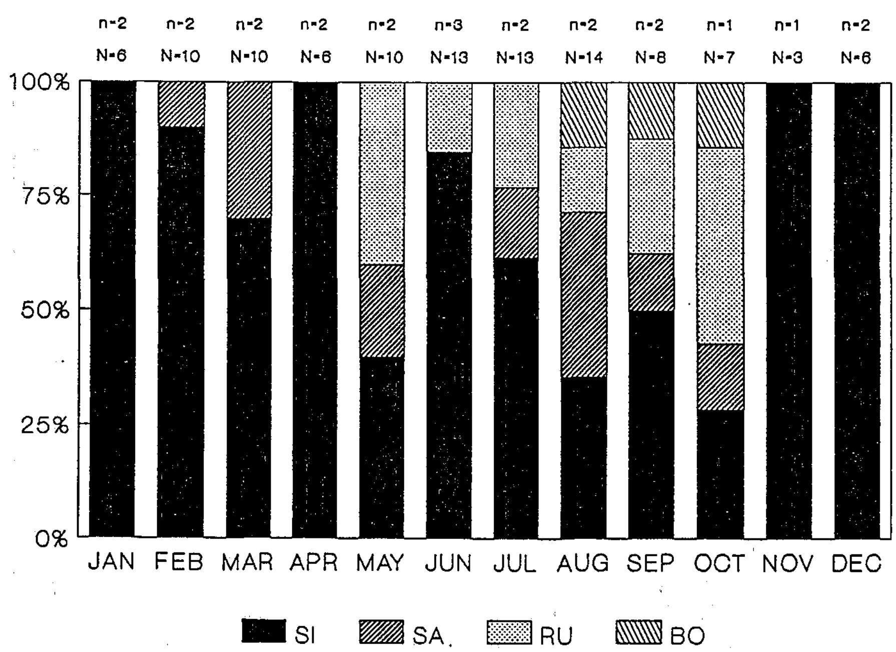

Figure 31. Frequency of substrate type at locations of radio-tagged razorback suckers, by month. Data were collected during 1986, 1987 and 1988 in the Grand Valley, Colorado. Substrate type codes: SI = silt; SA = sand; GR = gravel; RU = rubble; BO = boulder; BE = bedrock. N = number of observations; n = number of different razorback suckers.

SUMMARY

The 15-mile reach is habitat for two imperiled fish species, Colorado squawfish and razorback sucker. Some adult squawfish occur there year round, whereas others are found there only during the winter and spring or during the spawning season. Razorback suckers move there in spring from lower reaches, presumably to spawn. However, successful reproduction there appears to be very limited for both species. For squawfish, detectable spawning may only occur during infrequent years, and for razorback no young has yet been found. The few gravel-pit ponds and large backwaters within the 15-mile reach are extensively used by both squawfish and razorback during spring floods. For both species, the use of runs increases during the summer months, and pools are predominately used during winter. Razorback suckers appear to more strongly prefer deep-water habitats than do squawfish. During some years, some Colorado squawfish move out of the reach during the spawning season, then return shortly thereafter. Other squawfish move out of the 15-mile reach and spend the summer in the Colorado River upstream from the Grand Valley Diversion, or in the Gunnison River. These areas may be attractive because of the large pools there. Plunge pools below diversion dams may be good feeding and resting habitat; they might also serve as staging areas for squawfish using nearby spawning sites, such as cobble bars that often occur just downstream from plunge pools. From 1986 to 1988, abundance of larval and YOY Colorado squawfish decreased in the Grand Valley. Young of two other native species also decreased in abundance, while three common introduced species dramatically increased. It is not yet clear whether this trend will continue or whether these changes in abundance of young are natural short-term fluctuations related to yearly flow conditions.

RELATIVE IMPORTANCE OF THE 15-MILE REACH

Because of the high capture rate and the year-round presence of adult Colorado squawfish and razorback sucker, Valdez et al. (1982) considered the Grand Valley region of the Colorado and Gunnison rivers to be very important habitat for endangered fishes. As our data show, the 15-mile reach is an integral component of this larger Grand Valley region. Results of our studies indicate adult Colorado squawfish and razorback sucker travel among the three adjacent reaches in the Grand Valley. Such movement is evidently necessary to fulfill the various season-specific habitat needs of the fish. Thus loss of the 15-mile reach as habitat would be especially significant to the Colorado squawfish and razorback populations of the Grand Valley. The important habitats of the 15-mile reach need to be maintained; with proper management, the value of these habitats might be enhanced.

POSSIBLE LIMITING FACTORS

Adult Colorado Squawfish

Habitat

Spring

The habitat needs of adult squawfish apparently change throughout the year. The extensive use by squawfish of gravel-pit ponds and backwaters during spring may reflect their desire for a respite from high-velocity flood waters or an attraction to the warm waters that these habitats provide, as discussed later. Off-channel, low-velocity habitats thus may be important from April through June. The concentration of squawfish in certain large backwaters and flooded gravel pits during this time suggests that these habitats are limited in number. However, we do not know whether the availability of such habitats in spring could in some way limit the Colorado squawfish population in the 15-mile reach.

Summer

Summer is a critical time for Colorado squawfish. Metabolic requirements are high and the concurrent spawning season places large physiological demands on the fish. Runs are the habitats most used by squawfish during summer. Run habitat is common in the 15-mile reach; its availability is therefore probably not now a limiting factor. Though fish are often found in shallow water (< 3 ft) in summer, their use of deep water (> 4.5 ft) increases. Paradoxically, this increased use of deep water occurs at a time when flows and average depths in the 15-mile reach are at their lowest. Availability of deep water may be important during summer, particularly during those times when water clarity becomes high (discussed below).

Colorado squawfish spawn in summer, usually in July or August in the Grand Valley. Studies conducted in the Green River system suggest that suitable spawning habitat for squawfish includes a cobble bar adjacent to a deep pool (Tyus et al. 1987). Habitat of this type occurs in many areas of the 15-mile reach, although its actual suitability to squawfish for spawning is unknown. Availability of suitable spawning habitat could be one factor limiting reproduction in the 15-mile reach. The habitat at the one site ostensibly used for spawning in 1982 was significantly modified by the 1983 flood; since that time, no evidence of spawning in the reach has been found. However, spawning in the 15-mile reach may not be necessary to maintain a population of adult squawfish there; many of the adults there now may have colonized the area after having been hatched and reared in downstream reaches.

Fall-Winter

During October-November, when the irrigation season ends and many upstream diversions of water cease, flows in the 15-mile reach increase. This increases the depth of various habitats. Adult Colorado squawfish move to wintering sites during this time and their movements are then restricted to a relatively small area until spring. These sites are generally deep, low-velocity habitats, primarily pools. Some use is also made of runs and large backwaters. The low-velocity sites are covered with ice, primarily during January. Whether adults prefer ice cover or whether ice coincidentally forms on the low-velocity waters selected by fish is unknown. Availability of suitable wintering sites is probably not now a limiting factor for adult squawfish in the 15-mile reach.

Temperature

Environmental temperature is very important to all cold-blooded organisms, including fish. In upstream regions of historic range like the 15-mile reach, seasonal temperatures are generally well below the physiological optimum (25 C) of Colorado squawfish (Kaeding and Osmundson 1988). In response to this, squawfish may at times select habitats that are warmer than the main channel (Fig. 32). In the 15-mile reach, such habitats include backwaters and flooded gravel pits, which are used extensively in spring and may be as much as 10.5 C warmer than the main channel. Moreover, as pointed out by Kaeding and Osmundson (1988), low temperatures can

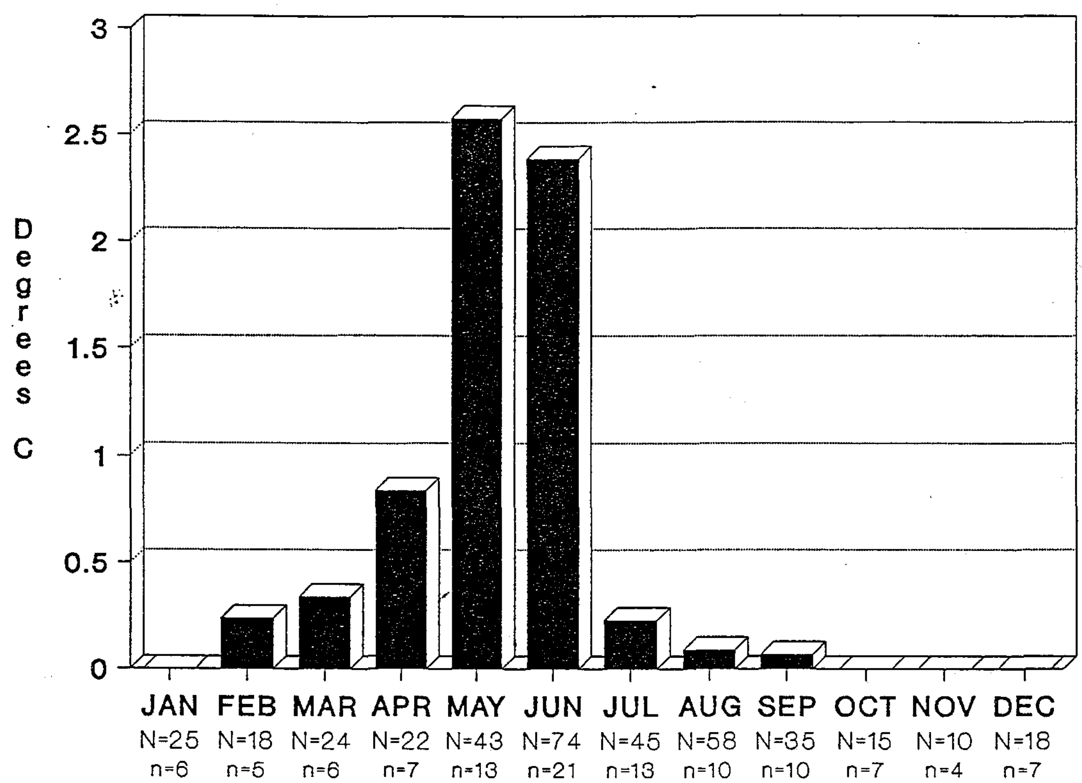

Figure 32. Mean difference between temperature at the location of captured or radio-tagged Colorado squawfish and the adjacent main river channel. Temperature differences were first averaged by month for individual fish; a mean of means was then calculated for each month. N = total number of observations; n = number of different fish.

result in slow growth and a decrease in the reproductive potential of the population because it takes longer for the fish to reach the size of sexual maturity. Slow growth also makes young fish vulnerable to predation for a longer period, thereby decreasing the likelihood of their surviving to maturity. Temperatures considered minimal for squawfish spawning (20 C) occur in the 15-mile reach, though often not until mid summer (Fig. 13). Thus the first growing season of the young produced there is especially short and the age-0 squawfish are quite small when they enter their first winter, another factor that may have an important effect on recruitment to the adult population (Kaeding and Osmundson 1988).

Contaminants

Numerous agricultural chemicals are used on lands in the Grand Valley, especially in orchards near the river. Summer rains may flush pesticides and herbicides into the river where they could be harmful to the endangered fishes, particularly to the young. Heavy metals may also be present in the Colorado River. Squawfish, a predator at the top of the food pyramid, would be at greatest risk of contaminant toxicity because of bioaccumulation. Currently there are no definitive data regarding levels of contaminants in squawfish or their prey. Although the importance of this problem to the endangered fishes is unknown, low summer flows in the 15-mile reach may serve to concentrate pollutants that enter the river.

Water Clarity

Colorado squawfish and razorback sucker evolved in the turbid environment of the Colorado River. Water clarity in the 15-mile reach may affect habitat use by adult squawfish. Our casual observations indicate water clarity in the 15-mile reach is often much greater than in other Colorado squawfish habitats downstream. Secchi disk visibility measured in 1987 and 1988 revealed a wide range of turbidity levels (Fig. 33). Spring runoff and spates from summer thunderstorms cause the river's silt load to dramatically increase and water clarity to decline. However, between such events, water clarity can become quite high. We regressed depth at fish location against water clarity and found a significant, though weak, positive relationship ($r = .29$; $P < .01$; n = 204). Although squawfish do not always use shallow-water habitats when turbidity is high, the correlation suggests that they are more likely to do so then. In August, we noted an unseasonably high use of shallow water (Fig. 24); regression of

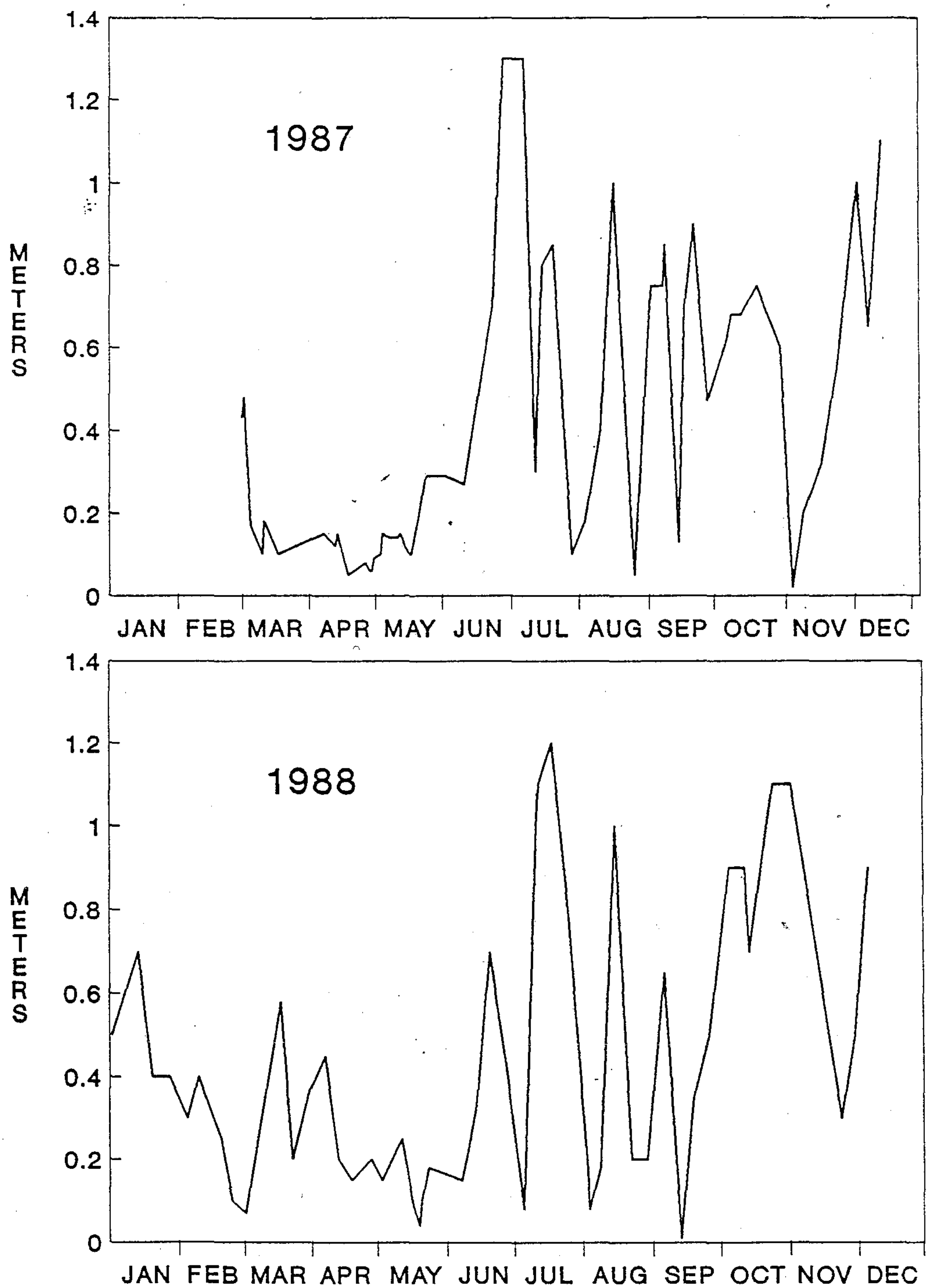

Figure 33. Water clarity in the 15-mile reach during 1987 and 1988, as measured by Secchi disk visibility. Measurements were taken between Colorado RM 174.4 and 175.2.

depth and Secchi visibility for August revealed a higher-than-average correlation ($r = .49$; $P < .05$; $n = 26$). During periods of high clarity, reduced light intensity at greater depths may provide cover for fish, much as turbid conditions otherwise might do.

Water clarity in the 15-mile reach may also be a problem for native fishes because of the introduction of sight-feeding predator fishes to the system. Clear water during summer may increase the vulnerability of young squawfish and razorbacks to such predation. Moreover, low flows in summer reduce the amount of backwater habitat and concentrate young fish, thus making them even more vulnerable to predation from piscivorous birds and fish.

Food Availability

It is not known whether food for Colorado squawfish or razorback sucker is limiting in the 15-mile reach. The movements of radio-tagged adults of both species, described earlier, might in part be related to differences in food availability among the river reaches. The availability of food is probably least important during winter months, when low temperatures reduce the metabolic demands of the fish.

Availability of Gravel-Pit Ponds

Squawfish use of warm off-channel habitats during spring may be an important behavioral mechanism by which they speed up gonadal maturation before the onset of the spawning season, or perhaps extend their limited growing season, in this their upstream region of range. Although flooded gravel pits may provide a source of warmer temperatures for Colorado squawfish and razorback sucker in the spring, they may also have a detrimental effect on these fishes. Both adult squawfish and razorback suckers have been found stranded in these ponds after flood waters recede. Moreover, if razorbacks spawn in these ponds, their young would be subject to predation from numerous introduced predators, including green sunfish (*Lepomis cyanellus*) and largemouth bass (*Micropterus salmoides*). Accordingly, Valdez and Wick (1982) and Osmundson (1987) recommended that gravel pits be sealed off from the river. To compensate for the loss of the beneficial aspects of these habitats, Valdez and Wick (1982) suggested the excavation of backwaters open to the river at all flow stages but having a graded bottom that allows complete, natural drainage with descending river flow. Whether such man-made habitats would have a beneficial effect on Colorado squawfish is unknown.

Large natural backwaters are also heavily utilized during spring. The creation and maintenance of large backwaters requires periodic high spring flows that cut side channels in the river floodplain; backwaters are then created when descending flows dewater the upstream end of these channels and the downstream end backs up with slack water.

Introduced Fishes

Introduced predatory fishes probably have important negative effects on the endangered fishes in the 15-mile reach and elsewhere in the Colorado River. Colorado squawfish grow slowly in the upper Colorado River and this probably exacerbates their vulnerability to predation from introduced species (Kaeding and Osmundson 1988). If resources such as food are limiting, competition with introduced species may also be a problem. However, which of the numerous introduced species have important negative effects on Colorado squawfish is unknown.

Angling

Mortality from angling is a potentially significant problem for adult Colorado squawfish in the 15-mile reach. Although there are no definitive data on the number of squawfish caught by fishermen, the close proximity to an urban area, the local popularity of fishing for channel catfish, and the vulnerability of squawfish to lures and bait could pose a serious threat to maintenance of the already low number of adults in the local population. Low summer flows could aggravate the situation by making squawfish more vulnerable to angling; not only are fish more concentrated, but fishermen access to the whole channel increases as river width and depth is reduced.

Razorback Sucker

Although the Colorado River of the Grand Valley, including the 15-mile reach, is the remaining stronghold of the razorback sucker in the upper Colorado River, very few fish have been captured there in recent years. Moreover, many of the razorbacks caught are recaptured individuals--fish that had previously been caught and tagged. Because recruitment of young razorback to this small adult population is evidently not occurring, the razorback of the Grand Valley are most assuredly nearing extirpation.

Ripe razorback sucker have been captured in old gravel-pit ponds throughout the Grand Valley. Razorbacks may have historically spawned in flooded pastures or ox-bow lakes during high water. However, many of these areas have been filled in or diked from the river. The lack of such habitats may be a bottleneck to the razorback population. The flooded gravel-pit ponds that razorbacks use during spring floods may not be entirely suitable as spawning habitat. Whether ripe fish successfully spawn in these gravel-pit ponds is unknown, although no young razorback has yet been collected from anywhere in the Grand Valley. This suggests that the probable bottleneck for the razorback population involves failure to successfully spawn or high mortality during the very early life stages. In the lower basin, researchers at Lake Mohave and Senator Wash Reservoir reported heavy predation by common carp on razorback sucker eggs (Minckley 1983). Such predation might result in low egg survival in the upper basin, where carp are common. Moreover, young razorbacks that may successfully hatch from eggs laid in pond or backwater environments would still be subject to predation, including that from introduced centrarchids and catfish. Marsh and Langhorst (1988) report complete elimination of previously abundant larval razorback from a backwater in Lake Mohave shortly after centrarchids and catfish gained access to the site.

RIVER MANAGEMENT OBJECTIVES

The 15-mile reach should be maintained as habitat for adult Colorado squawfish and razorback sucker. This will require that important habitats for these species be maintained through the provision of adequate flows. The present critical time period is the summer months, when flows are near their seasonal low and the physiological demands of the fish are high. Colorado squawfish use a diversity of habitat types at this time, though runs are used predominately. Razorback sucker mostly use low-velocity runs and pools during summer. Both species appear to require the availability of deep water, particularly razorbacks. However, we must emphasize that the most predominately used habitat types and conditions are not necessarily the only ones of importance or the only ones to be managed for. Species that require a combination of contiguous habitat types to meet life history needs may not be protected unless managers recognize the importance of these habitat combinations.

River management intended to maintain the adult habitat described above might also be useful for enhancing the spawning success and early-life survival of Colorado squawfish and razorback sucker in the 15-mile reach. For example, flows might be controlled to increase temperatures and thus promote spawning earlier in the year. Such temperature augmentation might ultimately improve the growth and survival of the fish. Assuring high flushing flows during spring may also be necessary to control the populations of introduced competitive or predatory fishes. These and other options need to be closely examined.

LITERATURE CITED

Archer, D. L., L. R. Kaeding, B. D. Burdick, and C. W. McAda. 1985. A study of the endangered fishes of the upper Colorado River. Final Report - Cooperative Agreement 14-16-0006-82-959. U.S. Department of the Interior, Fish and Wildlife Service, Grand Junction, Colorado.

Hamman, R. L. 1981. Spawning and culture of Colorado squawfish in raceways. Progressive Fish-Culturist 43(4):173-177.

Haynes, C. M., R. T. Muth, and T. P. Nesler. 1985. Identification of habitat requirements and limiting factors for Colorado squawfish and humpback chub. Final Report. Federal Aid Project. SE-3-4. Colorado Division of Wildlife, Ft. Collins, CO.

Kaeding, L. R., D. B. Osmundson. 1988. Interaction of slow growth and increased early-life mortality: an hypothesis on the decline of Colorado squawfish in the upstream regions of its historic range. Environmental Biology of Fishes 22:287-298.

Marsh, P. C., and D. R. Langhorst. 1988. Feeding and fate of wild larval razorback sucker. Environmental Biology of Fishes 21:59-67.

McAda, C. W. 1977. Aspects of the life history of three Catostomids native to the upper Colorado River basin. Master's thesis. Utah State University, Logan, Utah.

McAda, C. W., and R. S. Wydoski. 1980. The razorback sucker, *Xyrauchen texanus*, in the upper Colorado River basin, 1974-76. U.S. Fish and Wildlife Service Technical Paper 99.

Minckley, W. L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix, Arizona.

------. 1983. Status of the razorback sucker, *Xyrauchen texanus* (Abbott), in the lower Colorado River basin. The Southwestern Naturalist 28:126-187.

Osmundson, D. B. 1987. Growth and survival of Colorado squawfish (*Ptychocheilus lucius*) stocked in riverside ponds, with reference to largemouth bass (*Micropterus salmoides*) predation. Master's thesis. Utah State University, Logan, Utah.

Seethaler, K. H. 1978. Life history and ecology of the Colorado squawfish (*Ptychocheilus lucius*) in the upper Colorado River basin. Master's thesis, Utah State University, Logan, Utah.

Tyus, H. M. 1982. Fish radiotelemetry; theory and application for high conductivity rivers. U.S. Fish and Wildlife Service, Office of Biological Service, FWS/OBS82/38, Fort Collins, Colorado.

Tyus, H. M., R. L. Jones, and L. A. Trinca. 1987. Green River rare and endangered fish studies, 1982-1985. U. S. Fish and Wildlife Service, Final Report, Colorado River Fishes Monitoring Project, Vernal, Utah.

Valdez, R. A., P. G. Mangan, R. P. Smith, and B. C. Nilson. 1982. Upper Colorado River investigation (Rifle, Colorado to Lake Powell, Utah). U. S. Fish and Wildlife Service and Bureau of Reclamation, Final Report Part 2, Colorado River Fishery Project, Salt Lake City, Utah.

Valdez, R. A., and E. J. Wick. 1981. Natural vs manmade backwaters as native fish habitat. Pages 519-536 in V. D. Adams and V. A. Lamarra, editors. Aquatic Resources Management of the Colorado River Ecosystem. Ann Arbor Science Publishers, Ann Arbor, Michigan.

APPENDIX

Table 3. Definitions of habitat types.

<u>Backwaters</u>
Backwaters are calm areas adjacent to the river channel, and are often created when a declining water level cuts off flow at the top end of a side channel and the bottom end is filled with slack water backed up at the mouth. Mouths of backwaters were included in the backwater category unless a distinct counter-current (eddy) was present at the fish location.

<u>Gravel pits</u>
Flooded gravel pits are artificial backwater-like habitats that are available to riverine fish only during high water. They are calm protected areas, and those that are relatively shallow can become substantially warmer than the main channel, even more so than most natural backwaters.

<u>Eddies</u>
Often at the mouths of backwaters or coves and in steep-walled canyons, eddies form where the main current forms a distinct whirlpool or counter current.

<u>Pools</u>
Pools are calm areas in the river channel and are often deep; they may lie at the base of a riffle or off to one side of the main current. Velocity rather than depth was used to classify habitats as pools. We arbitrarily assigned mean velocities of 0.35 ft/second or less as a consistent indicator of pool rather than run or eddy habitat if a fish was located in a slow moving portion of the river channel.

<u>Shorelines</u>
If a fish was located in the river channel near shore, we would usually categorize the habitat as either a run, pool, etc. However, in some cases, the fish was so close to shore (< 0.5 m), that we concluded the habitat to be more influenced by the shoreline than the dominant habitat type nearby. Shoreline habitats were generally shallow and of lower velocity than the adjacent river channel.

<u>Runs</u>
A run is a stretch of relatively fast laminar flow in the river channel; it is often, but not always, relatively deep. Runs are by far the dominant habitat type in the Grand Valley.

<u>Riffles</u>
Riffles are shallow, fast-flowing areas where the water surface is broken into waves by obstructions wholly or partly submerged.

<u>Rapids</u>
Rapids occur where water is deep and fast-flowing; like riffles, the surface is broken into waves.

Table 4. Summary data for Colorado squawfish (CS) and razorback sucker (RZ) caught or seen while electrofishing (EL) and trammel netting (TR) during 1986,1987 and 1988 in the Grand Valley, Colorado. Disposition codes: BF = kept as brood fish; SN = seen but not captured; RT = radio tagged and released; RA = released without a radio tag. River codes: CO = Colorado River; GU = Gunnison River. Reproductive codes: T = tuberculated; E = expressible eggs present; M = expressible milt present.

Spp.	Date	River	RMI	Carlin Tag No.	Capture Gear	Disp.	Length (mm)	Repro. signs
				1986				
CS	860512	CO	168.7	2674	EL	BF	800	
CS	860514	CO	168.2	3136	EL	BF	650	
CS	860516	CO	174.2	3308	EL	BF	810	
CS	860516	CO	165.5	3393	EL	BF	595	
CS	860522	CO	175.1			SN		
CS	860522	CO	175.3			SN		
CS	860523	CO	174.5	3376	EL	BF	745	
CS	860523	CO	175.1	3336	TR	BF	551	
CS	860523	CO	175.1	2775	TR	BF	545	
CS	860530	CO	174.4	4116	EL	RT	541	
RZ	860603	CO	174.4	836	EL	RT	565	E
CS	860603	CO	174.4	3351	EL	RA	533	
CS	860603	CO	174.4	4092	TR	RT	693	T
CS	860603	CO	175.3	3353	EL	RA	476	
CS	860603	CO	174.4	4120	TR	RA	600	
CS	860603	CO	174.4	4111	TR	RT	556	
CS	860605	CO	174.4	3100	TR	RT	640	T
CS	860610	CO	174.4	4112	EL	RT	585	T
CS	860610	CO	174.4	4110	TR	RT	586	
RZ	860611	CO	174.4	939	EL	RT	525	T,M
CS	860811	GU	3.0		EL	RA		
CS	860812	GU	3.0	2728	EL	RA	582	
CS	861014	CO	167.2			SN		
CS	861014	GU	0.9			SN		
CS	861028	CO	173.5			SN		
CS	861105	CO	174.8			SN		
CS	861106	CO	173.8			SN		
				1987				
CS	870519	GU	2.5			SN		
RZ	870519	CO	168.2	2949	EL	RT	583	
CS	870526	CO	158.8	3296	EL	RA	760	
CS	870527	CO	179.1	4119	EL	RT	620	
RZ	870603	CO	172.5			SN		
RZ	870611	CO	178.3	4104	EL	RT	556	
CS	870611	CO	175.6	4110	EL	RA	585	T
CS	870611	CO	175.6			SN		
RZ	870612	CO	183.6	4098	EL	RT	496	
CS	870612	CO	175.7			SN		T
CS	870612	CO	175.5			SN		
CS	870612	CO	175.5			SN		
CS	870615	CO	175.2	4117	TR	RT	486	
CS	870615	CO	175.6			SN		
CS	870616	CO	175.2	4118	EL	RT	468	
CS	870616	CO	175.6	4093	TR	RT	521	T,M
CS	870619	CO	174.4			SN		
CS	870716	GU	3.0	2781	EL	RA	-	
CS	870716	GU	3.0		EL	RA	-	
CS	870716	GU	3.0			SN		
CS	870812	GU	3.0	4121	EL	RT	750	
CS	870813	GU	3.0	2728	EL	RT	608	
CS	870813	GU	3.0	4100	EL	RT	600	T
CS	870813	GU	3.0	3354	EL	RA	442	
CS	870813	GU	3.0	3129	EL	RA	510	
CS	870813	GU	3.0	3331	EL	RA	552	
CS	870825	GU	3.0	3343	EL	RA	431	
CS	870825	GU	3.0			SN		

Table 4. Continued

Spp.	Date	River	RMI	Carlin tag No.	Gear	Disp.	Length	Repro. signs
				1988				
RZ	880428	CO	174.4	5052	EL	BF	565	
RZ	880506	CO	175.2	5051	EL	BF	515	
CS	880510	GU	3.0	4122	EL	RT	566	
CS	880510	GU	3.0		EL	SN	999	
CS	880512	CO	180.5	4093	EL	RA	534	
CS	880512	CO	176.2	4101	EL	RT	556	T
CS	880517	CO	168.2	4761	EL	RT	679	T
CS	880517	CO	168.0		EL	SN		
CS	880518	CO	?		EL	SN		
CS	880524	CO	162.7		EL	SN		
CS	880524	CO	158.5		EL	SN		
CS	880526	CO	154.0		EL	SN		
CS	880526	CO	?		EL	SN		
CS	880527	CO	175.0	4112	TR	RA	590	T,M
CS	880527	CO	175.0	4118	TR	RA	485	T
CS	880527	CO	175.0	4781	TR	RT	636	T
CS	880527	CO	175.0	4750	TR	RT	566	T
CS	880527	CO	175.0	4734	TR	RT	603	T,M
CS	880527	CO	174.6	4101	EL	RA	999	
CS	880601	CO	175.2	4734	TR	RA	999	
CS	880601	CO	175.2	4117	TR	RA	510	T
CS	880601	CO	175.2	4743	TR	RT	545	T,M
CS	880601	CO	175.2	4793	TR	RT	629	
CS	880601	CO	175.2	4753	TR	RT	653	T,M
CS	880601	CO	175.2	4702	TR	RT	785	T
CS	880622	GU	3.0		EL	SN		

Table 5. Data for larval Colorado squawfish collected in 1986, 1987 and 1988.

Location[a]	Collection Date	TL (mm)	Estimated Age (days)	Estimated Hatching Date	Estimated Spawning Date
			1986		
CO RM 158.1	Aug 21	9.2	12.1	Aug 9	Aug 5
		10.1	15.1	Aug 6	Aug 2
		11.8	19.1	Aug 2	Jul 29
		13.8	21.8	Jul 30	Jul 26
CO RM 158.1	Aug 28	11.5	18.5	Aug 9	Aug 5
CO RM 163.7	Aug 28	12.4	20.1	Aug 8	Aug 4
		12.8	20.6	Aug 7	Aug 3
		14.8	22.7	Aug 5	Aug 1
GU RM 2.6	Aug 28	14.6	22.5	Aug 5	Aug 1
			1987		
CO RM 162.7	Jul 30	14.3	22.3	Jul 8	Jul 4
			1988		
CO RM 158.2	Jul 27	11.7	18.8	Jul 8	Jul 4

[a]CO = Colorado River; GU = Gunnison River

Table 6. Catch rates of fish species collected during young-of-the-year sampling in two adjacent Colorado River reaches, 1986. n = number of seine hauls.

	15-Mile Reach			18-Mile Reach		
	Mean fish/100 m^2	SD	n	Mean fish/100 m^2	SD	n
Colorado squawfish	0.0	-	12	4.0	7.9	14
Roundtail chub	75.0	80.7	11	21.8	8.5	4
Bluehead sucker	265.9	506.5	11	57.9	67.6	4
Flannelmouth sucker	4.0	5.8	11	2.5	2.1	4
White sucker	0.5	0.9	11	0.0	-	4
Common carp	0.0	-	11	1.8	2.0	4
Black bullhead	0.0	-	11	0.4	0.8	4
Largemouth bass	0.4	1.3	11	0.4	0.8	4
Green sunfish	1.3	2.6	11	11.9	23.8	4
Fathead minnow	208.5	234.8	11	77.6	23.0	4
Red shiner	66.2	107.4	11	36.3	31.4	4
Sand shiner	30.4	44.9	11	8.1	8.9	4
Speckled dace	43.8	70.0	11	22.1	25.4	4
Mosquitofish	1.0	3.5	11	0.0	-	4
Plains killifish	0.1	0.2	11	0.0	-	4
Brassy minnow	0.8	1.7	11	0.0	-	4

Table 7. Data for young-of-the-year Colorado squawfish (CS) collected from the Colorado River on 1 October 1986, 23 September 1987 and 20 September 1988.

River-mile location	No. CS collected	Total length (mm)	$\bar{x}$ TL (mm)	Std. dev.
		1986		
RM 162.6	2	19, 25	22.0	(4.2)
RM 158.2	3	23, 28, 24	25.0	(2.6)
RM 155.2	4	24, 27, 33, 23	26.8	(4.5)
RM 153.7	20	28, 25, 29, 26, 22 24, 20, 23, 25, 24 25, 20, 29, 23, 24 26, 25, 24, 20, 29	24.6	(2.8)
		1987		
RM 163.2	2	36, 39	37.3	(1.8)
RM 154.7	11	22, 26, 35, 28, 24 24, 26, 26, 25, 20 21	25.1	(4.0)
		1988		
RM 162.8	1	32	32	(-)

Table 8. Catch rates of fish species collected during young-of-the-year sampling in two adjacent Colorado River reaches, 1987. n = number of seine hauls.

	15-Mile Reach			18-Mile Reach		
	Mean fish/100 m^2	SD	n	Mean fish/100 m^2	SD	n
Colorado squawfish	0.0	-	10	2.8	9.3	16
Roundtail chub	0.8	1.3	9	99.3	46.0	4
Bluehead sucker	0.4	0.8	9	3.8	3.8	4
Flannelmouth sucker	0.8	1.2	9	5.3	4.0	4
White sucker	3.3	5.0	9	0.0	-	4
Common carp	0.5	1.5	9	1.6	2.2	4
Black bullhead	0.3	0.8	9	0.0	-	4
Largemouth bass	2.7	6.8	9	0.0	-	4
Green sunfish	0.2	0.5	9	0.4	0.7	4
Fathead minnow	52.5	60.1	9	702.5	889.8	4
Red shiner	13.0	13.7	9	187.3	205.7	4
Sand shiner	5.0	5.8	9	45.8	58.3	4
Speckled dace	0.0	0.0	9	2.2	4.4	4
Mosquitofish	3.0	7.5	9	0.0	-	4
Plains killifish	0.0	0.0	9	0.0	-	4
Brassy minnow	0.0	0.0	9	0.0	-	4

Table 9. Catch rates of fish species collected during young-of-the-year sampling in two adjacent Colorado River reaches, 1988. n = number of seine hauls.

	15-Mile Reach			18-Mile Reach		
	Mean fish/100 m^2	SD	n	Mean fish/100 m^2	SD	n
Colorado squawfish	0.0	-	12	0.1	0.5	14
Roundtail chub	18.3	18.7	12	0.9	1.1	14
Bluehead sucker	0.6	1.6	12	0.9	1.7	14
Flannelmouth sucker	1.3	2.4	12	0.4	1.1	14
White sucker	2.8	3.8	12	0.2	0.6	14
Common carp	3.6	4.7	12	3.1	5.6	14
Black bullhead	0.0	-	12	0.0	-	14
Largemouth bass	0.0	-	12	0.6	1.1	14
Green sunfish	0.3	0.9	12	0.8	1.7	14
Fathead minnow	809.6	1047.4	12	1426.0	1460.8	14
Red shiner	375.79	471.5	12	277.3	267.0	14
Sand shiner	250.5	360.3	12	71.6	147.9	14
Speckled dace	0.4	0.9	12	0.2	0.5	14
Mosquitofish	49.4	94.2	12	3.4	7.1	14
Plains killifish	0.0	-	12	0.0	-	14
Brassy minnow	0.3	0.9	12	0.0	-	14
Channel catfish	0.0	-	12	0.2	0.4	14

Table 10. Percent species composition of larval samples collected between 16 July and 28 August 1986, 13 July and 28 August 1987 and between 5 July and 10 August 1988, and pooled within three adjacent river reaches.

	Colorado R. 15-Mile Reach			Gunnison R. 2.2-Mile Reach			Colorado R. 18-Mile Reach		
	1986	1987	1988	1986	1987	1988	1986	1987	1988
Colorado squawfish	0.00	0.00	0.00	0.12	0.00	0.00	0.17	0.03	0.02
Roundtail chub	3.14	6.94	4.21	3.49	37.61	7.21	2.04	11.53	4.39
Bluehead sucker[a]	68.50	45.18	28.38	73.68	22.87	0.75	74.26	30.00	26.43
Flannelmouth sucker	2.69	0.49	8.50	0.96	1.14	0.25	0.75	0.23	0.74
White sucker	0.30	0.04	0.73	0.24	0.00	0.25	0.08	0.00	0.00
Unidentified sucker	0.00	0.00	0.00	0.00	0.00	0.00	1.11	0.00	0.00
Green sunfish	0.03	0.15	0.17	0.00	0.00	0.25	0.02	0.06	0.02
Black crappie	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00
Fathead minnow	1.40	7.02	9.45	0.24	0.64	31.84	5.40	25.71	19.23
Red shiner	1.64	18.93	18.59	0.12	10.55	23.38	1.48	16.92	37.44
Sand shiner	1.61	2.20	10.30	0.36	3.81	29.35	0.46	1.23	3.99
Speckled dace	20.10	18.82	18.25	20.67	23.38	4.98	15.15	14.01	7.26
Mosquitofish	0.48	0.19	1.12	0.00	0.00	0.25	0.00	0.20	0.19
Unidentified fish	0.12	0.04	0.30	0.15	0.00	1.49	0.02	0.09	0.28
No. fish	3349	2636	2329	832	787	402	4813	3427	4711
No. samples	49	42	43	8	12	12	58	54	51
No. fish/sample	68.8	62.8	54.2	85.0	63.6	33.5	83.9	63.3	92.4

[a]Includes some questionable specimens that the Larval Fish Laboratory tentatively believes are bluehead sucker; however, until techniques are developed to positively identify sucker of this size to species, the presence of razorback sucker larvae in these samples should be considered a possibility.

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Interaction of slow growth and increased early-life mortality: an hypothesis on the decline of Colorado squawfish in the upstream regions of its historic range

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Synopsis

The Colorado squawfish, *Ptychocheilus lucius,* the principal native piscivore of the Colorado River basin, was once widespread and abundant in large rivers and their major tributaries. It occurs today only in the upstream regions of its historic range and is threatened with extinction. Growth rate of the species there is much slower than its potential rate and the rate that might once have been typical in lower-basin rivers. We develop the hypothesis that the interaction of slow growth and increased early-life mortality is an important cause of the decline of Colorado squawfish in the upper basin. We use a growth-rate versus temperature relation for Colorado squawfish to compare temperature regimes of historic and present habitats, and we describe the strong, positive relation between our measure of temperature-regime suitability and first-year growth of Colorado squawfish in upper-basin rivers. The unusually small size of the age-0 fish going into winter might be an important factor affecting recruitment to the adult stock. Simulations showed how the effect of increased early-life mortality can be especially significant on populations of slow-growing fishes. Predation by introduced fishes, as well as other man-induced causes of increased early-life mortality, probably contributed importantly to the decline of Colorado squawfish in the remaining habitat. Management efforts that might help this endangered species to recover include water management to enhance temperatures for growth, and the control of important introduced fishes.

Introduction

The Colorado squawfish, *Ptychocheilus lucius,* was once widespread and abundant in large rivers and major tributaries of the Colorado River basin (Jordan 1891, Evermann & Rutter 1895, Jordan & Evermann 1896, Gilbert & Scofield 1898). Today, however, this principal native piscivore of the basin occurs naturally only in upstream regions of its historic range (Fig. 1) and is threatened with extinction (Seethaler 1978, Holden & Wick 1982, Tyus et al. 1982). Understanding both the causes of the population decline and the factors limiting the population is problematic yet essential to programs intended to recover the species. Although the extirpation of Colorado squawfish from its former

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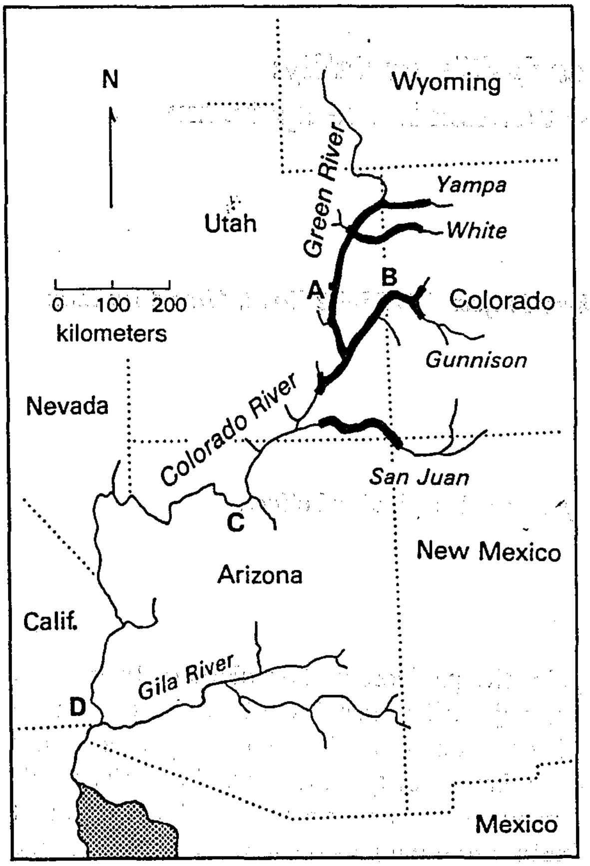

Fig. 1. The Colorado River basin, showing rivers that historically provided habitat for Colorado squawfish (light lines) and those that still support the species (heavy lines). (Modified from Seethaler 1978.) Sites of temperature-data collection are indicated in the Green River (A) and the upper (B), middle (C) and lower (D) Colorado River.

range is generally agreed to be a result of the widespread and often profoundly evident effects of water-resources development, the introduction of non-native fishes, and poor land-use practices (Miller 1961, Minckley & Deacon 1968, Minckley 1973), the causes of its decline to the present low levels in the remaining habitat are not so clearly evident nor well understood.

Among fishes, piscivores show an especially pronounced potential for rapid, early-life growth. This can be seen, for example, in two widely distributed piscivores, northern pike, *Esox lucius*, and largemouth bass, *Micropterus salmoides* (Fig. 2). Presumably a mechanism that has evolved to increase survival, such rapid growth reduces the period when fish are prey for other species and, in piscivores, it enables the use of a wider variety of prey (e.g. Keast 1985). Rapid, early-life growth is conspicuously lacking in the Colorado squawfish of the upper Colorado River basin, however (Fig. 2).

Growth rate in fishes is largely dependent upon the interaction of water temperature and food availability (e.g. Weatherley 1972). That this interaction might explain the slow growth of Colorado squawfish in upper-basin rivers became evident during a study of growth and survival of young Colorado squawfish in ponds by Osmundson (1987). In one test, 5-month-old Colorado squawfish 50–75 mm long stocked in a pond in which age-0 common carp, *Cyprinus carpio,* were abundant grew to an average length of 226 mm within one year; the largest was 304 mm long (Fig. 2). Osmundson attributed rapid growth in the pond to summer water temperatures nearly optimal for growth, plus abundant food. Such rapid growth had never before been reported for Colorado squawfish, and its observation led us to conclude that slow growth in upper-basin rivers was attributable to suboptimal conditions for growth in these upstream regions of the historic range. Among widely distributed species, such an effect is well known for populations that occur at high latitude and elevation where annual growth of fish can be much slower than the potential (e.g. Weatherley 1972).

We develop the hypothesis that the interaction of slow growth and increased early-life mortality is an important cause of the decline of Colorado squawfish in the upper Colorado River basin. In so doing, we use a growth-rate versus temperature relation for Colorado squawfish to compare temperature regimes of historic and present habitats, and we describe the relation between our measure of temperature-regime suitability and first-year growth of Colorado squawfish in upper-basin rivers. Simulation is used to show how the effects of increased early-life mortality can be especially significant on populations of slow-growing fishes, and we recommend management efforts to bring about the recovery of Colorado squawfish in its remaining habitat.

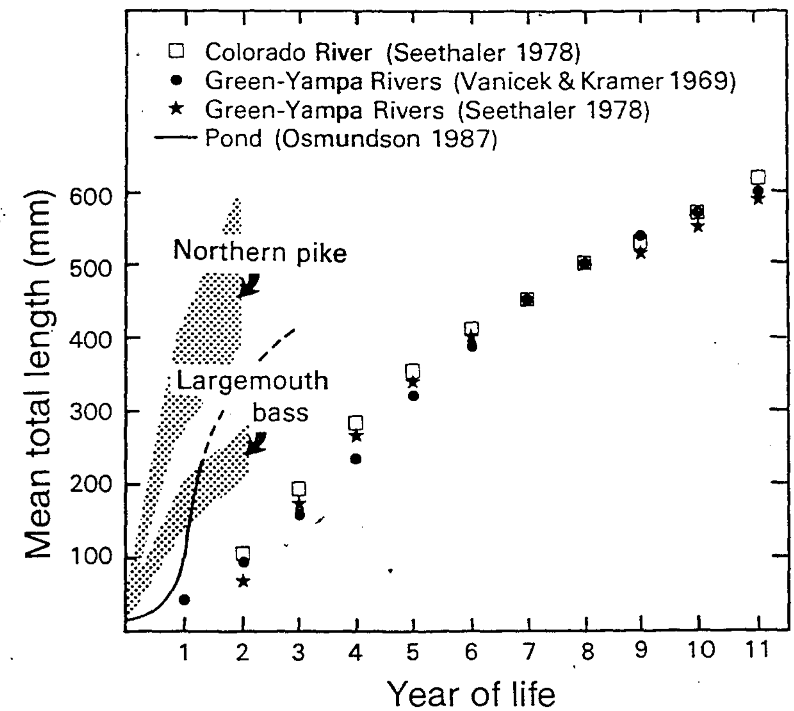

Fig. 2. Early-life growth of two widely distributed piscivores, northern pike and largemouth bass (shaded areas show the median 50% of the range of length-at-age values for these species provided by Carlander [1969, 1977]), compared to that of Colorado squawfish from the upper Colorado River basin (data derived by Vanicek & Kramer 1969, and Seethaler 1978, using scale annuli). Also shown is early-life growth of Colorado squawfish in a pond near Grand Junction, Colorado (Osmundson 1987). The broken line on the curve for pond fish shows estimated growth used in our simulations.

Methods

Temperature regime analysis

Black & Bulkley (1985a) studied the relation between constant temperature and growth of 45–100 mm long Colorado squawfish given excess food. They reported that growth was optimal at 25° C, and that growth at 15, 20, and 30° C was 18, 54, and 51% of optimum, respectively. Additional studies by Black & Bulkley (1985b) and Bulkley et al. (1981) indicated that 25° C was the preferred temperature, generally considered the optimum for many physiological processes including growth (e.g. Magnuson et al. 1979), for both yearling and adult Colorado squawfish. Our least-squares analysis of the published data of Black & Bulkley (1985a) suggested that growth ceases at temperatures below about 13° C, a value supported by observations on seasonal growth of Colorado squawfish in ponds (Osmundson 1987). We assigned suitability indices to the growth-rate versus temperature relation of Black & Bulkley (1985a) according to the percent of optimum growth that temperatures provided. Thus the suitability indices for temperatures of 25, 15, 20, and 30° C were 1.00, 0.18, 0.54, and 0.51, respectively, and those for 13° C or lower were zero. Indices for intervening temperatures were estimated by interpolation.

The growth-rate versus temperature relation for Colorado squawfish reported by Black & Bulkley (1985a) is symmetrical and triangular in shape, whereas those for other species often have a flat dome around the optimum temperature and an absolute value of the slope to the left of the optimum less than that to the right (e.g. Magnuson et al. 1979). Because we were concerned that the unusual shape of the Black & Bulkley (1985a) curve might affect our subsequent analyses, we performed preliminary analyses using several different modifications of the curve, each made to appear more typical. Results showed that these modifications had no important effect on the outcome of the analyses nor on our subsequent conclusions.

U.S. Geological Survey (USGS) annual reports were the source of temperature data for two upper-basin river reaches presently inhabited by Colorado squawfish (Fig. 1): the Green River near Green River, Utah (data for the years 1975–1983, 1985), and the upper Colorado River near the Colorado-Utah border (1979–1986). Temperatures at the Green River and upper-Colorado locations have not been affected by upstream water-development projects (Robert Green, Regional Hydrologist, U.S. Fish and Wildlife Service, Denver, Colorado, unpublished data). For the former range of Colorado squawfish, the few temperature data recorded before modification of temperature regimes by upstream dams are from the lower Colorado River near Yuma, Arizona, for the years 1917–1924 (Dill 1944), and from the middle Colorado River near Grand Canyon, Arizona (USGS annual reports for 1943–1947, 1957).

Because the temperature data from the lower, middle and upper-river reaches were not concurrent, we were concerned that possible long-term climatic changes might affect comparisons among these locations. We therefore analyzed climate data provided by the U.S. National Oceanic and Atmospheric Administration for 1901–1986 for Yuma and Flagstaff, Arizona, and Grand Junction, Colorado, monitoring stations near the sites of lower, middle and upper Colorado River data collection, respectively. Results showed that mean-annual air temperatures for the eight years for which historic lower-river temperature data were available were all cooler than the 86-yr mean for Yuma, and averaged 0.8° C less, whereas the six years during which the historic middle-river temperature data were collected were all warmer than the 86-yr average for Flagstaff, and averaged 0.8° C warmer. Of the ten years during which the Green River data were collected, four were cooler and six warmer than the 86-yr average for Grand Junction, and averaged 0.2° C warmer, whereas these respective data for the upper Colorado River location were two cooler, six warmer, and averaged 0.5° C warmer. Although we have no means of standardizing our river-temperature data to account for the effect of these climatic differences, such adjustment would increase the average temperatures that we report for the historic lower river and reduce them for the other locations.

River-temperature data were reduced to mean-monthly temperatures for each year of record and means were averaged within months to produce an average-annual temperature regime (the type of data provided by Dill [1944]) for each location. Because they consisted of once-daily measurements collected over a wide range of daylight hours, the Green River data had an uncorrectable bias toward the warmer temperatures that occur during daylight. However, our analyses of the continuously recorded data collected at the nearby upper Colorado River gauge indicated this bias was probably no more than 1° C. Using the suitability indices that we assigned to the growth-rate versus temperature relation of Black & Bulkley (1985a), we estimated the relative suitability of each temperature regime by summing the indices for its average-monthly temperatures.

Age-0 growth analysis

Mean total lengths of age-0 Colorado squawfish captured from the Green and upper Colorado rivers in fall (mid September-mid October) were obtained from Tyus et al. (1987) and from the U.S. Fish and Wildlife Service (USFWS) and Utah Division of Wildlife Resources (unpublished data). These data were compared to the relative suitability of the annual temperature regime for their respective rivers for the year of capture.

Population simulation

We used a simple simulation technique to demonstrate how growth rate can affect survival in populations of slow- and fast-growing fish. Beginning populations consisted of 1000 female larvae 10 mm long, which we arbitrarily accepted as being the offspring of one mature female. Our initial assumption was that, in fish of the slow-growing stock, growth rate, length at maturity, and age at maturity resembled these characteristics in upper-basin Colorado squawfish, whereas in the fast-growing stock, squawfish growth resembled that in Osmundson's pond (Fig. 2). First maturity of Colorado squawfish in the upper basin occurs at a length of about 428 mm and an age of about 6 years (Seethaler 1978) – a size that pond-raised fish might conceivably reach in about half that time (Fig. 2). For computational convenience, we assumed that maturity in both simulated stocks occurred at a length of 410 mm and the age of 6 years in slow-growing fish and 3 years for fast-growing fish. There are no definitive data on the survival of Colorado squawfish in its natural environment. In the simulations, we therefore assumed annual mortalities of 80, 90, 95 or 99% in the shortest length class (10–110 mm TL), and 20% in each of the three larger, 100 mm length classes. Although arbitrary, these rates were chosen because such rapid, early-life mortality and a reduced, constant rate for later ages is typical of many freshwater fishes (e.g. Weatherley 1972). Thus the important difference between our simulated populations was the length of time that fish remained in each length class, which was determined by growth rate. The number of fish that died in each length class was calculated as the product of the initial number of fish, mortality rate, and duration of time spent within the length class. For periods longer than 1 year, the number of deaths during the first year was calculated as described above, and deaths during the remaining time period were similarly calculated for fish that survived the first year.

Vital statistics for our simulated populations were calculated using equations provided by Krebs (1972):

$$G = (\Sigma\, l_x m_x x)/R_o$$
$$r = (\log_e R_o)/G, \text{ and } f = e^r,$$

where G = mean length of generation (the mean period between the birth of the parent and that of offspring); l_x = age-specific survival; m_x = age-specific effective birth rate; x = age in years; R_o = $\Sigma\, l_x m_x$ = net reproductive rate (the number of mature female offspring produced in the lifetime of a female parent); r = intrinsic rate of natural increase; and f = finite rate of increase (the multiplication factor by which the adult female stock will annually grow if that particular value of R_o is maintained). For these computations it was assumed that, beginning in the first year of maturity and continuing through age 10 (arbitrarily taken to be the age of last reproduction), each slow- and fast-growing female produces mature female offspring at an annual rate equal to the age-specific effective birth rate (m_x) for our simulated stocks when early-life mortality was 95 or 99%.

Development of the hypothesis

Temperature regime analysis

Although the temperature data used in our analyses do not reflect the precise temperatures that Colorado squawfish may experience throughout their life history, they nonetheless allow demonstration of the marked differences in suitability for Colorado squawfish growth among the temperature regimes of present and historic habitats. If growth of Colorado squawfish occurs only when water temperatures exceed 13° C, growing seasons in the upper-basin river reaches are less than 6 months, whereas they were 7 to 9 months in historic, pre-development, middle- and lower-basin reaches (Fig. 3). Comparisons among these temperature regimes are more useful, however, if their relative suitability for Colorado squawfish growth is considered. Such suitability was estimated as 3.2, 2.1, 3.9, and 4.9 for the Green River and the upper, middle, and lower Colorado River, respectively.

If the bias in the Green River data (Fig. 3) was as large as our worst-case estimate of 1° C, and we reduced these data by that amount, the Green River would continue to warm earlier and have warmer temperatures during the growing season than does the upper Colorado. Suitability of the Green River temperature regime would be 2.7, an average value 29% larger than that of the upper Colorado.

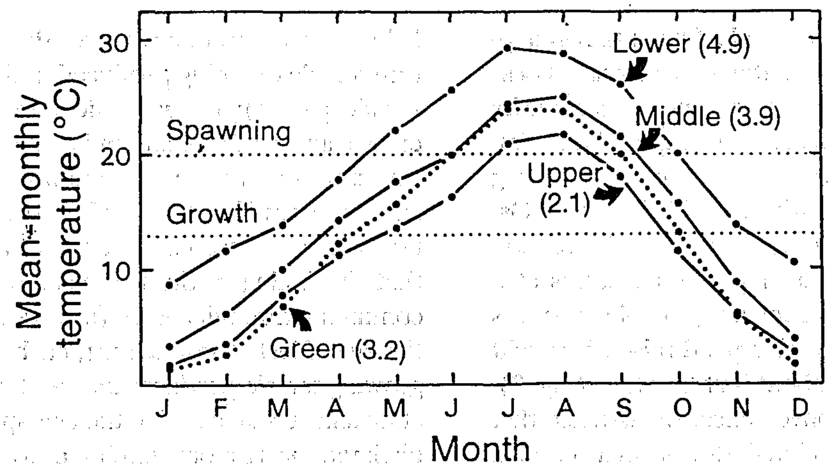

Fig. 3. Comparison of temperature regimes (average mean-monthly temperatures) of the historic lower and middle Colorado River and of the present upper Colorado and Green rivers. Horizontal lines are temperature thresholds for growth (13° C) and the onset of spawning (20° C) of Colorado squawfish. Numbers in parentheses are the relative availability of temperatures suitable for Colorado squawfish growth provided by each temperature regime (see text for explanation). See Figure 1 for sites of temperature-data collection.

Age-0 growth analysis

There was a highly significant, positive relation ($p<0.01$, $r = 0.95$) between the mean total length of age-0 Colorado squawfish captured in fall from the Green and Colorado rivers and the relative suitability of the temperature regime for the year of capture (Fig. 4). The coefficient of determination ($r^2 = 0.91$) indicated 91% of the variation in fish length was explained by variation in the suitability index.

Age-0 Colorado squawfish are most often captured from river backwaters (Holden & Stalnaker 1975). Although the temperature regimes of both backwater and main-channel habitats are largely dependent upon ambient air temperature and solar radiation and therefore are closely correlated with one another, backwaters generally have larger diel temperature variation than does the main channel (Robert Green, personal communication). Colorado squawfish might make diel movements between backwater and main-channel habitats to maximize the use of temperatures near their physiological optimum (e.g. Magnuson et al. 1979). The importance of such behavioral thermal regulation to the relation shown in Figure 4, which is based on main-channel temperatures, is unknown.

Population simulation

As one would expect, our simulations showed that fewer fish reach maturity as early-life mortality increases; more important, however, they showed that growth rate can have a pronounced effect on survival (Table 1). Markedly more fast-growing fish than slow-growing ones reach maturity at each rate of early-life mortality, and this disparity increases as early-life mortality increases. The potential effect of increased early-life mortality is therefore much greater in populations of slow-growing fish than in those of fast-growing fish.

The combined effect of low survival to maturity and advanced age at first maturity is reduced potential for population growth (Cole 1954), as predicted by our simulations (Fig. 5). Moreover, we illustrated in Figure 5 that growth potential of the populations of fast-growing fish is markedly greater than that of the slow-growing ones, especially when early-life mortality is 99%. Computation of vital statistics for our simulated populations is exemplified in the Appendix.

Although our simulations are useful for showing the importance of growth rate of individual fish as it can affect potential for population growth, they also provide examples in which the growth of the

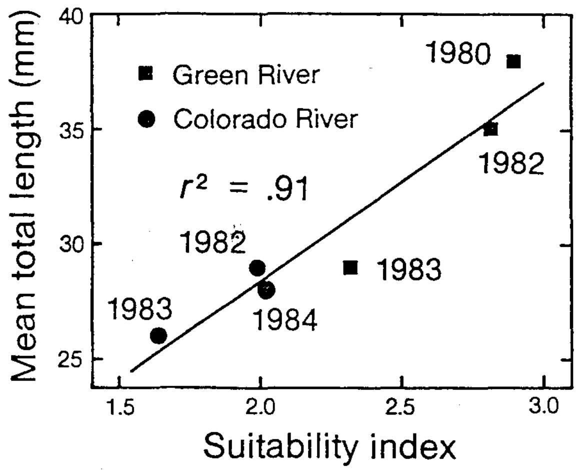

Fig. 4. Relation between the mean total length of age-0 Colorado squawfish in fall in the Green and Colorado rivers and the relative availability of temperatures suitable for growth (suitability index) for the year of capture. Year of data collection is given.

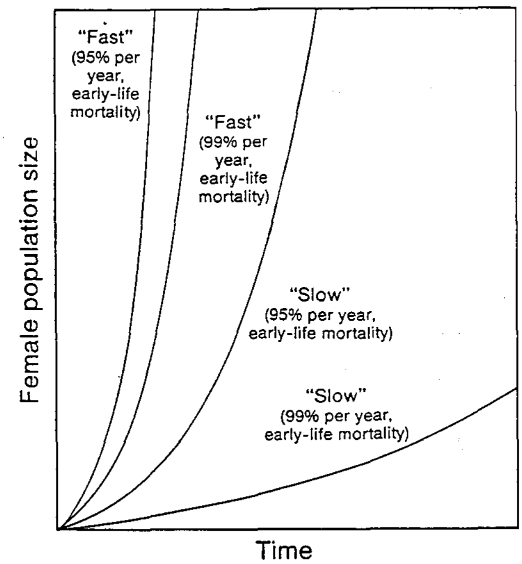

Fig. 5. Comparison of theoretical growth of populations of fast-growing, early-maturing female Colorado squawfish ('fast') with those of slow-growing, late-maturing fish ('slow'), in a limitless environment, under conditions of 95 or 99% early-life mortality.

theoretical populations is much greater than in present-day, upper-basin Colorado squawfish. Because that population is at best stable and perhaps declining (Holden & Wick 1982, Tyus et al. 1982), its net reproductive rate (R_o, the number of mature female offspring produced in the lifetime of a female parent) is no more than 1 – a condition far worse than that shown even by our simulated slow-growing population when early-life mortality is 99% (Appendix). Although the sustained, geometric growth indicated by our simulations (Fig. 5) does not occur in nature, the slopes of these curves provide an indication of the relative capacity of the

Table 1. Estimated survival (number of fish) in simulated populations of 1000 female Colorado squawfish that grow at different rates (S = slow; F = fast) and are subjected to different annual mortalities (80–99%) while at total lengths of 10–110 mm and to equal annual mortalities of 20% while in each of three longer length classes.[a]

Total length (mm)	Time in length class (years)		Assumed annual mortality of first length class, and growth-rate category							
			80%		90%		95%		99%	
	S	F	S	F	S	F	S	F	S	F
10–110	1.9	1.0	56	200	19	100	7.3	50	1.1	10
111–210	1.1	0.25	44	190	15	95	5.7	48	0.9	9.5
211–310	1.2	0.5	34	171	11	85	4.4	43	0.7	8.6
311–410	1.8	1.25	23	130	8	65	3.0	32	0.5	6.5
Production of mature females[b]	–	–	–	466	–	712	–	967	–	1200

[a] Initial population of 1000 female larvae 10 mm long were accepted as being the offspring of one mature female.
[b] Percentage by which fast-growing fish exceed slow-growing fish in producing mature females 410 mm long.

theoretical populations to bear additional mortality yet remain self-sustaining. As such, the capacity of the slow-growing population experiencing 99% early-life mortality is quite low.

Synthesis

The decline of Colorado squawfish and that of other native fishes of the southwestern U.S. has been attributed to alteration of discharge and temperature regimes downstream from dams and diversions, conversion of riverine ecosystems to lacustrine ones in the reservoirs upstream, introduction of non-native fishes, and altered water quality (Miller 1961, Minckley & Deacon 1968, Minckley 1973, Holden & Wick 1982). However, aside from the obvious detrimental effect of severe reduction in river discharge on Colorado squawfish, only the effect of unseasonably cold, hypolimnetic waters from dams has been demonstrated. Marsh (1985) showed that survival of Colorado squawfish embryos is appreciably reduced by low water temperatures such as those evident below mainstream Colorado River dams. However, this effect alone does not account for the Colorado squawfish decline to the present low numbers in its remaining habitat. Recent analyses of USGS records showed that dam operation did not reduce temperatures in most Colorado and Green river reaches still inhabited by Colorado squawfish (Robert Green, unpublished data). Nonetheless, the species is rare in these areas, and factors other than alteration of temperature regimes must therefore have brought about the presumed dramatic reduction of the stock in these river reaches. Our analyses are useful for developing the hypothesis that the interaction of slow growth and increased early-life mortality is an important cause of the decline of Colorado squawfish in the numerous upper-basin river reaches whose temperature regimes have not been importantly affected by the operation of upstream dams.

In their review of literature on Colorado squawfish, Behnke & Benson (1983) noted the slow growth of Colorado squawfish in upper-basin rivers and speculated that it was a recent phenomenon. They observed that the largest Colorado squawfish found today weigh about 7 kg, whereas early in this century squawfish weighing more than 20 kg apparently were not uncommon. Behnke & Benson (1983) hypothesized that a replacement of large, native prey fishes by introduced species that attain only small body size had caused a decline in Colorado squawfish food availability and growth rate. But fish need not grow rapidly to attain large size; they might also be slow-growing but long-lived. Moreover, to us Behnke & Benson's hypothesis seemed an unlikely explanation because prey species of a variety of sizes are abundant in upper-basin rivers (Holden & Stalnaker 1975, Tyus et al. 1982), although their actual availability to Colorado squawfish is unknown.

We believe a more plausible explanation is that the slow growth of Colorado squawfish in the upper basin is both historic and the result of suboptimal conditions for growth in these upstream regions of historic range. Temperature regimes in the former middle and lower Colorado River were more favorable to Colorado squawfish growth than are those of its present habitat (Fig. 3), although the availability of food and the rate of growth in these former habitats is unknown because squawfish were eliminated from these areas before such life-history information could be collected. Nonetheless, as judged by the growth rate of Colorado squawfish in Osmundson's (1987) pond (which had abundant food and a temperature regime with suitability of 3.6) it is reasonable to assume that annual growth in these former downstream areas was rapid.

We believe that in the historic Colorado River basin there was a marked longitudinal effect on growth of Colorado squawfish, most important on that of the age-0 fish. This belief is supported by the strong relation between size of age-0 Colorado squawfish in fall in upper-basin rivers and our measure of the relative suitability of the temperature regime for growth (Fig. 4). The actual cause of this relation might include a direct effect of temperature on Colorado squawfish metabolism, on the production of food organisms, on the time of spawning and length of the subsequent first-year growing season, or perhaps a combination of these factors. Serns (1982a, b) showed a similar relation between growth (as well as year-class strength) of age-0 walleye, *Stizostedion vitreum,* and smallmouth bass, *M. dolomieui,* and aspects of the annual water temperature regime. Water temperature is a cue for spawning of temperate-zone fishes. Colorado squawfish begin spawning when temperatures reach 20–22° C (Hamman 1981, Tyus & McAda 1984, Haynes et al. 1984) – normally during July or August in the upper basin (Fig. 3) – and embryos hatch 4–5 days later (Hamman 1981). As the relative suitability of the temperature regime increases, the date when spawning temperatures are achieved advances and the length of the growing season increases (Fig. 3). In the historic lower Colorado River, spawning temperatures were reached in early May (Fig. 3) and young fish had most of the longer growing season available for first-year growth. Although its precise causal factors are unknown, the relation shown in Figure 4 provides a perspective for the much larger differences in age-0 growth that probably occurred historically between the upper and lower basins.

In the upstream regions of historic range that constitute the remaining habitat of Colorado squawfish, the small size of the age-0 fish going into winter might be an important factor affecting recruitment to the adult stock. Studies on age-0 fish have shown that overwinter survival is directly related to fish size (Toneys & Coble 1979, Oliver et al. 1979, Shuter et al. 1980), and that first-year growth can directly affect adult year-class strength in smallmouth bass and largemouth bass (Shuter et al. 1980, Gutreuter & Anderson 1985). The largest age-0 largemouth bass most often recruit to the adult stock (Gutreuter & Anderson 1985 and references therein). If a similar relation holds true for Colorado squawfish in the upper basin, the more frequent occurrence in the Green River than in the Colorado of comparatively large age-0 young in fall (Fig. 4) might explain the relatively large adult squawfish stock of the Green (Holden & Stalnaker 1975, USFWS, unpublished data).

But examples probably exist of species that live under conditions well below their optimum for growth – where age-0 growth is slow and subsequent recruitment to the adult stock might be quite restricted – yet their populations are large. Our simulations provide insight into why this may no longer be the case for Colorado squawfish, a species presumed to have formerly had large populations in the upper basin. They show how slow growth in the upper basin can make Colorado squawfish there especially vulnerable to the effects of increased early-life mortality. Introduced fish species and other habitat manipulations of technologic man have doubtless contributed to increased early-life mortality of Colorado squawfish, though the precise nature of these negative interactions and their relative importance is unknown. River reaches inhabited by Colorado squawfish have been successfully colonized by numerous introduced species, including piscivores such as channel catfish, *Ictalurus punctatus,* green sunfish, *Lepomis cyanellus,* and largemouth bass (Holden & Stalnaker 1975, Tyus et al. 1982). Green sunfish, for example, can greatly suppress native cyprinid populations in rivers (Lemly 1985).

Our simulations also show how an increase in early-life mortality can reduce both the number of age groups (eliminating the oldest, largest fish) and the relative abundance of those that remain (Table 1) – changes that have indeed occurred in the upper-basin Colorado squawfish population. But why are the natural compensatory mechanisms that occur in populations of numerous other species not operating to offset the effects of increased early-life mortality on the Colorado squawfish population (e.g. McFadden 1977)? Most common among these are the related responses of increased growth and fecundity in the fish that escape early-life mortality. Each of these would have the effect of increasing the potential for population growth. Such compensatory responses would be anticipated if competition for resources had a limiting effect on growth and fecundity. However, if growth of Colorado squawfish in the upper basin is ultimately limited by the relative scarcity of optimal temperatures – a resource whose availability to individual fish is independent of population density – such compensatory mechanisms would not be operative. The capacity for compensatory responses in a population might be severely limited when conditions for growth of individual fish are appreciably less than optimal, as they are in the upstream regions of the historic range of Colorado squawfish.

Our observations suggest that the growth physiology and timing of spawning of the Colorado squawfish are not well adapted to the temperature regimes of upper-basin rivers (cf. Keast 1985). Nonetheless, the fish might have been common here under former, pristine conditions because early-life mortality then was relatively low and these life-history characteristics were not important impediments to population maintenance. Lack of strong directional selection then may have precluded evolution of phenotypes that grow more rapidly or spawn earlier in the year under upper-basin temperature regimes.

Management recommendations

Management recommendations for this endangered species are based on the arguments that we have made and include possible tests of our hypothesis.

Dams and reservoirs might be operated to increase both the length of the growing season and the availability of temperatures suitable for growth, and to stimulate earlier spawning. However, such enhancement must be cautiously considered because it might also benefit undesirable species – perhaps to the ultimate detriment of Colorado squawfish. Water-development programs that reduce available temperatures should of course be avoided.

Investigations should be conducted to determine the relation between the size of age-0 Colorado squawfish and overwinter survival. If an important relation occurs, it would provide useful objectives for possible growth-enhancement efforts.

Because elimination of introduced fishes is impracticable in a river system as large as the Colorado, concern must clearly be directed toward preventing introductions of additional, undesirable fishes to the already large non-native fauna. Investigations to determine which non-native fish species present problems for Colorado squawfish should be conducted. Perhaps ways can be found to reduce the negative effects of the important non-native fishes on the Colorado squawfish.

Appendix. Computation of vital statistics for simulated populations of fast(F)- and slow(S)-growing Colorado squawfish that mature at 3 and 6 years of age, respectively. It is assumed that, beginning in the first year of maturity and continuing through age 10, each slow-growing female produces 0.5 mature female offspring annually and each fast-growing female produces 6.5 – based on survival with 99% annual mortality in the smallest length class; see Table 1.[a]

x (age in years)	l_x		m_x		l_xm_x		l_xm_xx	
	S	F	S	F	S	F	S	F
0–2[b]	1.0	1.0	0	0	0	0	0	0
3	1.0	1.0	0	6.5	0	6.5	0	19.5
4	1.0	1.0	0	6.5	0	6.5	0	26.0
5	1.0	1.0	0	6.5	0	6.5	0	32.5
6	1.0	1.0	0.5	6.5	0.5	6.5	3.0	39.0
7	1.0	1.0	0.5	6.5	0.5	6.5	3.5	45.5
8	1.0	1.0	0.5	6.5	0.5	6.5	4.0	52.0
9	1.0	1.0	0.5	6.5	0.5	6.5	4.5	58.5
10	1.0	1.0	0.5	6.5	0.5	6.5	5.0	65.0
11	0.0	0.0	0	0	0	0	0	0
Sums					2.5	52	20	338

[a] For slow-growing population, $G = (\Sigma l_xm_xx)/R_o = 20/2.5 = 8$ years; $r = (\log_e R_o)/G = 0.916/8 = 0.115$; and $f = e^r = 1.121$. For fast-growing population, $G = 338/52 = 6.5$ years; $r = (\log_e 52)/G = 0.608$; and $f = 1.837$.

[b] Values apply to ages 0, 1 and 2.

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References cited

Behnke, R.J. & D.E. Benson. 1983. Endangered and threatened fishes of the upper Colorado River Basin. Coop. Exten, Serv., Colorado State University, Fort Collins, Bull. 503A. 38 pp.

Black, T. & R.V. Bulkley. 1985a. Growth rate of yearling Colorado squawfish at different water temperatures. Southwest. Nat. 30: 253–257.

Black, T. & R.V. Bulkley. 1985b. Preferred temperature of yearling Colorado squawfish. Southwest. Nat. 30: 95–100.

Bulkley, R.V., C.R. Berry, R. Pimentel & T. Black. 1981. Tolerance and preferences of Colorado River endangered fishes to selected habitat parameters. U.S. Fish & Wildl. Serv., Comp. Rpt., Contract 14–16–0008–1061 A-2, Utah Coop. Fish. Res. Unit, Utah State University, Logan. 57 pp.

Carlander, K.D. 1969. Handbook of freshwater fishery biology. Vol. 1. Iowa State University Press, Ames. 752 pp.

Carlander, K.D. 1977. Handbook of freshwater fishery biology. Vol. 2. Iowa State University Press, Ames. 431 pp.

Cole, L.C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29: 103–137.

Dill, W.A. 1944. The fishery of the lower Colorado River. Calif. Fish and Game 30: 109–211.

Evermann, B.W. & C. Rutter. 1895. Fishes of the Colorado basin. U.S. Fish Comm. Bull. 14(1894): 473–486.

Gilbert, C.H. & N.B. Scofield. 1898. Notes on a collection of fishes from the Colorado basin in Arizona. Proc. U.S. Natl. Mus. 20: 487–499.

Gutreuter, S.J. & R.O. Anderson. 1985. Importance of body size to the recruitment process in largemouth bass populations. Trans. Amer. Fish. Soc. 114: 317–327.

Hamman, R.L. 1981. Spawning and culture of Colorado squawfish in raceways. Prog. Fish-Cult. 43: 173–177.

Haynes, C.M., T.A. Lytle, E.J. Wick & R.T. Muth. 1984. Larval Colorado squawfish (*Ptychocheilus lucius* Girard) in the upper Colorado River basin, Colorado, 1979–1981. Southwest. Nat. 29: 21–33.

Holden, P.B. & C.B. Stalnaker. 1975. Distribution and abundance of mainstream fishes of the middle and upper Colorado River basin, 1967–1973. Trans. Amer. Fish. Soc. 104: 217–231.

Holden, P.B. & E.J. Wick. 1982. Life history and prospects for recovery of Colorado squawfish. pp. 98–108. *In:* W.H. Miller, H.M. Tyus & C.A. Carlson (ed.) Fishes of the Upper Colorado River System: Present and Future, Pub. West. Div., Amer. Fish. Soc., Bethesda.

Jordan, D.S. 1891. Report of exploration in Colorado and Utah during the summer of 1889, with an account of the fishes found in each of the river basins examined. Bull. U.S. Fish Comm. 9: 1–40.

Jordan, D.S. & B.W. Evermann. 1896. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47 (pt. 1): 1–1240.

Keast, A. 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. Env. Biol. Fish. 12: 119–129.

Krebs, C.J. 1972. Ecology: the experimental analysis of distribution and abundance. Harper and Row Publ., New York. 694 pp.

Lemly, A.D. 1985. Suppression of native fish populations by green sunfish in first-order streams of Piedmont North Carolina. Trans. Amer. Fish. Soc. 114: 705–712.

Magnuson, J.J., L.B. Crowder & P.A. Medvick. 1979. Temperature as an ecological resource. Amer. Zool. 19: 331–343.

Marsh, P.C. 1985. Effect of incubation temperature on survival of embryos of native Colorado River fishes. Southwest. Nat. 30: 129–140.

McFadden, J.T. 1977. An argument supporting the reality of compensation in fish populations and a plea to let them exercise it. pp. 153–183. *In:* W. Van Winkle (ed.) Proceedings of the Conference on Assessing the Effects of Power-plant-induced Mortality on Fish Populations, Pergamon Press, New York.

Miller, R.R. 1961. Man and the changing fish fauna of the American Southwest. Mich. Acad. Sci., Art. Lett. 46: 365–404.

Minckley, W.L. 1973. Fishes of Arizona. Sims Printing Co., Phoenix. 293 pp.

Minckley, W.L. & J.E. Deacon. 1968. Southwestern fishes and the enigma of 'endangered species.' Science 159: 1424–1432.

Oliver, J.D., G.F. Holeton & K.E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Trans. Amer. Fish. Soc. 108: 130–136.

Osmundson, D.B. 1987. Growth and survival of Colorado squawfish (*Ptychocheilus lucius*) stocked in riverside ponds, with reference to largemouth bass (*Micropterus salmoides*) predation. M.Sc. Thesis, Utah State University, Logan. 191 pp.

Seethaler, K. 1978. Life history and ecology of the Colorado squawfish (*Ptychocheilus lucius*) in the upper Colorado River basin. M.Sc. Thesis, Utah State University, Logan. 156 pp.

Serns, S.L. 1982a. Influence of various factors on density and growth of age-0 walleyes in Escanaba Lake, Wisconsin, 1958–1980. Trans. Amer. Fish. Soc. 111: 299–306.

Serns, S.L. 1982b. Relation of temperature and population density to first-year recruitment and growth of smallmouth bass in a Wisconsin Lake. Trans. Amer. Fish. Soc. 111: 570–574.

Shuter, B.J., J.A. MacLean, F.E.J. Fry & H.A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Trans. Amer. Fish. Soc. 109: 1–34.

Toneys, M.L. & D.W. Coble. 1979. Size-related, first winter mortality of freshwater fishes. Trans Amer. Fish. Soc. 108: 415–419.

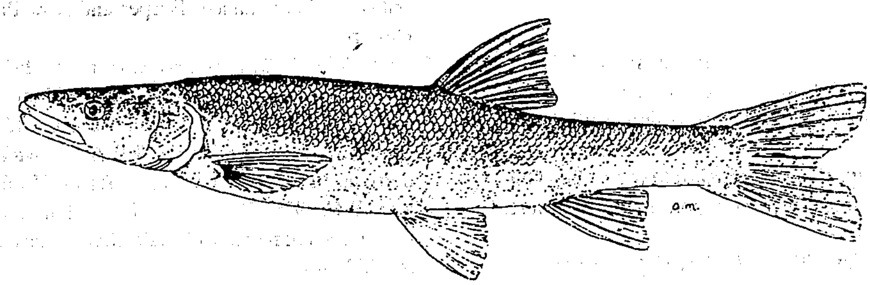
Tyus, H.M. & C.W. McAda. 1984. Migration, movements and habitat preferences of Colorado squawfish, *Ptychocheilus lucius*, in the Green, White, and Yampa rivers, Colorado and Utah. Southwest. Nat. 29: 289–299.

Tyus, H.M., B.D. Burdick, R.A. Valdez, C.M. Haynes, T.A. Lytle & C.R. Berry. 1982. Fishes of the upper Colorado River Basin: distribution, abundance, and status. pp. 12–70. *In:* W.H. Miller, H.M. Tyus & C.A. Carlson (ed.) Fishes of the Upper Colorado River System: Present and Future. Pub. West. Div., Amer. Fish. Soc., Bethesda.

Tyus, H.M., R.L. Jones & L.A. Trinca. 1987. Green River rare and endangered fish studies, 1982–1985. Final Rep. U.S. Fish & Wild. Serv., Vernal, Utah. 117 pp.

Vanicek, C.D. & R.H. Kramer, 1969. Life history of the Colorado squawfish, *Ptychocheilus lucius*, and the Colorado chub, *Gila robusta*, in the Green River in Dinosaur National Monument, 1964–1966. Trans. Amer. Fish. Soc. 98: 193–208.

Weatherley, A.H. 1972. Growth and ecology of fish populations. Academic Press, New York. 293 pp.



The Colorado squawfish, *Ptychocheilus lucius*, from Green River, Wyoming (from P.B. Moyle 1976, Inland Fishes of California).

APPENDIX C

Simulation of Physical Microhabitat versus Streamflow for adult Colorado squawfish (Ptychocheilus lucius) in the 15-mile reach of the Colorado River

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Introduction

One task of the U. S. Fish and Wildlife Service (FWS) is to develop year-round flow recommendations for the 15-mile reach at Palisade, Colorado, river mile 181.4-182.0. The recommendations will enhance adult habitat for Colorado squawfish (Ptychocheilus lucius). One method for simulating the amount of habitat available at a particular stream flow is the Physical Habitat Simulation Methodology (PHABSIM) system, part of the Instream Flow Incremental Methodology (IFIM). PHABSIM compares water depth, mean column velocity and substrate at various flow levels with the suitability of these parameters for fish use. Thus, the effects of proposed streamflow alterations on existing riverine habitat can be expressed (Bovee 1982).

This PHABSIM analysis follows three general steps to develop a flow recommendation. First, fish microhabitat utilization data are analyzed to develop suitability index (SI) curves which represent the relative use of various water depths, velocity and substrate during a fish life stage (i.e. adult Colorado squawfish in the 15-mile reach). Second, SI curves are compared with data collected along several transects to determine the relative amount of habitat available under various flow scenarios. These habitat conditions establish a baseline of habitat comparison for flow recommendations. Third, the feasibility of implementing recommended flows is evaluated based on existing water records.

In this analysis, habitat is considered for adult Colorado squawfish during the summer months of July, August and September, and a preliminary effort is made to address the "winter" months from October through April. Preliminary analyses suggest that a proposed flow window between 700 and 1200 cfs during July, August and September could maximize adult Colorado squawfish habitat in the 15-mile reach. In comparison to the flow records reviewed (virgin flows from 1950-1982 and actual flows from 1930-1987), a proposed flow of 700 cfs would decrease present flows by an average of 44 percent during July, August, and September but increase available habitat for Colorado squawfish adults by 45 percent during these months.

STEP 1: Suitability Index Curves

For adult Colorado squawfish, SI curves were derived by compiling and organizing microhabitat data into frequency histograms of habitat use. The data for construction of these SI curves were obtained from the Colorado River Fishery Project, Grand Junction, and consist of radiotelemetry observations of adult Colorado squawfish depth, velocity and substrate microhabitat use in pool, run, and riffle habitats in the 15 mile reach (Tables 1 and 2). Generally, SI curves are developed by combining data from all habitat types (pool, run, riffle, eddy, backwater, etc.); however, in this analysis, the limiting microhabitat, and hence the microhabitat evaluated for Colorado squawfish, is considered pools, runs and riffles (Kaeding, Response to questions posed by the Technical Group in Jim Bennett's memo of 13 April 1988). Further, only data collected from habitats modeled by the PHABSIM site cross sections--pools, riffles and runs--were used.

The raw data are prepared in frequency tables for summer (July, August and September) and winter (October through April) (Tables 3 and 4). Summer habitat use occurred at depths between 0.5 and 8.0 feet ($\bar{x}$ = to 3.76 ft; Tables 3 and 5), and velocities between 0 and 5.6 feet per second ($\bar{x}$ = to 1.57 feet per second; Table 3 and 5), over cobble substrate. In winter, depths between 0.5 and 10.5 feet ($\bar{x}$ = to 4.22 feet; Tables 4 and 6), and velocities ranging from 0.0 to 2.8 ft/sec ($\bar{x}$ = to 0.74 ft/sec), over silt and cobble substrates were used. Thus, in winter adult Colorado squawfish used deeper, lower velocity habitats. There also appears to be a shift from predominantly run habitat in the summer to a combination of pool and run habitats in the winter.

Table 1. Radiotelemetry observations collected by the Colorado River Fishery Project, Grand Junction, for Colorado squawfish (<u>Ptychocheilus lucius</u>) pool, run and riffle microhabitat use in the 15-mile reach during July, August and September.

POOL MICROHABITAT

Date	RM	Depth (ft)	Velocity (ft/s)	Substrate	Number Observations	Discharge* (cfs)
82/07/13	178.3	3.5	0.4	Rubble	9	5221
86/07/22	185.1	3.1	0.3	Sand/Rubble	1	6908
86/08/12	174.2	6.0	0.7	Rubble/Rubble	1	2003
86/08/19	174.2	5.0	0.8	Sand/Silt	1	2003
87/08/25	180.3	1.6	1.5	Rubble/Rubble	1	975
87/08/25	175.9	0.9	0.1	Rubble/Rubble	1	975
88/07/11	179.1	5.0	NA	Sand/Sand	1	NA**
88/07/25	173.4	2.0	0.1	Rubble/Boulder	1	NA
88/08/15	173.0	3.0	1.1	Rubble/Rubble	1	NA
88/09/13	171.2	4.3	0.1	Rubble/Silt	1	NA
88/09/13	175.1	3.0	0.3	Silt/Silt	1	NA

RIFFLE MICROHABITAT

Date	RM	Depth (ft)	Velocity (ft/s)	Substrate	Number Observations	Discharge (cfs)
85/08/29	178.3	1.0	1.7	Rubble	1	1961
85/07/30	172.5	1.3	3.2	Gravel/Rubble	1	5618
85/07/15	185.1	2.3	5.4	Rubble/Boulder	1	5618
86/08/15	187.5	0.8	0.8	Rubble/Rubble	1	2003
87/07/27	174.3	2.0	NA	Rubble/Rubble	1	1530
87/08/17	178.8	1.5	3.0	Rubble/Rubble	1	975
87/09/08	180.8	2.0	NA	Rubble/Rubble	1	634
87/09/18	181.9	1.8	2.5	Rubble/Boulder	1	634
88/07/11	178.3	3.8	NA	Rubble/Rubble	1	NA
88/08/29	175.4	1.9	2.2	Rubble/Rubble	1	NA

RUN MICROHABITAT

Date	RM	Depth (ft)	Velocity (ft/s)	Substrate	Number Observations	Discharge (cfs)
79/09/12	185.1	6.0	1.0	Gravel/Rubble	2	657
79/09/13	185.1	8.0	0.5	Gravel/Rubble	2	657
86/07/01	175.5	5.4	0.5	Rubble/Rubble	1	6908
86/07/16	174.5	3.0	3.5	Rubble/Rubble	1	6908
86/07/22	175.2	2.5	2.2	Rubble/Rubble	1	6908
86/07/29	174.4	4.2	1.0	Silt/Silt	1	6908

Table 1. Continued

86/07/30	188.2	NA	NA	Boulder/Rubble	1	6908
86/08/06	174.2	3.0	2.5	Rubble/Rubble	1	2003
86/09/03	174.3	4.0	1.2	Rubble/Boulder	1	1780
86/09/18	174.3	6.4	1.4	Rubble/Rubble	1	1780
86/09/30	174.2	7.0	2.0	Rubble/Gravel	1	1780
87/07/08	176.5	2.0	3.5	Rubble/Rubble	1	1530
87/07/09	174.2	5.9	0.8	Boulder/Silt	1	1530
87/07/13	174.5	1.9	1.4	Rubble/Boulder	1	1530
87/07/21	178.4	7.0	NA	NA/NA	1	1530
87/07/21	174.5	2.4	0.6	Sand/Sand	1	1530
87/07/27	174.9	6.1	NA	Rubble/Silt	1	1530
87/08/17	175.8	3.0	1.8	Rubble/Rubble	1	975
87/08/17	175.8	3.0	1.8	Rubble/Rubble	1	975
87/08/17	174.2	7.7	1.4	Sand/Sand	1	975
87/09/08	176.1	3.0	NA	Rubble/Rubble	1	634
87/09/18	176.5	4.5	0.0	Rubble/Rubble	2	634
88/07/05	181.3	2.5	3.3	Rubble/Rubble	1	NA
88/07/05	177.7	5.2	2.3	Rubble/Rubble	1	NA
88/07/05	177.7	4.1	2.8	Rubble/Rubble	1	NA
88/07/05	176.5	5.4	2.0	Rubble/Rubble	1	NA
88/07/11	179.1	4.6	NA	Rubble/Rubble	1	NA
88/07/11	178.6	5.5	NA	Rubble/Rubble	1	NA
88/07/18	179.1	3.6	0.8	Boulder/Boulder	1	NA
88/07/18	178.3	6.3	2.5	Rubble/Rubble	1	NA
88/07/18	174.2	2.7	1.7	Rubble/Gravel	1	NA
88/07/25	182.6	3.2	1.4	Rubble/Rubble	1	NA
88/07/25	178.2	5.2	2.6	Rubble/Boulder	2	NA
88/07/25	174.7	2.5	1.9	Rubble/Rubble	1	NA
88/08/02	178.2	1.8	3.0	Rubble/Rubble	1	NA
88/08/02	174.2	5.0	0.5	Rubble/Sand	1	NA
88/08/02	172.9	3.0	2.4	NA/NA	1	NA
88/08/08	174.4	2.5	1.2	Rubble/Rubble	1	NA
88/08/08	173.8	2.0	1.5	Rubble/Rubble	1	NA
88/08/08	172.4	1.9	0.4	Rubble/Boulder	1	NA
88/08/15	174.2	4.4	0.5	Rubble/Sand	1	NA
88/08/15	173.9	3.0	1.0	Rubble/Rubble	1	NA
88/08/22	176.2	2.0	1.9	Rubble/Rubble	1	NA
88/08/29	173.0	3.3	1.0	Boulder/Sand	1	NA
88/08/29	177.8	2.3	2.4	Rubble/Rubble	1	NA
88/08/29	174.0	2.8	1.8	Rubble/Rubble	1	NA
88/08/29	172.8	1.4	1.9	Rubble/Rubble	1	NA
88/09/06	171.2	5.0	1.0	Rubble/Rubble	1	NA
88/09/06	174.3	3.6	1.2	Sand/Sand	1	NA
88/09/19	176.7	5.0	1.5	Rubble/Rubble	1	NA
88/09/19	176.2	5.0	0.8	Boulder/Rubble	1	NA
88/09/26	172.3	3.3	1.3	Rubble/Rubble	1	NA
88/09/26	174.1	7.6	1.0	Rubble/Sand	1	NA
88/09/26	177.2	2.1	1.0	Bedrock/Rubble	1	NA

* Mean monthly discharge.
** Not available

Table 2. Radiotelemetry observations collected by the Colorado River Fishery Project, Grand Junction, for Colorado squawfish (Ptychocheilus lucius) pool and run microhabitat use in the 15-mile reach from October through April.

POOL MICROHABITAT

Date	RM	Depth (ft)	Velocity (ft/s)	Substrate	Number Observations	Discharge* (cfs)
86/10/07	175.9	1.5	0.3	Silt/Rubble	1	2204
86/10/07	174.4	3.9	0.2	Silt/Silt	1	2204
86/10/07	174.4	3.1	0.3	Silt/Silt	1	2204
86/11/04	174.5	3.0	0.5	Silt/Rubble	1	3198
86/11/05	174.5	5.0	0.2	Silt/Silt	1	3198
87/03/02	174.6	3.0	0.0	Sand/Sand	1	2513
87/04/16	179.1	0.8	0.2	Silt/Silt	1	3344
88/01/08	174.4	3.0	0.0	Silt/Silt	1	NA**
88/01/08	174.5	2.8	0.1	Silt/Silt	1	NA
88/01/13	174.5	2.5	0.0	Silt/Silt	1	NA
88/01/13	174.4	3.0	0.0	Silt/Silt	1	NA
88/01/19	174.4	3.0	0.0	Silt/Silt	1	NA
88/01/27	174.4	2.8	0.1	Silt/Silt	1	NA
88/02/04	174.5	1.4	0.0	Silt/Silt	1	NA
88/02/04	174.4	6.6	0.1	Silt/Boulder	1	NA
88/02/09	174.4	6.4	0.2	Gravel/Silt	1	NA
88/02/09	174.5	1.4	0.3	Silt/Silt	1	NA
88/02/19	174.4	4.0	0.3	Silt/Bedrock	1	NA
88/02/19	174.5	2.0	0.1	Silt/Silt	1	NA
88/02/19	176.7	3.0	0.1	Boulder/Silt	1	NA
88/02/24	174.4	3.8	0.4	Silt/Silt	1	NA
88/02/24	174.5	2.0	0.1	Silt/Silt	1	NA
88/02/24	176.7	3.8	0.2	Rubble/Silt	1	NA
88/03/01	174.4	4.3	0.1	Sand/Rubble	1	NA
88/03/10	174.4	4.0	0.2	Sand/Rubble	1	NA
88/03/10	176.5	4.2	0.7	Silt/Silt	1	NA
88/03/16	176.5	2.5	0.3	Silt/Rubble	1	NA
88/03/17	174.4	4.8	0.2	Boulder/Rubble	1	NA
88/03/31	174.4	3.8	0.0	Silt/Silt	1	NA
88/04/18	174.4	4.0	0.2	Silt/Silt	1	NA

Table 2. Continued

RUN HABITAT

Date	RM	Depth (ft)	Velocity (ft/s)	Substrate	Number Observations	Discharge* (cfs)
87/10/09	176.5	3.0	1.4	Rubble/Rubble	1	627
87/10/09	176.5	4.4	0.3	Rubble/Sand	1	627
87/10/09	174.4	3.5	0.8	Silt/Silt	1	627
87/10/09	174.3	2.7	0.8	Silt/Silt	1	627
88/10/07	184.2	4.0	0.8	Silt/Silt	1	NA**
88/01/11	177.0	7.5	1.8	Rubble/Rubble	1	NA
88/01/13	177.0	7.2	1.5	Silt/Rubble	1	NA
88/01/15	184.2	7.2	1.4	Rubble/Rubble	1	NA
88/01/21	177.0	7.4	1.2	Rubble/Silt	1	NA
88/01/22	184.2	7.0	1.1	Silt/Bedrock	1	NA
88/01/27	176.7	5.5	1.5	Rubble/Rubble	1	NA
88/01/27	174.4	2.6	1.0	Silt/Silt	1	NA
88/01/28	184.1	5.5	1.5	Rubble/Silt	1	NA
88/02/04	176.7	3.0	1.7	Rubble/Rubble	1	NA
88/02/05	184.1	6.0	1.4	Rubble/Silt	1	NA
88/02/09	176.7	3.0	1.1	Rubble/Rubble	1	NA
88/02/10	184.1	5.5	1.5	Rubble/Rubble	1	NA
88/02/19	184.1	7.4	0.7	Silt/Silt	1	NA
88/02/25	184.1	6.8	0.7	Silt/Rubble	1	NA
88/03/01	174.3	2.0	0.4	Sand/Silt	1	NA
88/03/01	176.6	2.8	0.5	Rubble/Silt	1	NA
88/03/02	184.1	6.9	0.7	Sand/Sand	1	NA
88/03/11	184.1	10.0	0.7	Boulder/Bedrock	1	NA
88/03/17	184.1	8.2	0.4	Silt/Boulder	1	NA
88/03/17	174.4	5.6	0.4	Sand/Sand	1	NA
88/03/22	174.4	2.4	1.1	Sand/Sand	1	NA
88/03/22	174.3	2.5	1.0	Sand/Sand	1	NA
88/03/23	177.2	3.0	1.8	Rubble/Silt	1	NA
88/03/23	183.4	4.1	0.7	Rubble/Silt	1	NA
88/03/29	177.3	4.0	1.0	Rubble/Silt	1	NA
88/03/31	182.7	4.5	2.6	Rubble/Rubble	1	NA
88/04/06	174.4	4.6	1.5	Sand/Sand	1	NA
88/04/06	174.4	2.6	0.9	Sand/Sand	1	NA
88/04/12	179.9	3.4	1.2	Gravel/Rubble	1	NA
88/04/25	178.8	2.9	1.5	Rubble/Rubble	1	NA
88/04/25	181.6	4.7	0.6	Sand/Sand	1	NA

* Mean monthly discharge
** Not available

Table 3. Radiotelemetry observations for Colorado squawfish (*Ptychocheilus lucius*) depth, velocity, and substrate microhabitat use in the 15-mile reach in pool, run, and riffle habitats during July, August and September.

DEPTH (FT)	FREQUENCY POOL	RUN	RIFFLE
0.0-0.49	0	0	0
0.5-0.99	1	0	1
1.0-1.49	0	1	2
1.5-1.99	1	3	3
2.0-2.49	1	6	3
2.5-2.99	0	6	0
3.0-3.49	3	10	0
3.5-3.99	1	2	1
4.0-4.49	1	4	0
4.5-4.99	0	2	0
5.0-5.49	2	8	0
5.5-5.99	0	2	0
6.0-6.49	1	4	0
6.5-6.99	0	0	0
7.0-7.49	0	2	0
7.5-7.99	0	2	0
>8.0	0	1	0
TOTAL:	11	53	10

SUBSTRATE	POOL	RUN	RIFFLE
1	0	0	0
2	0	0	0
3	1	1	0
4	3	3	0
5	0	2	1
6	7	39	9
7	0	5	0
8	0	1	0
9	0	0	0
TOTAL:	11	51	10

VELOCITY (FT/S)	FREQUENCY POOL	RUN	RIFFLE
0.0-0.19	3	1	0
0.2-0.39	2	0	0
0.4-0.59	1	5	0
0.6-0.79	1	1	0
0.8-0.99	1	3	1
1.0-1.19	1	7	0
1.2-1.39	0	4	0
1.4-1.59	1	6	0
1.6-1.79	0	1	1
1.8-1.99	0	6	0
2.0-2.19	0	2	0
2.2-2.39	0	1	1
2.4-2.59	0	4	1
2.6-2.79	0	1	0
2.8-2.99	0	1	0
3.0-3.19	0	1	1
3.2-3.39	0	1	1
3.4-3.35	0	2	0
3.6-3.79	0	0	0
3.8-4.19	0	0	0
4.2-4.39	0	0	0
4.4-4.59	0	1	0
4.6-5.19	0	0	0
5.2-5.39	0	0	0
5.4-5.59	0	0	1
>5.6	0	0	0
TOTAL:	10	48	7

SUBSTRATE CODE	DESCRIPTION
1	Plant detritus
2	Clay
3	Silt
4	Sand
5	Gravel
6	Rubble
7	Boulder
8	Bedrock
9	Other

Table 4. Radiotelemetry observations for Colorado squawfish (Ptychocheilus lucius) depth, velocity, and substrate microhabitat use in the 15-mile reach in pool and run habitats from October through April.

DEPTH (FT)	FREQUENCY POOL	FREQUENCY RUN
0.0- 0.49	0	0
0.5- 0.99	1	0
1.0- 1.49	3	0
1.5- 1.99	1	0
2.0- 2.49	2	2
2.5- 2.99	4	6
3.0- 3.49	6	5
3.5- 3.99	4	1
4.0- 4.49	5	4
4.5- 4.99	1	3
5.0- 5.49	1	0
5.5- 5.99	0	4
6.0- 6.49	1	1
6.5- 6.99	1	2
7.0- 7.49	0	4
7.5- 7.99	0	2
8.0- 8.49	0	1
8.5- 8.99	0	0
9.0- 9.49	0	0
9.5- 9.99	0	0
10.0-10.49	0	1
TOTAL:	30	36

SUBSTRATE	POOL	RUN
1	0	0
2	0	0
3	23	9
4	3	8
5	1	1
6	1	17
7	2	1
8	0	0
9	0	0
TOTAL:	30	36

VELOCITY (FT/S)	FREQUENCY POOL	FREQUENCY RUN
0.0-0.19	11	0
0.2-0.39	16	1
0.4-0.59	2	4
0.6-0.79	1	6
0.8-0.99	0	4
1.0-1.19	0	6
1.2-1.39	0	2
1.4-1.59	0	9
1.6-1.79	0	1
1.8-1.99	0	2
2.0-2.19	0	0
2.2-2.39	0	0
2.4-2.59	0	0
2.6-2.79	0	1
2.8-2.99	0	0
3.0-3.19	0	0
3.2-3.39	0	0
3.4-3.35	0	0
3.6-3.79	0	0
3.8-4.19	0	0
4.2-4.39	0	0
4.4-4.59	0	0
4.6-5.19	0	0
5.2-5.39	0	0
5.4-5.59	0	0
>5.6	0	0
TOTAL:	30	36

SUBSTRATE CODE	DESCRIPTION
1	Plant detritus
2	Clay
3	Silt
4	Sand
5	Gravel
6	Rubble
7	Boulder
8	Bedrock
9	Other

To produce SI curves for summer and winter adult Colorado squawfish microhabitat use, frequency bar graphs (developed form Tables 3 and 4) were smoothed by connecting the peak bars. Generally, the peak of a SI curve (the bin value assigned a suitability of one) occurs at the bar with the highest frequency of use. Thus, the resulting smoothed curve closely reflects the frequency bar graph, as in Figures 1 and 2 (Tables 5 and 6; Set A). However, to alleviate the radiotelemetry sampling bias towards shallow, low-velocity habitats and to reflect the range of habitat use in the 15-mile reach, the peak of the SI curve was extended to include the mean depth and velocity values (Table 7 and 8; Figures 3 and 4; Set B). Substrate is represented as a bar graph of habitat use.

Once the SI curves were developed, they were run through the HABTAT4 program, part of the Physical Habitat Simulation System for IBM-Compatible Micro Computers developed by BIO/WEST, Incorporated (Biowest 1987). The results of running curve Sets A and B are given in Tables 9 and 10. The highest habitat index value for curve Set A occurs at 1100 cfs for summer and 450 cfs for winter. The highest value for curve Set B occurs at 900 and 450 cfs for summer and winter, respectively.

Table 5. Set A: Coordinate pairs for the combined suitability index curves for pool, run, and riffle habitats in the 15-mile reach during July, August and September.

MICROHABITAT

DEPTH		VELOCITY		SUBSTRATE	
Value (ft)	Suitability Index	Value (ft/s)	Suitability Index	Code	Suitability Index
0.00	0.00	0.00	0.00	1	0.00
0.25	0.00	0.10	0.50	2	0.00
0.75	0.15	0.50	0.75	3	0.04
1.25	0.23	1.10	1.00	4	0.11
1.75	0.54	1.90	0.75	5	0.05
2.25	0.77	2.50	0.63	6	1.00
3.25	1.00	3.10	0.25	7	0.09
5.25	0.77	3.50	0.25	8	0.12
6.25	0.38	4.50	0.13	9	0.00
7.25	0.15	5.50	0.13		
7.75	0.15	5.70	0.00		
8.25	0.08	100.00	0.00		
8.75	0.08				
100.00	0.00				
mean	3.76	mean	1.57		
variance	3.26	variance	0.97		

SUBSTRATE CODE	DESCRIPTION
1	Plant detritus
2	Clay
3	Silt
4	Sand
5	Gravel
6	Cobble
7	Boulder
8	Bedrock
9	Other

Figure 1. Set A: Suitability index curves for adult Colorado squawfish (<u>Ptychocheilus lucius</u>) in the Colorado river at the 15-mile reach during July, August and September. The peak of the suitability curve has not been extended to include the mean water depth and velocity values.

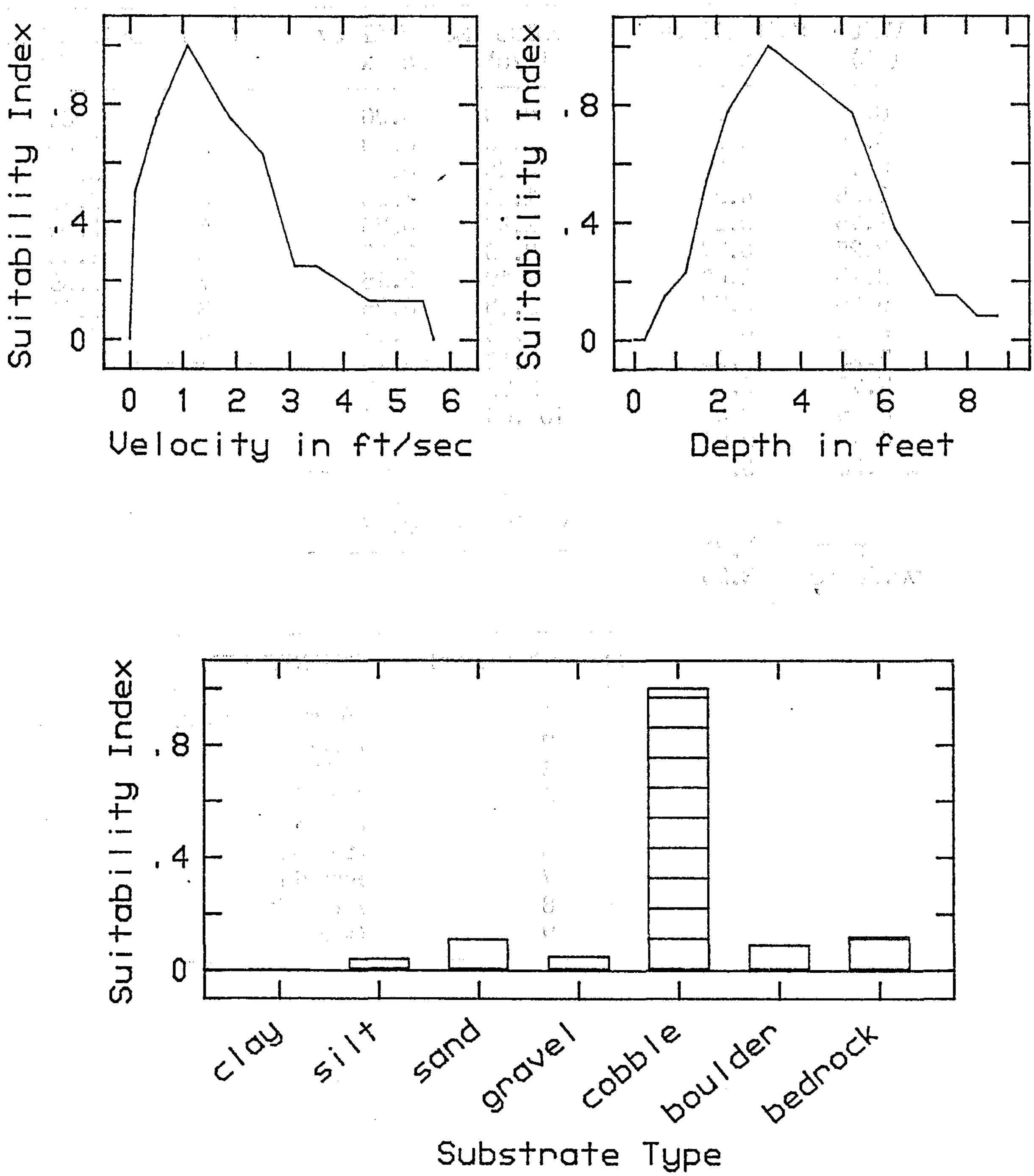


Table 6. Set A: Coordinate pairs for the combined suitability index curves for pool, run, and riffle habitats in the 15-mile reach during October through April.

MICROHABITAT

DEPTH		VELOCITY		SUBSTRATE	
Value (ft)	Suitability Index	Value (ft/s)	Suitability Index	Code	Suitability Index
0.00	0.00	0.00	0.00	1	0.00
0.25	0.00	0.10	0.65	2	0.00
0.75	0.09	0.30	1.00	3	1.00
1.25	0.27	1.50	0.53	4	0.34
2.25	0.36	1.90	0.12	5	0.06
2.75	0.91	2.70	0.06	6	0.56
3.25	1.00	2.90	0.00	7	0.09
4.25	0.91	100.00	0.00	8	0.00
4.75	0.36			9	0.00
7.25	0.36	mean	0.74		
7.75	0.18	variance	0.34		
8.25	0.09				
10.25	0.09				
10.75	0.00				
100.00	0.00				
mean	4.22				
variance	3.79				

SUBSTRATE CODE	DESCRIPTION
1	Plant detritus
2	Clay
3	Silt
4	Sand
5	Gravel
6	Cobble
7	Boulder
8	Bedrock
9	Other

Figure 2. Set A: Suitability index curves for adult Colorado squawfish (Ptychocheilus lucius) in the Colorado river at the 15-mile reach during October through April. The peak of the suitability curve has not been extended to include the mean water depth and velocity values.

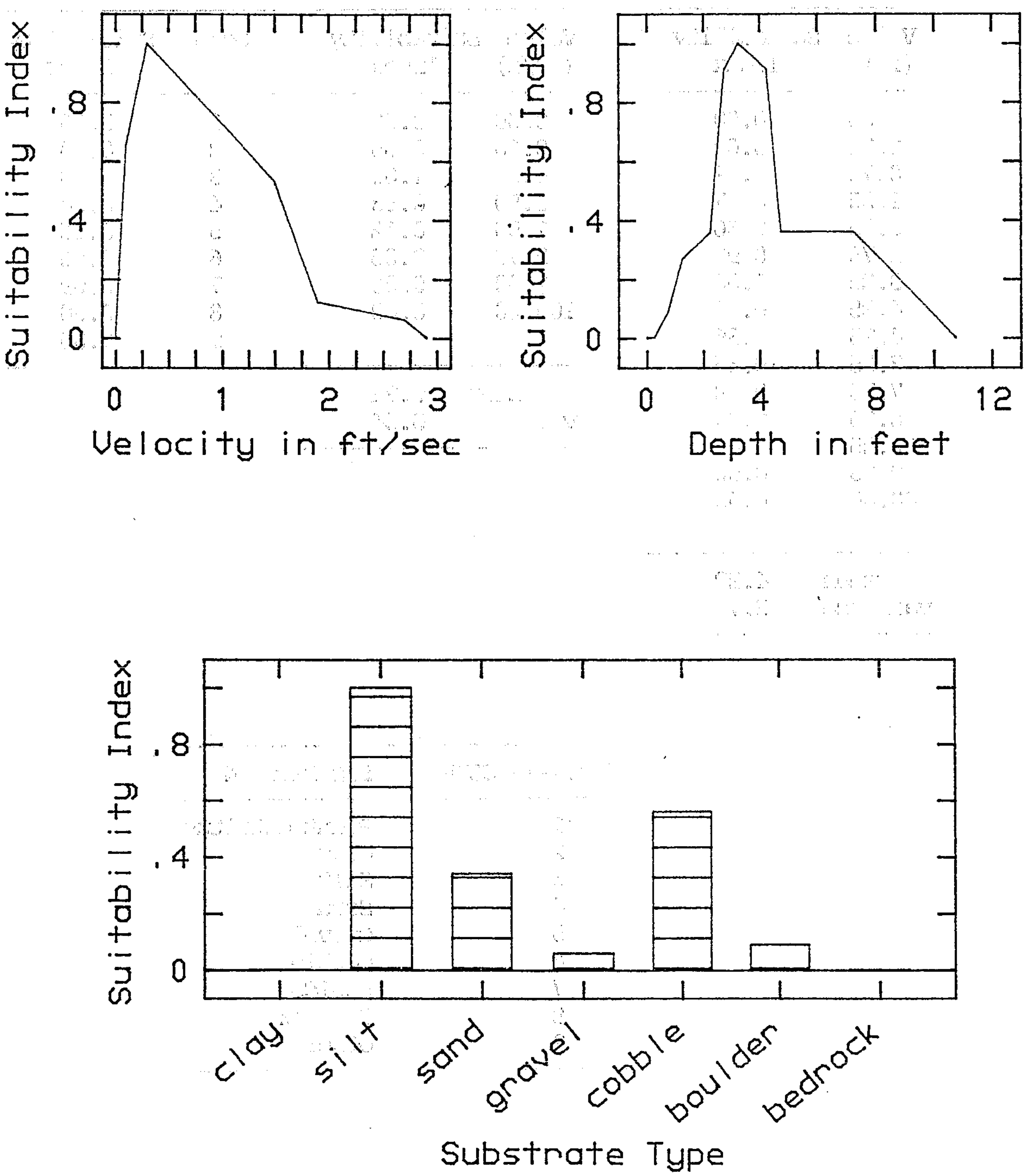


Table 7. Set B: Coordinate pairs for the combined suitability index curves for pool, run, and riffle habitats in the 15-mile reach during July, August and September.

MICROHABITAT

DEPTH		VELOCITY		SUBSTRATE	
Value (ft)	Suitability Index	Value (ft/s)	Suitability Index	Code	Suitability Index
0.00	0.00	0.00	0.00	1	0.00
0.25	0.00	0.10	0.50	2	0.00
0.75	0.15	0.50	0.75	3	0.04
1.25	0.23	1.10	1.00	4	0.11
1.75	0.54	1.57	1.00	5	0.05
2.25	0.77	1.90	0.75	6	1.00
3.25	1.00	2.50	0.63	7	0.09
3.76	1.00	3.10	0.25	8	0.12
5.25	0.77	3.50	0.25	9	0.00
6.25	0.38	4.50	0.13		
7.25	0.15	5.50	0.13		
7.75	0.15	5.70	0.00		
8.25	0.08	100.00	0.00		
8.75	0.00	mean	1.57		
100.00	0.00	variance	0.97		
mean	3.76				
variance	3.26				

SUBSTRATE CODE	DESCRIPTION
1	Plant detritus
2	Clay
3	Silt
4	Sand
5	Gravel
6	Cobble
7	Boulder
8	Bedrock
9	Other

Figure 3. Set B: Suitability index curves for adult Colorado squawfish (<u>Ptychocheilus lucius</u>) in the Colorado river at the 15-mile reach during July, August and September. The peak of the suitability curve has been extended to include the mean water depth and velocity values.

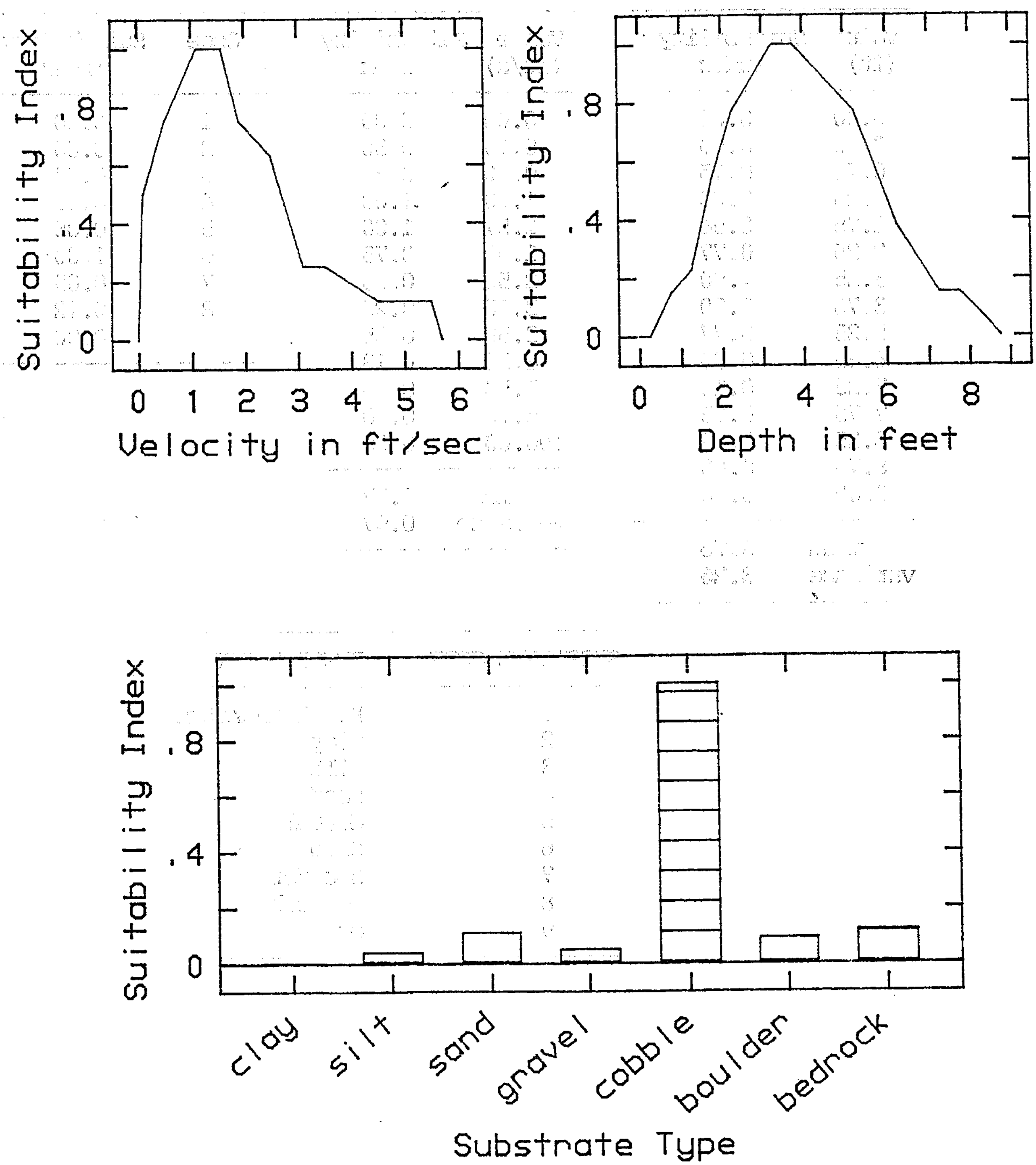


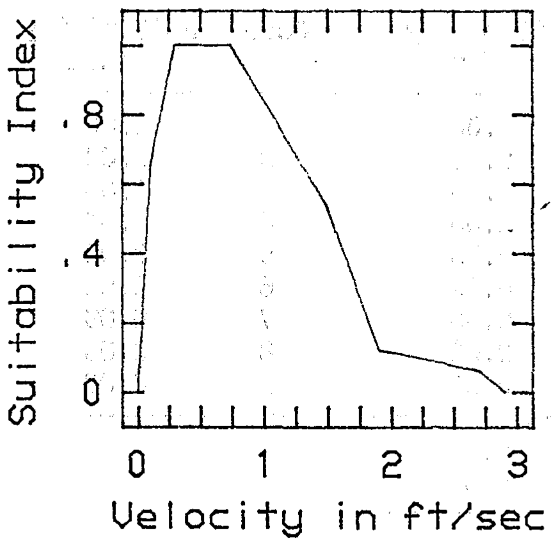
Table 8. Set B: Coordinate pairs for the combined suitability index curves for pool and run habitats in the 15-mile reach during October through April.

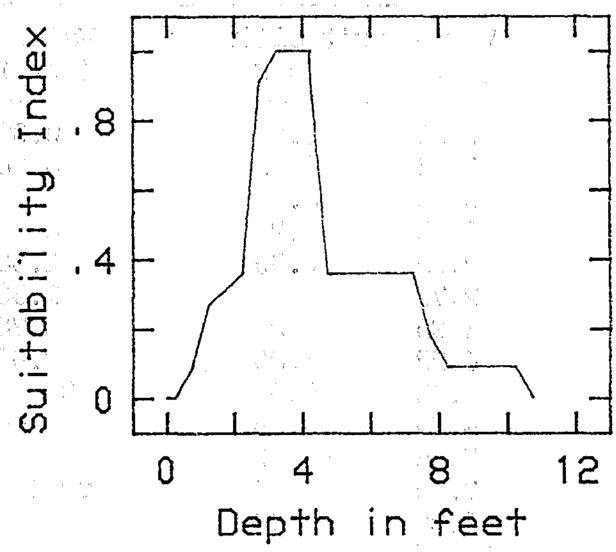
MICROHABITAT

DEPTH		VELOCITY		SUBSTRATE	
Value (ft)	Suitability Index	Value (ft/s)	Suitability Index	Code	Suitability Index
0.00	0.00	0.00	0.00	1	0.00
0.25	0.00	0.10	0.65	2	0.00
0.75	0.09	0.30	1.00	3	1.00
1.25	0.27	0.74	1.00	4	0.34
2.25	0.36	1.50	0.53	5	0.06
2.75	0.91	1.90	0.12	6	0.56
3.25	1.00	2.70	0.06	7	0.09
4.22	1.00	2.90	0.00	8	0.00
4.25	0.91	100.00	0.00	9	0.00
4.75	0.36				
7.25	0.36	mean	0.74		
7.75	0.18	variance	0.34		
8.25	0.09				
10.25	0.09				
10.75	0.00				
100.00	0.00				
mean	4.22				
variance	3.79				

SUBSTRATE CODE	DESCRIPTION
1	Plant detritus
2	Clay
3	Silt
4	Sand
5	Gravel
6	Cobble
7	Boulder
8	Bedrock
9	Other

Figure 4. Set B: Suitability index curves for adult Colorado squawfish (Ptychocheilus lucius) in the Colorado river at the 15-mile reach during October through April. The peak of the suitability curve has been extended to include the mean water depth and velocity values.





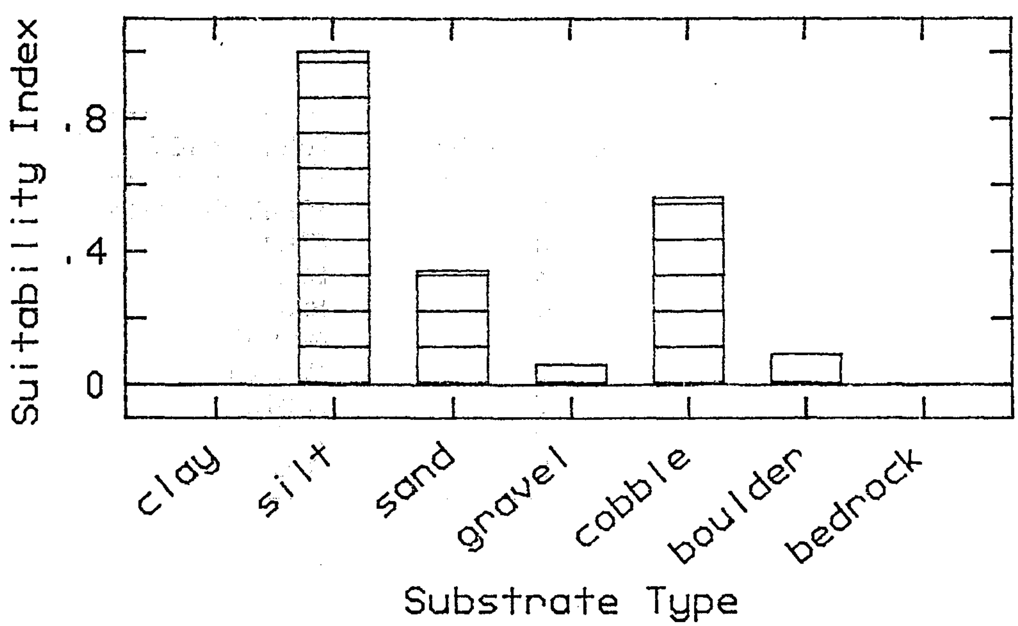


Table 9. Set A: Physical habitat (sq.ft./1000 linear ft. of stream) versus discharge relationship for adult Colorado squawfish in the 15 mile reach. The peak of the suitability curve has <u>not</u> been extended to include mean values.

	Discharge (cfs)	Physical Microhabitat July, Aug, Sep	Physical Microhabitat Oct through Apr
* 1	300.00	56028.64	24269.46
* 2	450.00	67296.86	* 25067.11 *
* 3	600.00	73952.05	23048.86
* 4	750.00	77237.37	19765.51
* 5	900.00	80319.25	17952.59
* 6	1100.00	* 80701.00 *	15509.92
* 7	1300.00	70045.51	13596.16
* 8	1500.00	64367.04	11034.96
* 9	2000.00	41300.50	6207.90
*10	2500.00	37543.22	6093.47
*11	3000.00	35959.93	6109.78
*12	3500.00	40846.59	7395.31
*13	4000.00	38744.78	7388.63
*14	4500.00	36790.31	7466.84
*15	5000.00	34460.90	7852.51
*16	5500.00	29545.45	8442.57
*17	6000.00	27549.20	9008.66
*18	6500.00	24881.62	9645.06
*19	7000.00	23843.78	9940.42
*20	7500.00	22924.88	9785.92
*21	8000.00	19515.84	9465.13
*22	8500.00	17834.88	9301.63
*23	9000.00	16270.96	9061.86
*24	9500.00	15751.91	8952.10
*25	10000.00	14556.03	8827.30
*26	12000.00	12402.97	7722.08
*27	14000.00	11863.88	6161.58
*28	16000.00	12123.08	5260.25

****

Table 10. Set B: Physical habitat (sq.ft./1000 linear ft of stream) versus discharge relationship for adult Colorado squawfish in the 15 mile reach at Palisade. The peak of the suitability curve has been extended to include the mean depth and velocity values.

	Discharge (cfs)	Physical Microhabitat July, Aug, Sep	Physical Microhabitat Oct through Apr
* 1	300.00	57592.22	26534.54
* 2	450.00	72156.56	* 27364.61 *
* 3	600.00	78080.21	25190.85
* 4	750.00	79808.09	21438.30
* 5	900.00	* 83254.01 *	19143.66
* 6	1100.00	83059.15	16349.70
* 7	1300.00	72721.34	14145.73
* 8	1500.00	66760.34	11477.27
* 9	2000.00	42288.81	6572.93
*10	2500.00	38492.04	6507.76
*11	3000.00	36770.83	6602.83
*12	3500.00	41825.69	7906.67
*13	4000.00	39583.34	7893.06
*14	4500.00	37552.72	7983.77
*15	5000.00	35261.92	8426.54
*16	5500.00	30270.20	9064.51
*17	6000.00	28334.02	9628.77
*18	6500.00	25742.38	10295.53
*19	7000.00	24675.67	10596.92
*20	7500.00	23685.78	10403.78
*21	8000.00	20046.39	10107.56
*22	8500.00	18197.25	9990.74
*23	9000.00	16546.07	9769.09
*24	9500.00	16034.47	9728.42
*25	10000.00	14870.52	9629.77
*26	12000.00	12821.08	8462.57
*27	14000.00	12242.39	6655.11
*28	16000.00	12299.16	5799.19

Step 2: Evaluation of Virgin, Actual and Proposed Habitat

The next step of this analysis is to evaluate how adult Colorado squawfish habitat has changed under a dynamic flow regime (virgin versus actual flows) and how a proposed flow regime may affect habitat. The summer and winter Tape 8's from curve Set A are combined with the virgin, actual and proposed flow records to produce monthly habitat time series which depict how habitat has changed over time. It must be stressed that this analysis is strictly limited to changes in depth, velocity and substrate, and that other changes (geomorphology, water temperature, species interactions, water quality, etc.) have also had important effects on the Colorado squawfish in the 15-mile reach, as well as elsewhere in the upper Colorado River.

The virgin (1952-1982) water records for the 15-mile reach were summarized by the Colorado Water Resources and Power Authority, Denver, Colorado, and received through George Smith, FWS hydrologist, Denver, Colorado. The virgin water record represents the historic (i.e. pre-water development) conditions in the 15-mile reach for which USGS flow records are available. The actual flow record is a recorded flow (i.e., Cameo Gage + Plateau Creek + Orchard Mesa Irrigation return flow - the Government Highline Canal and the Grand Valley Canal) and does not assume a full level of development for all projects that have received non-jeopardy biological opinions. It illustrates the variety of flow conditions experienced by squawfish in the Upper Colorado River.

Looking at the summary tables of habitat duration (Tables 11 and 12), it is evident that habitat for adult Colorado squawfish, as defined by depth, velocity and substrate, has increased by 50, 48 and 22 percent, respectively, for July, August and September under actual flow conditions, and that a proposed flow of 700 cfs would increase habitat by 89, 26 and 20 percent over actual during these respective months. Conversely, during October through April (Table 13), mean monthly habitat has decreased from 9 to 18 percent from November to March, and has increased 47 and 97 percent during April and October, respectively. A flow of 450 cfs would increase habitat between 45 and 209 percent throughout the winter months (Table 14). The duration plots for each month are provided in Appendix A-1 through A-4 and are available upon request.

Step 3: Evaluation of Virgin, Actual and Proposed Flow Regimes

The virgin (1952-1982) and actual (1930-1987) flow records used for the habitat and flow analyses are provided in Tables 15 and 16. If one looks at the summary table comparing flow duration during these two time periods (Table 17), it becomes apparent that the average monthly flow under actual conditions has been reduced between 19 and 63 percent during April through October, whereas from November through March flows have increased between 13 and 19 percent. The average monthly flow during July, August and September has been reduced by 39, 58 and 63 percent, respectively (Table 17). A flow of 450 cfs during October through April would reduce flow between 56 and 81 percent in all months. A proposed average monthly flow of 700 cfs during July, August and September would reduce the actual average flow by 84, 45, and 4 percent in July, August, and September, respectively (Table 18). The duration plots of each month are provided in Appendix A-5 and A-6 and are available upon request.

Table 11. Summary statistics of virgin (1951-1983) and actual (1930-1987) mean monthly habitat (i.e. weighted-usable-area (WUA)) in square feet per 1000 feet, in the 15-mile reach during July, August and September.

SUMMARY STATISTICS

MONTH	AVERAGE		MEDIAN		INDEX - A		INDEX - B	
	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA
JULY	26839.09	40357.60	27597.50	37599.00	18509.55	30447.21	26680.34	38845.25
AUGUST	40982.69	60511.67	38509.00	64679.00	37183.52	48865.34	39318.26	61212.89
SEPTEMBER	52113.59	63333.79	52095.50	66354.00	41184.75	55441.79	51237.91	64467.92

PERCENT EXCEEDENCE

MONTH	10		20		80		90	
	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA
JULY	39154.40	75049.80	37061.50	51461.20	13955.10	24045.80	13090.50	19360.40
AUGUST	54381.80	80459.00	41265.10	78782.60	36482.80	40882.60	35538.90	36467.00
SEPTEMBER	71521.00	79156.40	65363.80	75356.10	37322.90	51717.30	36896.70	39937.20

MONTH	CHANGE IN INDEX - A	CHANGE IN INDEX - B	CHANGE IN AVERAGE	CHANGE IN MEDIAN
JULY	64.49	45.59	50.37	36.24
AUGUST	31.42	55.69	47.65	67.96
SEPTEMBER	34.62	25.82	21.53	27.37

EXPRESSED AS PERCENT OF VALUE FOR FIRST DATA SET

* Index A is the average of the interval between the 50 and 90 percent duration.
Index B is the average of the interval between the 10 and 90 percent duration.

Table 12. Summary statistics of actual (1930-1987) and proposed mean monthly habitat (i.e. weighted-usable-area (WUA)), in square feet per 1000 feet, in the 15-mile reach during July, August and September.

SUMMARY STATISTICS

MONTH	AVERAGE		MEDIAN		INDEX - A		INDEX - B	
	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA
JULY	40357.60	76142.02	37599.00	76142.00	30447.21	76141.99	38845.25	76141.99
AUGUST	60511.67	76142.02	64679.00	76142.00	48865.34	76141.99	61212.89	76141.99
SEPTEMBER	63333.79	76142.02	66354.00	76142.00	55441.79	76141.99	64467.92	76141.99

PERCENT EXCEEDENCE

MONTH	10		20		80		90	
	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA
JULY	75049.80	76142.00	51461.20	76142.00	24045.80	76142.00	19360.40	76142.00
AUGUST	80459.00	76142.00	78782.60	76142.00	40882.60	76142.00	36467.00	76142.00
SEPTEMBER	79156.40	76142.00	75356.10	76142.00	51717.30	76142.00	39937.20	76142.00

MONTH	CHANGE IN INDEX - A	CHANGE IN INDEX - B	CHANGE IN AVERAGE	CHANGE IN MEDIAN
JULY	150.08	96.01	88.67	102.51
AUGUST	55.82	24.39	25.83	17.72
SEPTEMBER	37.34	18.11	20.22	14.75

EXPRESSED AS PERCENT OF VALUE FOR FIRST DATA SET

Index A is the average of the interval between the 50 and 90 percent duration.
* Index B is the average of the interval between the 10 and 90 percent duration.

Table 13. Summary statistics of virgin (1951-1982) and actual (1930-1987) mean monthly habitat (i.e. weighted-usable-area, in square feet per 1000 feet, in the 15-mile reach during October through April.

SUMMARY STATISTICS

MONTH	AVERAGE		MEDIAN		INDEX - A		INDEX - B	
	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA
OCTOBER	8750.84	17269.72	7685.00	17513.00	6612.44	13882.62	8420.42	17661.51
NOVEMBER	8955.59	8115.68	9345.50	7386.00	7304.29	6447.71	8878.53	7786.75
DECEMBER	11275.62	9414.19	11227.00	9220.00	10041.09	7237.35	11316.01	9116.88
JANUARY	12670.66	10570.53	13077.50	10514.00	11420.35	8572.19	12751.55	10468.21
FEBRUARY	12844.53	10536.07	13231.50	10552.00	11791.89	8596.40	12962.68	10470.84
MARCH	11123.44	9538.61	11278.50	9529.00	9570.73	7229.59	11210.87	9301.39
APRIL	6632.44	9746.21	6184.50	8447.00	6128.59	7011.45	6451.66	9266.17

PERCENT EXCEEDENCE

MONTH	10		20		80		90	
	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA	Virgin WUA	Actual WUA
OCTOBER	12749.70	24541.80	12184.90	23038.40	6136.30	11003.70	6100.40	8208.20
NOVEMBER	11920.00	10845.80	11178.40	10056.40	6206.90	6151.50	6163.10	6111.00
DECEMBER	13709.70	14103.60	13248.20	11726.80	9501.00	6204.90	8416.00	6168.40
JANUARY	14851.80	14591.60	14517.50	13507.00	10848.80	7252.60	10173.80	6179.20
FEBRUARY	15374.10	14265.80	14693.70	13088.90	10932.20	6930.10	9503.00	6183.80
MARCH	14058.30	13652.00	13691.60	12638.50	9009.30	6196.70	6972.60	6100.00
APRIL	7821.10	15445.00	7205.50	13157.30	6104.90	6192.80	6098.40	6136.60

MONTH	CHANGE IN INDEX - A	CHANGE IN INDEX - B	CHANGE IN AVERAGE	CHANGE IN MEDIAN
OCTOBER	109.95	109.75	97.35	127.89
NOVEMBER	-11.73	-12.30	-9.38	-20.97
DECEMBER	-27.92	-19.43	-16.51	-17.88
JANUARY	-24.94	-17.91	-16.57	-19.60
FEBRUARY	-27.10	-19.22	-17.97	-20.25
MARCH	-24.46	-17.03	-14.25	-15.51
APRIL	14.41	43.62	46.95	36.58

EXPRESSED AS PERCENT OF VALUE FOR FIRST DATA SET

Table 14. Summary statistics of actual (1930-1987) and proposed mean monthly habitat (i.e. weighted-usable-area (WUA)), in square feet per 1000 feet, in the 15-mile reach during October through April.

SUMMARY STATISTICS

MONTH	AVERAGE		MEDIAN		INDEX - A		INDEX - B	
	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA
OCTOBER	17269.72	25066.98	17513.00	25067.00	13882.62	25066.99	17661.51	25067.01
NOVEMBER	8115.68	25066.98	7386.00	25067.00	6447.71	25066.99	7786.75	25067.01
DECEMBER	9414.19	25066.98	9220.00	25067.00	7237.35	25066.99	9116.88	25067.01
JANUARY	10570.53	25066.98	10514.00	25067.00	8572.19	25066.99	10468.21	25067.01
FEBRUARY	10536.07	25066.98	10552.00	25067.00	8596.40	25066.99	10470.84	25067.01
MARCH	9538.61	25066.98	9529.00	25067.00	7229.59	25066.99	9301.39	25067.01
APRIL	9746.21	25066.98	8447.00	25067.00	7011.45	25066.99	9266.17	25067.01

PERCENT EXCEEDENCE

MONTH	10		20		80		90	
	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA	Actual WUA	Proposed WUA
OCTOBER	24541.80	25067.00	23038.40	25067.00	11003.70	25067.00	8208.20	25067.00
NOVEMBER	10845.80	25067.00	10056.40	25067.00	6151.50	25067.00	6111.00	25067.00
DECEMBER	14103.60	25067.00	11726.80	25067.00	6204.90	25067.00	6168.40	25067.00
JANUARY	14591.60	25067.00	13507.00	25067.00	7252.60	25067.00	6179.20	25067.00
FEBRUARY	14265.80	25067.00	13088.90	25067.00	6930.10	25067.00	6183.80	25067.00
MARCH	13652.00	25067.00	12638.50	25067.00	6196.70	25067.00	6100.00	25067.00
APRIL	15445.00	25067.00	13157.30	25067.00	6192.80	25067.00	6136.60	25067.00

MONTH	CHANGE IN INDEX - A	CHANGE IN INDEX - B	CHANGE IN AVERAGE	CHANGE IN MEDIAN
OCTOBER	80.56	41.93	45.15	43.13
NOVEMBER	288.77	221.92	208.87	239.39
DECEMBER	246.36	174.95	166.27	171.88
JANUARY	192.42	139.46	137.14	138.42
FEBRUARY	191.60	139.40	137.92	137.56
MARCH	246.73	169.50	162.79	163.06
APRIL	257.52	170.52	157.20	196.76

EXPRESSED AS PERCENT OF VALUE FOR FIRST DATA SET

Table 15. Virgin (1952-1982) mean monthly flows, in cfs, in the Colorado River at Palisade, river mile 181.4-182.0.

YEAR	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC
1951	1231.00	1339.00	1431.00	2305.00	10123.00	18339.00	9884.00	3769.00	1736.00	1891.00	1673.00	1543.00
1952	1499.00	1389.00	1562.00	5078.00	17382.00	27911.00	8339.00	4992.00	2722.00	1767.00	1677.00	1450.00
1953	1517.00	1289.00	1483.00	2038.00	6843.00	19006.00	5718.00	3353.00	1419.00	1413.00	1655.00	1356.00
1954	1335.00	1294.00	1237.00	2465.00	6555.00	4965.00	2657.00	1427.00	1520.00	2122.00	1658.00	1344.00
1955	1187.00	1206.00	1385.00	2851.00	8074.00	10268.00	4547.00	3007.00	1275.00	1222.00	1490.00	1361.00
1956	1192.00	1116.00	1479.00	3280.00	14510.00	14674.00	3364.00	1927.00	871.00	1123.00	1346.00	1190.00
1957	1252.00	1334.00	1314.00	2362.00	10641.00	29184.00	21225.00	6321.00	2766.00	2270.00	2008.00	1725.00
1958	1255.00	1516.00	1709.00	2594.00	16695.00	16749.00	3568.00	1810.00	1470.00	1370.00	1477.00	1286.00
1959	1240.00	1282.00	1291.00	2051.00	7580.00	16921.00	4613.00	2434.00	1569.00	2515.00	2004.00	1449.00
1960	1227.00	1305.00	1988.00	4777.00	8762.00	16553.00	4796.00	2055.00	1390.00	1535.00	1537.00	1320.00
1961	1127.00	1191.00	1268.00	1722.00	7544.00	11350.00	3068.00	2223.00	3701.00	3979.00	2277.00	1611.00
1962	1401.00	1843.00	1636.00	8737.00	16658.00	19973.00	10746.00	3324.00	1784.00	1831.00	1833.00	1486.00
1963	1335.00	1408.00	1502.00	2500.00	7515.00	6580.00	2333.00	2465.00	1740.00	1364.00	1426.00	1154.00
1964	948.00	938.00	1039.00	1905.00	9265.00	11491.00	5161.00	2898.00	1593.00	1367.00	1524.00	1405.00
1965	1401.00	1319.00	1281.00	2809.00	10234.00	22613.00	13587.00	5329.00	3098.00	2777.00	2038.00	1823.00
1966	1447.00	1287.00	1707.00	2673.00	8383.00	7006.00	2974.00	1871.00	1266.00	1631.00	1514.00	1328.00
1967	1278.00	1179.00	1608.00	2540.00	7246.00	14076.00	6825.00	2330.00	2036.00	1803.00	1636.00	1488.00
1968	1281.00	1338.00	1359.00	1956.00	6541.00	19712.00	6017.00	4308.00	2011.00	1884.00	1727.00	1496.00
1969	1515.00	1323.00	1331.00	4552.00	13189.00	12798.00	7500.00	2657.00	2078.00	2556.00	1999.00	1637.00
1970	1517.00	1402.00	1390.00	2231.00	17058.00	19512.00	7764.00	2992.00	3104.00	2776.00	2235.00	1917.00
1971	1845.00	1501.00	1910.00	4890.00	9624.00	21228.00	8980.00	3166.00	2720.00	2296.00	1909.00	1772.00
1972	1715.00	1717.00	2159.00	3097.00	8806.00	17445.00	4395.00	2270.00	2567.00	2681.00	2177.00	1771.00
1973	1540.00	1510.00	1689.00	2021.00	11782.00	20060.00	11246.00	3751.00	2145.00	1979.00	1902.00	1564.00
1974	1662.00	1584.00	1946.00	3048.00	15474.00	15911.00	5953.00	2702.00	1592.00	1863.00	1808.00	1551.00
1975	1473.00	1492.00	1704.00	2408.00	7890.00	18311.00	13324.00	3547.00	2097.00	1923.00	1883.00	1653.00
1976	1558.00	1641.00	1792.00	2858.00	8804.00	11864.00	5285.00	2828.00	2080.00	2125.00	1662.00	1484.00
1977	1400.00	1372.00	1258.00	2166.00	4449.00	5841.00	1844.00	1497.00	1257.00	1569.00	1433.00	1414.00
1978	1205.00	1110.00	1413.00	3413.00	9727.00	23720.00	9274.00	2650.00	1522.00	1385.00	1406.00	1289.00
1979	1131.00	1186.00	1509.00	3097.00	13347.00	22425.00	10551.00	3491.00	1808.00	1660.00	1804.00	1645.00
1980	1558.00	1700.00	1717.00	3014.00	12327.00	21344.00	7193.00	2413.00	1748.00	1584.00	1557.00	1401.00
1981	1185.00	1103.00	1148.00	2151.00	4683.00	9610.00	3311.00	1449.00	1587.00	1767.00	1478.00	1299.00
1982	1346.00	1150.00	1413.00	2354.00	8995.00	18611.00	10624.00	4152.00	3132.00	2717.00	2246.00	1712.00

Table 16. Actual (1930-1987) mean monthly flows in cfs, in the Colorado River at Palisade, river mile 181.4-182.0

YEAR	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC
1930	1546.00	1562.00	1632.00	1919.00	7747.00	11963.00	3540.00	973.00	599.00	949.00	1870.00	1704.00
1931	1190.00	1228.00	1294.00	1057.00	3986.00	3439.00	799.00	210.00	84.00	471.00	1517.00	1232.00
1932	1546.00	1562.00	1632.00	1919.00	7747.00	11953.00	3540.00	967.00	599.00	949.00	1870.00	1704.00
1933	1331.00	1368.00	1406.00	1438.00	5243.00	7609.00	1901.00	451.00	320.00	648.00	1651.00	1471.00
1934	1450.00	1408.00	1489.00	2368.00	8930.00	2767.00	37.00	34.00	31.00	27.00	1079.00	1037.00
1935	1039.00	990.00	1032.00	1102.00	4690.00	19911.00	6162.00	1009.00	555.00	697.00	1634.00	1243.00
1936	1252.00	1238.00	1261.00	4786.00	18128.00	14373.00	4073.00	2274.00	641.00	687.00	1554.00	1287.00
1937	1180.00	1298.00	1479.00	1766.00	11429.00	8526.00	3429.00	532.00	552.00	933.00	1802.00	1549.00
1938	1346.00	1341.00	1957.00	4147.00	13758.00	24082.00	6902.00	1258.00	1812.00	942.00	1836.00	1762.00
1939	1551.00	1395.00	1876.00	2778.00	12769.00	9548.00	1487.00	100.00	311.00	476.00	1349.00	1053.00
1940	1047.00	1134.00	1295.00	1576.00	7949.00	7396.00	1032.00	33.00	321.00	944.00	1502.00	1263.00
1941	1114.00	1262.00	1375.00	1455.00	15573.00	12615.00	3589.00	824.00	705.00	1891.00	2241.00	1808.00
1942	1536.00	1644.00	1713.00	5368.00	12605.00	19919.00	5116.00	741.00	84.00	489.00	1687.00	1437.00
1943	1307.00	1386.00	1477.00	3306.00	7245.00	14358.00	4729.00	1684.00	595.00	749.00	2014.00	1785.00
1944	1245.00	1372.00	1341.00	1127.00	8826.00	14358.00	4718.00	497.00	33.00	549.00	1767.00	1645.00
1945	1327.00	1352.00	1572.00	1126.00	9261.00	12462.00	6625.00	3209.00	590.00	1009.00	2203.00	1969.00
1946	1833.00	1681.00	1666.00	4149.00	6262.00	10217.00	2756.00	566.00	145.00	936.00	1808.00	2011.00
1947	1374.00	1530.00	1788.00	2205.00	12781.00	16202.00	10393.00	2390.00	1012.00	1455.00	2366.00	1979.00
1948	1924.00	1988.00	1928.00	3670.00	14841.00	12904.00	3532.00	1089.00	93.00	699.00	1878.00	1551.00
1949	1662.00	1563.00	1646.00	2706.00	8586.00	17186.00	8172.00	1489.00	663.00	991.00	1892.00	1688.00
1950	1554.00	1660.00	1941.00	2786.00	5831.00	12064.00	2893.00	498.00	471.00	489.00	1697.00	1626.00
1952	1584.00	1487.00	1839.00	4655.00	15440.00	21489.00	5773.00	2985.00	1430.00	862.00	1892.00	1675.00
1953	1652.00	1467.00	1656.00	1425.00	4589.00	13723.00	3215.00	1608.00	243.00	527.00	1696.00	1528.00
1954	1576.00	1503.00	1526.00	1504.00	3680.00	1857.00	767.00	178.00	280.00	918.00	1661.00	1356.00
1955	1220.00	1212.00	1411.00	1524.00	5355.00	6152.00	1878.00	1009.00	218.00	334.00	1587.00	1485.00
1956	1327.00	1327.00	1699.00	2249.00	10041.00	9194.00	1219.00	316.00	36.00	351.00	1390.00	1192.00
1957	1307.00	1417.00	1330.00	1701.00	8661.00	23868.00	16299.00	4028.00	1248.00	1176.00	2165.00	1756.00
1958	1569.00	1815.00	2061.00	2208.00	13672.00	12496.00	1561.00	244.00	330.00	524.00	1603.00	1460.00
1959	1587.00	1613.00	1352.00	1133.00	5214.00	9972.00	1883.00	601.00	304.00	1097.00	1966.00	1636.00
1960	1639.00	1604.00	2208.00	3378.00	6011.00	9804.00	1922.00	378.00	253.00	607.00	1671.00	1664.00

Table 16. CONTINUED

YEAR	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC
1961	1605.00	1548.00	1373.00	814.00	4534.00	5601.00	658.00	352.00	1559.00	2211.00	2244.00	2010.00
1962	1890.00	2521.00	2631.00	8084.00	13599.00	13862.00	7374.00	1481.00	626.00	1713.00	2516.00	1942.00
1963	1630.00	1628.00	1635.00	1229.00	3799.00	2547.00	238.00	368.00	455.00	456.00	1530.00	1166.00
1964	942.00	969.00	1055.00	921.00	5589.00	6349.00	2059.00	978.00	547.00	604.00	1583.00	1555.00
1965	1527.00	1428.00	1401.00	1923.00	6695.00	14431.00	8427.00	2961.00	1588.00	1695.00	2404.00	2337.00
1966	1908.00	1831.00	2219.00	1592.00	4903.00	3127.00	1000.00	423.00	304.00	664.00	1582.00	1454.00
1967	1430.00	1368.00	1726.00	1377.00	3973.00	7641.00	3145.00	694.00	674.00	754.00	1775.00	1673.00
1968	1504.00	1574.00	1547.00	1344.00	4181.00	11500.00	2656.00	2201.00	677.00	1007.00	1950.00	1734.00
1969	1781.00	1590.00	1586.00	3420.00	7998.00	7253.00	4292.00	973.00	817.00	1798.00	2266.00	2039.00
1970	1779.00	1784.00	1925.00	1740.00	12947.00	12858.00	4386.00	1214.00	1756.00	1736.00	2661.00	2353.00
1971	2316.00	2058.00	2489.00	4245.00	7416.00	13696.00	5807.00	1388.00	1489.00	1385.00	2378.00	2182.00
1972	2145.00	2119.00	2497.00	2066.00	5040.00	9643.00	2003.00	778.00	1094.00	1580.00	2604.00	2127.00
1973	1947.00	1919.00	2049.00	1227.00	9036.00	13570.00	7775.00	1884.00	996.00	1342.00	2427.00	2129.00
1974	2051.00	1988.00	2527.00	2328.00	10379.00	9520.00	3106.00	1078.00	711.00	1092.00	2160.00	1922.00
1975	1789.00	1788.00	2024.00	1756.00	5328.00	11508.00	7728.00	1722.00	961.00	1196.00	2271.00	2015.00
1976	1921.00	2040.00	2266.00	1842.00	5255.00	6093.00	1903.00	882.00	850.00	1133.00	1962.00	1821.00
1977	1724.00	1550.00	1261.00	896.00	1002.00	1343.00	250.00	214.00	272.00	428.00	1350.00	1413.00
1978	1291.00	1318.00	1544.00	2074.00	5838.00	12927.00	4293.00	658.00	408.00	649.00	1878.00	1520.00
1979	1345.00	1518.00	1818.00	2141.00	8927.00	14169.00	6985.00	1393.00	657.00	1051.00	2158.00	2021.00
1980	1831.00	1981.00	2024.00	2414.00	9488.00	13942.00	3852.00	836.00	657.00	765.00	1827.00	1685.00
1981	1400.00	1197.00	1162.00	1011.00	1853.00	3899.00	781.00	244.00	453.00	780.00	1624.00	1447.00
1982	1552.00	1392.00	1569.00	1474.00	5809.00	10489.00	5221.00	1898.00	1639.00	1772.00	2550.00	1963.00
1983	1806.00	1806.00	1942.00	1489.00	8479.00	25252.00	15458.00	5295.00	1446.00	1496.00	2629.00	2476.00
1984	2303.00	2269.00	2652.00	3243.00	19455.00	21679.00	13912.00	5068.00	2859.00	2518.00	3350.00	3086.00
1985	2693.00	2466.00	2932.00	5504.00	15506.00	15937.00	5618.00	1961.00	1028.00	1974.00	3024.00	2501.00
1986	2464.00	2772.00	3387.00	6286.00	12627.00	15749.00	6908.00	2003.00	1780.00	2204.00	3198.00	2625.00
1987	2258.00	2253.00	2513.00	3344.00	7654.00	6489.00	1530.00	973.00	634.00	627.00	2233.00	1879.00

Table 17. Summary statistics of virgin (1951-1983) and actual (1930-1987) mean monthly flows, in cfs, in the Colorado River at Palisade river mile 181.4-182.0.

SUMMARY STATISTICS

MONTH	AVERAGE		MEDIAN		INDEX - A		INDEX - B	
	Virgin flow	Actual flow	Virgin flow	Actual flow	Virgin flow	Actual flow	Virgin flow	Actual flow
JANUARY	1368.84	1607.84	1340.50	1554.00	1247.26	1396.82	1360.49	1578.02
FEBRUARY	1355.12	1615.47	1328.50	1550.00	1242.57	1397.64	1343.91	1578.01
MARCH	1520.56	1783.09	1481.00	1656.00	1356.32	1483.95	1504.22	1734.02
APRIL	2998.22	2426.58	2567.00	1919.00	2280.60	1493.58	2746.00	2183.46
MAY	10209.56	8494.04	9130.00	7747.00	7946.81	5767.30	9970.96	8170.83
JUNE	16439.09	11640.02	17183.00	11963.00	13118.45	8480.70	16482.69	11383.99
JULY	7083.31	4338.72	5985.00	3540.00	4386.87	2145.30	6598.88	3829.13
AUGUST	2981.50	1264.82	2765.00	973.00	2300.52	586.54	2858.83	1068.93
SEPTEMBER	1981.37	727.98	1766.00	599.00	1555.48	388.26	1921.81	662.36
OCTOBER	1960.78	1017.65	1847.00	936.00	1594.72	671.32	1901.94	965.44
NOVEMBER	1749.97	1982.14	1675.00	1878.00	1563.09	1697.76	1732.16	1942.24
DECEMBER	1497.62	1747.91	1485.00	1688.00	1378.31	1517.39	1491.01	1719.44

PERCENT EXCEEDENCE

MONTH	10		20		80		90	
	Virgin flow	Actual flow	Virgin flow	Actual flow	Virgin flow	Actual flow	Virgin flow	Actual flow
JANUARY	1589.20	2126.20	1519.30	1891.80	1203.70	1307.00	1168.80	1196.00
FEBRUARY	1658.70	2106.80	1510.60	1925.20	1185.30	1339.60	1114.20	1230.00
MARCH	1920.80	2509.80	1709.80	2075.70	1290.00	1374.80	1251.70	1294.20
APRIL	4810.90	4573.00	3293.30	3382.20	2141.00	1332.50	2001.50	1106.80
JULY	11869.40	8092.60	10558.30	6902.60	3358.70	1525.70	2878.90	784.60
AUGUST	4513.20	2846.80	3752.80	1904.30	2042.20	377.00	1716.10	220.00
SEPTEMBER	3099.80	1582.20	2720.20	1109.40	1464.90	279.20	1272.30	103.40
OCTOBER	2734.70	1792.80	2519.10	1504.40	1410.20	546.80	1366.10	472.00
NOVEMBER	2194.40	2593.20	2004.40	2367.20	1488.80	1601.40	1430.90	1519.60
DECEMBER	1771.30	2306.00	1658.90	2015.60	1327.20	1446.00	1288.10	1247.00

MONTH	CHANGE IN INDEX - A	CHANGE IN INDEX - B	CHANGE IN AVERAGE	CHANGE IN MEDIAN
JANUARY	11.99	15.99	17.46	15.93
FEBRUARY	12.48	17.42	19.21	16.67
MARCH	9.41	15.28	17.27	11.82
APRIL	-34.51	-20.49	-19.07	-25.24
JULY	-51.10	-41.97	-38.75	-40.85
AUGUST	-74.50	-62.61	-57.58	-64.81
SEPTEMBER	-75.04	-65.53	-63.26	-66.08
OCTOBER	-57.90	-49.24	-48.10	-49.32
NOVEMBER	8.62	12.13	13.27	12.12
DECEMBER	10.09	15.32	16.71	13.67

EXPRESSED AS PERCENT OF VALUE FOR FIRST DATA SET

Table 18. Summary statistics of actual (1930-1987) and proposed mean monthly flows, in cfs, in the Colorado River at Palisade river mile 181.4-182.0.

SUMMARY STATISTICS

MONTH	AVERAGE		MEDIAN		INDEX - A		INDEX - B	
	Actual flow	Proposed flow	Actual flow	Proposed flow	Actual flow	Proposed flow	Actual flow	Proposed flow
JANUARY	1607.84	450.00	1554.00	450.00	1396.82	450.00	1578.02	450.00
FEBRUARY	1615.47	450.00	1550.00	450.00	1397.64	450.00	1578.01	450.00
MARCH	1783.09	450.00	1656.00	450.00	1483.95	450.00	1734.02	450.00
APRIL	2426.58	450.00	1919.00	450.00	1493.58	450.00	2183.46	450.00
MAY	8494.04	8494.04	7747.00	7747.00	5767.30	5767.30	8170.83	8170.83
JUNE	11640.02	11640.02	11963.00	11963.00	8480.70	8480.70	11383.99	11383.99
JULY	4338.72	700.00	3540.00	700.00	2145.30	700.00	3829.13	700.00
AUGUST	1264.82	700.00	973.00	700.00	586.54	700.00	1068.93	700.00
SEPTEMBER	727.98	700.00	599.00	700.00	388.26	700.00	662.36	700.00
OCTOBER	1017.65	450.00	936.00	450.00	671.32	450.00	965.44	450.00
NOVEMBER	1982.14	450.00	1878.00	450.00	1697.76	450.00	1942.24	450.00
DECEMBER	1747.91	450.00	1688.00	450.00	1517.39	450.00	1719.44	450.00

PERCENT EXCEEDENCE

MONTH	10		20		80		90	
	Actual flow	Proposed flow	Actual flow	Proposed flow	Actual flow	Proposed flow	Actual flow	Proposed flow
JANUARY	2126.20	450.00	1891.80	450.00	1307.00	450.00	1196.00	450.00
FEBRUARY	2106.80	450.00	1925.20	450.00	1339.60	450.00	1230.00	450.00
MARCH	2509.80	450.00	2075.70	450.00	1374.80	450.00	1294.20	450.00
APRIL	4573.00	450.00	3382.20	450.00	1332.50	450.00	1106.80	450.00
MAY	14624.40	14624.40	12770.20	12770.20	5026.30	5026.30	4025.00	4025.00
JUNE	19917.40	19917.40	14562.80	14562.80	6475.00	6475.00	3531.00	3531.00
JULY	8092.60	700.00	6902.60	700.00	1525.70	700.00	784.60	700.00
AUGUST	2846.80	700.00	1904.30	700.00	377.00	700.00	220.00	700.00
SEPTEMBER	1582.20	700.00	1109.40	700.00	279.20	700.00	103.40	700.00
OCTOBER	1792.80	450.00	1504.40	450.00	546.80	450.00	472.00	450.00
NOVEMBER	2593.20	450.00	2367.20	450.00	1601.40	450.00	1519.60	450.00
DECEMBER	2306.00	450.00	2015.60	450.00	1446.00	450.00	1247.00	450.00

MONTH	CHANGE IN INDEX - A	CHANGE IN INDEX - B	CHANGE IN AVERAGE	CHANGE IN MEDIAN
JANUARY	-67.78	-71.48	-72.01	-71.04
FEBRUARY	-67.80	-71.48	-72.14	-70.97
MARCH	-69.68	-74.05	-74.76	-72.83
APRIL	-69.87	-79.39	-81.46	-76.55
MAY	0.00	0.00	0.00	0.00
JUNE	0.00	0.00	0.00	0.00
JULY	-67.37	-81.72	-83.87	-80.23
AUGUST	19.34	-34.51	-44.66	-28.06
SEPTEMBER	80.29	5.68	-3.84	16.86
OCTOBER	-32.97	-53.39	-55.78	-51.92
NOVEMBER	-73.49	-76.83	-77.30	-76.04
DECEMBER	-70.34	-73.83	-74.25	-73.34

EXPRESSED AS PERCENT OF VALUE FOR FIRST DATA SET

Literature Cited

BIO/WEST Incorporated. 1987. PCSIM Physical Habitat Simulation System for IBM-Compatible Micro Computers. BIO/WEST Incorporated, Logan, Utah. Unpublished document.

Bovee, K. D. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. Instream Flow Information Paper 12. U. S. Fish and wildlife Service, FWS/OBS-82/26. 248 pp.

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MAY 17 1988

Memorandum

To: Regional Hydrologist, Division of Water Resources, Region 6

From: Supervisory Hydrologist, Division of Water Resources, Region 6

Subject: Water Storage on the Descending Hydrograph as identified in the draft report on Development of Biologically Defensible Flow Recommendations for the Maintenance and Enhancement of Colorado Squawfish in the "15-Mile" Reach of the Upper Colorado River During July, August and September

At the direction of the Colorado River Recovery Implementation Coordinator in a memorandum dated April 29, 1988, I have made an evaluation of the feasibility and practicality of encouraging water storage on the descending hydrograph.

Reservoirs physically capable of storing water of the magnitude necessary to influence the flow and temperature regimes in the fifteen-mile reach are Green Mountain, Dillon, Ruedi, Granby, and Shadow Mountain. These reservoirs are located high in the basin and store predominantly during peak runoff. Because of their location, high in the basin, they are dependant on a limited drainage area and cannot afford to gamble on filling each year.

Under Colorado water right administration, each reservoir is granted a once yearly fill right. Normal administration is to have the reservoirs located high in the basin fill first, even if they have a low water right priority. Downsteam reservoirs are filled next, and if there is not sufficient water to fill downstream reservoirs with senior rights, water is called down from upsteam reservoirs with junior rights. This allows the State to optimize reservoir storage under most water year conditions.

Having established how reservoirs are administered in Colorado, we can now look at how water storage on the descending hydrograph would be affected by this administration during dry, average, and wet years. We will also try to hypothesize how the administration and operation of reservoirs might be modified to accommodate descending hydrograph storage.

DRY YEARS

During dry years, there is not much opportunity for changes in storage patterns. The peak flows typically come earlier in the year and are reduced in magnitude and duration. This is generally of little concern because data collected to date indicates that optimal temperature conditions are present in dry years.

WET YEARS

During wet years, most reservoirs are operated on two criteria, to fill, and to prevent spills which damage the spillway. This type of operation moves water storage to the descending hydrograph as reservoir operators work toward filling later in the year. Since this type of operation is currently in practice, there is little room for additional storage in the descending limb without additional storage facilities above the fifteen-mile reach.

AVERAGE YEARS

Average years have the most potential for moving depletions to the descending hydrograph, but they also have the most associated water allocation problems. The problems are with convincing senior right holders to delay storage based upon runnoff forecasts; and if they do delay, they will be precluding other junior water right holders from storing. The junior water right holders would be adamantly opposed to such a plan because there is a significantly higher probability that they would not get their full allocation. With most of the senior storage high in the basin, senior right holders would be reluctant to let juniors downstream fill first because it is difficult to effect an exchange mechanism on a year-to-year basis. Prediction techniques would also have to be significantly improved to accommodate a change in present storage practices.

/S/ GEORGE R. SMITH

cc: ARD-FWE (John Hamill) (60153)

Appendix E

Table 1. Persons who commented on drafts of this report.

Name	Affiliation	Date if responded with letter
Jim Bennett and Tom Nesler	CDOW	25 April 1988
Bob Burdick	USFWS	
John Hamill	USFWS	
Denise Hann	USFWS	
Bob Jacobsen and Bill Martin	USFWS	
Alan Mauzy	Wyoming Water Dev. Com.	19 April 1988 7 Feb 1989
Lee Mills	USFWS	
Pat Nelson	USFWS	2 May 1988
Tom Pitts	Water Users	29 April 1988 6 July 1988 8 Mar 1989
Keith Rose	USFWS	
John Shields	Wyoming State Eng. Office	22 April 1988 8 July 1988 31 Jan 1989
Clair Stalnaker	USFWS	
Robert Wigington	The Nature Conservancy	28 Feb 1989
Raymond Willms	USBR	1 Mar 1989