EVALUATION OF A METHODOLOGY FOR RECOMMENDING INSTREAM FLOWS FOR FISHES

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EVALUATION OF A METHODOLOGY FOR RECOMMENDING
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PREFACE

This research was funded by the United States Fish and Wildlife Service, Office of Biological Services, as a part of Phase II of their Stream Evaluation Project. Phase II dealt with the quantification of instream flow needs and an evaluation of methodologies for streams of western United States. The approach taken in this particular study was to make instream flow recommendations for fishes of a warm-water stream, Glover Creek, in southeast Oklahoma, and to test the validity of some critical assumptions of the methodology (the incremental method) employed.

I thank Dr. O. Eugene Maughan, who served as chairman of my graduate committee, for his guidance and encouragement during this research and for his prompt and careful reviews of earlier drafts of the dissertation. Sincere thanks are also offered to Dr. Michael D. Clady for serving on my graduate committee and for always being helpful in all phases of this research, from the tedious field work to the final editorial reviews of the manuscript. I also thank Dr. Ronald W. McNew, Dr. Rudolph J. Miller, and Dr. Robert J. Mulholland, who served on my graduate committee, for their technical assistance, constructive criticisms, and editorial reviews of the manuscript.

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To my wife, Martha, I express my sincerest gratitude for her encouragement, support, and understanding throughout my graduate studies, for her help with field work, and for typing the final copy of this dissertation.

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CHAPTER I

INTRODUCTION

Few streams in the United States are uninfluenced by man's activities. Natural flows have been modified by irrigation diversions, changing land-use practices, construction of flood control and water supply reservoirs, and increased demands for generation of electricity using hydro-electric, fossil fuel, and nuclear power. Native stream fishes, which are adapted to natural, unregulated flow regimes and have preferences for a rather limited range of velocities, depths, substrates, or temperatures, have been impacted by stream flow modifications that alter these variables. Coupled with the increasing modification of streams is an increasing demand for recreational fishing and habitat preservation for native fishes. Methodologies must be developed that will enable fishery biologists to recommend flow regimes that will maintain or enhance this valuable natural resource and its fisheries.

Reservation of a minimum instream flow is dependent on a legal right to water for fish and wildlife. Currently surface water rights may be legally obtained only for out-of-stream beneficial uses under appropriative water doctrine and the question of legal right of water for instream uses, such as fisheries, has only recently been considered (Dewsnup and Jensen 1977; Dewsnup et al. 1977; Doerksen 1977). Future conflicts over reserving instream flows for fisheries may require court action for resolution. Therefore, methodologies used for making instream flow recommendations must be based on sound ecological theory and be thoroughly field tested to establish legal credibility. Furthermore, from a practical standpoint, the methodology must be designed so that it can be implemented easily by the field biologist and will provide relevant information for negotiating water allocations and mitigation.

There are two general categories of methodologies for determination of instream flow requirements. The first category includes reconnaissance level methodologies which rely on existing records (i. e., United States Geological Survey gaging records) and require little or no field work. The second category includes the intensive on-site field approaches. The latter procedures usually evaluate the ecological requirements of indicator species and determine to what extent these requirements are met at various stream flow levels. A plethora of methods of this type have resulted in confusion over which methodology is best (Orsborn and Allman 1976; Stalnaker and Arnette 1976). In 1976, the United States Fish and Wildlife Service established the Instream Flow Group (IFG) and charged them to evaluate these different types of methodologies and develop a comprehensive state-of-the-art method for determining instream flows. The result was the IFG incremental method. This method consists of a system of deterministic and statistical models for habitat analysis, complete with computer software (PHABSIM = Physical Habitat Simulation System) and interpretive techniques. To date, the incremental method has been applied in 339 river reaches by 71 agencies throughout the United States (Cooperative Instream Flow Service Group 1979). However, no studies have been designed with the explicit purpose of testing the validity of the method in a warm-water stream and the scarcity of quantitative data on habitat preferences of warm-water stream fishes limits its use in these habitats.

Therefore, the objectives of this research were (1) to develop habitat suitability criteria for fishes of Glover Creek; (2) to test some of the assumptions inherent in the IFG incremental method; and (3) to make monthly instream flow recommendations for Glover Creek below the proposed Lukfata Lake Dam for maintenance of the existing smallmouth bass (*Micropterus dolomieui*) fishery.

CHAPTER II

INCREMENTAL METHOD

Numerous methods have been proposed by various state and federal agencies for making instream flow recommendations (Orsborn and Allman 1976; Stalnaker and Arnette 1976). Although some of the approaches are quite different, the problems they address are the same, viz., what is the stream flow necessary for instream uses, and what are the effects on fish habitat of alteration of the flow regime. The incremental method was developed by the Cooperative Instream Flow Service Group as a synthesis and refinement of the concepts previously used for making instream flow recommendations (Collings et al. 1970; Waters 1976; Bovee et al. 1977).

The need for a method that could be applied in a wide variety of situations made it essential to limit the variables considered to those which would be common to all instream flow investigations, namely velocity, depth, substrate, and temperature. The effects of these variables on the distribution and abundance of stream organisms and their relations to stream flow have been emphasized by Needham and Usinger (1956), Minckley (1963), Hynes (1970), Fraser (1972), Ward (1976), Gorman and Karr (1978), and Ward and Stanford (1979). The incremental method utilizes a hydraulic simulation technique to predict depths, velocities, and substrates within a stream reach at different stream flows. From this simulation, and knowledge of habitat preferences, the amount of usable (or suitable) habitat for a given fish species can be determined. Instream flows can then be recommended based on the effect on fish habitat of incremental changes in stream flow.

To use the incremental method the preferred habitat of all life stages of species of interest must be defined in relation to depth, velocity, substrate, and sometimes temperature. Bovee and Cochnauer (1977) suggest that a frequency analysis can be used to construct the habitat suitability curves. Data on the measurements of depth, velocity, and substrate at individual capture locations are arranged into frequency distributions for each habitat variable and an optimum range, defined as the interval having the greatest frequency of captures, is given a weighting factor of one. Weighting factors for the suitability for use in all other intervals are calculated by dividing the frequency of observations in each interval by the mean frequency within the optimum range.

Flow recommendations are based on the amount of usable habitat in relation to discharge. Several investigators had previously used planimetric mapping techniques to measure the amount of usable habitat (Collings et al. 1970; Bovee 1975), but this procedure is very time consuming and requires field measurements at each flow of interest. The amount of time needed to measure the amount of usable habitat in a stream reach can be reduced by representing the stream reach as shown in Figure 1 and using a computer program to determine the amount of area having particular combinations of depth, velocity, and substrate types at each flow. Depth, velocity, and substrate type within each interval along the transects are extended half way to the nearest upstream and downstream transects (Figure 1). Surface area of each segment is then equal to the length times the width. Hence, the amount of surface area having

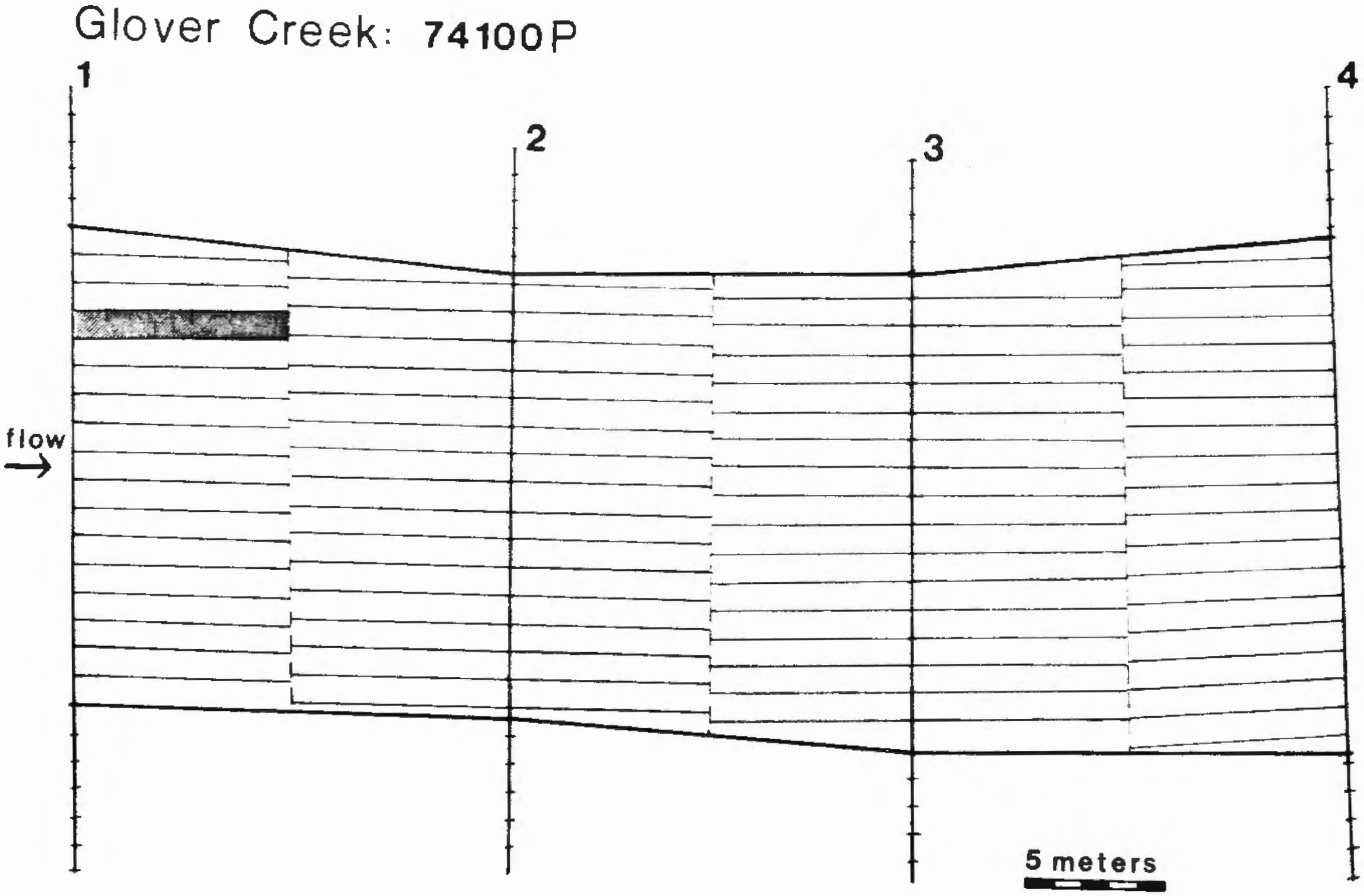

Figure 1. Conceptual view of a stream reach as it is represented in a computer program.

a particular combination of depth, velocity, and substrate can easily be computed. To eliminate the need for field measurements at each flow of interest, one of two hydraulic simulation techniques can be used for estimating the depths and velocities within the stream reach in relation to discharge: the Water Surface Profile (WSP) program (United States Bureau of Reclamation 1968), and the IFG4 program (Main 1978a). The WSP program, which utilizes the Manning equation (Chow 1959) to predict velocities based on one set of field measurements, has been used successfully by Cochnauer (1976), Dooley (1976), Elser (1976), and White (1976). However, the WSP program has limited accuracy and is difficult to calibrate. The second technique, IFG4 (Main 1978a), is more accurate but requires at least two sets of field measurements (Bovee and Milhous 1978).

Details on the field techniques and data requirements of the IFG4 program are presented by Bovee and Milhous (1978) and Main (1978a). In general, data are obtained by taking stream bed elevations along transects at fixed intervals with a level and level rod to obtain a cross-sectional profile (Figure 2). Elevations are measured relative to a benchmark established near the study area and on a permanent object, e.g., tree root, bridge. These objects are given an arbitrary reference elevation. Depth, velocity, and substrate are then measured at the same intervals along transects at two or more flows encompassing the flows of interest. Water surface elevations (stage) relative to the benchmark are also measured at each transect and at each flow. These data are used as input to the IFG4 program (Main 1978a), which establishes linear regression equations for the $\log_{10}$ (stage) versus $\log_{10}$ (discharge) relations for each transect (Figure 3) and $\log_{10}$ (velocity) versus $\log_{10}$ (discharge) relations for each segment (Figure 4). These relationships

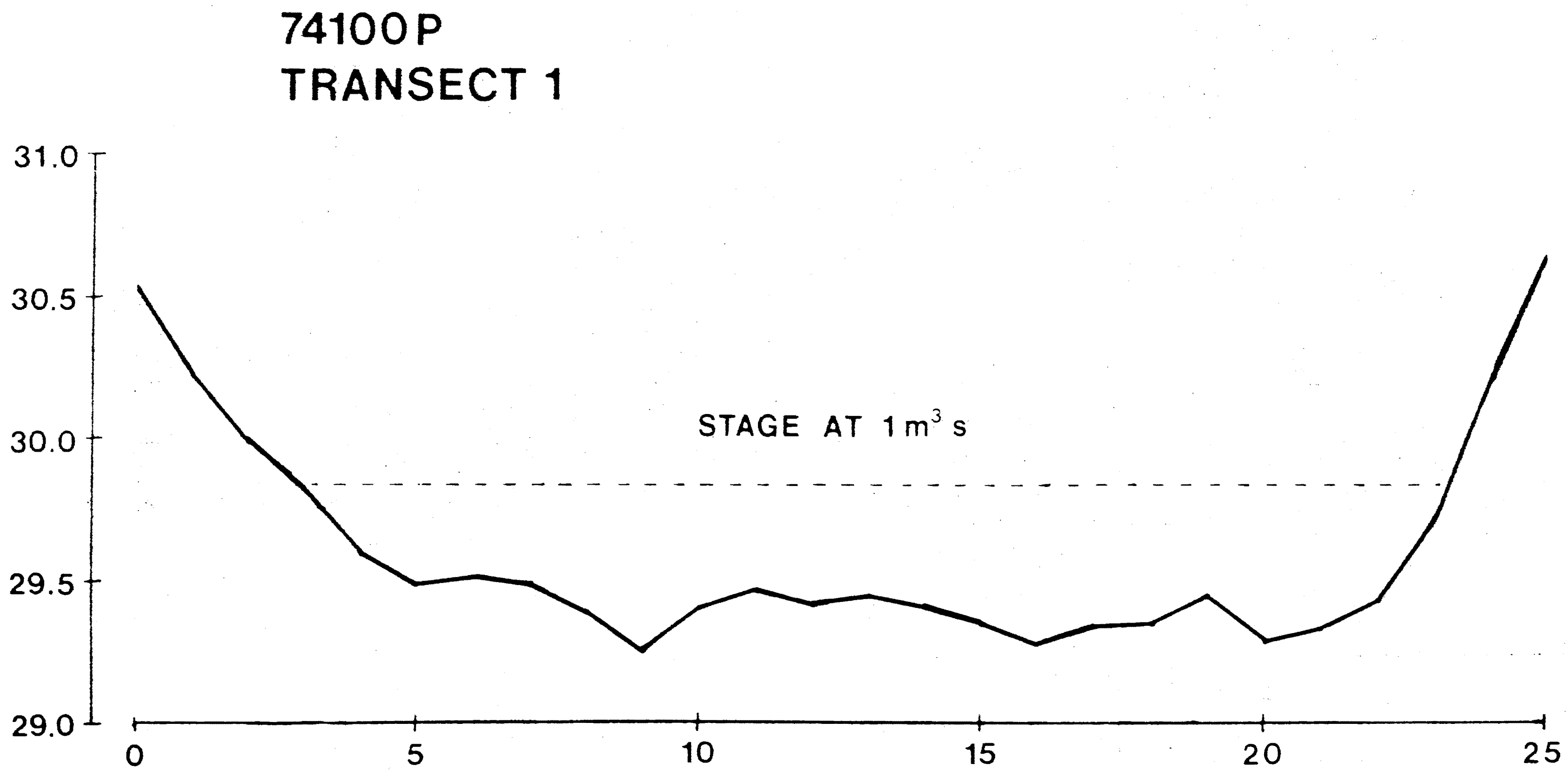

Figure 2. Cross-sectional profile at a transect. Scale in meters is exaggerated.

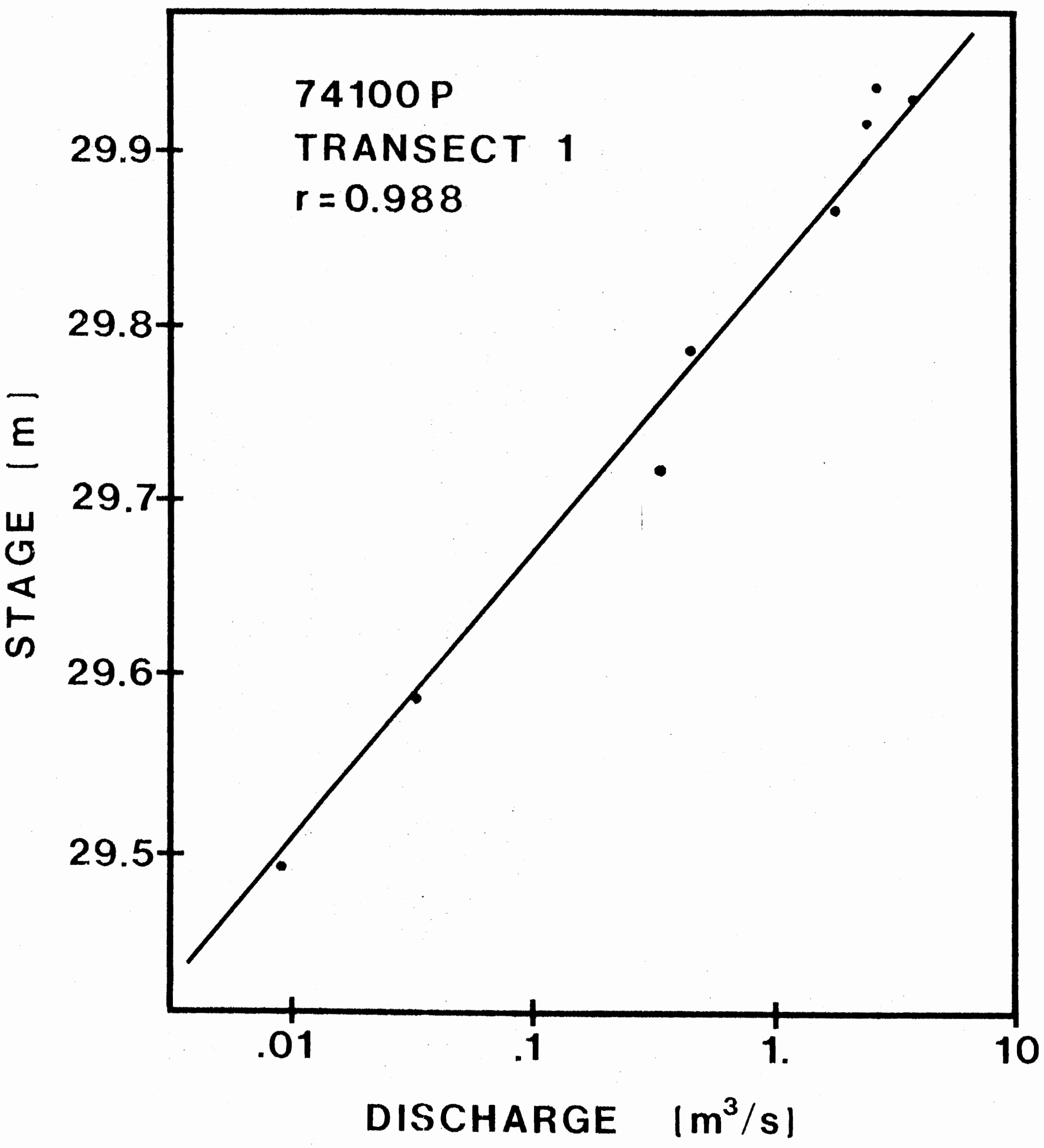

Figure 3. Stage-discharge relationship for a transect.

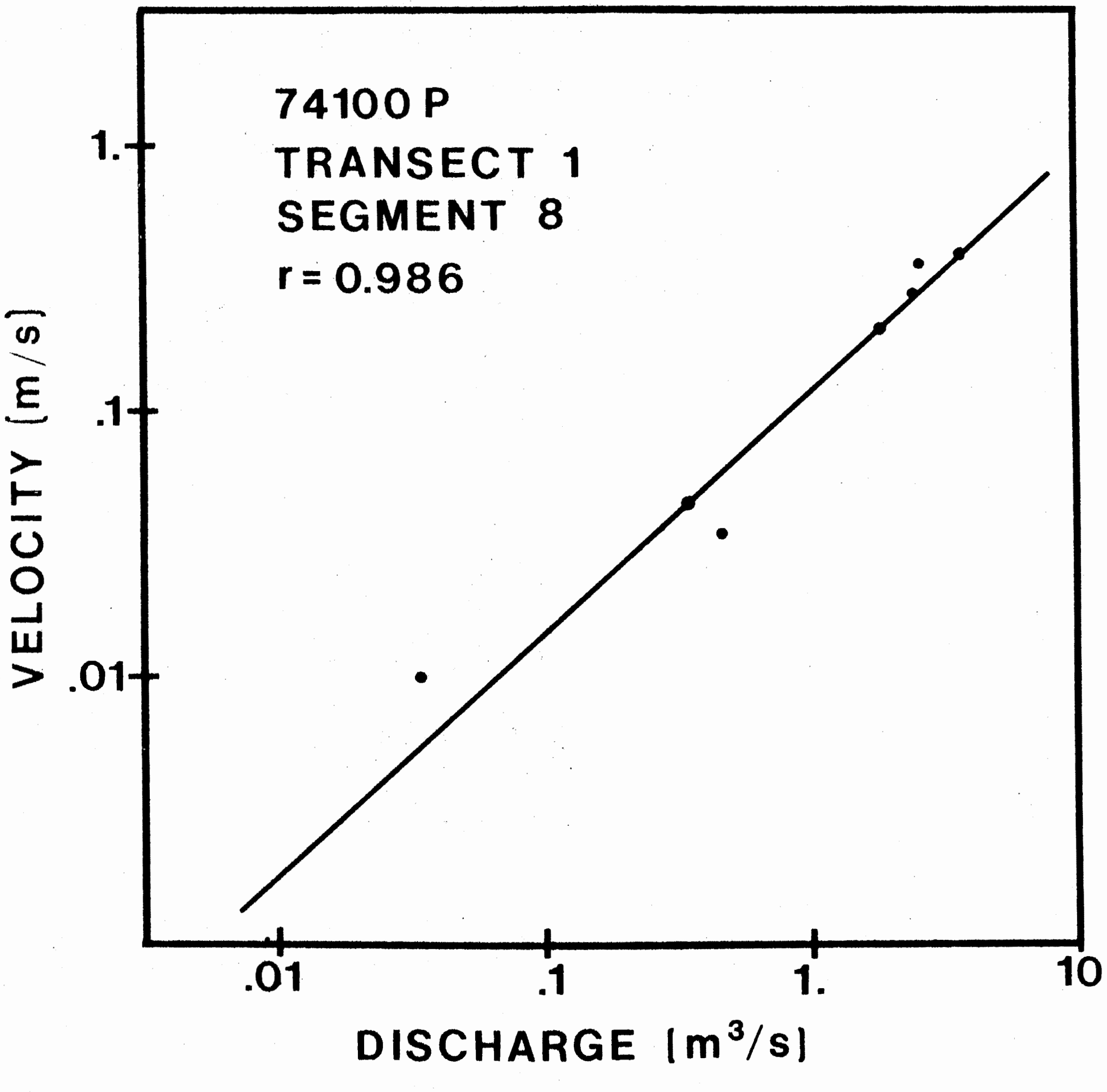

Figure 4. Velocity-discharge relationship of a particular segment on a transect.

allow the water surface elevation (stage) to be determined for any discharge, and the depths at every segment along transects to be obtained by subtraction (Figure 2). Velocity in each segment can then be estimated by the $\log_{10}$ (velocity) versus $\log_{10}$ (discharge) relation for that particular segment (Figure 4). For segments in which there are fewer than two velocity measurements, Manning's equation is used to predict velocity. Using estimated depths and velocities, discharge can be computed and compared with the desired discharge as a check on the reliability of the estimates. The ratio of desired discharge to computed discharge based on estimates is called an adjustment factor and is used to adjust velocities so that desired and computed discharges agree.

Substrate data, distances between transects, estimated depths and velocities at various discharges, and suitability curves for life stages of species of interest are used as input to the IFG3 or Habitat program (Main 1978b). Suitability curves are used to compute a composite weighting factor for suitability, which is the product of the individual weighting factors for the depth, velocity, and substrate in each rectangular segment of the stream reach (Figure 1). The composite weighting factor is multiplied by the surface area having that particular combination of depth, velocity, and substrate and the sum of these products over all segments of the stream reach is called the weighted usable area. Weighted usable area is an index of the quantity and quality of usable habitat. By computing weighted usable area for a wide range of flows, the impact on fish habitat of changes in the flow regime can be determined or an instream flow can be recommended (Stalnaker 1979; Trihey 1979).

Any methodology of this type should be robust, so that minor violations of the assumptions do not limit the usefulness of the outcome.

The objectives of this research were to test the assumptions and determine the robustness of the method. The following are the assumptions of the methodology: (1) depth, velocity, and substrate are the most important habitat variables affecting fish distribution and abundance when considering changes in stream flow regimes; (2) the stream channel is not altered by changes in flow regime; (3) depth, velocity, and substrate are independent in their influence on habitat selection of fishes. This assumption allows one to calculate the composite weighting factor as the product of individual weighting factors; (4) the stream can be modeled by using one or more representative sample reaches of the stream; and (5) there is a positive, linear relationship between weighted usable area and fish standing crop or habitat use.

CHAPTER III

DESCRIPTION OF STUDY AREA

Glover Creek (Figure 5), located in McCurtain County in southeastern Oklahoma, is the last major uncontrolled tributary of the Little River System. The creek drains an area of about 876 km^2, the upper region of which is mountainous, characterized by sharp ridges and steep slopes. Downstream areas of the basin are more characteristic of low fertile flatlands. Rock formations of the basin consist of sandstones, shales, limestones, and cherts.

Long, hot summers and short, mild winters characterize the climate of the region. Average annual air temperature is 17.2 C, with monthly averages of 27.8 C in July and 6.7 C in January. Average annual precipitation is about 127 cm while runoff averages 47 cm (United States Army Corps of Engineers 1975).

Most of the drainage area supports an oak-hickory-pine forest (Rice and Penfound 1959); although, at the present time, clear-cutting and replanting with pine is diminishing the number of hardwoods. Commercial timber harvesting is the principle economic activity and much of the watershed is owned or leased by the Weyerhauser Company. A small percentage of the area is in pasture or under cultivation.

Glover Creek rises in the Ouachita Mountains, near the LeFlore-McCurtain county line, then flows south before emptying into the Little River. Elevations range from 103 meters above mean sea level at the

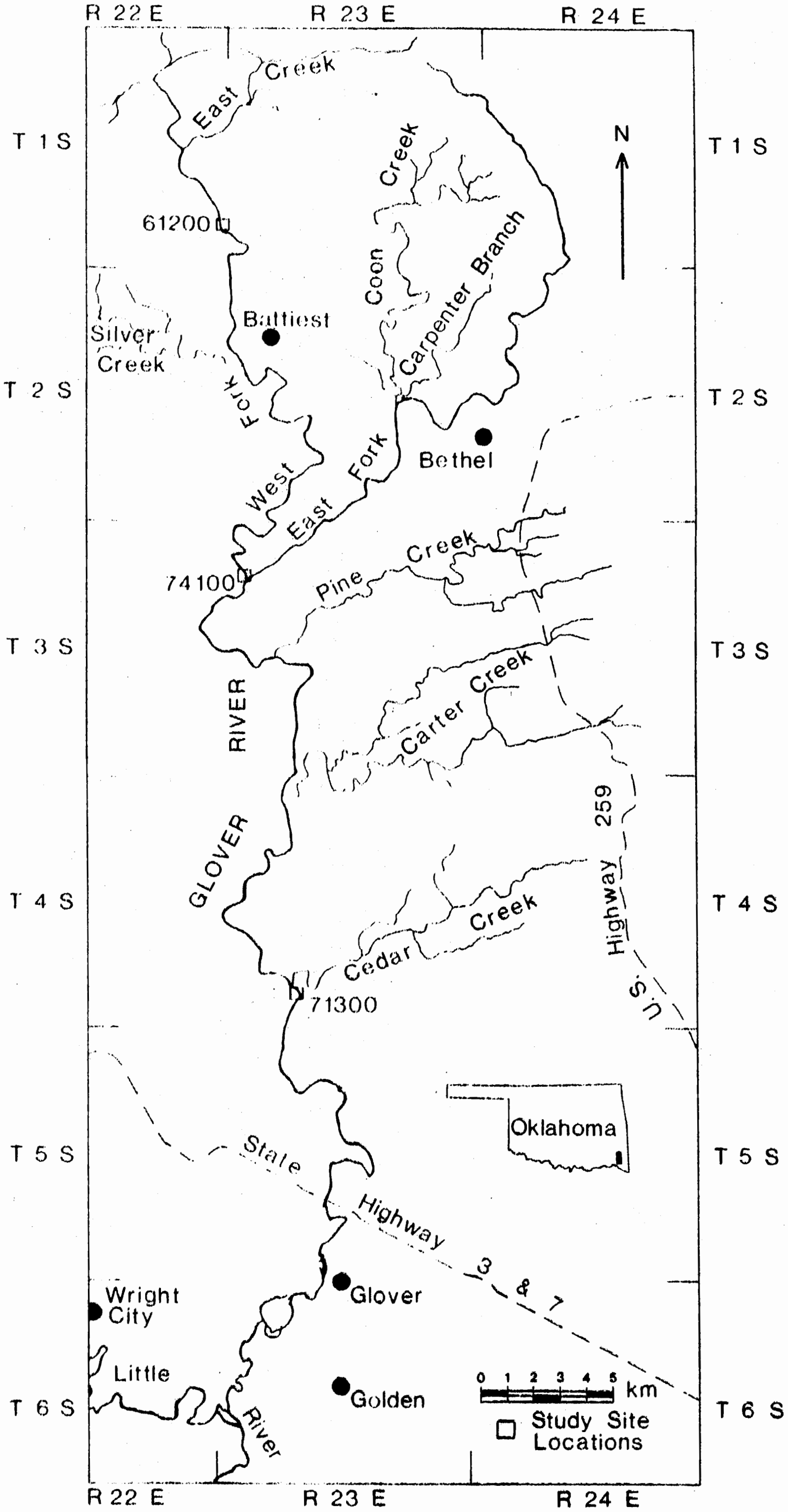

Figure 5. Glover Creek study area.

mouth to 610 m at the source. The average gradient is 2.3 m/km, and ranges from 18.9 m/km in the upper reaches to 0.95 m/km near the mouth. The main stem of Glover Creek from the mouth to the confluence of the East and West Forks is 53 km long; the length of the East and West Forks, respectively, are approximately 35 and 33 km. Other major tributaries, Pine, Carter, and Cedar creeks, drain the eastern portion of the watershed.

Above the United States Geological Survey stream gage located on the Highway 3 and 7 bridge, the drainage encompasses an area of 816 km^2 and has had an average discharge of 12.912 m^3/s and a median discharge of 3.171 m^3/s for 1937 through 1973 (United States Army Corps of Engineers 1975). Median monthly flows ranged from 0.680 m^3/s in August to 22.628 m^3/s in May.

Below the Carter Creek confluence the stream habitat is mostly deep, long pools separated by shallow, relatively narrow riffles. Above the Carter Creek confluence the stream habitat consists of fewer pool and riffle areas and more shallow and wide bedrock bottom pools separated by low bedrock falls and chutes (United States Army Corps of Engineers 1975). Frequent flooding in all areas keeps the stream well-scoured with bedrock, large boulders, and rubble, the predominate substrate types. During the summer, extensive beds of water willow (*Justicia* sp.) develop in shallow, slow current areas.

Water quality in Glover Creek is very good (Oklahoma State Department of Health 1977). Dissolved oxygen remains near saturation year round and pH is usually near 7 (Appendix A). Turbidity and suspended solids are generally low and the water is quite clear. However, during high flows, turbidity and suspended solids increase markedly (Appendix A).

Glover Creek supports a diverse fish community. Taylor and Wade (1972) collected 50 species, the most abundant of which were bigeye shiner (*Notropis boops*), ribbon shiner (*N. fumeus*), longear sunfish (*Lepomis megalotis*), stoneroller (*Campostoma anomalum*), green sunfish (*L. cyanellus*), and orangebelly darter (*Etheostoma radiosum*). The primary game fish is smallmouth bass. In addition, most of Glover Creek is designated as critical habitat for the threatened leopard darter (*Percina pantherina*; United States Fish and Wildlife Service 1978), a species that is endemic to the Little River system in southeastern Oklahoma and southwestern Arkansas. Fishing, canoeing, and swimming are the principal recreational uses of the stream.

The topography of the upper portion of the watershed results in rapid runoff, and an average of three floods per year occur on the lower Glover Creek. Flooding has been estimated to cause an average of about $1,083,900 of damages annually (United States Army Corps of Engineers 1975). To avoid these flood damages, Lukfata Lake was authorized by the Flood Control Act in 1958; however, funds were never appropriated. The authorized damsite is located about 1.6 river km downstream from the mouth of Cedar Creek (Figure 5). Opposition from environmental groups and recreationists resulted in identification of an alternate damsite (0.5 river km downstream from Carter Creek). Since Glover Creek is designated as critical habitat for the threatened leopard darter, the possibility of appropriation for the Lukfata Lake project in the near future is remote.

CHAPTER IV

HABITAT SUITABILITY CURVES FOR FISHES OF GLOVER CREEK

Introduction

One of the major limitations in assessing the impact of stream flow changes and subsequent habitat alteration on fishes is the lack of quantitative information on habitat requirements of individual species. Intensive data collection efforts and evaluation of critical assumptions will be required before methodologies for the determination of instream flow requirements can be implemented and the resulting instream flow reservations justified in court (Lamb 1977). These methodologies, such as the incremental method, all involve determining the habitat (depth, velocity, substrate) requirements for the major life history stages of target species and converting this information into flow recommendations for these life stages.

Habitat suitability curves have been developed for fishes of the family Salmonidae (Bovee 1978) and some other fish species (Bovee, unpublished) based on existing data. However, there is very little suitable information for developing habitat suitability curves for fishes of Glover Creek. Furthermore, the assumption of independence of habitat variables in the selection of microhabitats by fishes has not been adequately tested even though it is the basis for weighted usable area calculations. The objectives of this portion of the study were (1) to develop habitat suitability curves for several fish species of Glover

Creek; (2) to test the assumption of independence of variables in habitat selection by fishes; and (3) to determine differences in the habitat preferences of different size groups of the same species.

Methods

Collection of habitat data was concentrated on five species: freckled madtom (Noturus nocturnus), orangebelly darter, stoneroller, smallmouth bass, and green sunfish. Fishes were sampled quarterly from January 1978 through September 1979 using a boat-mounted pulsed DC electrofishing unit with hand-held electrodes, and a pulsed DC backpack electrofisher (Smith-Root Type VII). Most of the data were collected at adjacent riffle and pool sites located at 61200 and 74100, although data on the less abundant species (freckled madtom and smallmouth bass) were obtained at 14 additional sites throughout the stream (Figure 6). Capture locations were marked with small bouys which were color-coded by species so that depth, current velocity, and substrate type could later be determined. Depth (cm) was measured with a metric wading rod; current velocity (cm/s) was measured at 0.6 of the depth from the water surface with a pygmy current meter; and substrate type was classified according to a modified Wentworth scale and given a numerical code (Bovee and Cochnauer 1977). Mixtures of substrates were given intermediate code values. Habitat data were collected in this manner for the freckled madtom, orangebelly darter, stoneroller, and smallmouth bass. Smallmouth bass were classified as juvenile (<150 mm total length, TL) and adult (>150 mm TL).

Angling was also used to collect habitat information for those species vulnerable to angling, i. e., smallmouth bass and green sunfish.

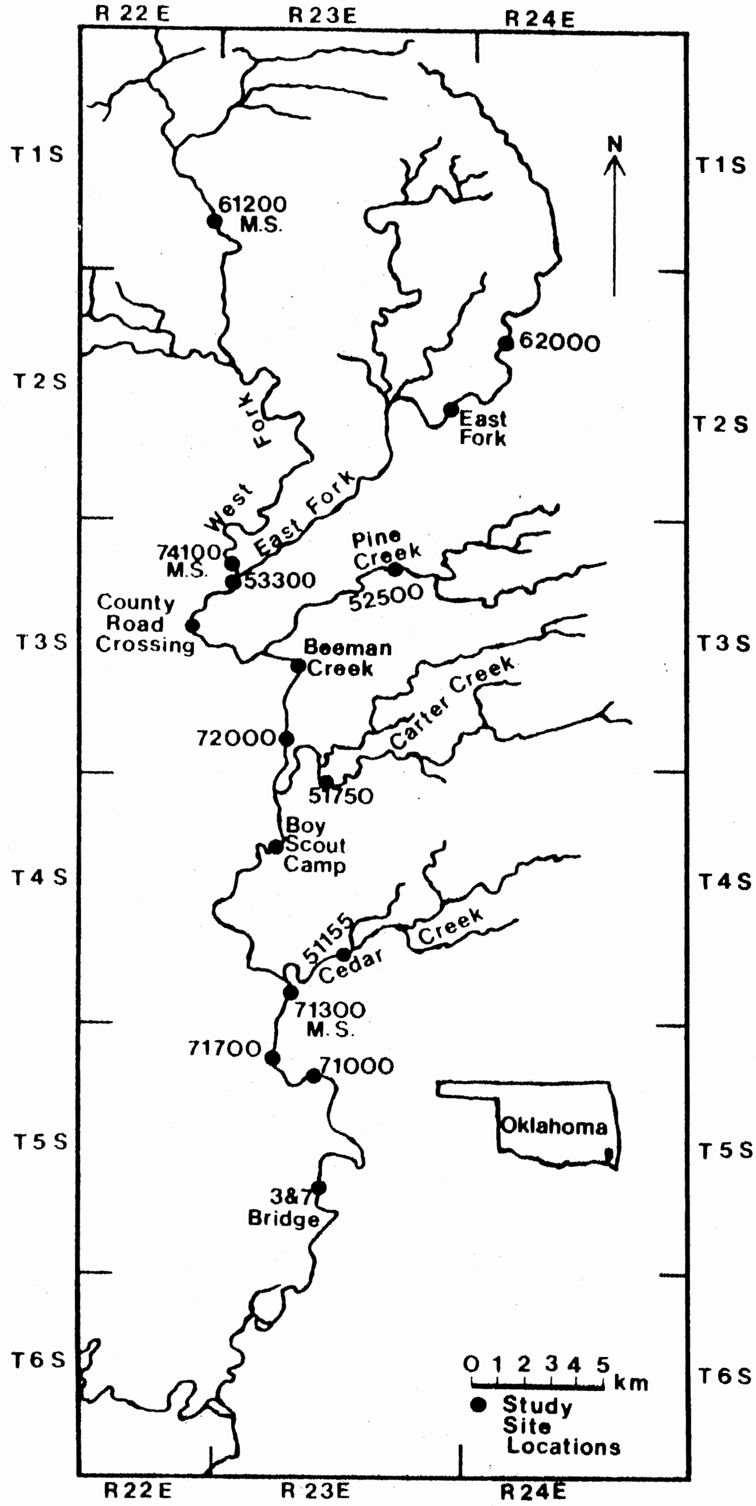

Figure 6. Location of study sites on Glover Creek.

Angling during canoe float trips provided the opportunity to sample a wide variety of habitats which otherwise would have been impossible because of the limited access to Glover Creek. The stream reach from the County Road Crossing to the Boy Scout Camp was sampled on May 19-20, 1979, and the reach from the Boy Scout Camp to access road 71000 was sampled on August 2-3, 1979 (Figure 6). A total of about 27 stream kilometers were sampled by biologists fishing with artificial lures. At the locations where fish struck, depth, surface velocity, and substrate type were determined. Surface velocity (V_s in cm/s), measured by timing a float, was converted to velocity at 0.6 depth ($V_{.6}$) by the equation: $V_{.6} = 1.1199\ V_s^{.8842}$ ($r=0.943$; $P<0.0001$), which was derived from field data on Glover Creek.

For adult smallmouth bass and green sunfish, suitability curves were developed in the following manner. Depth, velocity, and substrate frequency distributions were tabulated for each species and a chi-square test was used to determine if the distribution was significantly different from a uniform distribution over the range of the habitat variable. If this test indicated significant deviation from uniform, then the optimum range was assigned a weighting factor of one, and weighting factors for other intervals were obtained by dividing the frequencies in other intervals by the average frequency in the optimum range (Bovee and Cochnauer 1977). Suitability curves were then drawn to fit the weighting factor data. If there was no significant deviation from uniform, then a curve was drawn to indicate a suitability of one over the observed range of that habitat variable.

For juvenile and adult smallmouth bass, green sunfish, and freckled madtom, the assumption of independence of depth, velocity, and substrate frequency distributions was tested with a chi-square test for independence (Conover 1971:154-156). Contingency tables were set up to test the independence of: depth and velocity, depth and substrate, and velocity and substrate.

To account for the bias associated with the habitat availability at the time of sampling, depth, velocity, and substrate were estimated using the IFG4 hydraulic simulation program (Main 1978a), which had been calibrated for each main site. Calibration data were collected quarterly from November 1977 through September 1979. For each sampling period, the amount of area sampled in each depth, velocity, and substrate interval was computed.

For juvenile smallmouth bass and the freckled madtom, the frequencies in one-way depth, velocity, and substrate tables were divided by the amount of area sampled in each interval for an estimate of relative density. Suitability curves were then drawn based on weighting factors calculated from the relative density estimates.

For the orangebelly darter and the stoneroller, data were sufficient to estimate actual densities in relation to depth, velocity, and substrate. Therefore, for each main site, population estimates were made quarterly by the removal method (Carle and Strub 1978). Frequencies in one-way depth, velocity, and substrate tables for each site were multiplied by the ratio of the estimated population size to the actual number of fish that were captured and for which habitat data were recorded. The adjusted frequencies were summed over all sites and seasons and divided by the amount of surface area sampled in all sites and seasons in the respective interval for an estimate of the average density (number/m^2) in various depth, velocity, and substrate intervals. Suitability curves were then drawn based on weighting factors calculated from these density estimates.

For juvenile smallmouth bass, freckled madtom, orangebelly darter, and the stoneroller, a chi-square test for goodness fit (Conover 1971: 186-194) was used to test the null hypothesis that the one-way frequency distributions have the same distribution as the amount of area sampled; that is, densities do not vary over the sampled range of the habitat variable.

Data on the stoneroller and orangebelly darter for the spring 1979, and summer 1979 sampling periods were sufficient to analyze for the extent of the effects of each two-way interaction on density. Numbers and area sampled were tabulated in a three-way table using 10 cm depth intervals, 10 cm/s velocity intervals, and 0.5 substrate intervals. Midpoints of the depth and velocity intervals were used as values for depth and velocity. Exponential polynomial functions were chosen to fit to the density data. Numbers (N) were adjusted to N+1, and areas sampled were adjusted to Area+1, so the dependent variable modeled was actually (N+1)/(Area+1). This variable, (N+1)/(Area+1), is a biased estimate of density. The bias is negative at densities greater than one, and positive at densities less than one. A natural logarithm transformation of (N+1)/(Area+1) was then done so that the exponential polynomial function could be fitted by multiple linear regression. The order of the polynomial used was the one that gave the best fit to the marginal densities. An exponential polynomial function was then derived to relate density to depth, velocity, substrate, and the two-way interactions between depth, velocity, and substrate. The significance of the interactions was tested using a partial F test (Draper and Smith 1966), which tests the significance of including a variable after all other variables have already been included in the model. Reductions in the mean square error due to inclusion of the interaction terms were also calculated.

Results

Smallmouth Bass - Adult

Adult smallmouth bass were most frequently captured at depths from 40 to 100 cm in slow to moderate current velocities (0-19 cm/s), near boulder substrates (Figure 7). Data based on electrofishing were biased towards the shallower depths since habitat greater than 120 cm deep could not be sampled with the gear used. The depth frequency distributions based on electrofishing data was significantly different than that based on angling data according to the chi-square test for independence ($P<0.001$). Although the angling data may have some bias associated with it, the dashed depth suitability curve based only on angling data (Figure 7) probably is more representative of the habitat of adult smallmouth bass in Glover Creek. The velocity frequency distribution based on electrofishing data was also significantly different than that based on angling data ($P<0.025$). Much of this difference could be attributed to the very low flow conditions in summer and fall 1978, during which 31 of the 73 adult smallmouth bass captured by electrofishing were collected. If the data from summer and fall 1978 were omitted, the electrofishing velocity distribution would not be significantly different than the angling velocity distribution ($P>0.25$). Also, angling was conducted at flows which offered a wider range and probably a more uniform distribution of velocities for the fish to select from; flows during angling

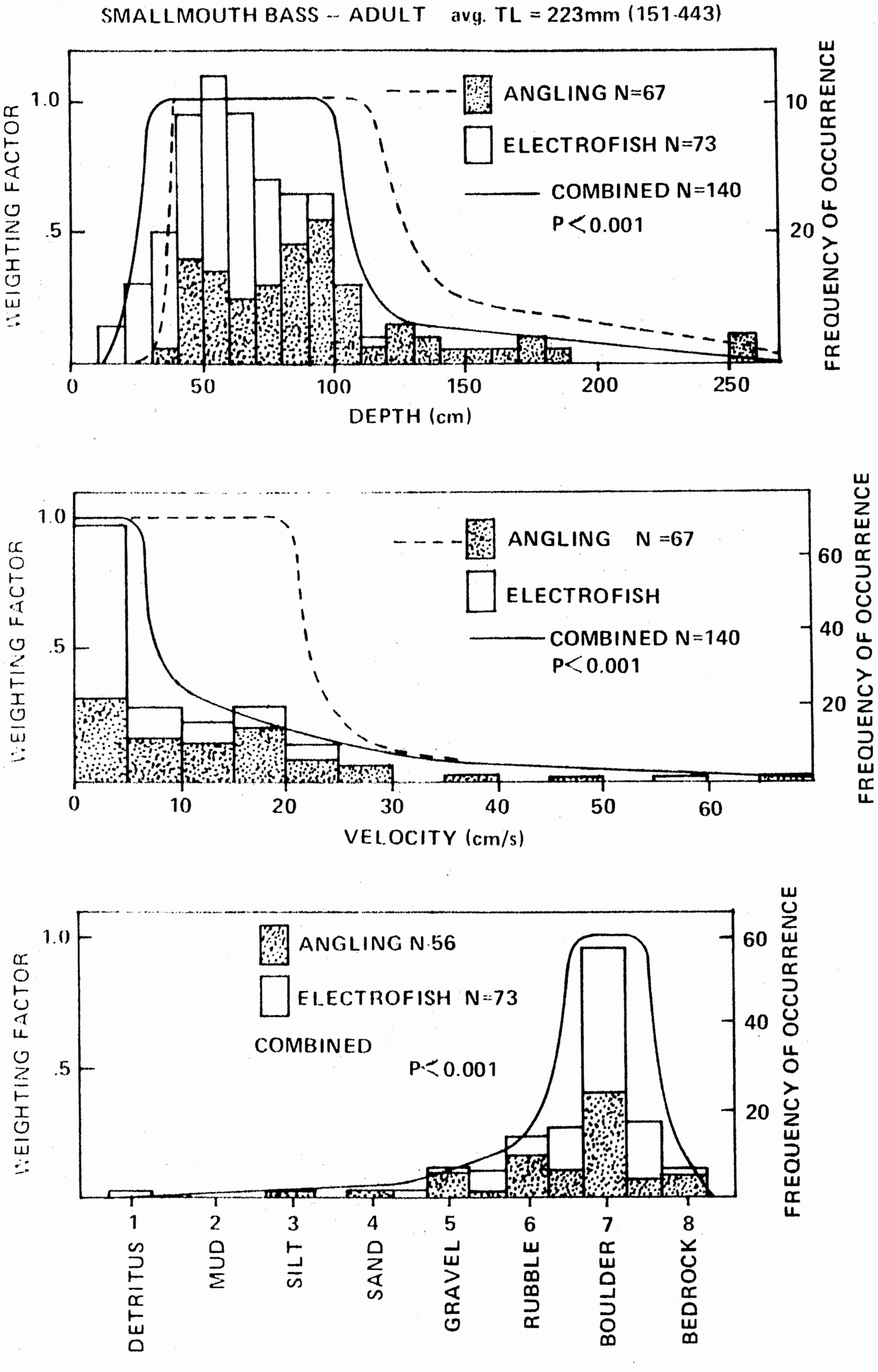

Figure 7. Depth, velocity, and substrate frequency distributions and suitability curves for adult smallmouth bass in Glover Creek.

collections were at levels which were exceeded only 36 to 37% of the time during the period of record (1961-74). Therefore, the dashed velocity suitability curve appears to be more accurate. In contrast, there was no significant difference (P>0.25) between the substrate frequency distribution based on electrofishing data and that based on angling data. Therefore, the combined data were used to develop the substrate suitability curve.

Observed frequencies of adult smallmouth bass in relation to depth and velocity were not significantly different than the expected frequencies under the assumption of independence, although the observed significance level (P=0.088) was low enough to indicate slight dependencies (Table 1). At shallow depths (<45 cm) adult smallmouth bass were captured at lower velocities (<5 cm/s) more frequently but at greater depths were captured at higher velocities more frequently than would be expected.

For depth and substrate, the assumption of independence was rejected at an observed significance level of 0.025 (Table 2). Adult smallmouth bass utilized smaller substrates (1.0-6.5) more frequently than expected at shallow depths and utilized larger substrates (7.0-8.0) more frequently than expected in deeper areas. In contrast, the assumption of independence of velocity and substrate in habitat selection by adult smallmouth bass was not rejected (P>0.25; Table 3).

Smallmouth Bass - Juvenile

Juvenile smallmouth bass were most abundant in relatively shallow areas, usually in or near riffles, with velocities from 10-20 cm/s, over substrates ranging from gravel to boulder. Densities varied significantly

Table 1. Observed frequencies of adult smallmouth bass and expected frequencies (in parentheses) assuming independence of depth and velocity.

	Velocity (cm/s)			
Depth (cm)	0-4	5-14	15-69	Totals
15-44	21 (14.09)	3 (7.25)	5 (7.66)	29
45-59	15 (15.06)	7 (7.75)	9 (8.19)	31
60-74	10 (13.60)	11 (7.00)	7 (7.40)	28
75-260	22 (25.26)	14 (13.00)	16 (13.74)	52
Totals	68	35	37	140

T = 11.09 (6 df) P = 0.088

Table 2. Observed frequencies of adult smallmouth bass and expected frequencies (in parentheses) assuming independence of depth and substrate.

Depth (cm)	Substrate				Totals
	1.0-5.5	6.0 & 6.5	7.0	7.5 & 8.0	
15-44	9 (4.02)	10 (6.69)	8 (12.72)	2 (5.35)	29
45-59	1 (4.15)	9 (6.92)	15 (13.15)	5 (5.54)	30
60-74	2 (3.46)	4 (5.77)	14 (10.96)	5 (4.62)	25
75-260	6 (6.37)	7 (10.62)	20 (20.17)	13 (8.49)	46
Totals	18	30	57	24	130

$T = 20.68$ (9 df) $P<0.025$

Table 3. Observed frequencies of adult smallmouth bass and expected frequencies (in parentheses) assuming independence of velocity and substrate.

	Substrate				
Velocity (cm/s)	1.0-5.5	6.0 & 6.5	7.0	7.5 & 8.0	Totals
0-4	13 (9.21)	12 (15.35)	28 (29.16)	13 (12.28)	66
5-14	1 (4.19)	7 (6.98)	16 (13.26)	6 (5.58)	30
15-69	4 (4.60)	11 (7.67)	13 (14.58)	5 (6.14)	33
Totals	18	30	57	24	129

T = 7.31 (6 df) P>0.25

over the range of depths ($P<0.001$) and velocities ($P<0.005$) sampled, but did not vary significantly ($P>0.10$) over the substrate range sampled (Table 4). Habitat suitability curves were fit to the relative density data (Figure 8), thereby eliminating bias that would have been in the curves if the raw frequency data had been used. This bias would have been greatest in the velocity and substrate curves because the distributions of the amount of area sampled over the range of velocities and substrates were non-uniform (Table 4). Although relative densities were not highest at velocities from 0-9 cm/s and over rubble-boulder substrate, habitat suitability would have been highest in these ranges if the raw frequency data were the basis for defining the suitability curves.

Depth and velocity were independent in the habitat selection by juvenile smallmouth bass ($P = 0.085$), but the contingency table indicates some slight dependencies in the data (Table 5). At depths less than 25 cm, juvenile smallmouth bass utilized higher velocities (15-39 cm/s) more frequently than expected, and at depths greater than 25 cm, they utilized higher velocities less frequently than would be expected. The test for independence of depth and substrate indicated significant differences between observed and expected frequencies ($P<0.005$; Table 6) with juvenile smallmouth bass utilizing progressively larger substrates at greater depths. In the test for independence of velocity and substrate, no significant differences were found between observed and expected frequencies ($P>0.25$; Table 7).

To determine if there were any differences in the depths, velocities, and substrate types utilized by different length groups of smallmouth bass, chi-square tests for independence were performed. There was a definite trend for the smallmouth bass to utilize microhabitats of

Table 4. Total area sampled, frequency of capture, and relative density of juvenile smallmouth bass in relation to depth, velocity, and substrate type in Glover Creek, January 1978 to September 1979.

Variable and interval	Area sampled (m^2)	Frequency	Relative density (Frequency/Area)
Depth (cm)			
0- 9	2,253	8	.004
10-19	2,466	40	.016
20-29	2,688	25	.009
30-39	2,220	13	.006
40-49	1,425	12	.008
50-59	1,340	11	.008
60-69	956	8	.008
70-79	849	2	.002
80-89	847	0	.000
≥ 90	1,400	5	.004
	16,444	124	
		T=43.9 (9 df) P<0.001	
Velocity (cm/s)			
0- 9	10,336	86	.008
10-19	2,168	23	.011
20-29	1,368	10	.007
30-39	792	5	.006
40-49	474	0	.000
50-59	517	0	.000
60-69	332	0	.000
70-79	190	0	.000
80-89	178	0	.000
90-119	90	0	.000
	16,445	124	
		T=17.3 (5 df) P<0.005	
Substrate			
Detritus	20	0	.000
Sand	188	0	.000
Sand-Gravel	34	0	.000
Gravel	319	4	.012
Gravel-Rubble	2,059	20	.010
Rubble	3,177	22	.007
Rubble-Boulder	6,412	42	.007
Boulder	2,989	31	.010
Boulder-Bedrock	209	1	.005
Bedrock	1,038	4	.004
	16,445	124	
		T=7.5 (5 df) P>0.10	

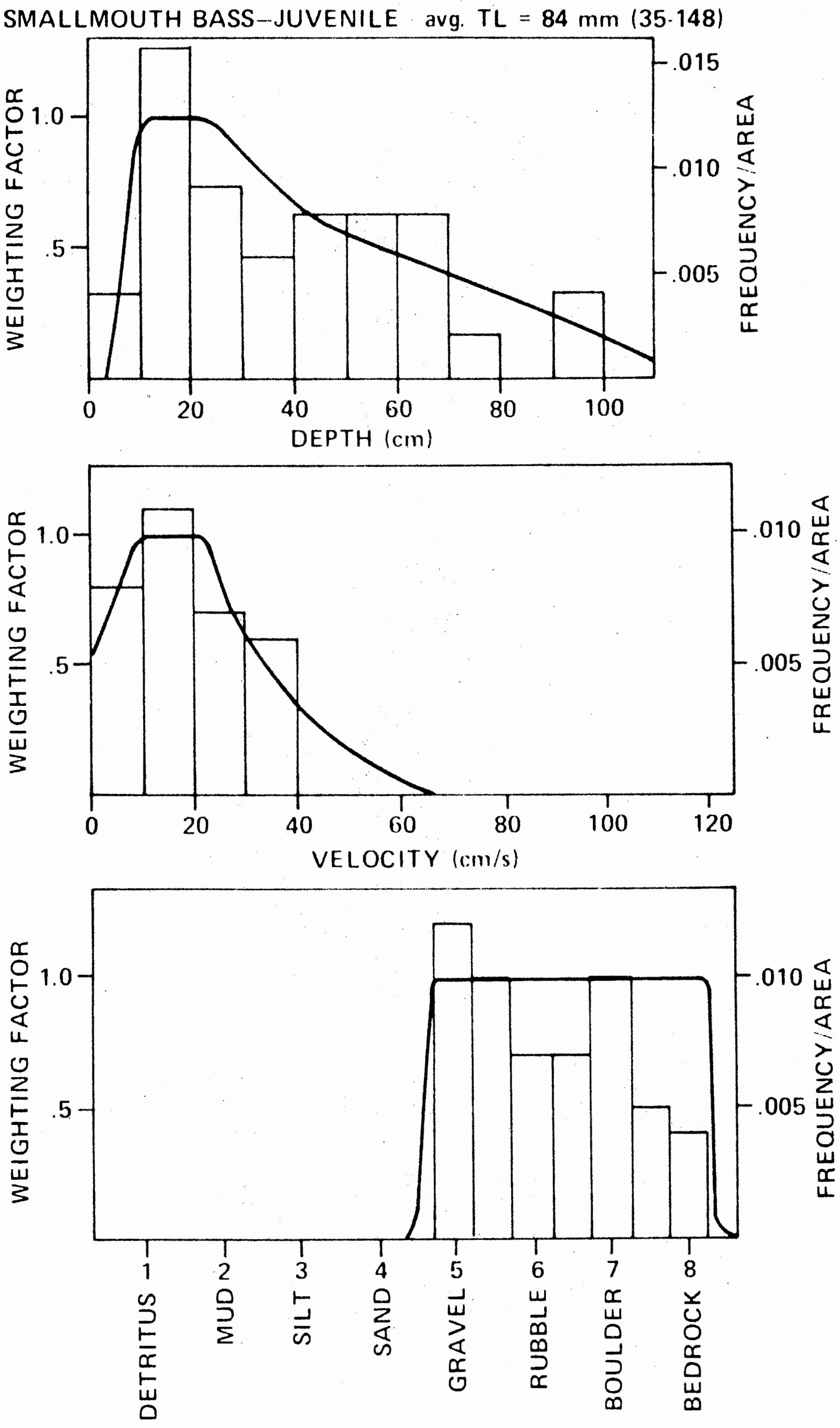

Figure 8. Relative density estimates and suitability weighting factors in relation to depth, velocity, and substrate, for juvenile smallmouth bass in Glover Creek.

Table 5. Observed frequencies of juvenile smallmouth bass and expected frequencies (in parentheses) assuming independence of depth and velocity.

	Velocity (cm/s)			
Depth (cm)	0-4	5-14	15-39	Totals
5-14	13 (13.84)	5 (6.29)	8 (5.87)	26
15-24	13 (19.69)	11 (8.95)	13 (8.36)	37
25-34	13 (10.11)	5 (4.60)	1 (4.29)	19
35-54	13 (12.24)	5 (5.56)	5 (5.19)	23
55-110	14 (10.11)	4 (4.60)	1 (4.29)	19
Totals	66	30	28	124

T = 14.00 (8 df) P = 0.085

Table 6. Observed frequencies of juvenile smallmouth bass and expected frequencies (in parentheses) assuming independence of depth and substrate.

	Substrate				
Depth (cm)	5.0 & 5.5	6.0	6.5	7.0, 7.5, & 8.0	Totals
5-14	7 (5.03)	7 (4.61)	8 (8.81)	4 (7.55)	26
15-24	10 (7.16)	7 (6.56)	16 (12.53)	4 (10.74)	37
25-34	3 (3.68)	4 (3.37)	8 (6.44)	4 (5.52)	19
35-54	2 (4.45)	2 (4.08)	7 (7.79)	12 (6.68)	23
55-110	2 (3.68)	2 (3.37)	3 (6.44)	12 (5.52)	19
Totals	24	22	42	36	124
T = 28.64	(12 df)	P<0.005			

Table 7. Observed frequencies of juvenile smallmouth bass and expected frequencies (in parentheses) assuming independence of velocity and substrate.

Velocity (cm/s)	Substrate 5.0 & 5.5	6.0	6.5	7.0, 7.5, & 8.0	Totals
0-4	11 (12.77)	13 (11.71)	26 (22.36)	16 (19.16)	66
5-14	6 (5.81)	5 (5.32)	8 (10.16)	11 (8.71)	30
15-39	7 (5.42)	4 (4.97)	8 (9.48)	9 (8.13)	28
Totals	24	22	42	36	124

T = 3.57 (6 df) P>0.25

greater depths as they grew (Table 8), and the differences between observed and expected frequencies were significant ($P<0.001$). The greatest change in the preferred depth range occurred between smallmouth bass less than 100 and those greater than 100 mm TL. Conversely, in the test for independence of fish length and velocity, no significant differences were found between observed and expected frequencies ($P>0.10$; Table 9). In the test for independence of fish length and substrate type, there were significant differences between observed and expected frequencies ($P<0.001$; Table 10). Smallmouth bass less than 100 mm TL utilized substrates of gravel-rubble, rubble, and rubble-boulder (5.5, 6.0, and 6.5) more frequently than expected and those greater than 100 mm TL utilized substrates of boulder, boulder-bedrock, and bedrock (7.0, 7.5, and 8.0) more frequently than expected.

Green Sunfish - Adult

A total of 254 adult green sunfish were captured by angling in Glover Creek, usually in areas 40 to 120 cm deep, with little or no current (0-4 cm/s), and boulder substrate (Figure 9). Within the optimum depth range there were no significant differences ($P>0.25$) between observed and expected frequencies assuming a uniform distribution.

Because the adult green sunfish ranged in size from 75 to 243 mm TL, chi-square tests for independence of fish length and habitat use were performed. There was significant evidence to reject the null hypothesis that depth at capture locations is independent of fish length ($P<0.025$; Table 11). Green sunfish greater than 200 mm TL were captured at depths of 80-119 cm more frequently, and green sunfish less than 140 mm TL were captured at depths less than 80 cm more frequently than would be expected

Table 8. Observed frequencies of smallmouth bass and expected frequencies (in parentheses) assuming independence of fish length and the water depth at capture locations.

Total length (mm)	Depth (cm)						Totals
	5-19	20-34	35-49	50-64	65-84	85-260	
35-99	23 (7.87)	21 (10.40)	10 (10.40)	2 (10.68)	3 (9.28)	2 (12.37)	61
100-149	3 (4.00)	6 (5.29)	4 (5.29)	11 (5.43)	4 (4.71)	3 (6.29)	31
150-199	1 (6.71)	5 (8.87)	13 (8.87)	11 (9.11)	14 (7.91)	8 (10.54)	52
200-249	1 (5.81)	4 (7.67)	6 (7.67)	10 (7.88)	8 (6.84)	16 (9.12)	45
250-450	0 (3.61)	1 (4.77)	4 (4.77)	4 (4.90)	4 (4.26)	15 (5.68)	28
Totals	28	37	37	38	33	44	217

T = 116.30 (20 df) $P<0.001$

Table 9. Observed frequencies of smallmouth bass and expected frequencies (in parentheses) assuming independence of fish length and the current velocity at capture locations.

Total length (mm)	Velocity (cm/s)					Totals
	0-4	5-9	10-14	15-19	20-69	
35-99	41 (29.52)	5 (8.43)	4 (7.31)	5 (8.15)	6 (7.59)	61
100-149	11 (15.00)	6 (4.29)	6 (3.71)	5 (4.14)	3 (3.86)	31
150-199	21 (25.16)	10 (7.19)	5 (6.23)	7 (6.95)	9 (6.47)	52
200-249	18 (21.77)	8 (6.22)	6 (5.39)	6 (6.01)	7 (5.60)	45
250-450	14 (13.55)	1 (3.87)	5 (3.36)	6 (3.74)	2 (3.48)	28
Totals	105	30	26	29	27	217

T = 20.77 (16 df) P>0.10

Table 10. Observed frequencies of smallmouth bass and expected frequencies (in parentheses) assuming independence of fish length and substrate type at capture locations.

Total length (mm)	Substrate						Totals
	1.0-5.0	5.5	6.0	6.5	7.0	7.5 & 8.0	
35-99	1 (4.15)	15 (5.92)	16 (9.48)	22 (13.03)	6 (21.91)	1 (6.52)	61
100-149	1 (2.11)	0 (3.01)	3 (4.82)	7 (6.62)	16 (11.14)	4 (3.31)	31
150-199	7 (3.19)	0 (4.56)	7 (7.30)	5 (10.04)	22 (16.88)	6 (5.02)	47
200-249	4 (2.85)	4 (4.08)	4 (6.52)	5 (8.97)	16 (15.09)	9 (4.48)	42
250-450	1 (1.70)	1 (2.43)	2 (3.88)	5 (5.34)	14 (8.98)	2 (2.67)	25
Totals	14	20	32	44	74	22	206

T = 75.98 (20 df) P<0.001

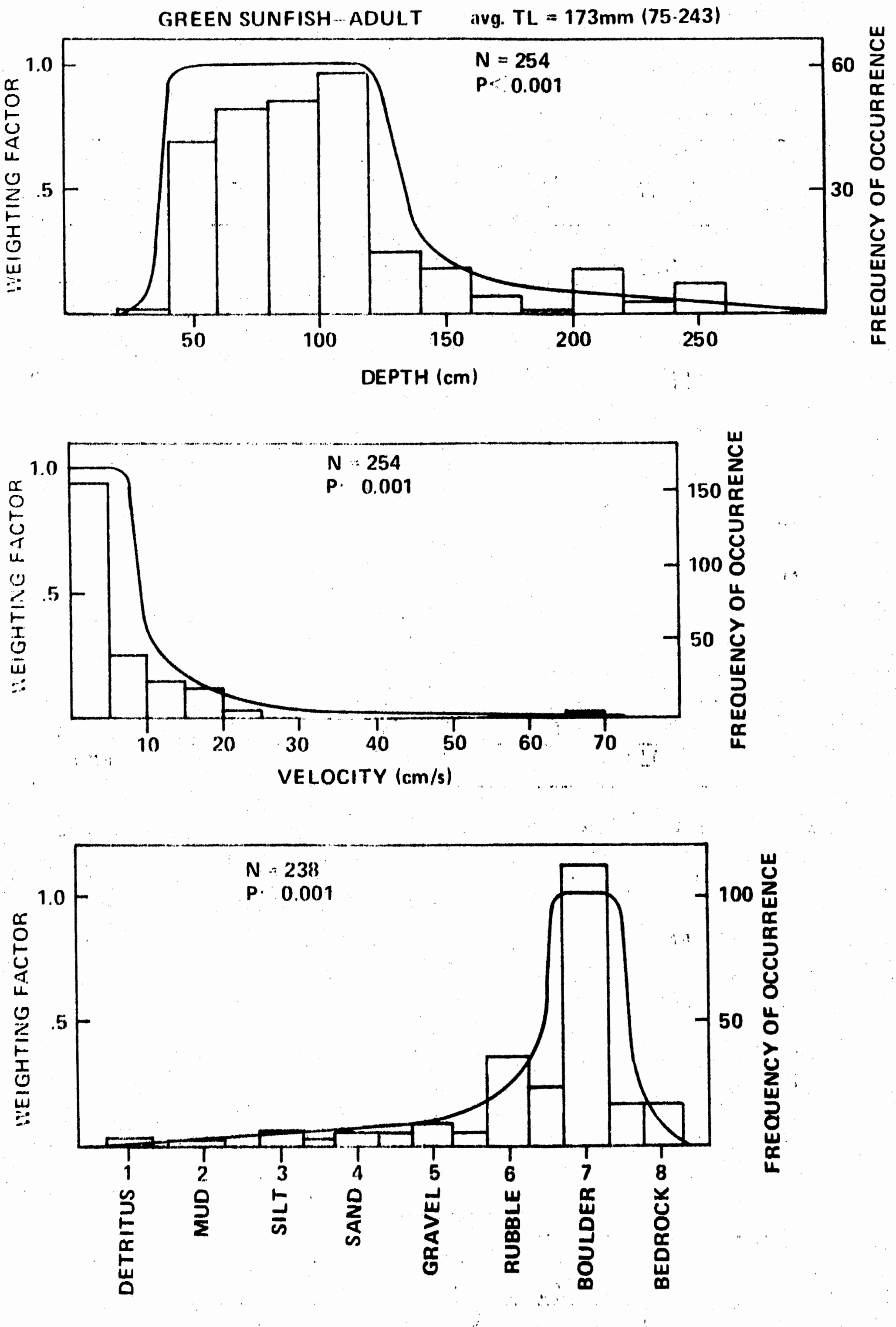

Figure 9. Depth, velocity, and substrate frequency distributions and suitability curves for adult green sunfish in Glover Creek.

Table 11. Observed frequencies of green sunfish and expected frequencies (in parentheses) assuming independence of fish length and depth at capture locations.

Total length (mm)	Depth (cm)			Totals
	< 80	80-119	≥ 120	
< 140	22 (15.81)	14 (18.70)	7 (8.50)	43
140-159	16 (12.50)	13 (14.78)	5 (6.72)	34
160-179	29 (23.53)	22 (27.83)	13 (12.65)	64
180-199	14 (16.54)	21 (19.56)	10 (8.89)	45
≥ 200	12 (24.63)	40 (29.13)	15 (13.24)	67
Totals	93	110	50	253

T = 19.41 (8 df) $P<0.025$

if depth of capture was independent of fish length. Velocity at capture locations was independent of fish length (P>0.25; Table 12), but substrate at capture locations and fish length were not independent (P<0.025; Table 13). Green sunfish less than 140 mm TL utilized rubble (6.0) more frequently and boulder-bedrock and bedrock (7.5 and 8.0) less frequently than would be expected assuming independence.

In the test for independence of depth and velocity in the habitat selection by adult green sunfish, the observed significance level was 0.061 (Table 14). At shallow depths green sunfish utilized velocities greater than 10 cm/s more frequently, and at greater depths utilized velocities less than 10 cm/s more frequently than would be expected if depth and velocity were independent. Depth at capture locations was related to substrate (P<0.025; Table 15). At shallow depths green sunfish utilized substrates ranging from sand-gravel (4.5) to rubble-boulder (6.5) more frequently than would be expected if depth and velocity were independent. The observed significance level for the test for independence of velocity and substrate was 0.072 (Table 16). The major difference between observed and expected frequencies was for substrates from detritus to sand (1.0-4.0). At velocities less than 10 cm/s, green sunfish utilized these finer substrates more frequently, and at velocities greater than 10 cm/s, they utilized the smaller substrate types less frequently than would be expected if velocity and substrate were independent.

Freckled Madtom

Freckled madtoms were almost always captured in shallow riffle habitat. Relative densities were greatest at depths from 10-19 cm, velocities

Table 12. Observed frequencies of green sunfish and expected frequencies (in parentheses) assuming independence of fish length and velocity at capture locations.

Total length (mm)	Velocity (cm/s) 0	1-10	>10	Totals
< 140	28 (25.83)	7 (8.16)	8 (9.01)	43
140-159	20 (20.43)	4 (6.45)	10 (7.12)	34
160-179	40 (38.45)	12 (12.14)	12 (13.41)	64
180-199	27 (27.04)	12 (8.54)	6 (9.43)	45
≥ 200	37 (40.25)	13 (12.71)	17 (14.04)	67
Totals	152	48	53	253

T = 6.32 (8 df) P>0.25

Table 13. Observed frequencies of green sunfish and expected frequencies (in parentheses) assuming independence of fish length and substrate at capture locations.

Total length (mm)	Substrate					Totals
	1.0-5.5	6.0	6.5	7.0	7.5 & 8.0	
< 140	3 (6.08)	15 (5.91)	2 (3.88)	18 (18.90)	2 (5.23)	40
140-159	7 (4.86)	3 (4.73)	2 (3.10)	16 (15.12)	4 (4.19)	32
160-179	7 (9.57)	9 (9.30)	8 (6.11)	32 (29.77)	7 (8.24)	63
180-199	10 (6.23)	4 (6.06)	4 (3.98)	16 (19.38)	7 (7.98)	41
≥ 200	9 (9.27)	4 (9.01)	7 (5.92)	30 (28.83)	11 (7.98)	61
Totals	36	35	23	112	31	237

T = 30.03 (16 df) P<0.025

Table 14. Observed frequencies of adult green sunfish and expected frequencies (in parentheses) assuming independence of depth and velocity.

Depth (cm)	Velocity (cm/s)		Totals
	0-9	≥ 10	
< 80	60 (73.59)	26 (19.41)	93
80-119	89 (87.05)	21 (22.95)	110
≥ 120	45 (40.36)	6 (10.64)	51
Totals	201	53	254

T = 5.68 (2 df) P = 0.061

Table 15. Observed frequencies of adult green sunfish and expected frequencies (in parentheses) assuming independence of depth and substrate.

	Substrate						
Depth (cm)	1.0-4.0	4.5-5.5	6.0	6.5	7.0	7.5 & 8.0	Totals
< 80	6 (6.66)	10 (6.66)	18 (12.94)	14 (8.50)	31 (41.41)	9 (11.83)	88
80-119	6 (7.71)	7 (7.71)	13 (15.00)	7 (9.86)	56 (48.00)	13 (13.71)	102
≥ 120	6 (3.63)	1 (3.63)	4 (7.06)	2 (4.64)	25 (22.59)	10 (6.45)	48
Totals	18	18	35	23	112	32	238

T = 21.97 (10 df) P<0.025

Table 16. Observed frequencies of adult green sunfish and expected frequencies (in parentheses) assuming independence of velocity and substrate.

Velocity (cm/s)	Substrate						Totals
	1.0-4.0	4.5-5.5	6.0	6.5	7.0	7.5 & 8.0	
0-9	18 (14.14)	14 (14.14)	31 (27.50)	15 (18.07)	84 (88.00)	25 (25.14)	187
≥ 10	0 (3.86)	4 (3.86)	4 (7.50)	8 (4.93)	28 (24.00)	7 (6.86)	51
Totals	18	18	35	23	112	32	238

T = 10.28 (5 df) P = 0.072

from 20-39 cm/s, in substrates of sand-gravel, gravel, and gravel-rubble (Table 17). The null hypothesis that densities do not vary over the sampled range of the habitat variable was rejected ($P<0.001$) for each habitat variable (Table 17). The suitability curves for the freckled madtom (Figure 10) are based on data which show that they were indeed selecting a particular range of each habitat variable while avoiding other ranges.

The majority of these data (79 of 115 observations) were collected during summer 1979 and therefore the suitability curves are most representative of summer habitat utilization. Based on length frequencies, most of the freckled madtoms captured during summer 1979 were probably young of the year. To determine if there were any differences in habitat selection between freckled madtoms less than 40 mm TL and those greater than 40 mm TL, chi-square tests for independence were performed for length versus depth, length versus velocity, and length versus substrate. In only 49 of the 115 observations were the length measurements associated with the observed depth, velocity, and substrate data. The average total length of these fish was 43 mm and the range was 16-98 mm. No significant differences were found between the depth, velocity, or substrate frequency distributions for freckled madtoms less than and those greater than 40 mm total length (Tables 18, 19, and 20). The same suitability curves (Figure 10) can thus be applied to both the juvenile and adult stages.

Frequency distributions of the depths and velocities utilized by freckled madtoms were not independent (Table 21). At depths greater than 20 cm, freckled madtoms used areas with higher velocities (>20 cm/s) more frequently than would be expected under the assumption of indepen-

Table 17. Total area sampled, frequency of capture, and relative density of the freckled madtom in relation to depth, velocity, and substrate type in Glover Creek, January 1978 to September 1979.

Variable and interval	Area sampled (m^2)	Frequency	Relative density (Frequency/Area)
Depth (cm)			
0- 9	2,253	32	.014
10-19	2,466	50	.020
20-29	2,688	27	.010
30-39	2,220	2	.001
40-49	1,425	2	.001
50-59	1,340	1	.001
60-69	956	0	.000
70-79	849	1	.001
80-89	847	0	.000
≥ 90	1,400	0	.000
	16,444	115	
		T=134.9 (9 df) $P<0.001$	
Velocity (cm/s)			
0- 9	10,336	32	.003
10-19	2,168	32	.015
20-29	1,368	24	.018
30-39	792	15	.019
40-49	474	1	.002
50-59	517	5	.010
60-69	332	4	.012
70-79	190	1	.005
80-89	178	0	.000
90-119	90	1	.011
	16,445	115	
		T=79.2 (5 df) $P<0.001$	
Substrate			
Detritus	20	0	.000
Sand	188	0	.000
Sand-Gravel	34	1	.029
Gravel	319	4	.012
Gravel-Rubble	2,056	33	.016
Rubble	3,177	32	.010
Rubble-Boulder	6,412	37	.006
Boulder	2,989	8	.003
Boulder-Bedrock	209	0	.000
Bedrock	1,038	0	.000
	16,445	115	
		T=46.9 (5 df) $P<0.001$	

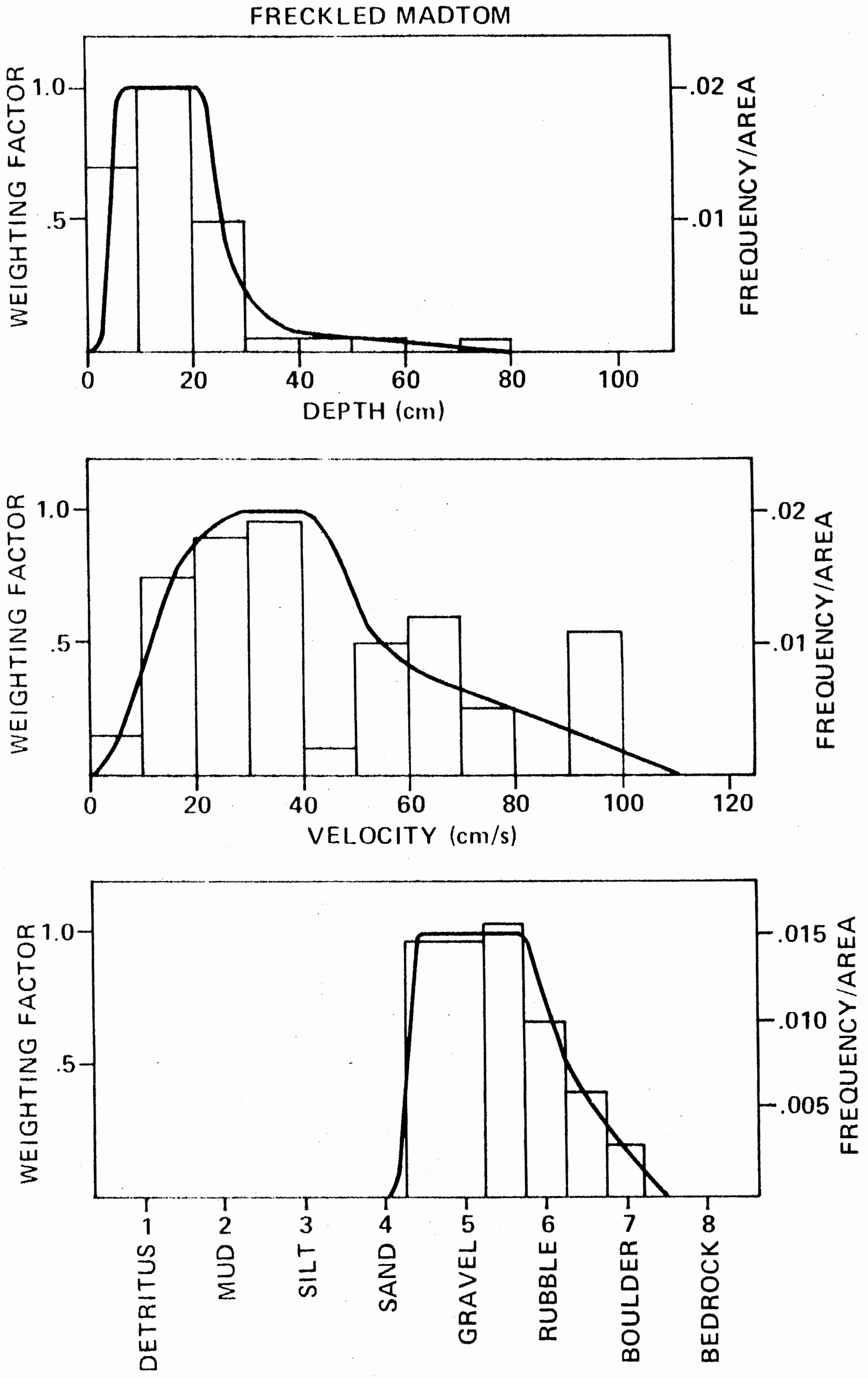

Figure 10. Relative density estimates and suitability weighting factors in relation to depth, velocity, and substrate, for the freckled madtom in Glover Creek.

Table 18. Observed frequencies of freckled madtoms and expected frequencies (in parentheses) assuming independence of total length (TL) and the water depth (cm) at capture locations.

TL (mm)	Depth (cm) 0-19	 20-39	 40-79	Totals
< 40	20 (16.53)	6 (8.82)	1 (1.65)	27
≥ 40	10 (13.47)	10 (7.18)	2 (1.35)	22
Totals	30	16	3	49

T = 4.20 (2 df) P>0.10

Table 19. Observed frequencies of freckled madtoms and expected frequencies (in parentheses) assuming independence of total length (TL) and current velocity (cm/s) at capture locations.

	Velocity (cm/s)			
TL (mm)	0-19	20-39	≥ 40	Totals
< 40	10 (10.47)	14 (11.57)	3 (4.96)	27
≥ 40	9 (8.53)	7 (9.43)	6 (4.04)	22
Totals	30	21	9	49

T = 2.91 (2 df) P>0.10

Table 20. Observed frequencies of freckled madtoms and expected frequencies (in parentheses) assuming independence of total length (TL) and substrate at capture locations.

	Substrate				
TL (mm)	4.5 & 5.0	5.5	6.0	6.5 & 7.0	Totals
< 40	3 (2.76)	10 (8.26)	11 (9.92)	3 (6.06)	27
≥ 40	2 (2.24)	5 (6.74)	7 (8.08)	8 (4.94)	22
Totals	5	15	18	11	49

T = 4.57 (3 df) P>0.10

Table 21. Observed frequencies of freckled madtoms and expected frequencies (in parentheses) assuming independence of depth and velocity.

Depth (cm)	Velocity (cm/s)			Totals
	0-19	20-39	≥ 40	
0-19	51 (45.64)	25 (27.81)	6 (8.56)	82
20-70	13 (18.36)	14 (11.19)	6 (3.44)	33
Totals	64	39	12	115

T = 7.39 (2 df) P<0.025

dence ($P<0.025$; Table 21). Therefore, the velocity suitability curve (Figure 10) would probably not be the same at depths less than and greater than 20 cm. The depth frequency distribution was independent of substrate type ($P>0.25$; Table 22) and the velocity frequency distribution was independent of substrate type ($P>0.10$; Table 23).

Stoneroller

Stonerollers were most frequently captured in or near riffles or raceways. The null hypothesis that densities of the stoneroller do not vary over the sampled range of the habitat variable was rejected for each habitat variable ($P<0.001$; Table 24). Densities were greatest at depths from 10-19 cm, velocities from 10-19 cm/s, and over gravel substrate (Figure 11). Velocities from 10 to 49 cm/s were judged to be the optimum range for the suitability curve (Figure 11) since observed frequencies in these intervals were greater than the expected frequencies under the null hypothesis. A weighted average density ($0.18/m^2$) was calculated for this interval and weighting factors for other intervals were calculated by dividing the density by 0.18. Since a relatively small amount of area of gravel substrate was sampled (Table 24), the optimum substrate types were judged to be gravel and gravel-rubble and weighting factors were scaled to a weighted average density ($0.19/m^2$) over gravel and gravel-rubble. The amount of area sampled over detritus substrate was under-estimated because of its ephemeral nature and, therefore, density of the stoneroller over detritus was inflated. Also, since the density estimate for detritus was based on so few fish (Table 24), it was not included in developing the suitability curve (Figure 11).

During the spring 1979, the stoneroller population had a very low

Table 22. Observed frequencies of freckled madtoms and expected frequencies (in parentheses) assuming independence of depth and substrate.

	Substrate					
Depth (cm)	4.5 & 5.0	5.5	6.0	6.5	7.0	Totals
0-19	4 (3.56)	24 (23.53)	22 (22.82)	28 (26.38)	4 (5.70)	82
20-70	1 (1.44)	9 (9.47)	10 (9.18)	9 (10.62)	4 (2.30)	33
Totals	5	33	32	37	8	115

T = 2.44 (4 df) P>0.25

Table 23. Observed frequencies of freckled madtoms and expected frequencies (in parentheses) assuming independence of velocity and substrate.

Velocity (cm/s)	Substrate				Totals
	4.5 & 5.0	5.5	6.0	6.5 & 7.0	
0-19	2 (2.78)	16 (18.36)	15 (17.81)	31 (25.04)	64
20-39	3 (1.70)	15 (11.19)	11 (10.85)	10 (15.26)	39
≥ 40	0 (0.52)	2 (3.44)	6 (3.34)	4 (4.70)	12
Totals	5	33	32	45	115

T = 9.852 (6 df) P>0.10

Table 24. Total area sampled, and estimated number and density of the stoneroller in relation to depth, velocity, and substrate type in Glover Creek, January 1978 to September 1979.

Variable and interval	Area sampled (m^2)	Number	Number/m^2
Depth (cm)			
0- 9	2,253	394	.175
10-19	2,466	1,131	.459
20-29	2,688	293	.109
30-39	2,220	78	.035
40-49	1,425	44	.031
50-59	1,340	10	.007
60-69	956	2	.002
70-79	849	1	.001
80-89	847	0	.000
≥ 90	1,400	0	.000
	16,444	1,953	
		T=3298.4 (9 df) P<0.001	
Velocity (cm/s)			
0- 9	10,336	1,056	.102
10-19	2,168	435	.201
20-29	1,368	228	.166
30-39	792	106	.134
40-49	474	74	.157
50-59	517	33	.064
60-69	332	8	.023
70-79	190	6	.033
80-89	178	2	.013
90-119	90	4	.046
	16,445	1,952	
		T=251.7 (9 df) P<0.001	
Substrate			
Detritus	20	3	.155
Sand	188	0	.000
Sand-Gravel	34	0	.000
Gravel	319	80	.251
Gravel-Rubble	2,059	364	.177
Rubble	3,177	335	.105
Rubble-Boulder	6,412	744	.116
Boulder	2,989	412	.138
Boulder-Bedrock	209	7	.035
Bedrock	1,038	6	.006
	16,445	1,951	
		T=296.3 (7 df) P<0.001	

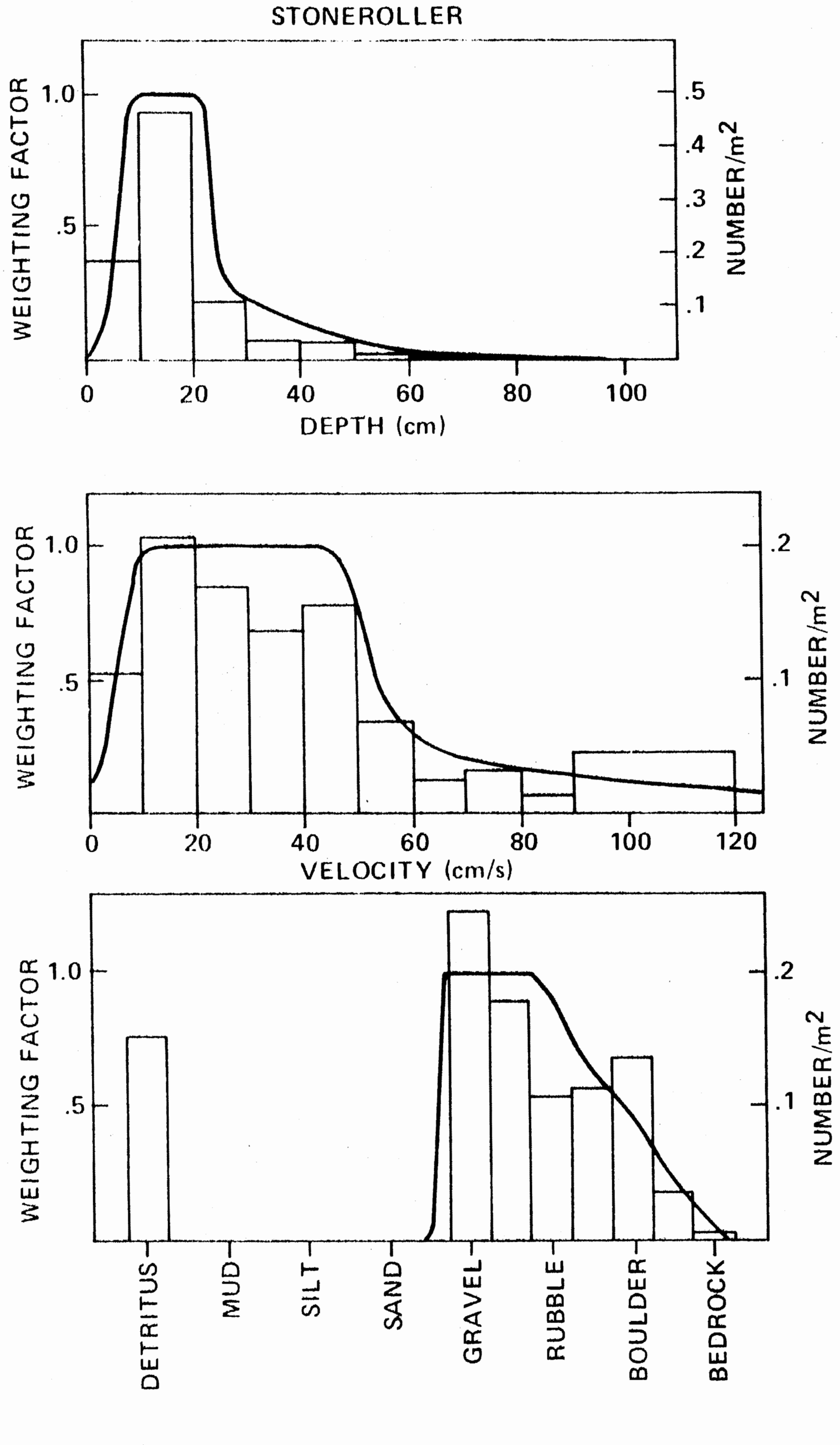

Figure 11. Density estimates and suitability weighting factors in relation to depth, velocity, and substrate, for the stoneroller in Glover Creek.

estimated density ($0.07/m^2$), and the exponential polynomial function of depth, velocity, substrate, and their interactions explained only 21.8% of the variation in density ($R^2=0.218$; Tables 25 and 26). The only variable which was significant after adjusting for all other variables was the depth-velocity interaction (DxV; P=0.0029; Table 25). Inclusion of this interaction term decreased the mean square error by 6%, from 1.6564 to 1.5543, and increased the R^2 value from 0.160 to 0.218. Partial correlation between density of the stoneroller and DxV was positive indicating that at higher depths the response surface would shift so that the maximum densities would occur at higher velocities. This significant depth-velocity interaction violates the assumption of independence which is inherent in the weighted usable area calculation used in the incremental methodology. The low amount of variation (21.8%) explained by depth, velocity, substrate, and their interactions, indicates that either these variables were not the most important variables affecting stoneroller distribution during spring 1979, or that the stoneroller population was below the carrying capacity of the stream at this point in time.

The exponential polynomial function, which was derived for the stoneroller during spring 1979 (Table 26), defines the response surface of density at various habitat conditions. However, this function cannot be reliably applied for depth, velocity, or substrate types outside the ranges which were sampled (Table 24).

During the summer 1979, the stoneroller population had a higher estimated density ($0.41/m^2$) and the exponential polynomial function explained 66.7% of the variation in density ($R^2=0.667$; Tables 27 and 28). A fourth-order series of depth terms was used in this model and therefore the exponential polynomial function does not hold at depths greater than

Table 25. Analysis of variance for multiple regression analysis of the dependent variable, $\log_e[(N+1)/(Area+1)]$ for the stoneroller, and independent variables: depth (D), D^2, velocity (V), V^2, substrate (S), S^2, DxV, DxS, and VxS, for spring 1979.

Source	df	Sum of squares	Mean square	F	P
Regression	9	53.7243	5.9694	3.84	0.0003
Error	124	192.7344	1.5543		
Correction total	133	246.4587			
		Sequential (Type I)			
D	1	32.6080	32.6080	20.98	0.0001
D^2	1	0.2174	0.2174	0.14	0.7091
V	1	1.6936	1.6936	1.09	0.2986
V^2	1	1.5885	1.5885	1.02	0.3140
S	1	0.2842	0.2842	0.18	0.6697
S^2	1	0.8857	0.8857	0.57	0.4518
DxV	1	14.0563	14.0563	9.04	0.0032
DxS	1	2.0034	2.0034	1.29	0.2584
VxS	1	0.3871	0.3871	0.25	0.6186
		Partial (Type IV)			
D	1	0.0030	0.0030	0.00	0.9653
D^2	1	3.1926	3.1926	2.05	0.1543
V	1	0.0043	0.0043	0.00	0.9583
V^2	1	0.6797	0.6797	0.44	0.5097
S	1	0.0139	0.0139	0.01	0.9247
S^2	1	0.0343	0.0343	0.02	0.8821
DxV	1	14.3217	14.3217	9.21	0.0029
DxS	1	2.3406	2.3406	1.51	0.2221
VxS	1	0.3871	0.3871	0.25	0.6186

Table 26. Estimates of the parameters of the exponential polynomial function relating density of the stoneroller, spring 1979, to depth (D), velocity (V), substrate (S), and their interactions. The model is $(N+1)/(Area+1) = \exp\left[\beta_0 + \beta_1 D + \beta_2 D^2 + \beta_3 V + \beta_4 V^2 + \beta_5 S + \beta_6 S^2 + \beta_7 DxV + \beta_8 DxS + \beta_9 VxS\right]$.

Variable	Parameter	Estimate
	β_0	-2.420064
D	β_1	-2.110190×10^{-3}
D^2	β_2	2.824449×10^{-4}
V	β_3	4.049990×10^{-3}
V^2	β_4	-2.239968×10^{-4}
S	β_5	0.157933
S^2	β_6	2.369075×10^{-2}
DxV	β_7	1.323058×10^{-3}
DxS	β_8	-9.861233×10^{-3}
VxS	β_9	-5.880265×10^{-3}

Table 27. Analysis of variance for multiple regression analysis of the dependent variable, $\log_e[(N+1)/(Area+1)]$ for the stoneroller, and independent variables: depth (D), D^2, D^3, D^4, velocity (V), V^2, substrate (S), S^2, DxV, DxS, and VxS, for summer 1979.

Source	df	Sum of squares	Mean square	F	P
Regression	11	280.9481	25.5407	14.38	0.0001
Error	79	140.3029	1.7760		
Corrected total	90	421.2509			
		Sequential (Type 1)			
D	1	146.0791	146.0791	82.25	0.0001
D^2	1	1.5998	1.5998	0.90	0.3455
D^3	1	42.7340	42.7340	24.06	0.0001
D^4	1	30.7010	30.7010	17.29	0.0001
V	1	17.3568	17.3568	9.77	0.0025
V^2	1	3.0765	3.0765	1.73	0.1919
S	1	0.8276	0.8276	0.47	0.4968
S^2	1	0.0491	0.0491	0.03	0.8684
DxV	1	24.6837	24.6837	13.90	0.0004
DxS	1	4.8554	4.8554	2.73	0.1022
VxS	1	8.9850	8.9850	5.06	0.0273
		Partial (Type IV)			
D	1	13.7202	13.7202	7.73	0.0068
D^2	1	13.4928	13.4928	7.60	0.0073
D^3	1	13.3650	13.3650	7.53	0.0075
D^4	1	11.7540	11.7540	6.62	0.0120
V	1	6.9282	6.9282	3.90	0.0517
V^2	1	5.2407	5.2407	2.95	0.0897
S	1	2.3790	2.3790	1.34	0.2506
S^2	1	4.6681	4.6681	2.63	0.1089

Table 27. (Continued).

Source	df	Sum of squares	Mean square	F	P
DxV	1	32.3557	32.3557	18.22	0.0001
DxS	1	10.4012	10.4012	5.86	0.0178
VxS	1	8.9850	8.9850	5.06	0.0273

Table 28. Estimates of the parameters of the exponential polynomial function relating density of the stoneroller, summer 1979, to depth (D), velocity (V), substrate (S), and their interactions. The model is $(N+1)/(Area+1) = \exp[\beta_0 + \beta_1 D + \beta_2 D^2 + \beta_3 D^3 + \beta_4 D^4 + \beta_5 V + \beta_6 V^2 + \beta_7 S + \beta_8 S^2 + \beta_9 DxV + \beta_{10} DxS + \beta_{11} VxS]$.

Variable	Parameter	Estimate
	β_0	1.749429
D	β_1	0.343397
D^2	β_2	$-13.733793 \times 10^{-3}$
D^3	β_3	21.904521×10^{-5}
D^4	β_4	$-10.799299 \times 10^{-7}$
V	β_5	0.225512
V^2	β_6	$- 1.195159 \times 10^{-3}$
S	β_7	- 2.267743
S^2	β_8	0.280705
DxV	β_9	6.523762×10^{-3}
DxS	β_{10}	$-22.989572 \times 10^{-3}$
VxS	β_{11}	$-37.016870 \times 10^{-3}$

60 cm because of the bi-modal nature of the fourth-order polynomial.

Most of the variables and all of the interaction terms in the model for summer 1979 were judged significant by the partial F tests (Table 27). Inclusion of the interaction terms in the model decreased the mean square error by 19%, from 2.181 to 1.776, and increased the R^2 value from 0.575 to 0.667. The most significant interaction was again the depth-velocity interaction. Without the depth-velocity interaction term in the model the R^2 would have been only 0.590, whereas without the depth-substrate and velocity-substrate interactions the R^2 values would have been 0.642 and 0.646, respectively. The assumption of independence, especially of depth and velocity, was invalid for the stoneroller and the importance of these interactions was greater in summer 1979 than in spring 1979.

Orangebelly Darter

Orangebelly darters were most common in shallow riffles and raceways. The null hypothesis that densities do not vary over the sampled range of the habitat variable was rejected for each habitat variable (Table 29; $P<0.001$). Densities of the orangebelly darter were greatest at depths from 10-19 cm, velocities from 40-49 cm/s, and over gravel substrate (Figure 12). As with the stoneroller data, the density estimate over detritus was not used for developing the substrate suitability curve (Figure 12). Weighted average density ($0.37/m^2$) was calculated for the optimum substrate range (gravel and gravel-rubble) and weighting factors for other substrate types were scaled to this value.

During the spring 1979, the orangebelly darter population had an estimated density of $0.29/m^2$. The exponential polynomial function with

Table 29. Total area sampled, and estimated number and density of the orangebelly darter in relation to depth, velocity, and substrate type in Glover Creek, January 1978 to September 1979.

Variable and interval	Area sampled (m^2)	Number	Number/m^2
Depth (cm)			
0- 9	2,253	540	.240
10-19	2,466	1,278	.518
20-29	2,688	606	.225
30-39	2,220	327	.147
40-49	1,425	102	.071
50-59	1,340	19	.014
60-69	956	2	.002
70-79	849	0	.000
80-89	847	1	.001
≥ 90	1,400	0	.000
	16,444	2,875	
		T=2590.9 (9 df) P<0.001	
Velocity (cm/s)			
0- 9	10,336	1,331	.129
10-19	2,168	527	.243
20-29	1,368	388	.284
30-39	792	261	.330
40-49	474	172	.363
50-59	517	88	.170
60-69	332	57	.172
70-79	190	25	.132
80-89	178	18	.101
90-119	90	8	.089
	16,445	2,875	
		T=491.3 (9 df) P<0.001	
Substrate			
Detritus	20	11	.555
Sand	188	0	.000
Sand-Gravel	34	2	.070
Gravel	319	203	.636
Gravel-Rubble	2,059	674	.327
Rubble	3,177	421	.133
Rubble-Boulder	6,412	1,078	.168
Boulder	2,989	479	.160
Boulder-Bedrock	209	4	.018
Bedrock	1,038	3	.003
	16,445	2,876	
		T=924.8 (7 df) P<0.001	

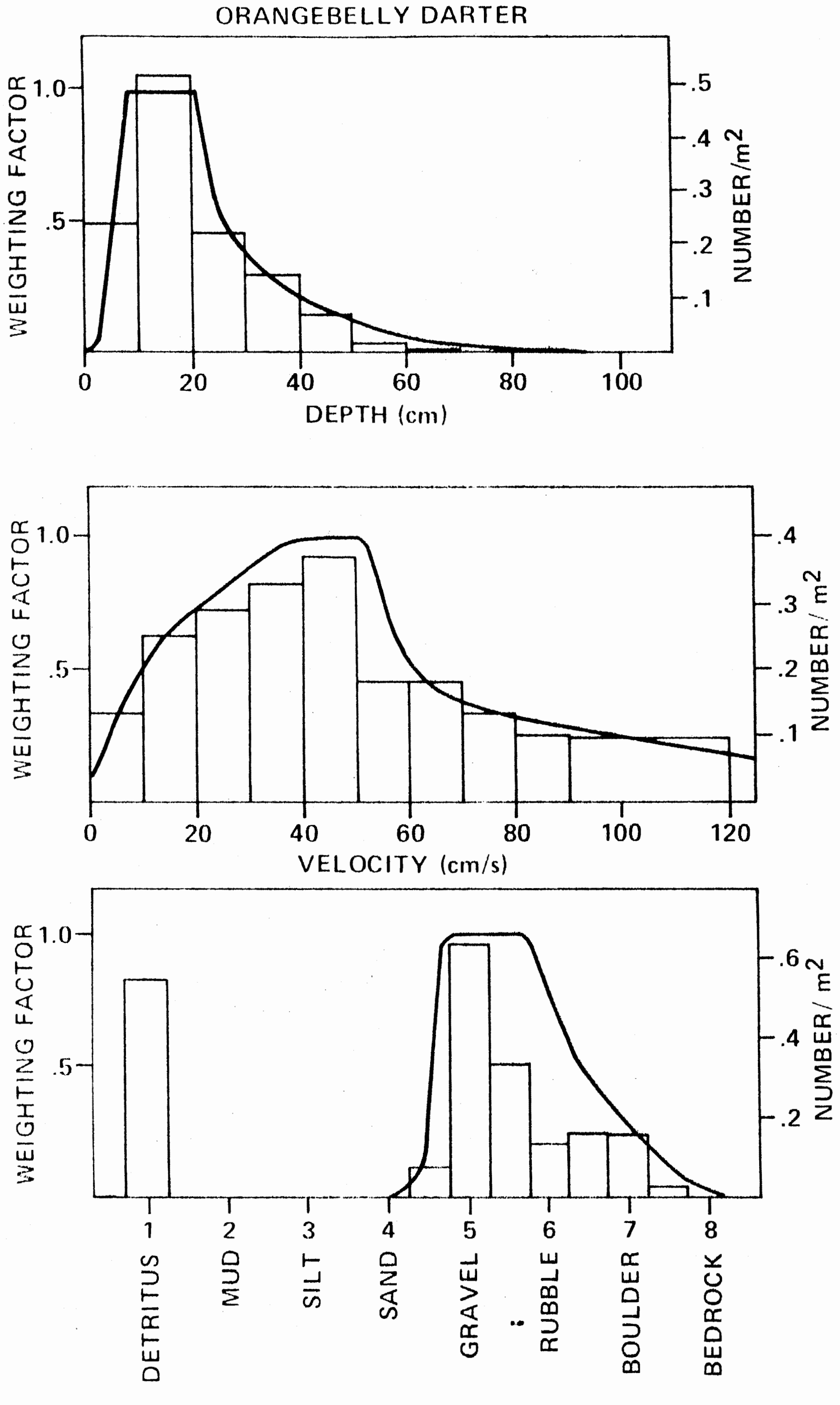

Figure 12. Density estimates and suitability weighting factors in relation to depth, velocity, and substrate, for the orangebelly darter in Glover Creek.

a third-order series of depth terms, fourth-order series of velocity terms, second-order series of substrate terms, and interaction terms explained 39.9% of the variation in density (R^2=0.399; Tables 30 and 31). None of the interaction terms significantly improved the fit of the model to the data (Table 30). Based on partial F tests, all velocity terms ($P<0.005$) and all depth terms ($P<0.10$) were significant, but the substrate terms were not (Table 30). Apparently within the range of substrates sampled (gravel to bedrock), substrate was not the most important variable. Depth and velocity were definitely important in affecting the distribution of orangebelly darters during spring 1979. However, considering the amount of variation explained (39.9%), either other factors were also equally important or the orangebelly darter population was below the carrying capacity of the stream at this point in time.

Because of the range of each habitat variable sampled and the use of third- and fourth-order terms in the model, the exponential polynomial function (Table 31) which defines the response surface of density at various habitat conditions for spring 1979 cannot be reliably applied at depths greater than 80 cm, velocities greater than 65 cm/s, or substrate types smaller than sand.

During the summer 1979, the orangebelly darter population had an estimated density of 0.41/m^2. An exponential polynomial function with a fourth-order series of depth terms, second order series of velocity and substrate terms, and interaction terms explained 71.1% of the variation in density (R^2=0.711; Tables 32 and 33). Only the depth terms, and the depth-velocity interaction term (DxV) were judged significant ($P<0.005$) by the partial F tests (Table 32). Inclusion of the depth-velocity interaction term in the model decreased the mean square error

Table 30. Analysis of variance for multiple regression analysis of the dependent variable, $\log_e[(N+1)/(Area+1)]$ for the orange-belly darter, and independent variables: depth (D), D^2, D^3, velocity (V), V^2, V^3, V^4, substrate (S), S^2, DxV, DxS, and VxS, for spring 1979.

Source	df	Sum of squares	Mean square	F	P
Regression	12	234.4422	19.5369	9.07	0.0001
Error	164	353.4210	2.1550		
Corrected total	176	587.8632			
		Sequential (Type I)			
D	1	131.6940	131.6940	61.11	0.0001
D^2	1	24.6170	24.6170	11.42	0.0009
D^3	1	16.9249	16.9249	7.85	0.0057
V	1	29.3432	29.3432	13.62	0.0003
V^2	1	0.0017	0.0017	0.00	0.9774
V^3	1	10.1998	10.1998	4.73	0.0310
V^4	1	14.5282	14.5282	6.74	0.0103
S	1	0.6805	0.6805	0.32	0.5749
S^2	1	2.5331	2.5331	1.18	0.2799
DxV	1	0.1144	0.1144	0.05	0.8180
DxS	1	2.2801	2.2801	1.06	0.3052
VxS	1	1.5252	1.5252	0.71	0.4014
		Partial (Type IV)			
D	1	8.3079	8.3079	3.86	0.0513
D^2	1	8.1453	8.1453	3.78	0.0536
D^3	1	6.3287	6.3287	2.94	0.0885
V	1	21.9680	21.9680	10.19	0.0017
V^2	1	22.1231	22.1231	10.27	0.0016
V^3	1	19.2645	19.2645	8.94	0.0032
V^4	1	15.9487	15.9487	7.40	0.0072

Table 30. (Continued).

Source	df	Sum of squares	Mean square	F	P
S	1	0.0293	0.0293	0.01	0.9074
S^2	1	0.0226	0.0226	0.01	0.9186
DxV	1	0.5828	0.5828	0.27	0.6037
DxS	1	3.5157	3.5157	1.63	0.2033
VxS	1	1.5252	1.5252	0.71	0.4014

Table 31. Estimates of the parameters of the exponential polynomial function relating density of the orangebelly darter, spring 1979, to depth (D), velocity (V), substrate (S), and their interactions. The model is $(N+1)/(Area+1) = \exp\left[\beta_0 + \beta_1 D + \beta_2 D^2 + \beta_3 D^3 + \beta_4 V + \beta_5 V^2 + \beta_6 V^3 + \beta_7 V^4 + \beta_8 S + \beta_9 S^2 + \beta_{10} DxV + \beta_{11} DxS + \beta_{12} VxS\right]$.

Variable	Parameter	Estimate
	β_0	$- 4.416257$
D	β_1	0.131039
D^2	β_2	$- 2.216020 \times 10^{-3}$
D^3	β_3	1.370094×10^{-5}
V	β_4	0.266026
V^2	β_5	$- 8.245234 \times 10^{-3}$
V^3	β_6	11.107827×10^{-5}
V^4	β_7	$- 4.709585 \times 10^{-7}$
S	β_8	0.214365
S^2	β_9	1.770406×10^{-2}
DxV	β_{10}	1.972065×10^{-4}
DxS	β_{11}	$-10.953525 \times 10^{-3}$
VxS	β_{12}	$- 7.310504 \times 10^{-3}$

Table 32. Analysis of variance for multiple regression analysis of the dependent variable, $\log_e[(N+1)/(Area+1)]$ for the orange-belly darter, and independent variables: depth (D), D^2, D^3, D^4, velocity (V), V^2, substrate (S), S^2, DxV, DxS, and VxS, for summer 1979.

Source	df	Sum of squares	Mean square	F	P
Regression	11	275.8517	25.0774	18.82	0.0001
Error	84	111.9345	1.3326		
Corrected total	95	387.7861			
		Sequential (Type I)			
D	1	148.3077	148.3077	111.30	0.0001
D^2	1	6.5568	6.5568	4.92	0.0292
D^3	1	49.4814	49.4814	37.13	0.0001
D^4	1	24.4257	24.4257	18.33	0.0001
V	1	22.5535	22.5535	16.93	0.0001
V^2	1	4.3260	4.3260	3.25	0.0752
S	1	0.3391	0.3391	0.25	0.6153
S^2	1	0.7365	0.7365	0.55	0.4593
DxV	1	14.9442	14.9442	11.21	0.0012
DxS	1	1.7229	1.7229	1.29	0.2587
VxS	1	2.4578	2.4578	1.84	0.1781
		Partial (Type IV)			
D	1	16.1789	16.1789	12.14	0.0008
D^2	1	18.4096	18.4096	13.82	0.0004
D^3	1	15.0541	15.0541	11.30	0.0012
D^4	1	11.9702	11.9702	8.98	0.0036
V	1	2.6295	2.6295	1.97	0.1638
V^2	1	3.3306	3.3306	2.50	0.1176
S	1	0.1453	0.1453	0.11	0.7421
S^2	1	0.0019	0.0019	0.00	0.9699

Table 32. (Continued).

Source	df	Sum of squares	Mean square	F	P
DxV	1	11.7020	11.7020	8.78	0.0040
DxS	1	3.0108	3.0108	2.26	0.1366
VxS	1	2.4578	2.4578	1.84	0.1781

Table 33. Estimates of the parameters of the exponential polynomial function relating density of the orangebelly darter, summer 1979, to depth (D), velocity (V), substrate (S), and their interactions. The model is $(N+1)/(Area+1) = \exp[\beta_0 + \beta_1 D + \beta_2 D^2 + \beta_3 D^3 + \beta_4 D^4 + \beta_5 V + \beta_6 V^2 + \beta_7 S + \beta_8 S^2 + \beta_9 DxV + \beta_{10} DxS + \beta_{11} VxS]$.

Variable	Parameter	Estimate
	β_0	-5.952499
D	β_1	0.380049
D^2	β_2	$-15.442515 \times 10^{-3}$
D^3	β_3	22.622678×10^{-5}
D^4	β_4	$-10.661934 \times 10^{-7}$
V	β_5	0.102666
V^2	β_6	-4.892682×10^{-4}
S	β_7	0.545803
S^2	β_8	5.440317×10^{-3}
DxV	β_9	3.176670×10^{-3}
DxS	β_{10}	$-11.334102 \times 10^{-3}$
VxS	β_{11}	$-14.448920 \times 10^{-3}$

by 8%, from 1.454 to 1.333, and increased the R^2 value from 0.681 to 0.711. Partial correlation between density of the orangebelly darter and DxV was positive indicating that at higher depths the response surface would shift so that maximum densities would occur at higher velocities. This significant interaction violates the assumption of independence which is inherent in the weighted usable area calculation.

The exponential polynomial function (Table 33) for summer 1979 cannot be reliably applied at depths greater than 60 cm or substrate types smaller than sand.

Discussion

There are several potential biases associated with development of habitat suitability curves for instream flow methodologies. The first type of bias arises when the distributions of the depth, velocity, and the substrate types sampled deviate from uniform. The second bias arises when sampling efficiencies vary over the range of each habitat variable. To deal with the first bias, relatively equal amounts of area must be sampled in each depth, velocity, and substrate interval, and then the frequency analysis technique (Bovee and Cochnauer 1977) can be applied. Most streams, however, do not always have a uniform distribution of depth, velocity and substrate, and therefore data on habitat availability must be collected to determine the amounts of area sampled over each habitat variable. Relative density estimates can then be calculated and the habitat suitability curves developed with relative density estimates will be free of this bias. The potential biases due to differential sampling efficiencies vary with species and therefore the discussion of these biases is broken down by species and life stages. The remainder of the discussion on each species deals with the problems associated with application of the habitat suitability criteria: independence of habitat variables; changes in habitat preferences among length groups; differences between localized populations; and physical habitat variables as limiting factors.

Smallmouth Bass - Adult

For the adult smallmouth bass, there were differences in the depth and velocity distributions determined from angling and electrofishing data, although both curves showed the same general trends. Both depth suitability curves declined markedly at depths greater than 120 cm (Figure 7) due to the lack of any current at these depths.

The velocity suitability curve based on angling data is probably the more reliable of the two velocity curves (Figure 7). Evidence from other investigators supports this conclusion since the optimum velocity range determined in this curve (0-20 cm/s) is similar to velocity ranges where adult smallmouth bass have been observed in streams (Munther 1970; Klauda 1975).

There were no differences between substrate frequency distributions determined by angling and electrofishing, and therefore the bias in the substrate curve due to sampling efficiencies is of no major concern. However, since boulder substrate was the predominant substrate type in Glover Creek and the most frequent substrate type at capture locations of adult smallmouth bass, bias due to non-uniform sampling distributions may be present. For example, other studies have indicated the importance of gravel and rubble substrates in addition to boulder substrate for smallmouth bass (Reynolds 1965; Paragamian 1978); however, the apparent selection for boulder substrates may, in fact, be related to cover. Adult smallmouth bass spend most of their time (79-91%) in position-holding and shelter-using behaviors in areas of low to moderate current velocities (Klauda 1975) and, in Glover Creek, boulders may provide cover and areas of reduced current.

The depth-substrate interaction, which was the only significant two-way interaction for adult smallmouth bass, may result from the changing depth and substrate preferences of smallmouth bass as they grow rather than from an interaction between depth and substrate preferences. In this study, larger smallmouth bass utilized microhabitats of greater depths and with larger substrate types than did the smaller individuals. However, there is not enough data to test if the depth-substrate interaction is still significant among larger sized fish. It is also possible that some of the depth-substrate interaction was caused by systematic error in classifying substrate types in deeper water, since the same interaction was also significant for juvenile smallmouth bass and adult green sunfish. At greater depths, water clarity sometimes prevented accurate distinction between rubble and boulder sized substrates. Until more data is collected, independence will have to be assumed for adult and juvenile smallmouth bass and adult green sunfish.

Smallmouth Bass - Juvenile

Except for the interaction of depth and substrate, the data did not indicate any significant deviations from the assumption of independence of habitat variables in habitat selection by juvenile smallmouth bass.

Juvenile smallmouth bass selected shallower areas of the stream and utilized smaller substrate types (gravel and rubble) than did adults and the greatest shift in habitat use occurred at 100 mm total length. In other species, such as the bluegill (Lepomis macrochirus), similar differences in the habitat utilized by different length groups have been attributed to predation forcing smaller fish into cover (Werner et al. 1977). For smallmouth bass, however, these differences may be related to the distribution of prey items, such as aquatic insects (Surber 1941; Lachner 1950; Pflieger 1966; Paragamian 1973), which are more abundant in the riffle habitats of streams (Surber 1939; O'Connell and Campbell 1953).

Green Sunfish - Adult

Suitability curves for adult green sunfish were based entirely on angling data and could not be adjusted for any bias due to non-uniform distributions because habitat availability data were absent. The depth and velocity suitability curves probably have no significant biases due to non-uniform distributions since a variety of depths and velocities were sampled at flow levels which were exceeded 36-37% of the time during the period of record (1961-1974). Preference for low velocity (0-5 cm/s) and moderate depths (40-120 cm) was also noted by Minckley (1963), Jones (1970), and Moyle and Nickols (1973), who found green sunfish most often in slow velocity pools.

In this study, green sunfish were found most frequently near boulder substrate, the predominant substrate in Glover Creek; however, other authors have found them over all substrates (Jenkins and Finnell 1957; Trautman 1957; Moyle and Nickols 1973). The preferences for boulder substrate may indicate a cover seeking response since Summerfelt (1967) noted this species was invariably associated with cover and in Glover

Creek potential cover was provided by boulders and, in some cases, undercut banks.

Different sized green sunfish occupied different depths and substrates, but not velocities. Larger green sunfish tended to select areas of greater depth and larger substrate types. The trend was the same as that observed for smallmouth bass. Social hierarchies in green sunfish are such that larger individuals dominate smaller individuals (Greenberg 1947). Therefore, rank in the dominance hierarchies may affect the habitat use of individual green sunfish and smallmouth bass as it does in two species of trout, *Salmo* (Jenkins 1969). The results of future studies relating social structure with habitat use would have implications for development of suitability criteria for fishes with a social structure. If dominant individuals are inhabiting the preferred areas and other individuals occupy less suitable habitat, the preferred habitat of the dominant individuals may in fact be the most preferred habitat of that species. Future attempts to refine habitat suitability criteria should, therefore, consider the influence of social structure on habitat selection.

Freckled Madtom

Suitability curves for the freckled madtom in Glover Creek agree with the observations of Pflieger (1975a) and Smith (1979) that they are found in gravel-bottomed riffle areas with moderate currents. Cross (1967), however, found the species more frequently over muddy areas with a sluggish current in Kansas, and Orth and Jones (1980) found the species in similar habitat in western Oklahoma. These differences in habitat indicate some plasticity in the habitat requirements of the freckled madtom. Differing habitat preferences could be attributed to the lack of gene flow between isolated populations, which has been observed for other species by Echelle et al. (1975) and Smith et al. (1976). In fact, Taylor (1969:79-81) noted that the freckled madtom tends to form distinctive localized populations. Although different habitat preferences between isolated populations of the same species may not be common, habitat suitability curves developed on a regional or site-specific basis would have more reliability than those developed over all habitats.

Stoneroller

No quantitative studies on habitat selection by the stoneroller are available for comparisons, although related studies indicated that the stoneroller prefers riffle habitat of headwater streams (Lewis and Elder 1953; Metcalf 1959; Smith and Powell 1971). Other studies (Lennon and Parker 1960; Layher et al. 1978) have noted the importance of gradient, which may reflect the preference for a certain range of depth, velocity, and substrate since each is related to gradient. Layher et al. (1978: 338) found that gradient and mean depth were the two most important variables affecting standing crops of the stoneroller in Kansas streams. In the Great Smoky Mountains National Park, Tennessee and North Carolina, the stoneroller did not occur in creeks with a gradient of more than 44 m/km, but were common in fast-flowing areas of stream reaches with lower gradients, 13-44 m/km (Lennon and Parker 1960). The lowest gradient section sampled, however, was still 13 m/km, and the stoneroller does inhabit streams of lower gradient. An average density of 0.21/m^2, calculated from the data of Lennon and Parker, was between the spring and summer density estimates for the stoneroller in the Glover Creek study areas, which had gradients somewhere between 2.3 and 18.9 m/km.

There is a potential bias in the depth and velocity curves for the stoneroller which was due to pooling data from all seasons. Population density of the stoneroller was much lower during the winter and spring sampling periods, at which time there was more habitat present at higher velocities at all depths. Conversely, during summer sampling periods, when density was higher, there was less habitat present at higher velocities. Therefore the density estimates for the upper range of velocities were based mostly on winter and spring data. Furthermore, during the summer most of the areas with a moderate current were relatively shallow. Therefore, the decline in suitability at depths greater than 20 cm and velocities greater than 50 cm/s may not be as steep as indicated by the data (Figure 11).

Similarity in habitat preferences of different subspecies of stoneroller must be established before these curves can be generally applied. Two supspecies of the stoneroller are generally recognized: the Ohio stoneroller, _C. a. anomalum_, and the central stoneroller, _C. a. pullum_. Although the stoneroller from Glover Creek is _C. a. pullum_, the suitability curves may be applicable to _C. a. anomalum_ since general habitat preferences of the two subspecies are similar (Burr 1976).

Depth, velocity, substrate, and their interactions explained considerably more of the variation in stoneroller density during summer 1979 (66.7%) than in spring 1979 (21.8%). Densities were very low during spring 1979 (0.07/m^2), which may account for the lack of significance. Previous conditions such as low flow conditions during summer and fall 1978 and high winter and spring flows may be related to the low density of stonerollers during spring 1979, at which time populations were probably below carrying capacity. Low flows could increase mortality indirectly by forcing stonerollers into marginal habitats, shallow pools, where they are more vulnerable to predation. Stonerollers have been identified in the stomachs of spotted bass, *Micropterus punctulatus*, and largemouth bass, *M. salmoides* (Scalet 1977). High flows might possibly cause mortality either directly by bombardment with moving bedload or indirectly due to increased stress and fatigue brought on by continually swimming against the current.

The fact that depth, velocity, substrate, and their interactions explained 66.7% of the variation during the summer 1979 strengthens the assumption that these variables are important, at least during summer conditions. However, the significant depth-velocity interaction indicates that the assumption of independence of these two variables for the stoneroller would lead to some error in weighted usable area. The degree of error would probably be greatest the farther depth and velocity are from the optimum. Assuming independence of depth and substrate, and velocity and substrate would also lead to error, though, based on the data for Glover Creek, it would be less than that due to assuming independence of depth and velocity.

The interaction of depth and velocity affects the distribution of the stoneroller. At shallow depths and high velocities the stoneroller may not be able to maintain position and feed efficiently, since at a given velocity, as depth decreases, turbulence would increase. Conversely, at higher depths turbulence would decrease and, the stoneroller may be able to maintain in habitats with higher mean column velocities. Also, since the stoneroller feeds on the stream bottom, during feeding they are actually in areas of lower velocity than if they fed at the mean column velocity.

The effect of assuming independence of depth, velocity, and substrate, on the weighted usable area calculations and the ultimate flow recommendation cannot be accurately determined for the stoneroller until a multivariate suitability function can be derived that holds for all regions of depth, velocity, and substrate space. The effect on the ultimate flow recommendation may not be great when one considers that suitable habitat conditions are still closely approximated. Recommended flows based on the assumption of independence should still provide suitable habitat for the species.

Orangebelly Darter

Little quantitative data exist on the habitat preferences of the orangebelly darter. Scalet (1973) estimated densities of the orangebelly darter to be $2.66/m^2$ in raceway habitat, and noted that as many as $10/m^2$ may occupy the more preferred areas within the raceways. This population density is considerably higher than the estimated densities of the orangebelly darter in Glover Creek during spring ($0.29/m^2$) and summer ($0.41/m^2$), 1979. However, the density estimates for Glover Creek apply to all habitat types encountered (pool, riffle, raceway). Average densities in more suitable habitat (depth: 10-30 cm; velocity: 20-60 cm/s; substrate: gravel to boulder) were $0.52/m^2$ and $1.94/m^2$ in spring and summer 1979, respectively. These estimates are still less than the density reported by Scalet (1973). In spite of density differences, the habitat in which Scalet (1973) found the orangebelly darter in the Blue River, Oklahoma, was similar to that for the orangebelly darter in Glover Creek (Figure 12). Apparently the subspecies of orangebelly darter in Glover Creek,

E. r. radiosum, has similar habitat requirements to the subspecies in the Blue River, E. r. cyanorum. Differing habitat preferences between isolated populations, therefore, do not seem to be a problem, even though there is little gene flow between populations of the orangebelly darter in different drainages (Echelle et al. 1975).

There is potentially some bias in the depth and velocity suitability curves since the high velocities were typically present only at lower population densities during winter and spring. Therefore the decline in suitability at depths greater than 20 cm and velocities greater than 50 cm/s may not be as steep as indicated by the data (Figure 12).

The fact that less of the variation in density of the orangebelly darter could be explained by depth, velocity, substrate, and their interactions, in spring than in summer 1979 supports the hypothesis that usable habitat or space is limiting for darter populations only during summer months. Usable habitat may be limiting populations directly, or indirectly by limiting either the production or drift of aquatic insects, which in turn may affect the territory size and density. Competition with other darter species during non-breeding seasons is probably non-existent since the next most abundant darters in Glover Creek (channel darter, Percina copelandi, and leopard darter, P. pantherina) are present at extremely low densities and occupy different microhabitats (Jones et al. 1979; Orth and Maughan 1980, and unpublished data). Therefore, the assumption that depth, velocity, and substrate are important variables affecting distribution of the orangebelly darter is supported by the summer data. During the spring, either other factors were equally important, or the orangebelly darter population was below the carrying capacity of the stream. Predation as a factor affecting distribution can probably be ruled out since predation on orangebelly darters was never detected in a study of the food habits of potential predators (Scalet 1974). Since adults of many aquatic insects typically emerge during the spring, limited populations of the immature aquatic insects at this time (Orth and Maughan, unpublished data) may also have affected the distribution of orangebelly darters.

The depth-velocity interaction effect on density of the orangebelly darter was the only significant interaction and was only significant during summer 1979. Lack of significance of the depth-velocity interaction during spring 1979 may be related to the fact that physical factors (depth, velocity, and substrate) were less important during spring 1979.

During summer 1979 the significant depth-velocity interaction may be related to the need for a certain range of current velocity in the microhabitat of the orangebelly darter. Since orangebelly darters live and feed among the substrate of the stream bottom, velocity at the bottom must be fast enough to facilitate respiration for both the darter and its prey items and yet not so fast that the organisms are bombarded with bedload movement. As depth increases, the mean column velocity necessary to provide velocity within a suitable range on the stream bottom increases. In addition, other factors may have had an influence during the summer period but not during the spring. Oxygen, which was typically super-saturated during the spring but below saturation during the summer, may have been one such factor. For example, critical oxygen tension as high as 6.1 ppm was reported for _E_. _rufilineatum_, a darter that occurs in fast-water habitats (Ultsch et al. 1978). Another possibility is that oxygen was limiting the distribution of the prey of the orangebelly darter (aquatic insects; Scalet 1972). In aquatic insects of the

Ephemeroptera, Trichoptera, and Plecoptera, current speed and the limiting oxygen concentration are inversely related (Ambühl 1959, 1961, 1962; cited by Hynes 1970) so that at faster current velocity the minimum oxygen levels for survival decrease (Knight and Gaufin 1963, 1964; Philipson 1954). This phenomenon may also hold for stream fishes, such as the orangebelly darter, though it has not yet been documented (Hynes 1970).

Although inclusion of the depth-velocity interaction term only decreased the mean square error by 8% for summer 1979 data, the error in assuming independence when calculating weighted usable area would be greater the farther depth and velocity are from the optimum. However, the effect of this error on recommending minimum flows may not be great since the region of optimum habitat is still closely approximated and, therefore, recommended flows would provide suitable habitat. Instream flow methodologies previously used depth and velocity criteria consisting of simply a definition of a suitable range (Collings et al. 1970; Smith 1973; Thopmson 1974; Bovee et al. 1977) and, therefore, the multiplication of suitability weighting factors is an improvement. However, research on the changes in minimum flow recommendation caused by assuming independence for various types and degrees of interaction is necessary to help those using the incremental method to decide when it would be safe to assume independence. It should be recognized that data requirements for developing multivariate suitability functions for just three variables and their interactions will be great; however, accurate assessment of the effects of altered flows depends on an accurate description of habitat requirements.

Flow recommendations have previously been developed with the incremental method, assuming independence, and have yielded reasonable recommendations (Pruitt and Nadeau 1978; Wegner 1979; McNatt et al. 1980). However, the present study indicated that the interaction of depth and velocity had an important effect on the distribution of three of the five species studied. Therefore, the effect on flow recommendations of ignoring this interaction needs further investigation. Of greater concern, however, may be the consideration of the importance of other variables in instream flow assessments. Suitability curves developed for depth, velocity, and substrate, define necessary conditions for these species, but in all cases suitability based only on these variables may not be sufficient for survival. This criticism of the incremental method was also raised by Patten et al. (1979). However, until research efforts are successful in determining how many and which variables are sufficient for survival of target species of fishes, and until models are developed that can be parameterized to predict the values of these variables in relation to discharge, the incremental method offers one practical tool.

CHAPTER V

RELATIONSHIPS BETWEEN USABLE HABITAT AND STANDING CROP FOR FISHES OF GLOVER CREEK

Introduction

No previous studies have established a relationship between usable habitat (as defined by the product of depth, velocity, and substrate weighting factors) and biomass of any warm-water stream fish. Yet the existence of a positive, linear relation between weighted usable area and standing crop is a necessary assumption for recommending instream flows with the incremental method. If there is no positive, linear relation between weighted usable area and biomass of fishes, then factors other than these parameters of habitat are limiting populations and instream flows cannot be reliably based on the amount of weighted usable area. If, however, a positive, linear relation is established, then it may be possible to estimate the level of fish biomass that could be sustained at different discharge levels.

Studies on the relations between physical factors and standing crops of stream fishes have been concentrated on salmonids in cold-water streams (Lewis 1969; Burns 1971; Burton and Wesche 1974; Wesche 1974; Nickelson 1976; Platts 1976; White et al. 1976; Binns and Eiserman 1979). Although the results of these studies may not be directly applicable to warm-water streams, some of the same mechanisms may be operating. Chapman (1966) speculated that during the summer, the density of drift-feeding salmonids is regulated by a space-food, and sometimes a space-shelter, mechanism. In areas of higher velocities, drift-feeding salmonids require less space to obtain needed food; therefore, territory size is reduced, population densities can be higher, and both food and space interact to regulate population density. In addition there may be a minimal spatial requirement of individuals regardless of food supply, so that when space is extremely limited or fish are present at extremely high densities, space will become the sole factor regulating density. Space could also act to regulate density because of limited shelter from predation and, during seasons of high flow, limited shelter from excessive currents. Since such needs as protection from currents should vary with season, the mechanisms which regulate density probably also vary seasonally. Chapman's hypotheses seem to be supported by laboratory experiments, which showed that density of young rainbow trout, Salmo gairdneri, increased and territory size decreased as prey abundance increased (Slaney and Northcote 1974), as well as field studies which showed that population density of salmonids was related to the habitat attributes of the stream affecting amount of usable habitat (Lewis 1969; Burns 1971; Nickelson 1976; Binns and Eiserman 1979). Weighted usable area, which also measures the amount of usable habitat, was positively correlated with the biomass of brown trout, Salmo trutta, in eight Wyoming streams (Stalnaker 1979).

For warm-water stream fishes, there have been a limited number of studies that attempted to relate habitat suitability to density. Matthews and Hill (1979) found that temperature, current velocity, and depth had the greatest influence on the habitat selection by the red shiner, Notropis lutrensis. Gorman and Karr (1978) found a positive relationship between habitat structure, as defined by depth, velocity, and substrate, and fish species diversity. Although both of these studies emphasized the importance of physical factors as they influence habitat selection, neither demonstrated that usable space had any regulatory effect on population density. Paragamian (1978), however, did find a curvilinear relationship between the standing crop of smallmouth bass and proportions of suitable substrate (gravel and rubble) in an Iowa stream. This relationship may indicate a space-food mechanism if, in this case, the food of smallmouth bass (insects, fish, and crayfish) was also more abundant in habitats with gravel and rubble substrate, as some studies have indicated (Surber 1939; Bovbjerg 1970).

The instream flow methodology assumes that populations are limited by usable habitat, but the importance of this factor remains to be verified. Theoretically, limiting factors may vary with different species and seasons. Therefore, the objective of this portion of the study was to determine the extent to which usable habitat (or space), as measured by weighted usable area, was limiting biomass standing crop of fishes during different seasons in Glover Creek.

Methods

The relation between weighted usable area and standing crop was examined for four of the fish species for which habitat suitability curves had been previously developed: smallmouth bass (juvenile and adult), freckled madtom, stoneroller, and orangebelly darter.

Four study sites were chosen, two riffles and two pools. The riffle sites initially chosen were located at sites 74100 and 71300 (Figure 5), and were designated 74100R and 71300R, respectively. Site designations correspond to the number of the nearest logging road. In the spring 1978, site 71300R was abandoned due to high flows and replaced with site 61200R (Figure 5). The pool sites, designated 61200P and 74100P, were located immediately downstream from riffle sites 61200R and 74100R, respectively. An additional site was utilized during summer 1979 for the orangebelly darter at 72000 (Figure 6). This site contained riffle, raceway, and pool habitats and data used to develop the suitability curves were not taken from this location.

Population estimates for juvenile and adult smallmouth bass, freckled madtom, stoneroller, and orangebelly darter were made four times per year from November 1977 to September 1979. Sites were blocked at the upstream and downstream ends with a block net (6.4 mm mesh) to prevent movement of fish into and out of the study area. Fishes were captured using one of two types of electroshocking gear: a boat-mounted generator and variable voltage pulsator with hand-held electrodes; and a Smith-Root Type VII backpack electroshocker. Pulsed direct current was used with both of these units. The boat-mounted unit was always used in the pools, but was used in the riffles only when the water level was such that the boat could be maneuvered through the riffle. Fishes were captured on three or more units of effort and held in floating live bags outside of the block net. Data on the number of fish captured on each unit of effort was used to estimate population size by a maximum weighted likelihood technique (Carle and Strub 1978). Total lengths (mm) and individual weights (grams) were measured for all smallmouth bass. For the smaller fishes, total lengths were measured from a sub-sample and group weights were measured. Estimated biomass was then calculated for each species, except for the smallmouth bass in which biomass of juveniles and adults was calculated separately.

At each site, four to six permanent transects were established, along which to measure habitat characteristics. Bed elevations were surveyed with a builder's level and level rod at one meter intervals along each transect. At the same time the substrate type at each interval was classified and given a numerical code (Bovee and Cochnauer 1977). During each sampling period, depth and velocity were measured at the same intervals, and water surface elevation was measured at each transect. Depth was measured with a metric wading rod and the mean column velocity was measured at 0.6 of the depth from the water surface with a pygmy current meter. These data were used to calibrate the IFG4 hydraulic simulation program which fits power functions to the stage-discharge data for each transect and to the velocity-discharge data for each one-meter segment of each transect (Main 1978a). The IFG4 model was used to estimate the depths and velocities at the time of sampling, which was often at a different discharge than the one at which depths and velocities were measured. Weighted usable areas for smallmouth bass (juvenile and adult), freckled madtom, stoneroller, and orangebelly darter, at the time of sampling, were then calculated based on the habitat suitability curves developed in the previous chapter. Computations of weighted usable area were done using the Habitat program (Main 1978b).

For each season, the biomass of each species or life stage per weighted usable area was averaged over all sites. This enabled comparisons between seasons on the amount of biomass relative to the amount of usable habitat. Also, for each season, the estimated biomass of each species or life stage per total surface area was regressed against weighted usable area expressed as a percentage of the total surface area, and correlation coefficients were calculated.

Results and Discussion

Smallmouth Bass - Juvenile

Biomass of juvenile smallmouth bass (<150 mm total length) and biomass per weighted usable area followed the same trend as weights of individual juveniles, being lowest in summer and increasing through fall, winter, and spring (Table 34). Values of biomass per weighted usable area are relatively low, ranging from 0.74 kg/hectare in summer to 2.03 kg/hectare in spring. These data indicate that the amount of usable habitat is probably not limiting abundance. Two other lines of evidence support this hypothesis. Biomass of juvenile smallmouth bass per total area was not correlated with weighted usable area during any season (Figure 13). The correlation for winter approached significance (P=0.057), but elimination of a single high data point would have resulted in a nonsignificant correlation. The other line of evidence supporting the hypothesis that usable habitat was not limiting abundance was that the abundance of juvenile smallmouth bass in summer 1979 was much higher than abundance in summer 1978, yet the amount of weighted usable area varied by less than 3% between the two summers (Table 34).

Abundance of smallmouth bass less than 200 mm was related to the proportions of suitable substrate (gravel and rubble) in an Iowa stream (Paragamian 1978), but in Glover Creek, the presence of suitable substrate was probably never a limiting factor for juveniles. This conclusion follows because, based on substrate suitability curves (Figure 8), almost all the substrate in the study areas was suitable, with only minimal amounts of sand and silt. In contrast, Paragamian's data set included

Table 34. Total estimated biomass (grams), weighted usable area (m^2), and biomass per weighted usable area (kg/hectare) for juvenile smallmouth bass in Glover Creek, November 1977 to September 1979.

Season	Biomass (grams)	Weighted usable area (m^2)	Biomass per weighted usable area (kg/hectare)
Fall			
Nov-Dec 1977	123	866.07	1.42
Oct 1978	27	657.23	0.41
Combined	150	1,523.30	0.98
Winter			
Jan-Mar 1978	130	755.60	1.72
Jan 1979	12	410.86	0.29
Combined	142	1,166.46	1.22
Spring			
Apr 1978	109	487.76	2.23
Apr-Jun 1979	94	513.99	1.83
Combined	203	1,001.75	2.03
Summer			
Jul 1978	25	873.61	0.29
Aug-Sep 1979	103	852.49	1.21
Combined	128	1,726.10	0.74

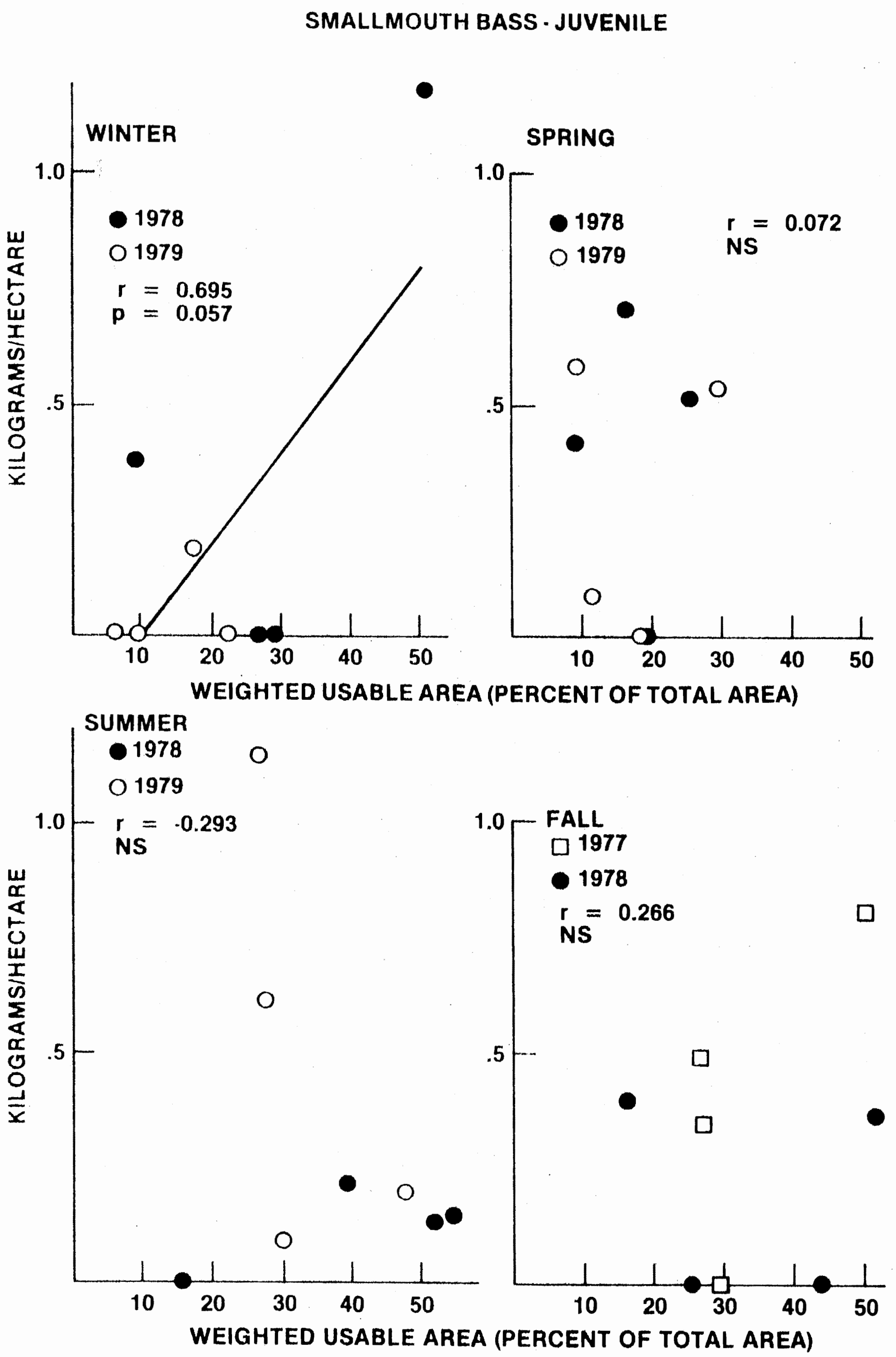

Figure 13. Correlations between standing crop of juvenile smallmouth bass and weighted usable area for each season.

several sites in areas of marginal smallmouth bass habitat containing vast stretches of silt and sand.

Juvenile smallmouth bass abundance in Glover Creek was most likely limited by factors other than habitat. Other investigators have established the negative influence of low temperatures during the first year of life on recruitment of smallmouth bass in lakes in northern latitudes (Fry and Watt 1957; Forney 1972; Clady 1975), but this factor probably did not limit reproduction in Glover Creek, which is at the southern edge of the range of smallmouth bass. Food for juvenile smallmouth bass was probably adequate since Mauck (1972) found that, during their first year, smallmouth bass in Glover Creek grew faster than the averages for smallmouth bass in Missouri (Purkett 1958) and the Little River system, Oklahoma (Finnell et al. 1956). In streams, such as Glover Creek, flooding during or after the spawning period seems to be a dominant factor influencing survival of eggs and fry (Surber 1939, 1943; Cleary 1956; Funk and Fleener 1974; Larimore 1975; Pflieger 1975b). Timing of spring floods in Glover Creek, may likewise have limited reproduction of smallmouth bass such that the influence of usable habitat for juveniles was not important.

Smallmouth Bass - Adult

Biomass of adult smallmouth bass per weighted usable area, as well as total estimated biomass, was highest during fall and summer, and lowest during winter and spring (Table 35). The decrease in the total biomass during the winter period may be due to movements rather than mortality because total biomass increased in the spring, summer, and fall more than would be expected simply from recruitment of juveniles to the

Table 35. Total estimated biomass (grams), weighted usable area (m^2), and biomass per weighted usable area (kg/hectare) for adult smallmouth bass in Glover Creek, November 1977 to September 1979.

Season	Biomass (grams)	Weighted usable area (m^2)	Biomass per weighted usable area (kg/hectare)
Fall			
Nov-Dec 1977	1,120	701.94	15.96
Oct 1978	1,743	443.39	39.31
Combined	2,863	1,145.33	25.00
Winter			
Jan-Mar 1978	310	683.59	4.53
Jan 1979	0	785.45	0.00
Combined	310	1,469.04	2.11
Spring			
Apr 1978	896	801.97	11.17
Apr-Jun 1979	286	807.05	3.54
Combined	1,182	1,609.02	7.35
Summer			
Jul 1978	1,707	491.15	34.76
Aug-Sep 1979	323	695.75	4.64
Combined	2,030	1,186.90	17.10

adult size and growth of adults. Munther (1970) found that during late fall and winter, at temperatures below 15.5 C, smallmouth bass were concentrated in deep pools. In contrast, study pools on Glover Creek were relatively shallow (mean depth less than 1 meter), and during the winter months adult smallmouth bass may have sought out deeper pools. Residence in deeper pools during winter and early spring would provide more protection from high flows during a time when adult smallmouth bass are typically less active (Klauda 1975).

No comparable data on biomass of adult smallmouth bass per weighted usable area are available from other studies. Biomass per total surface area has been estimated by other workers but these estimates would be less than the corresponding biomass per weighted usable area, although the degree of this difference cannot be determined. Funk (1975) summarized thirty-five standing crop estimates of smallmouth bass in streams and found that the mean biomass per total area was 9.5 kg/hectare, and the range was 0.2 to 46.3 kg/hectare. The mean of the eleven highest sites was 18.0 kg/hectare. Considering that the aforementioned estimates of biomass per total area are underestimates of the biomass per weighted usable area, my estimates of biomass per weighted usable area (Table 35) are relatively low. Only during the summer and fall periods did biomass per weighted usable area in Glover Creek approach that typically found elsewhere for biomass per total area.

Mauck (1972) estimated the standing crop of smallmouth bass in Glover Creek at 19.6 kg/hectare in a relatively shallow pool and 54.6 kg/hectare in a deeper pool. These greater estimates could be due to the more downstream location of Mauck's sites, the different sampling technique used (prima cord explosives), or temporal variation in standing crop.

In addition to low estimates of biomass per weighted usable area, the lack of any significant correlations between biomass per total area and weighted usable area for any season (Figure 14) suggests that usable habitat was not limiting abundance of adult smallmouth bass in Glover Creek. Also, differences between estimated biomass in different years was not related to the amount of weighted usable area for any season (Table 35). Adult smallmouth bass were, however, always absent or nearly so at sites with weighted usable area less than 5% of the total surface area (Figure 14). Therefore, presence of adult smallmouth bass may be limited by usable habitat when conditions are marginal. In Glover Creek, habitat for adult smallmouth bass becomes marginal at the extremely high and low flows, and then usable habitat is a prime limiting factor. For example, flows were near zero during summer 1978 and the few data points fell on a straight line (Figure 14). As stated earlier, timing of spring flooding in Glover Creek may have limited reproduction in previous years to the extent that the amount of usable habitat for adults was not limiting. If so, then production of several large year classes of smallmouth bass might result in the amount of usable habitat and its influence on food during the growing season and shelter during high flows limiting smallmouth bass abundance.

Another explanation for the lack of significant correlations between weighted usable area and standing crop is that adult smallmouth bass use different microhabitats for feeding and resting (Munther 1970). Since the suitability curves (Chapter IV) were not developed at this level of resolution, they are a composite description of the two microhabitats. The resulting values of weighted usable area may, therefore, be an

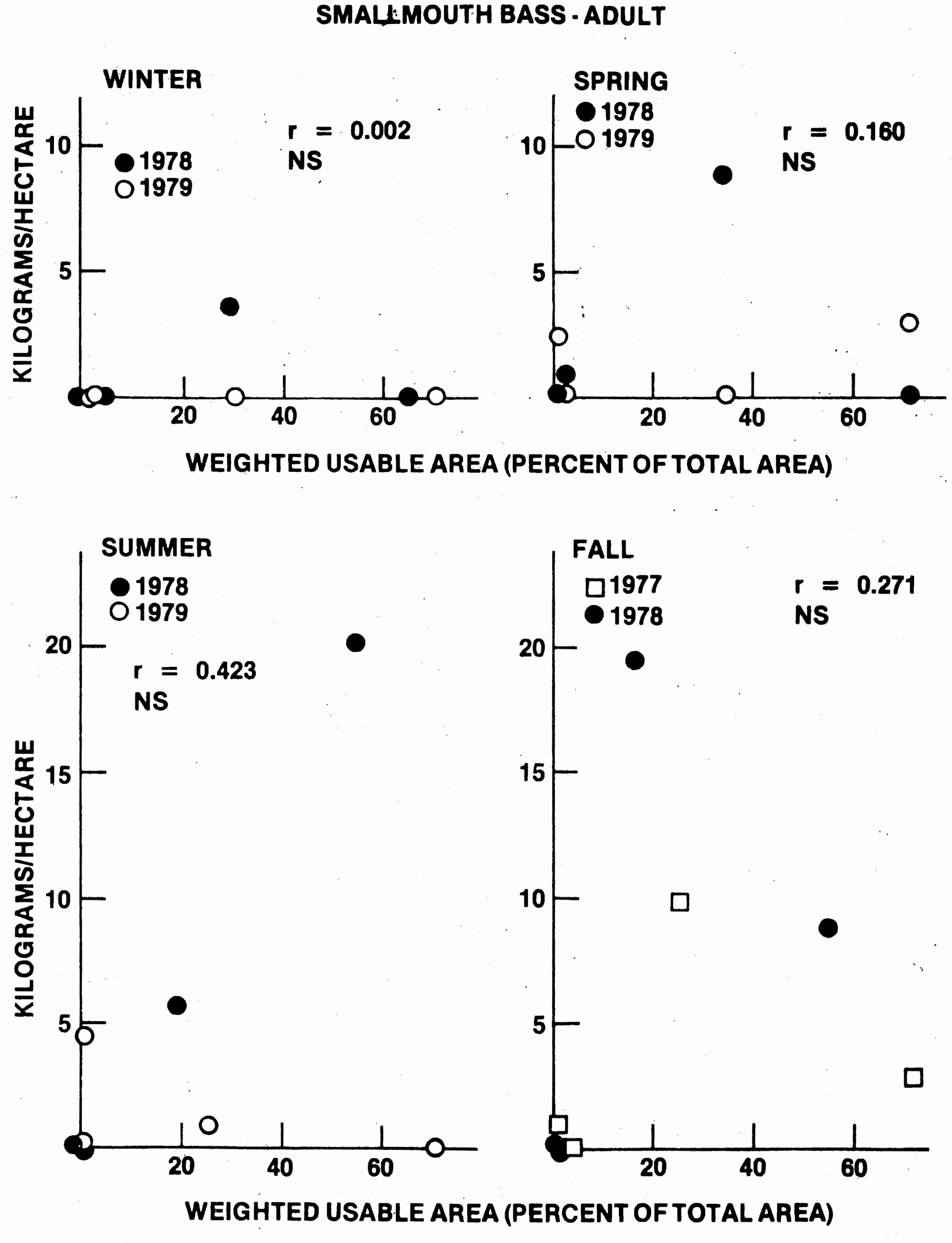

Figure 14. Correlations between standing crop of adult smallmouth bass and weighted usable area for each season.

inaccurate measure of actual usable habitat. Furthermore, other variables which influence the abundance of smallmouth bass, such as cover (Haines and Butler 1969; Hickman 1975), were not considered and this may have resulted in an inaccurate measurement of usable habitat.

Freckled Madtom

Biomass per weighted usable area was highest during summer (4.96 kg/hectare), followed by spring (2.82), fall (1.79), and winter (0.78) (Table 36). Differences between the estimated total biomass between years within the summer and fall sampling periods seem to be related to the amount of weighted usable area (Table 36). Furthermore, there were significant positive correlations between biomass per total area and weighted usable area (percentage of total area) for summer ($r=0.927$; $P<0.001$), and fall ($r=0.754$; $P<0.050$), and near-significant correlation for spring ($r=0.682$; $P=0.064$) (Figure 15). The seasons in which the correlations between biomass and weighted usable area were significant were also the seasons of highest biomass (Figure 15; Table 36), and the most likely seasons of maximum growth of the freckled madtom. The slope of the regression was greatest for the summer data indicating that the influence of usable habitat on biomass of freckled madtoms was greatest during the summer period.

The mechanism by which usable habitat influences populations of madtoms is not known. However, it is clear that habitat influences are significant, especially during the summer, and therefore the assumption of a positive relation between weighted usable area and standing crop is supported for the freckled madtom.

Table 36. Total estimated biomass (grams), weighted usable area (m^2), and biomass per weighted usable area (kg/hectare) for the freckled madtom in Glover Creek, November 1977 to September 1979.

Season	Biomass (grams)	Weighted usable area (m^2)	Biomass per weighted usable area (kg/hectare)
Fall			
Nov-Dec 1977	32	226.66	1.41
Oct 1978	9	2.51	35.86
Combined	41	229.17	1.79
Winter			
Jan-Mar 1978	33.5	226.63	1.48
Jan 1979	2	226.01	0.09
Combined	35.5	452.64	0.78
Spring			
Apr 1978	97	293.98	3.30
Apr-Jun 1979	68	292.01	2.33
Combined	165	585.99	2.82
Summer			
Jul 1978	17	10.20	16.67
Aug-Sep 1979	86	197.42	4.36
Combined	103	207.62	4.96

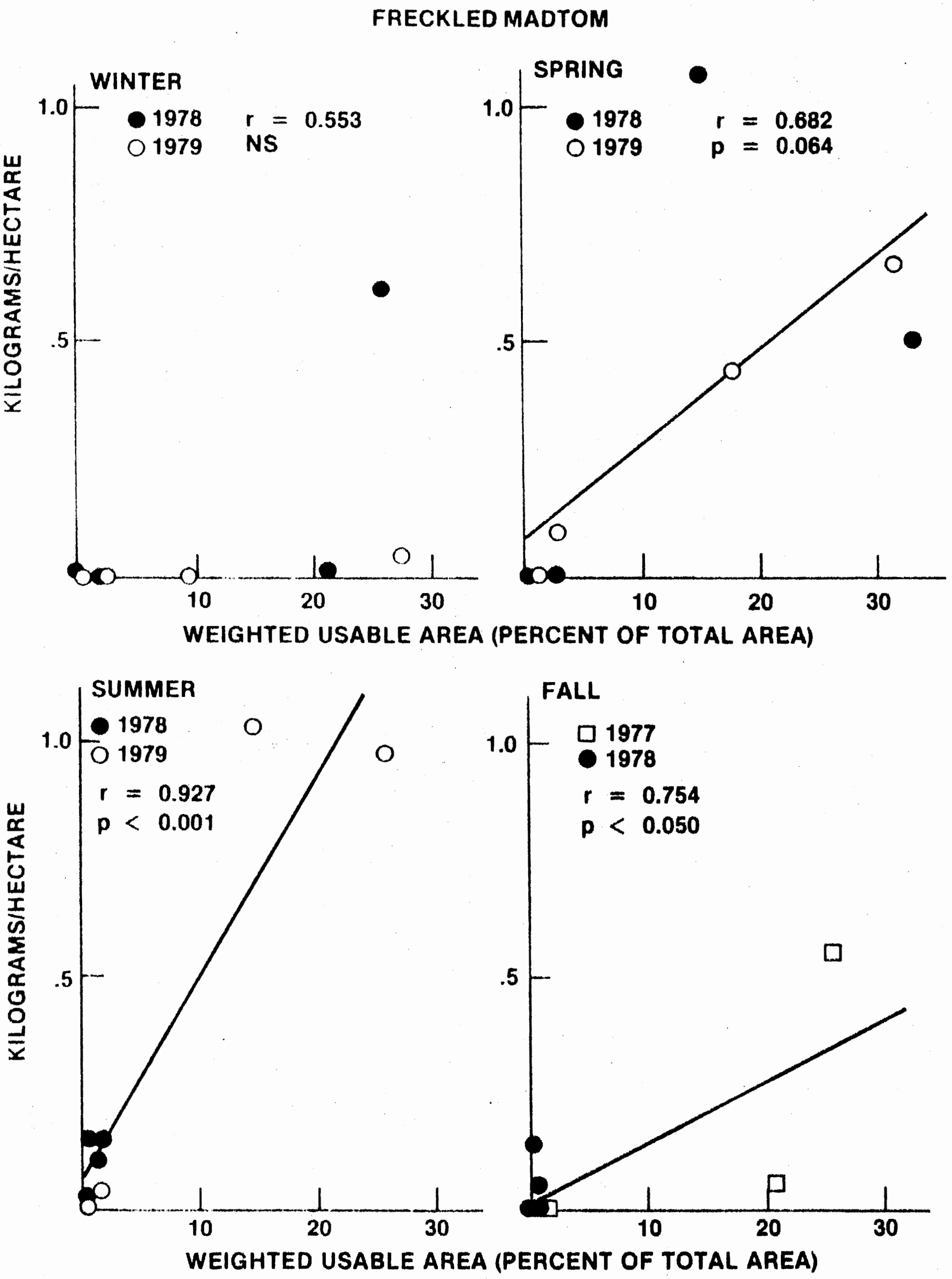

Figure 15. Correlations between standing crop of the freckled madtom and weighted usable area for each season.

Stoneroller

Biomass of the stoneroller per weighted usable area was greatest during the summer (108.81 kg/hectare), and decreased from summer to fall (34.92), winter (15.99), and spring (9.83) (Table 37). Usable habitat was most likely limiting during the summer and fall when biomass per usable habitat was highest. During the summer and fall, the total estimated biomass for different years corresponded to the amounts of weighted usable area (Table 37). Biomass per total area and weighted usable area (percentage of the total area) were correlated for the winter, summer, and fall periods (Figure 16). The slope was greatest for the summer data indicating that the influence of usable habitat on standing crop of stonerollers was greatest during the summer.

The stoneroller is similar to the freckled madtom, and most minnows and darters in that it is a relatively small fish that reaches maturity early (Moyle and Li 1979) and can respond quickly to favorable environmental conditions. The stoneroller feeds on algae and detritus (Kraatz 1923; Wynes 1979), and is probably not limited by food supply because, in general, most herbivores are not food-limited (Hairston et al. 1960). Usable habitat could probably limit abundance of stonerollers through predation. In optimum habitat, shallow riffles with gravel and rubble substrate, predation by fishes would be less efficient than it would be in shallow pools. As riffles dry up, stonerollers are forced to move into shallow pools where they are more vulnerable to predation by fishes and other vertebrate predators.

The decrease in the biomass of stonerollers during winter and spring (Table 37) could probably be due to some agent of mortality related to high currents associated with winter and spring flows. Therefore, shelter

Table 37. Total estimated biomass (grams), weighted usable area (m^2), and biomass per weighted usable area (kg/hectare) for the stoneroller in Glover Creek, November 1977 to September 1979.

Season	Biomass (grams)	Weighted usable area (m^2)	Biomass per weighted usable area (kg/hectare)
Fall			
Nov-Dec 1977	1,295	405.72	31.92
Oct 1978	298	50.48	59.03
Combined	1,593	456.20	34.92
Winter			
Jan-Mar 1978	1,069	406.96	26.27
Jan 1979	149	354.77	4.20
Combined	1,218	761.73	15.99
Spring			
Apr 1978	489	422.67	11.57
Apr-Jun 1979	390	471.22	8.28
Combined	879	893.89	9.83
Summer			
Jul 1978	2,009	119.94	167.50
Aug-Sep 1979	3,536	392.83	90.01
Combined	5,545	512.77	108.81

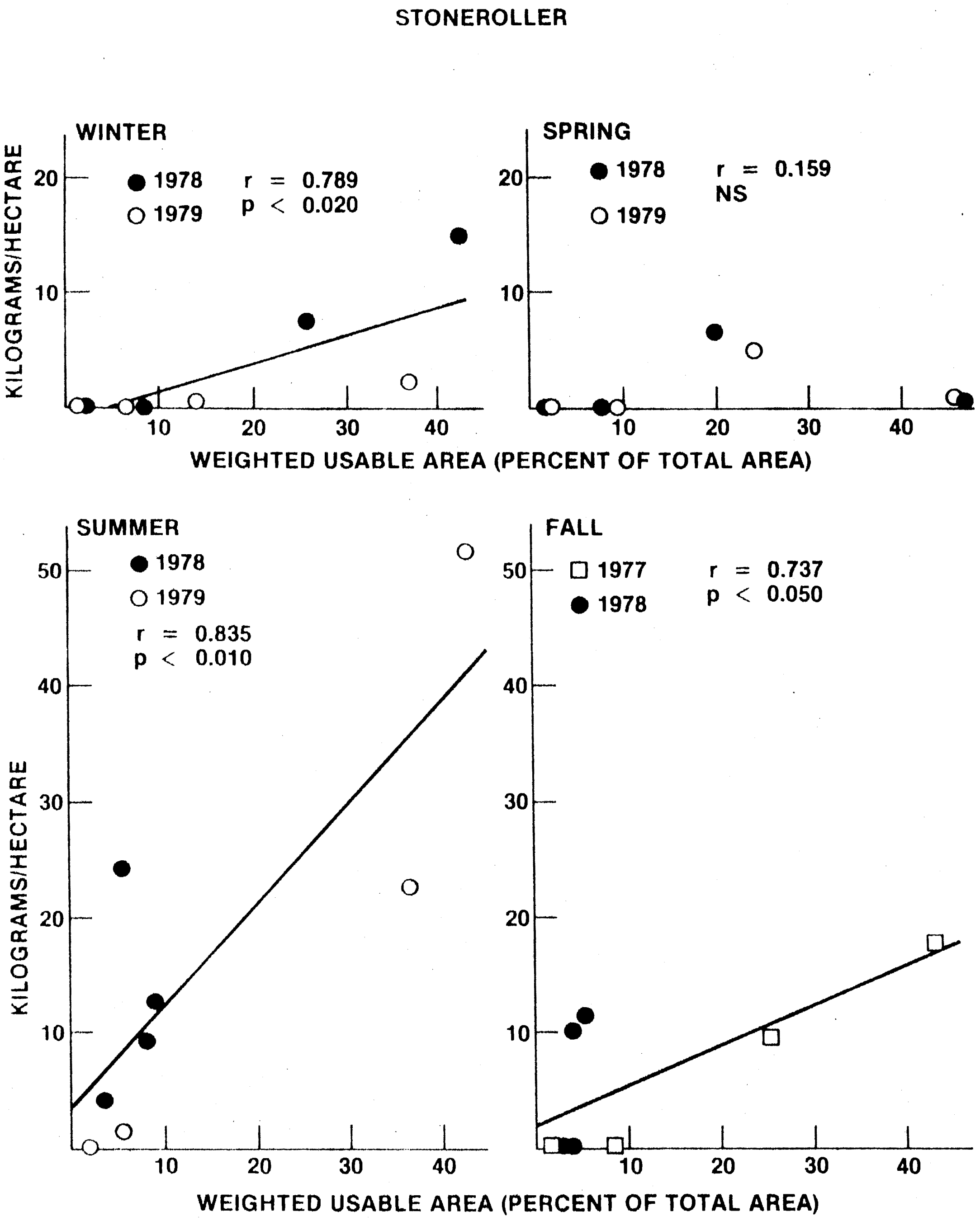

Figure 16. Correlations between standing crop of the stoneroller and weighted usable area for each season.

from excessive currents is another potential limiting factor. Winter and spring samples were taken when flows were low enough to permit efficient sampling such that the conditions limiting usable habitat were not measured.

For the summer 1978 and fall 1978 data the effect of the error in assuming independence is apparent (Figure 16). During these seasons there was little difference in the weighted usable area (percentage of total area) between the four sites, although riffle sites had much higher standing crops. In addition, the depth of water in riffle sites was extremely shallow and less velocity would have been necessary to provide suitable habitat. Despite this error, significant correlations resulted when data from both years were combined (Figure 16).

Orangebelly Darter

Biomass of the orangebelly darter per weighted usable area was highest during the summer (61.45 kg/hectare) and ranged from 12.09 to 19.26 kg/hectare during other seasons (Table 38). Only during the summer was the estimated total biomass for different years related to the amount of weighted usable area. During the summer 1978 weighted usable area was 67.73 m^2 and biomass was 383 grams, whereas during summer 1979 weighted usable area was 309.84 m^2 and biomass was 1,937 grams (Table 38). There were significant correlations between biomass per total area and weighted usable area (percentage of total area) for both the winter ($r=0.764$; $P<0.050$) and the summer ($r=0.835$; $P<0.010$), although the slope of the regression was much greater for the summer data (Figure 17). As was found for the freckled madtom and the stoneroller, it appears as though the influence of usable habitat on the abundance of the orangebelly

Table 38. Total estimated biomass (grams), weighted usable area (m^2), and biomass per weighted usable area (kg/hectare) for the orangebelly darter in Glover Creek, November 1977 to September 1979.

Season	Biomass (grams)	Weighted usable area (m^2)	Biomass per weighted usable area (kg/hectare)
Fall			
Nov-Dec 1977	135	263.21	5.13
Oct 1978	455	43.19	105.35
Combined	590	306.40	19.26
Winter			
Jan-Mar 1978	480	259.09	18.53
Jan 1979	195	299.04	6.52
Combined	675	558.13	12.09
Spring			
Apr 1978	129	339.71	3.80
Apr-Jun 1979	976	377.87	25.83
Combined	1,105	717.58	15.40
Summer			
Jul 1978	383	67.73	56.55
Aug-Sep 1979	1,937	309.84	62.52
Combined	2,320	377.57	61.45

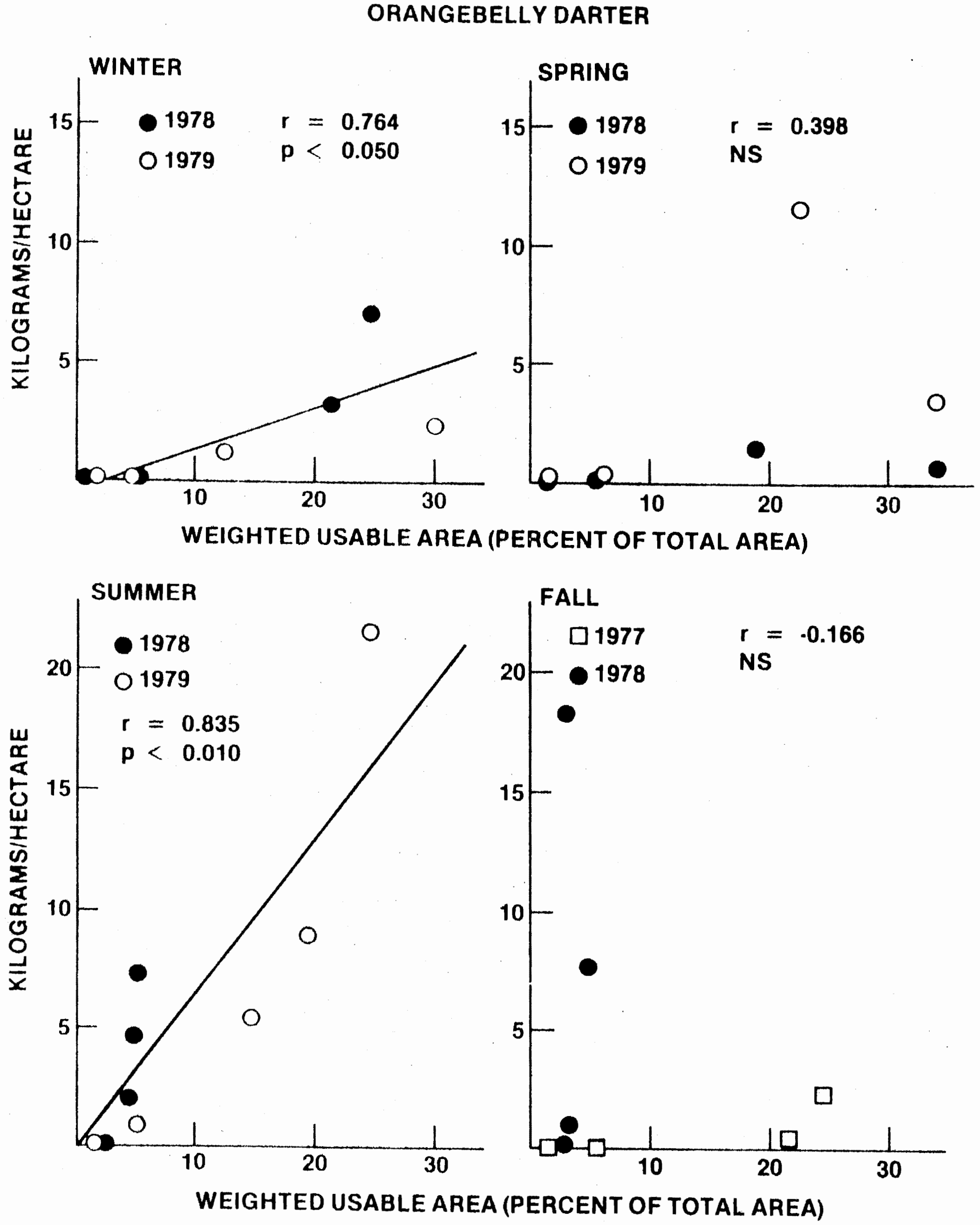

Figure 17. Correlations between standing crop of the orangebelly darter and weighted usable area for each season.

darter was greatest during the summer. Darters have developed a life history strategy of small size and rapid maturity (Moyle and Li 1979). Consequently, darter populations in small streams have high production to biomass ratios (Lotrich 1973; Small 1975), which may allow the orangebelly darter to respond quickly to favorable summer habitat. Abundance of orangebelly darters was probably limited in a different manner from that for either the freckled madtom or the stoneroller. Winn (1958) found that, even during the non-breeding season, two darters closely related to the orangebelly darter, *E. spectabile* and *E. caeruleum*, were territorial in aquaria and, in their respective habitats, individuals were found separated by 20 cm or more. The fantail darter, *E. flabellare*, also sets up non-reproductive territories in aquaria (Seifert 1963). During the summer, when usable habitat typically declines, individuals probably defend a territory in suitable habitat. As usable habitat becomes more limited, and darters whose territories have become unsuitable begin to move to more suitable, but occupied, areas in the riffle, aggressive behavior might increase, resulting in the subordinate darters having to remain in unsuitable habitat. To determine whether or not this spatial requirement is related to food supply as it is in young rainbow trout (Slaney and Northcote 1974) would require experimental verification.

The error due to assuming independence of depth and velocity is apparent from the summer and fall 1978 data. Weighted usable area for riffle sites were lower than they would have been if the depth-velocity interaction had been considered because the riffles were unusually shallow, and therefore the velocity required to provide suitable habitat conditions would be less than that indicated by the velocity suitability curve (Figure 12). The two highest standing crops in summer 1978 and in fall 1978 were for riffle sites, but weighted usable area varied little among sites (Figure 17). The error does not alter the conclusion that usable habitat was limiting the abundance of the orangebelly darter.

To summarize these findings, usable habitat was correlated with the abundance of the freckled madtom, stoneroller, and orangebelly darter most markedly during the summer, but was not correlated with the abundance of juvenile or adult smallmouth bass during any season. These findings support the hypothesis that usable habitat, especially during the summer, limits the abundance of the three riffle-dwelling fishes studied--freckled madtom, stoneroller, and orangebelly darter. Usable habitat was not limiting the abundance of smallmouth bass. The riffle-dwelling species are obligate stream fishes, whereas the smallmouth bass is adapted to both stream and lake environments. Furthermore, the riffle-dwelling species apparently utilize similar microhabitats for both feeding and resting, whereas the smallmouth bass is not adapted to resting in the same microhabitats in which it feeds. It would not be surprising then that limiting factors would be different for the two groups. The riffle-dwelling species evolved and adapted to warm-water stream environments that are characterized by extreme fluctuations in discharge (Starret 1951; Paloumpis 1958; Larimore et al. 1959; Metcalf 1959; Rinne 1975; Harrell 1978). Typically the season of lowest flow, which limits usable habitat, is during the summer, and it is at this time that the influence of usable habitat is most clear. The use of the weighted usable area-discharge relation to recommend instream flows is best justified for those riffle-dwelling fishes for which relations between standing crop and weighted usable area have been established. Further research to establish criteria for sufficient habitat conditions for the smallmouth bass is warranted.

CHAPTER VI

INSTREAM FLOW RECOMMENDATIONS FOR FISHES OF GLOVER CREEK

Introduction

In the event that the proposed Lukfata Lake is built, flow recommendations will be needed to maintain the diverse fish community and substantial fishery for smallmouth bass in Glover Creek. However, recommendation of instream flows in Glover Creek is hampered since none of the instream flow methodologies, including the incremental method, have been adequately tested on the variety of fishes present in streams of this type. Previously, minimum flow releases from impoundments have been based on the adequacy of flows during dry years without concern for the needs of fishes. A reliable and defensible methodology is urgently needed to prevent degradation of stream resources. This chapter deals with the application of the incremental method to recommend instream flows for Glover Creek and comparison of the incremental method with two other methods for recommending instream flows.

Methods which have been developed for recommending instream flows range in complexity from (1) those reconnaissance-level approaches based on historical discharge records requiring no field studies, to (2) threshold methods which examine a few habitat variables in critical cross-sections, and finally to (3) the multiple transect approaches which base flow recommendations on the relation between the amount or quality of usable habitat for a given species in relation to discharge (Stalnaker and Arnette 1976; Stalnaker 1979).

The Montana method (Tennant 1976), the most widely used of the reconnaissance-level methods, has been applied to warm-water and cold-water streams in the Midwest, Great Plains, and Intermountain West. Based on field studies in Montana, Wyoming, and Nebraska, Tennant (1976) found that habitat quality was remarkably similar in most streams carrying the same percentage of their average annual flow, and therefore percentages of the average annual flow were recommended that would provide suitable habitat. In general, ten percent of the average annual flow was recommended as a minimum instantaneous flow to provide short-term survival habitat. Thirty percent of the average annual flow was recommended to maintain good habitat; 60 to 100 percent for optimum habitat; and 200 percent for flushing flows. These percentages were modified for the wet and dry seasons in the Northern Great Plains (Tennant 1976). Although the Montana method does not provide specific information on the effects of altered flows on fish habitat, it has the advantage of requiring no field studies, which allows recommendations to be made early in the planning process.

The wetted perimeter approach provides information on the effects of different flows on fish rearing habitat at critical cross-sections of the stream. Wetted perimeter is the length of wetted contact between the stream and its channel, measured perpendicular to the direction of flow. In a rectangular cross-section, a plot of wetted perimeter versus discharge shows a rapid increase in wetted perimeter from zero discharge to an inflection point beyond which further increases in discharge result in only minor increases in wetted perimeter. Minimum flows for fish rearing have been set near the inflection point in the wetted perimeter-discharge curve (Collings 1974; Cochnauer 1976). The rationale for this approach is that riffle areas are the first areas of the stream seriously affected by reduced discharges and therefore these areas are usually selected for the wetted perimeter method. The principal advantage of the wetted perimeter approach is that it requires relatively little field work. However, without information on velocities, it is difficult to determine whether the habitat at the recommended flow is suitable.

In the third level of complexity, several methodologies have been developed to relate the amount or quality of usable habitat to discharge (Collings et al. 1970; Wesche 1973, 1974; Nickelson 1976; Waters 1976; Bovee et al. 1977; Stalnaker 1979). These methodologies differ in the level to which they define habitat needs of fishes, the manner in which suitabile habitat is measured, and the method used for predicting habitat conditions at different discharge levels. The incremental method uses a hydraulic simulation technique to estimate depths and velocities at different flows (Bovee and Milhous 1978) and can be used for any life stages of fish species for which habitat needs are defined (Stalnaker 1979; Trihey 1979). This flexibility to consider any life stages is an advantage since one or more life stages or critical periods of time are often known to be limiting and instream flows can be based on these needs. For example, most instream flow reservations in California have been based on spawning and passage requirements of anadromous salmon (<u>Oncorhynchus</u> spp.) and steelhead (<u>Salmo gairdneri</u>), and summer low flow habitat of trout (<u>Salmo</u> spp.; Hazel 1976).

To recommend instream flows below the proposed Lukfata Lake dam, limiting factors must be recognized and flows recommended to reduce the influence of the limiting factor. For the freckled madtom, stoneroller, and orangebelly darter, usable habitat was found to be important during all seasons, but most limiting during the summer (Chapter V). For the smallmouth bass, usable habitat was apparently not limiting. However, with alteration of natural flows usable habitat for smallmouth bass may become limiting. Since Glover Creek is designated as critical habitat for the threatened leopard darter (United States Fish and Wildlife Service 1978), flow recommendations will also consider the habitat needs of adult leopard darters. Possibilities of funding for the Lukfata Lake project in the near future are remote because of the critical habitat designation for Glover Creek.

Methods

A stream reach, located immediately downstream from access road 72000 and about 3 river kilometers above the proposed damsite, was chosen for the study (Figure 6). Since Carter Creek empties into the stream between study site 72000 and the damsite, the ratio of the drainage area above the damsite to that above site 72000 is 1.15 and the flow at the damsite would be approximately 1.15 times greater than that at site 72000.

Five permanent transects were established to sample riffle (transects 1, 2), run (transects 3, 4), and pool (transect 5) habitats. These transects were placed perpendicular to the direction of flow. A permanent benchmark was established and given an arbitrary reference elevation. Stream bed elevations, relative to the benchmark, were measured with a builder's level and level rod at one meter intervals along each transect. At the same fixed intervals along each transect, substrate type was classified according to a modified Wentworth scheme and given a numerical code (Bovee and Cochnauer 1977). Mean column velocities, measured at 0.6 of the depth from the water surface, were measured with a pygmy current meter at the same fixed intervals of each transect at flows of 0.057, 0.283, 2.379, and 3.342 m^3/s. Water surface elevation (stage) was measured at the thalweg of each cross-section at the same flows. Power functions were fitted to these data for the stage-discharge relation at each transect, and the velocity-discharge relation at each one meter segment along each transect, using the IFG4 program (Main 1978a). Weighted usable areas for selected species and life stages were computed for twelve different flows ranging from 0.10 to 7.00 m^3/s, using the Habitat program (Main 1978b). Habitat suitability curves for juvenile and adult smallmouth bass, freckled madtom, stoneroller, and orangebelly darter, developed in Chapter IV, were used to calculate weighted usable areas. For the adult leopard darter, weighted usable area calculations were based on the preliminary habitat suitability curves in Appendix B. Preliminary habitat suitability curves for the spawning and fry stages of the smallmouth bass were also used (K. D. Bovee, Cooperative Instream Flow Service Group, unpublished; Appendix B). Plots of weighted usable area versus discharge were used to base recommendations of a minimum flow for each life stage. For each month, the recommended minimum flow was the greatest of the minimum flows for all life stages.

Wetted perimeter was also measured at each flow for one of the riffle transects. The inflection point of the wetted perimeter-discharge curve, the minimum rearing flow, was determined by someone who had no knowledge of the flow recommendations based on the other methods tested.

The Montana method was also applied based on the average annual flow of 10.5 m^3/s, estimated for the damsite location (United States Army

Corps of Engineers 1975). Ten percent of the average annual flow was recommended for the period from July through December, and thirty percent of the average annual flow was recommended for the period from January through June.

Results

The total amount of wetted surface area within the study site increased rapidly from 423 m^2 at 0.10 m^3/s to 846 m^2 at 0.60 m^3/s and then increased slowly at higher discharges to 980 m^2 at 7.00 m^3/s (Figure 18). The suitability of the habitat is more important than the amount of wetted area for the purposes of making instream flow recommendations, but the wetted area-discharge curve (Figure 18) is needed to compare weighted usable area with total area.

Weighted usable area-discharge curves for the freckled madtom, stoneroller, and orangebelly darter were similar (Figures 19, 20, and 21), as were their suitability curves (Figures 10, 11, and 12). In general, all three species prefer shallow riffle areas, with gravel and rubble substrate. The amount of this type of habitat increased rapidly from 0.10 to 0.30 m^3/s. Consequently, flows were 0.30 m^3/s for the freckled madtoms and 0.50 m^3/s for the stoneroller and orangebelly darter.

A minimum flow 0.90 m^3/s was recommended so that usable habitat would not be limited for the adult leopard darter (Figure 22). Weighted usable area was a relatively high percentage of the total area at this flow (49%; Figure 18).

Weighted usable area curves for life stages of smallmouth bass indicate that the flow requirements are highest for the spawning stage (Figure 23). Typical spawning months for smallmouth bass in Oklahoma are

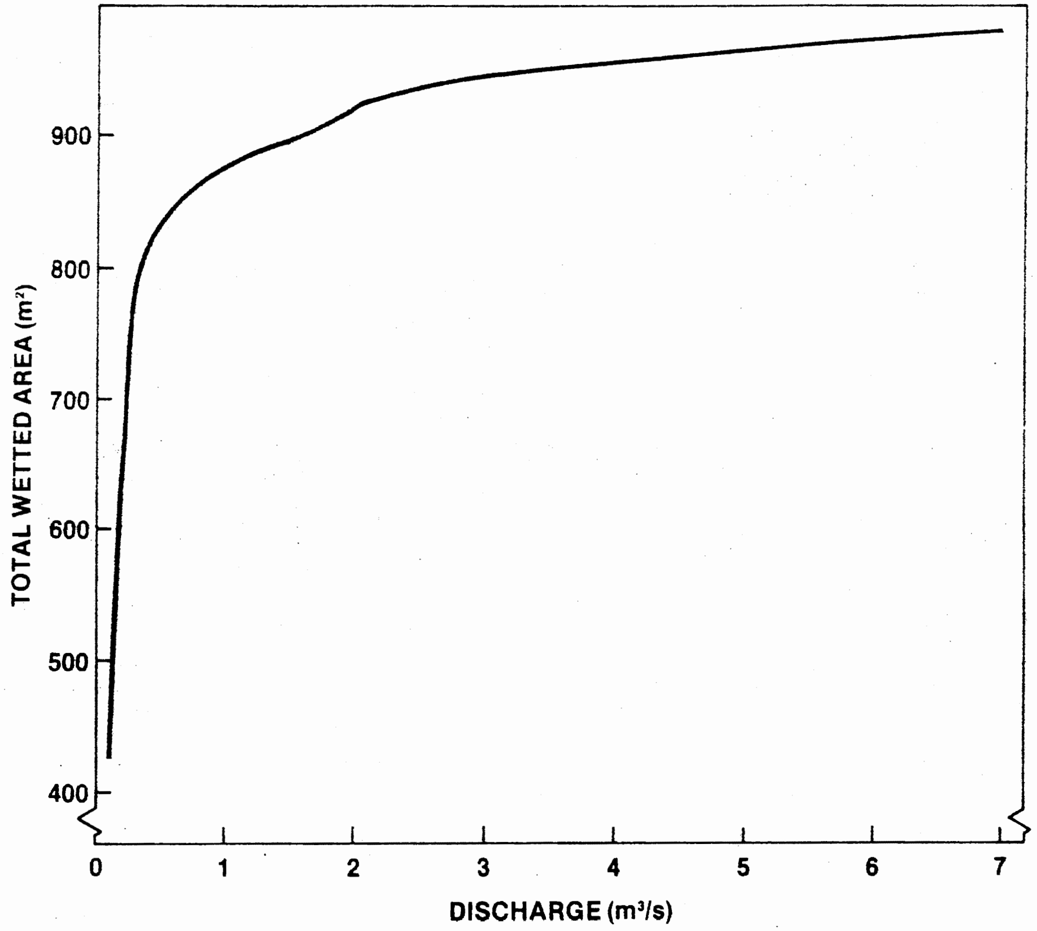

Figure 18. Relationship between total wetted area and discharge for site 72000, Glover Creek.

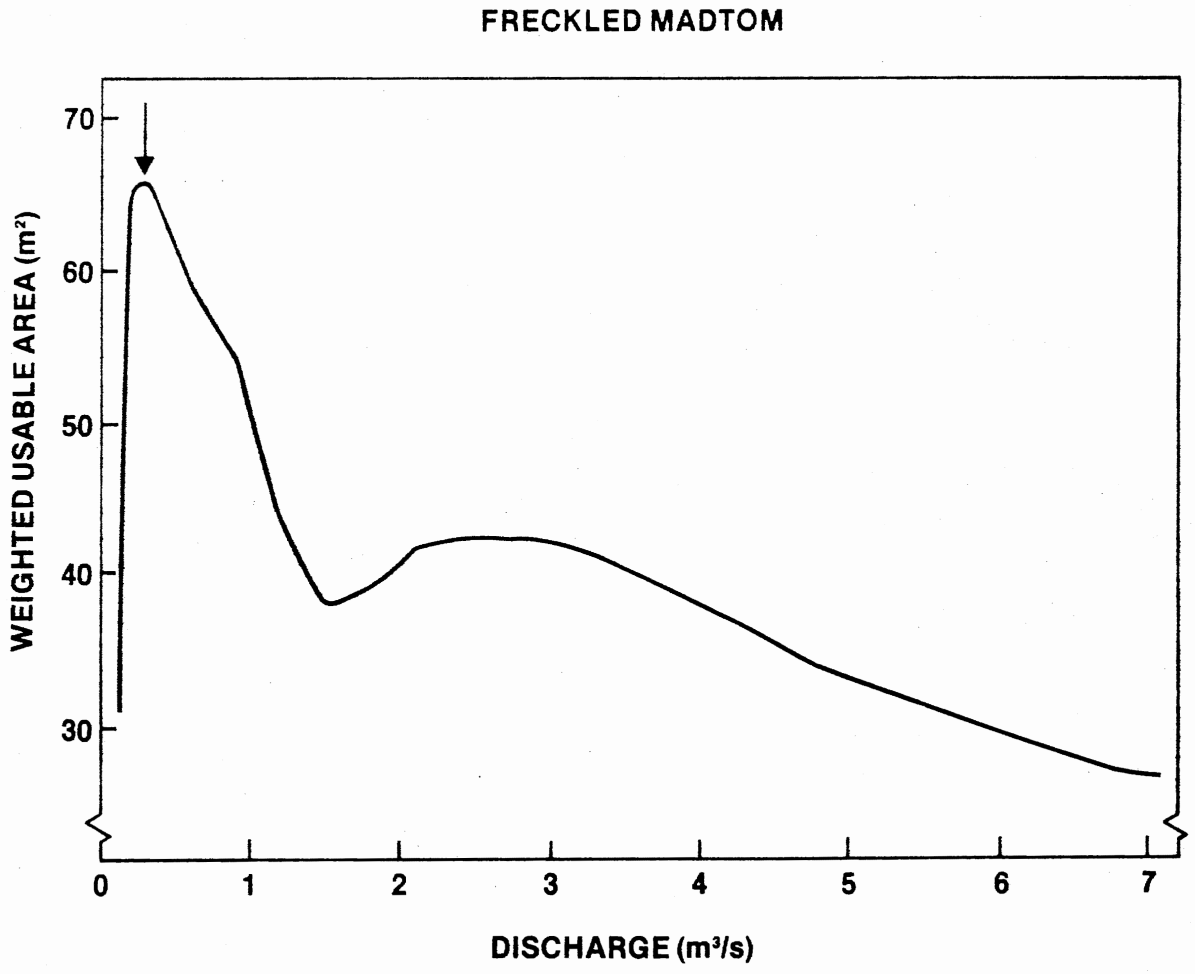

Figure 19. Relationship between weighted usable area for the freckled madtom and discharge for site 72000, Glover Creek.

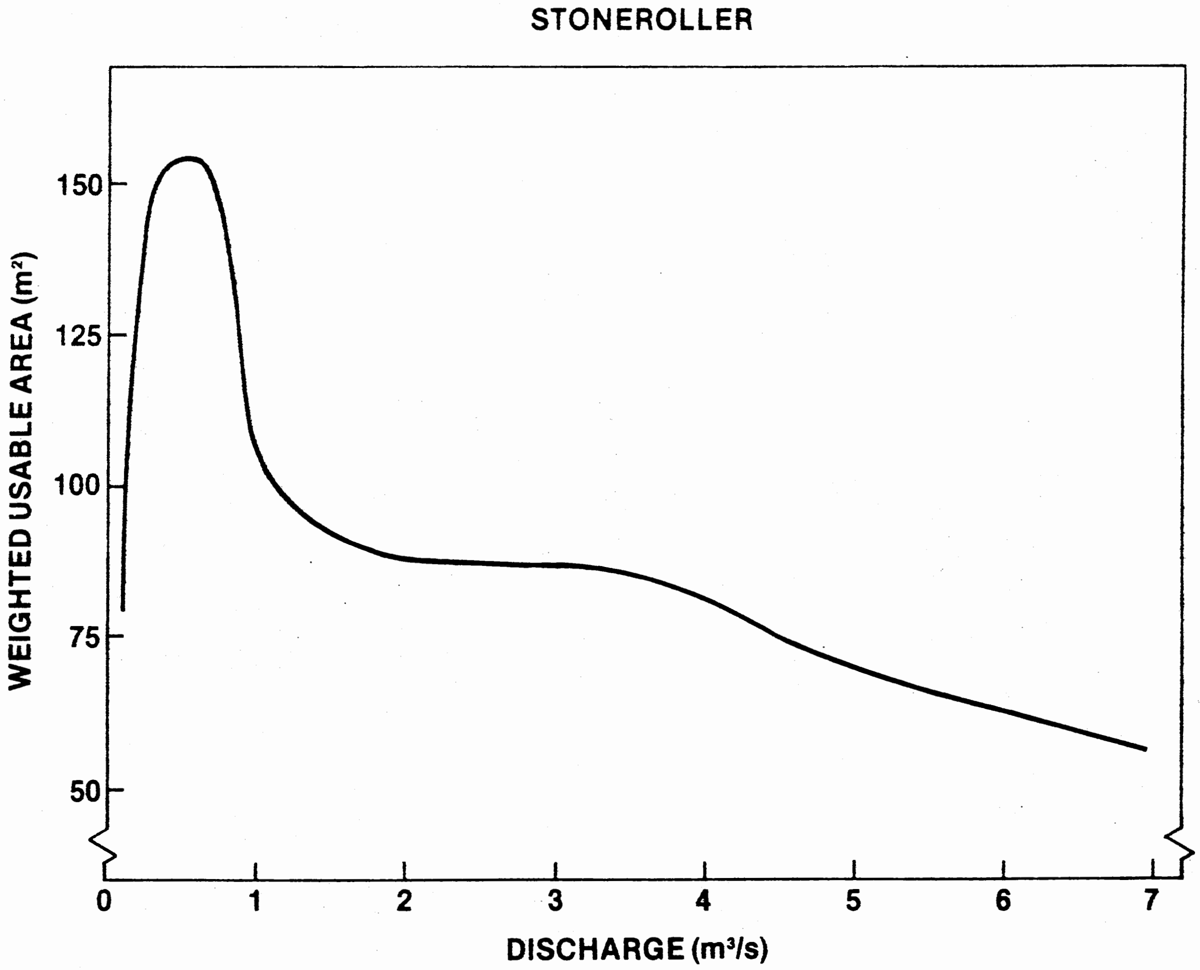

Figure 20. Relationship between weighted usable area for the stoneroller and discharge for site 72000, Glover Creek.

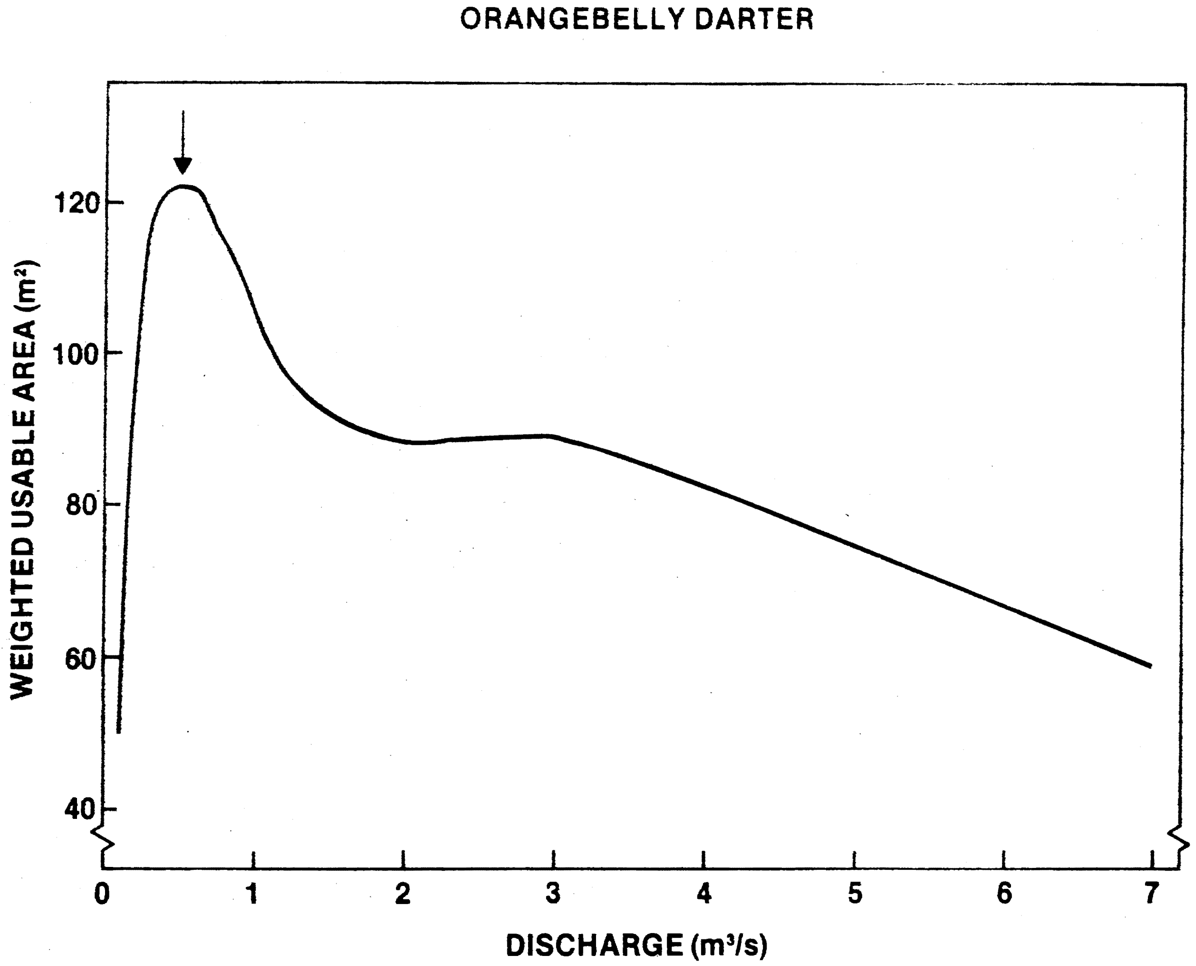

Figure 21. Relationship between weighted usable area for the orangebelly darter and discharge for site 72000, Glover Creek.

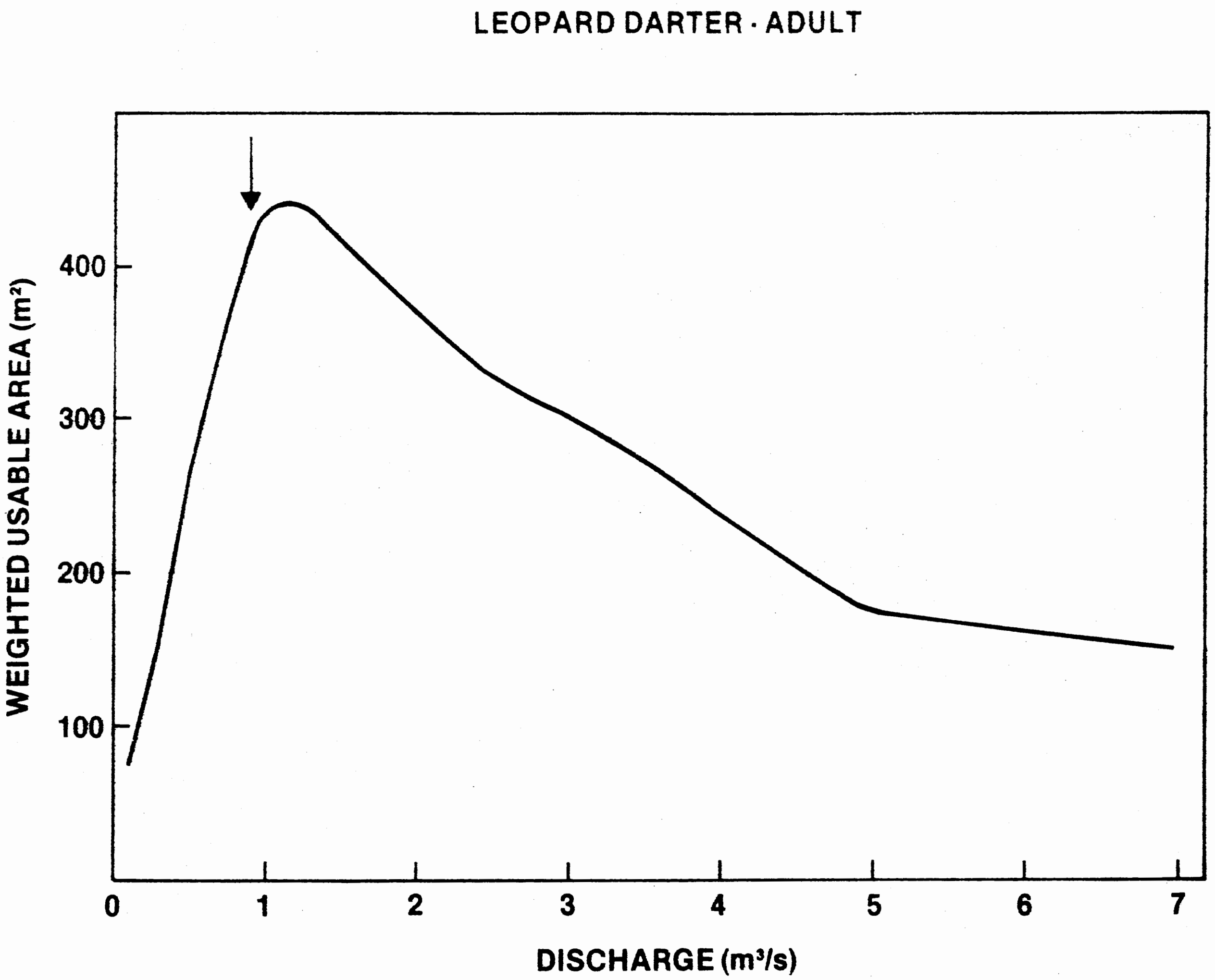

Figure 22. Relationship between weighted usable area for the leopard darter and discharge for site 72000, Glover Creek.

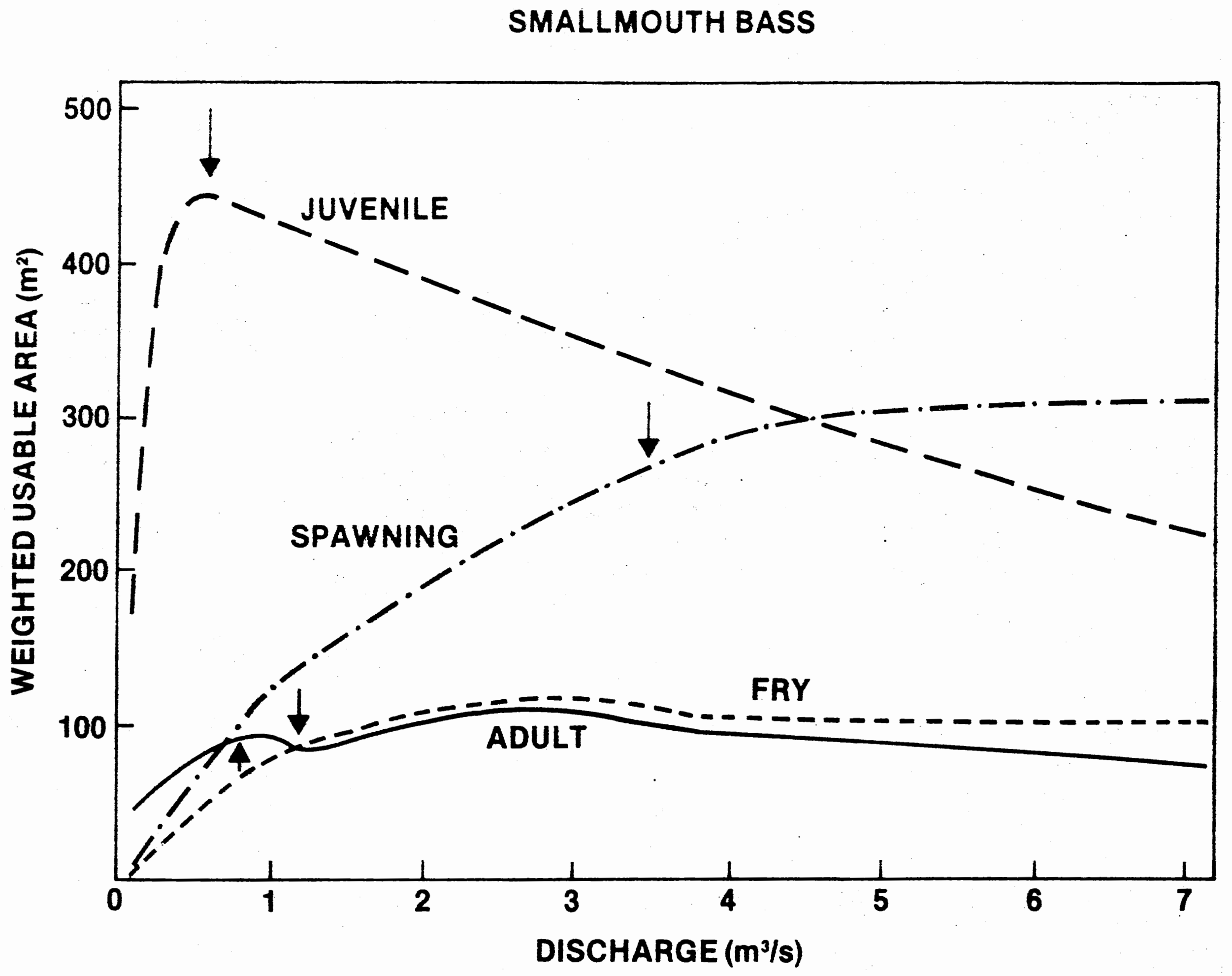

Figure 23. Relationships between weighted usable area for life stages of smallmouth bass and discharge for site 72000, Glover Creek.

April and May (Miller and Robison 1973). However, since smallmouth bass may continue to re-nest through June after earlier nest failures (Pflieger 1966, 1975b), flows for the spawning and fry stages were recommended for April, May, and June. A minimum flow of 1.2 m^3/s was recommended for smallmouth bass fry, and a minimum flow of 3.5 m^3/s was recommended for spawning. Weighted usable area for adult smallmouth bass varied little over the entire range of flows; however since there was a slight decrease in weighted usable area at flows below 0.80 m^3/s, that flow was recommended as a minimum (Figure 23). Weighted usable habitat for juvenile smallmouth bass was highest at 0.60 m^3/s and since usable habitat declined so steeply at lower discharges, a minimum flow of 0.6 m^3/s was recommended (Figure 23).

Based on the five fish species considered in this study, the recommended minimum flow regime was 0.9 m^3/s for July through March and 3.5 m^3/s for April through June (Table 39). A flushing flow of 12.0 m^3/s was recommended for March based on the approximate median monthly flow at the damsite for March (United States Army Corps of Engineers 1975). However, the duration of flushing flows necessary to transport accumulated silt is unknown. The flushing flow was much greater than the maximum flow for which the velocity-discharge and stage-discharge relations could be safely extrapolated, and therefore the suitability of the habitat at 12.0 m^3/s could not be accurately determined. The minimum flow regime would result in a minimum average annual flow of 2.48 m^3/s which is less than 25% of the estimated average annual flow (10.5 m^3/s) at the damsite (United States Army Corps of Engineers 1975). This minimum flow regime assures adequate availability of water during a typical water year and also mimics to some extent the seasonal pattern of flows

Table 39. Recommended minimum instantaneous flows (m^3/s) for Glover Creek at site 72000.

Species/Life stage	Recommended monthly flow (m^3/s) Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Average annual
Freckled madtom	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	
Stoneroller	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	
Orangebelly darter	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	
Leopard darter	0.90	0.90	0.90	0.90	0.90	0.90	0.90	0.90	0.90	0.90	0.90	0.90	
Smallmouth bass													
Spawning				3.50	3.50	3.50							
Fry				1.20	1.20	1.20							
Juvenile	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	
Adult	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	
Flushing flow[a]			12.00										
Recommended minimum monthly flows (median conditions)	0.90	0.90	12.00	3.50	3.50	3.50	0.90	0.90	0.90	0.90	0.90	0.90	2.48
Recommended minimum monthly flows (low-flow conditions)	0.50	0.50	3.60[b]	1.20	1.20	1.20	0.50	0.50	0.50	0.50	0.50	0.50	0.93

[a] Median monthly flow during March

[b] Monthly flow exceeded 90% of the time during March recommended for flushing during low-flow conditions

(Figure 24). Minimum flows recommended for median conditions were substantially less than the median monthly flows for November through May (Table 39, Figure 24). The minimum flow recommended for July through October was slightly higher than the median monthly flows for July and August, similar to the median monthly flow for September, and slightly below that for October. Under low flow conditions (approximately 1 in 10 year low flows), a contingency flow regime (Table 39) could provide some habitat for the fishes of Glover Creek, although it would be deleterious to the fish populations if adopted on an annual basis.

The wetted perimeter-discharge curve for one of the riffle transects had an inflection point at a discharge of 0.90 m^3/s (Figure 25). Therefore, based on the wetted perimeter method, the minimum flow for fish rearing would be 0.90 m^3/s. This recommendation agreed exactly with the recommendations of the incremental method for the July through February period (Table 40). The wetted perimeter method did not, however, permit recommendations of spawning flows.

The recommendations based on the Montana method agreed closely with those based on the incremental method for all months except January and February (Table 40). The same flushing flows was recommended since the wetted perimeter approach and the incremental method do not allow for estimation of a flushing flow.

Discussion

Implementation of the three methods used in this study vary greatly in cost and time required, yet for the low flow season (July through December) the flow recommendations based on each method were similar. Application of these results should be used with caution until comparable

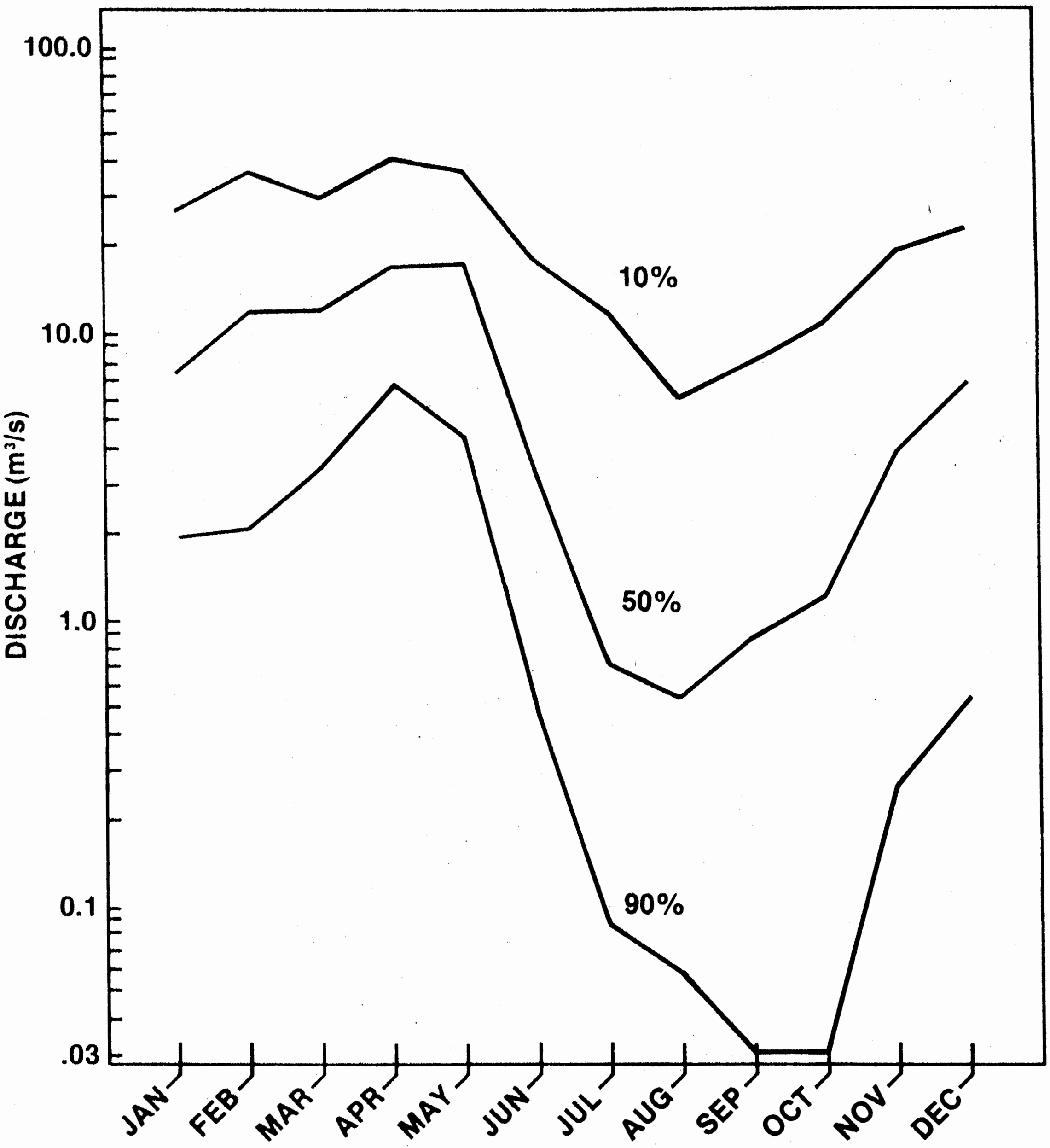

Figure 24. Hydrograph of monthly flows exceeded 10, 50, and 90 percent of the time during the period of record (1937-74) at the proposed Lukfata Lake damsite.

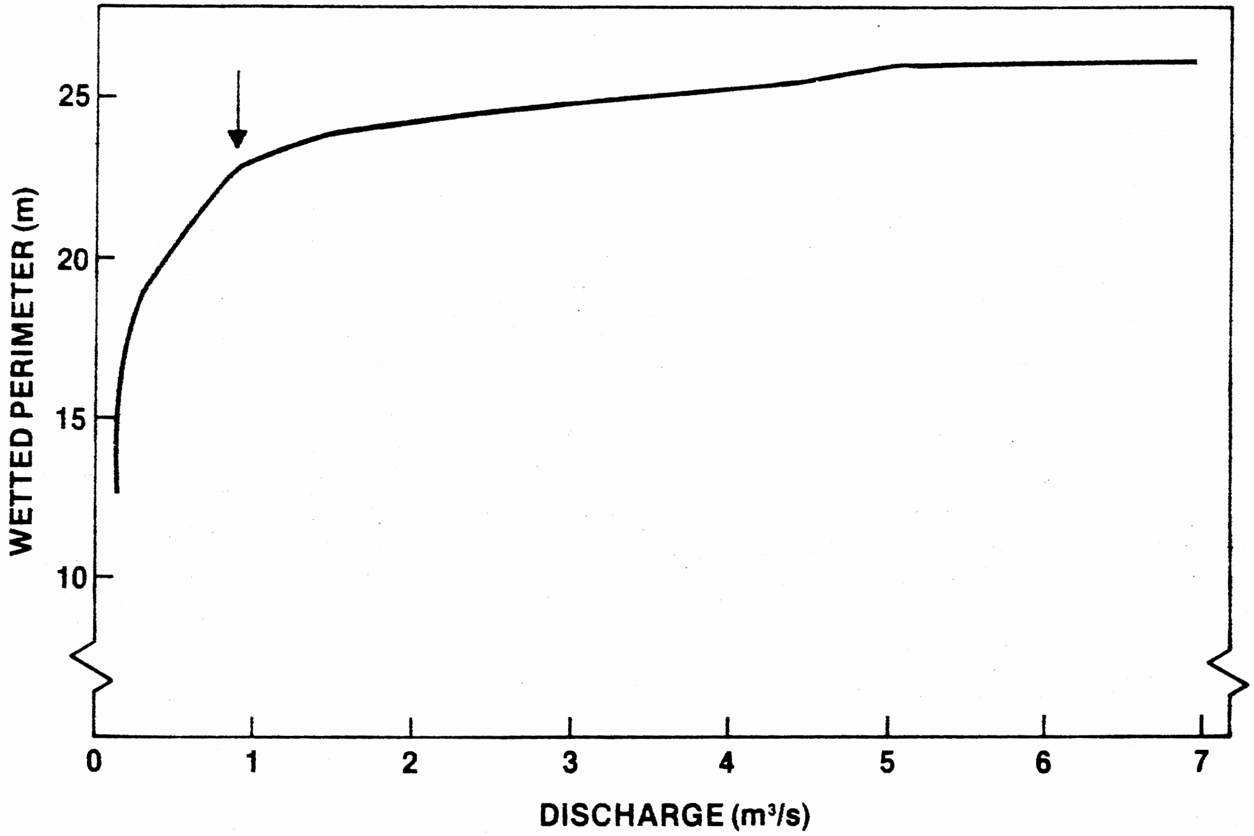

Figure 25. Wetted perimeter in relation to discharge for site 72000, Glover Creek.

Table 40. Comparison of recommended minimum monthly flow regimes based on the Montana (Tennant) method, the wetted perimeter method, and the IFG incremental method, with the median monthly and 1-in-10 year monthly low flows for 1937 to 1974 at the proposed Lukfata Lake damsite.

	Recommended flow regimes (m^3/s)			Historical
Month	Analysis of records (Montana-Tennant)	Single cross-section (wetted perimeter)	Multiple cross-section (incremental method)	flows (m^3/s)
(Median conditions)				(median)
January	3.16	0.90	0.90	7.476
February	3.16	0.90	0.90	12.036
March	12.00	12.00	12.00	12.319
April	3.16	0.90	3.50	17.700
May	3.16	0.90	3.50	18.096
June	3.16	0.90	3.50	3.200
July	1.05	0.90	0.90	0.708
August	1.05	0.90	0.90	0.538
September	1.05	0.90	0.90	0.878
October	1.05	0.90	0.90	1.246
November	1.05	0.90	0.90	3.936
December	1.05	0.90	0.90	6.853
Average annual	2.84	1.82	2.48	
(1-in-10 year low flow conditions)				(1-in-10 year low flows)
January	1.05	0.90	0.50	1.982
February	1.05	0.90	0.50	2.124
March	3.60	3.60	3.60	3.568
April	1.05	0.90	1.20	6.599
May	1.05	0.90	1.20	4.333
June	1.05	0.90	1.20	0.481

Table 40. (Continued).

	Recommended flow regimes (m^3/s)			Historical flows (m^3/s)
Month	Analysis of records (Montana-Tennant)	Single cross-section (wetted perimeter)	Multiple cross-section (incremental method)	
(1-in-10 year low flow conditions)				(1-in-10 year low flows)
July	1.05	0.90	0.50	0.088
August	1.05	0.90	0.50	0.059
September	1.05	0.90	0.50	0.031
October	1.05	0.90	0.50	0.031
November	1.05	0.90	0.50	0.269
December	1.05	0.90	0.50	0.538
Average annual	1.26	1.12	0.93	

studies substantiate these findings for other types of streams. In addition, both the Montana method and the wetted perimeter method should be restricted to reconnaissance level planning purposes, since neither provides any information on the effects of altered flows on fish habitat. This shortcoming limits the alternatives available to water resource managers. The incremental method offers more flexibility in this regard since the effects on fish habitat of any conceivable flow regime can be evaluated.

The effect of the recommended flow regime on the water level in the proposed Lukfata Lake has not been considered in this study. However, water level fluctuation has a dramatic effect on the recruitment of reservoir fishes and manipulation of water levels to inundate suitable spawning and nursery habitat and allow for successful reproduction of reservoir fishes has proven to be a useful management technique (Keith 1975; Benson 1976; Groen and Schroeder 1978; Nelson 1978). Management of river-reservoir ecosystems should involve flow recommendations for the downstream community as well as concurrent evaluation and recommendation of water level regimes for the biota of the reservoir. Therefore, the incremental method offers the advantage of evaluating alternative flows that would be compatible with water level manipulations for reservoir fisheries and reservoir operations.

The validity of the flow recommendations made for Glover Creek depends on how well the assumptions of the incremental method were met. Also, the validity of the recommendations may be questioned because the lack of information on the habitat requirements of life stages of other fish species prevented consideration of their instream flow needs. Over 50 species of fish have been recorded from Glover Creek (Taylor and Wade

1972), but instream flow recommendations were based on only five of these. The implicit assumption is that adequate protection of the habitat for these fishes will also result in habitat protection for the other species. This concept of indicator species for instream flow assessments has been suggested by Stalnaker and Arnette (1976) and Bovee et al. (1977), although the validity of such an approach has never been tested. There are, however, indications that some species are more sensitive to flow alterations than others (Spence and Hynes 1971; Trautman and Gartman 1974; Holden and Stalnaker 1975; Bovee et al. 1977; Edwards 1978; Holden 1979). All of the species for which flow recommendations were made in this study, except for the smallmouth bass, are obligate stream fishes, and therefore should be quite sensitive to alterations in the natural flow regime. Information on the requirements of all life stages of some of these fishes is still incomplete so the flow recommendations for these species must be regarded as tentative. For example, nothing is known of the habitat requirements of the spawning and early life stages of the threatened leopard darter. Therefore, flows to provide habitat for adult leopard darters will not permit survival of the species if habitat for successful reproduction is not available.

The assumptions inherent in this application of the incremental method were (1) depth, velocity, and substrate are the most important variables affecting fish distribution and abundance when considering changes in the flow regime; (2) the stream channel is not altered by changes in the flow regime; (3) depth, velocity, and substrate are independent in their influence on habitat selection by fishes; (4) the stream can be modeled by using one representative sample reach; and (5) there is a positive, linear relation between weighted usable area and standing crop or habitat use.

The first assumption is a tenuous one, especially when dealing with flow alterations due to impoundment since chemical conditions as well as energy sources are altered below reservoirs (Hannan 1979; Webster et al. 1979). Flow alterations that change light or thermal regimes, chemical water quality, or organic matter inputs would result in changes in the stream community structure (Cummins 1979) and the relative importance of these alterations as compared to changes in weighted usable area has not yet been investigated. Lukfata dam is designed to have multilevel outlets to allow lake water to be released from various depths in order to maintain downstream temperatures that are as natural as possible (United States Army Corps of Engineers 1975). Also, the projected inflow to storage ratio is relatively high (6:1) and should not significantly decrease nutrient concentrations downstream (United States Army Corps of Engineers 1975). The impoundment would probably decrease the particulate organic matter concentration immediately downstream from the dam (Webster et al. 1979); however, it cannot yet be predicted how the alteration in the energy base would in turn alter food web relations and fish community structure, and if this influence would be more important than the influence of changes in weighted usable area. With this level of uncertainty, the only prudent approach for biologists and planners is to recommend flows that would ensure that usable habitat is not the limiting factor, recognizing the potential ramifications of alterations of other ecosystem components.

The interactions of other variables, such as temperature and dissolved oxygen, with flow must also be recognized. The potential for low concentrations of dissolved oxygen and excessive temperatures is greater at low flows during summer. During winter the potential for formation of frazile or anchor ice is greater at low flows and should be an added consideration in colder regions (Bovee et al. 1977). These problems have not been observed in Glover Creek at flows approximating those recommended.

The amount of cover provided by stream banks and instream structures also changes with discharge; however, these changes were not evaluated in the present study. The effect of cover on abundance of fishes has been documented for both cold-water (Saunders and Smith 1962; Lewis 1969; Wesche 1974) and warm-water stream fishes (Hickman 1975). Attempts are being made to incorporate suitability criteria for cover types into weighted usable area calculations of the incremental method (K. D. Bovee, Cooperative Instream Flow Service Group, personal communication).

The second assumption of this application of the incremental method was that the morphometry of the channel would not change with the altered flow regime. The Glover Creek channel is mostly boulder and bedrock and seems relatively stable. However, this assumption is never strictly valid since all stream channels will eventually degrade. Impoundments might speed this process since reservoirs typically release clearer water, which may cause more erosion of the channel downstream, and they also block the downstream movement of larger-sized sediment particles (Simon 1979).

Of major concern is the effect of reduced flood flows on accumulated sediment in the stream, since there are several small tributaries below the proposed damsite which would carry sediment to the main channel. Smith (1976) noted that reduced flood flows in the Trinity River resulted in siltation of gravel beds used for spawning and pools used for nesting by trout and salmon, as well as allowing encroachment of riparian vegetation in the channel. Research is essential to develop methods to estimate the duration and magnitude of flushing flows needed to scour silt from pools and the interstices of the substrate in riffles (Grenney and Porcella 1976) since production of typical stream insects in riffles depends on the presence of silt-free interstitial spaces (Ward 1976).

The assumption of independence, especially of depth and velocity, was invalid for the freckled madtom, stoneroller, and orangebelly darter (Chapter IV), and this violation of the assumption undoubtedly affected the shape of the weighted usable area curves. At higher discharges the amount of weighted usable area for these three species declined more rapidly than it would have if interactions had been considered. At discharges greater than about 0.5 m^3/s, the depth and velocity in riffle areas of the study reach would begin to exceed the optimum ranges as defined by the habitat suitability curves (Figures 10, 11, and 12). However, due to the depth-velocity interaction, at greater velocities the preferred depth range would be at greater depths. Therefore, the error in assuming independence of depth and velocity resulted in lower estimates of weighted usable area at the higher discharges. The amount of weighted usable area probably still declines at the higher discharges, although less abruptly than indicated by the curve. In this case, the effect on the minimum flow recommendation does not appear to be great. The influence of high flows on usable habitat cannot, however, be accurately determined because of the error due to assuming independence. Future attempts to determine habitat suitability criteria should utilize a multivariate suitability function which takes into account the interactions among habitat variables (Voos 1980).

The fourth assumption of this application was that the stream reach sampled for habitat measurements is representative of the habitat types available in the stream. This assumption was not strictly met since deep, sluggish pool habitat was not represented in this reach. Most of the pool habitat in Glover Creek consists of relatively shallow, rock-bottom pools with a noticeable current. The representative reach concept is especially critical when dealing with fishes which are mobile enough (e.g., smallmouth bass) to seek out more favorable habitats when local conditions become unsuitable. For fishes like the orangebelly darter, this is probably less of a problem since they move little (Scalet 1973). Although the application of stratified sampling concepts for choosing representative reaches has been introduced by Bovee and Milhous (1978), further research is necessary to establish the most efficient sampling scheme and an appropriate number of sample reaches.

The validity of the assumption of a positive, linear relation between weighted usable area and standing crop depends on the validity of the assumption of independence and the assumption that depth, velocity, and substrate are the most critical variables. There is little doubt that usable habitat would be limiting at extremely low levels of weighted usable area, due to marginal habitat conditions or extremely low or high flows. However, above a certain level of weighted usable area, other factors may become overriding. The most important question with regard to making instream flow recommendations is: Within what range of weighted usable area is usable habitat the overriding factor? For three of the species considered in this study, there is evidence that usable habitat is the limiting factor within the range of typical summer flows (Chapter V). Also, high winter and spring flows can further limit abundance through influence on usable habitat. However there have not been enough tests of the relation between weighted usable area and standing crops to generalize about the extent to which this assumption is valid.

The use of weighted usable area for other life stages (spawning, fry, juvenile) has not been tested for warm-water stream fishes. The assumption is that there are direct relations between the weighted usable area for spawning and the number of successful nests; weighted usable area for fry and number of fry produced; and weighted usable area for juveniles and number or standing crop. Factors controlling successful reproduction and survival of young black basses, *Micropterus* spp., are much more complex than this assumption implies (Eipper 1975; Pflieger 1975b; Shuter et al. 1980). Tests of this assumption for the spawning and early life stages are urgently needed to determine if an alternative approach needs to be developed.

CHAPTER VII

SUMMARY AND CONCLUSIONS

Natural stream flow regimes have been altered by a variety of man's activities, and therefore fish populations in streams have also changed. To protect the instream values of stream resources in the face of continued modification of streams and increased demands for water, methodologies for recommending instream flows have been developed. The incremental method developed by Cooperative Instream Flow Service Group, United States Fish and Wildlife Service, is one such methodology. Application of the incremental method in warm-water streams is limited because there have been no field tests of the validity of the assumptions, and there is a scarcity of the type of quantitative information needed on habitat preferences of warm-water stream fishes.

The objectives of this research were (1) to develop habitat suitability curves for selected fishes of Glover Creek; (2) to test the assumption of independence of habitat variables in the selection of microhabitats by fishes; (3) to investigate the relationship between weighted usable area and fish standing crop; and (4) to make monthly instream flow recommendations for the fishes of Glover Creek. Glover Creek was chosen for the study because it supports a high quality fishery for smallmouth bass, is designated as critical habitat for the threatened leopard darter, and is the site for the proposed Lukfata Lake.

Habitat (depth, velocity, and substrate) suitability curves were developed for the smallmouth bass (juvenile and adult), adult green sunfish, freckled madtom, stoneroller, and orangebelly darter. Two types of bias were noted. The first type of bias arises when the distributions of depth, velocity, and substrate types sampled deviate from uniform and frequency of capture distributions are used to derive habitat suitability curves. This bias was adjusted for by dividing frequencies by the amount of area sampled within each interval. The second type of bias recognized was that due to differential sampling efficiencies over the range of the particular habitat variable being considered. This bias may be minimized by using several different sampling techniques, but care must be exercised to prevent over-representation by any single method.

For each species studied, the assumption of independence was violated for at least one of the three possible two-way combinations (depth-velocity, depth-substrate, velocity-substrate). Violation of the independence assumption appeared to be greatest for the interaction of depth and velocity preferences for the freckled madtom, stoneroller, and orangebelly darter. In each of these species, the optimum velocity range increased with increasing depth. The reason that depth and velocity preferences were not independent for these species is probably because their microhabitat is in or near the stream bottom and mean column velocities were measured rather than bottom velocities. The effect of violation of this assumption on the minimum flow recommendation did not appear to be great, although the suitability of the habitat at other flows could not be reliably determined. Research on the effects of assuming independence for various types and degrees of interaction would enable those using the incremental method to decide when it might be appropriate to assume independence.

There were differences in the habitat used by different size groups of conspecifics for the smallmouth bass and green sunfish. These differences may be partially the result of size-related dominance hierarchies. If further research shows that the preferred habitat of the dominant individuals is actually the most preferred habitat of the species, then density of all individuals may be an inappropriate criterion on which to base suitability criteria.

Although suitability curves for depth, velocity, and substrate define necessary conditions, suitability based only on these three variables will not always indicate that sufficient conditions exist to permit survival of a particular life stage (Patten et al. 1979). The incremental method assumes that populations are limited by usable habitat. Part of this research was aimed at determining the extent to which usable habitat, as measured by weighted usable area, was limiting standing crops of fishes during different seasons. For the smallmouth bass, adults and juveniles, there were no significant correlations between weighted usable area and standing crop for any season. Standing crops of adults were, however, always near zero at sites where weighted usable area was less than 5% of the total surface area. Therefore, presence of adult smallmouth bass was limited by usable habitat only where habitat conditions were marginal. Also, since habitat for smallmouth bass would become marginal at the extremely high and low flows, only then would usable habitat be a prime limiting factor. For the freckled madtom, stoneroller, and orangebelly darter, correlations between weighted usable areas and standing crops were significant during the summer. There were also significant correlations during some of the other seasons but it appeared that usable habitat limited the abundance of freckled madtoms, stonerollers, and orangebelly darters most markedly during the summer. Probable mechanisms were different for each species. The amount of usable habitat to provide shelter from excessive currents during high winter and spring flows may have been an additional limiting factor, especially for the stoneroller. In warm-water streams, which are characterized by extreme fluctuations in discharge, usable habitat is probably the prime factor limiting fish populations, however its influence is most intense at the extremes of high and low flows.

The incremental method was used to recommend monthly flows for the freckled madtom, stoneroller, orangebelly darter, leopard darter, and all life stages of the smallmouth bass for a stream reach near the proposed Lukfata Lake damsite. In addition the wetted perimeter method and the Montana (Tennant) method were also applied to make flow recommendations. Flow recommendations based on each method were remarkably similar for the low flow season (July through December) and recommended flows were present during typical water years. The validity of the assumptions made in this application of the incremental method was discussed. However, a major question still unresolved is what duration and magnitude of flushing flows would be required to scour silt from pools and the interstices of the substrate in riffles, yet prevent major mortality and displacement of stream fishes. In streams, such as Glover Creek, measurements of velocities and water surface elevations are not possible at high flows. Therefore, predictions of depths and velocities at high flows are the least accurate; yet their effects on fishes and fish habitat cannot be disregarded.

Further research is warranted to improve the accuracy of techniques for assessing the effects of habitat modifications and flow alterations, and to enable fishery managers to recommend instream flows to optimize the value of the stream fishery. Specific recommendations for areas of needed research, which became apparent during the course of this study, are outlined below.

1. Simulation studies could provide insight into the effects on the final flow recommendation of assuming independence of habitat preferences for various types and degrees of interaction.
2. Field investigations designed to determine the extent of interaction of habitat variables for various fish species would, when coupled with the results of the first research area, allow investigators to determine, for the species of interest, whether independence can be safely assumed or whether multivariate suitability functions including the interactions must be developed.
3. A greater understanding of the manner in which social structure influences habitat use or limits population density would enable fishery managers, through habitat modification or flow manipulation, to manage for populations with a size structure to provide quality angling. Similar studies on interspecific interactions would help prevent further situations where exotic competitor species replace the native fauna after habitat or flow modifications.
4. Studies on the mechanisms regulating population density of warm-water stream fishes are needed in order to determine necessary and sufficient conditions for these species.
5. When variables describing necessary and sufficient conditions are determined, studies can then be aimed at examining the relationships of these variables to discharge.

6. Research is essential to develop methods to estimate the duration and magnitude of flushing flows needed to scour silt from pools and the interstices of the substrate in riffles.
7. Comparison of the flow recommendations based on field studies with those based on reconnaissance level-methodologies would help test the validity of these reconnaissance-level methodologies, which are extremely important for early planning purposes.

The results of my research suggest that some refinements of the incremental methodology would permit more reliable estimation of minimum instream flow requirements. First, the assumption of independence of variables in habitat selection by fishes proved invalid. As a first-step approximation the assumption of independence can be made; however, as more data are obtained multivariate suitability functions, which take into account the interaction of variables, should be developed. Second, definition of habitat requirements should be aimed toward determining sufficient conditions for each life stage, i.e., what variables and what range of each comprise sufficient conditions for growth and survival of that life stage (Patten et al. 1979), rather than determining the requirements for only depth, velocity, and substrate. The use of weighted usable area-discharge curves for recommending instream flows is justified only for those species in which the variables considered in calculations of weighted usable areas include those which are limiting.

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APPENDICES

APPENDIX A

WATER QUALITY DATA FOR GLOVER CREEK

Table 41. Water quality data for Glover Creek at the State Highways 3 and 7 bridge (U. S. Geological Survey 1977, 1978).

Date	Time	Discharge (cfs)	Specific conductance (μmhos)	pH	Temperature (C)	Turbidity (JTU)	D.O. (mg/l)	Percent saturation	Chemical oxygen demand (mg/l)	Hardness CaMg (mg/l)	Calcium CO_3 (mg/l)
5 Nov 1975	1430	7.5	140	8.0	18.0	5	9.3	101	4	79	67
3 Dec 1975	1430	16.0	125	7.8	14.0	2	10.7	107	8	65	50
16 Jan 1976	-	29.0	-	-	-	16	-	-	24	59	31
3 Feb 1976	1300	24.0	70	7.2	10.5	7	11.4	106	59	11	11
3 Mar 1976	1500	60.0	68	7.5	19.0	12	9.0	101	13	<2	<2
7 Apr 1976	1430	97.0	55	8.1	19.0	8	9.1	102	15	<1	<1
7 May 1976	1300	1300.0	47	8.1	20.0	7	9.0	103	<4	30	19
2 Jun 1976	1400	638.0	45	7.9	22.5	25	8.3	104	30	21	12
7 Jul 1976	1330	57.0	55	7.6	32.0	10	7.3	100	7	60	10
4 Aug 1976	1315	3.0	-	7.0	28.0	2	-	-	12	48	38
8 Sep 1976	1400	50.0	64	8.0	27.0	6	8.2	105	12	13	13
12 Oct 1976	1645	25.0	70	6.7	20.5	7	9.6	107	11	16	
9 Nov 1976	1600	48.0	71	6.7	12.5	14	11.0	105	9	97	
14 Dec 1976	1430	983.0	42	-	7.0	15	11.7	97	16	12	
19 Jan 1977	1330	579.0	31	7.2	1.0	12	12.6	87	5	93	
2 Feb 1977	1400	214.0	33	6.6	4.5	9	10.4	80	8	11	
8 Mar 1977	1700	597.0	-	7.7	12.5	13	10.8	102	5	10	
13 Apr 1977	1135	96.0	63	7.2	21.0	5	9.1	101	1	-	
10 May 1977	1030	251.0	40	6.1	22.0	9	8.3	94	2	10	
8 Jun 1977	1140	16.0	78	7.0	27.5	5	6.7	85	7	33	
27 Jul 1977	1545	14.0	135	7.3	28.5	0	7.8	101	10	44	
2 Aug 1977	1530	305.0	54	6.7	27.5	18	7.3	92	24	23	
13 Sep 1977	1745	5.9	88	8.3	28.0	2	6.3	82	14	49	

Table 42. Water quality data for site 61200P, Glover Creek.

Date	Discharge (m^3/s)	Temperature (C)	Dissolved oxygen (mg/l)	Percent saturation	Turbidity (JTU)	Suspended solids (mg/l)	Secchi disc transparency (cm)	Specific conductance (µmhos/cm)	pH
30 Oct 1977	0.014	19.0	7.4	78	23	6.0	48	85.0	
13 Jan 1978	∿0.010	0.5	15.9	110	15	0.5	–[a]	67.4	
13 Mar 1978	1.326	8.5	12.6	107	11	0	>80	48.0	
8 Apr 1978	0.373	20.5	9.3	102	8	1.5	–[a]	80.0	6.52
21 Jul 1978	0.000	26.0	6.9	83	15	7.0	–[a]		
21 Jul 1978[b]		26.0	6.9	83	6	1.0			
23 Oct 1978	0.000	16.0	10.4	104	13	4.0	–[a]	85.0	
30 Dec 1978		6.0			6	2.0	–[a]	52.0	
4 May 1979	1.359	15.0			13	3.0	–[a]	56.0	
18 Jul 1979	∿2.000	23.0			23	77.0	20	52.0	
18 Jul 1979 - Bluff Creek					8	1.0	–[a]	67.0	
8 Aug 1979	0.085	20.0			11	2.0	>110	63.0	

[a] Transparency greater than maximum depth

[b] Data for upstream pool

Table 43. Water quality data for site 74100R, Glover Creek.

Date	Discharge (m^3/s)	Temperature (C)	Dissolved oxygen (mg/l)	Percent saturation	Turbidity (JTU)	Suspended solids (mg/l)	Secchi disc transparency (cm)	Specific conductance (μmhos/cm)	pH
10 Dec 1977	0.271	4.5	13.7	105	19	0	>100	90.0	
9 Jan 1978	∿0.300	5.0	14.0	108	15	0.5	–[a]	75.5	6.75
14 Mar 1978	4.409	11.3	14.4	130	11	0	–[a]	67.5	6.67
15 Apr 1978	2.060	17.0	10.5	107	10	3.0	–[a]		6.50
13 Jul 1978	0.034	28.0	5.9	74	11	2.0	–[a]	95.0	
21 Oct 1978	0.008	16.0	10.0	100	8	2.0	–[a]	121.0	
30 Dec 1978		8.0	–		4	1.0	–[a]	67.0	
5 May 1979	∿7.000	16.5	–		23	26.0	22	80.0	
27 Jun 1979	2.985	24.0	–		36	77.0	20		
8 Aug 1979	0.283	25.0	–		11	3.0	–[a]	76.0	

[a] Transparency greater than maximum depth

Table 44. Water quality data for site 74100P, Glover Creek.

Date	Discharge (m^3/s)	Temperature (C)	Dissolved oxygen (mg/l)	Percent saturation	Turbidity (JTU)	Suspended solids (mg/l)	Secchi disc transparency (cm)	Specific conductance (μmhos/cm)	pH
30 Oct 1977	low	18.2	8.8	93	21	2.0	132		
17 Nov 1977	.337	13.6	11.2	106	15	5.0	67	82.5	
9 Jan 1978	∿ .300	5.0	13.4	104	11	2.5	–[a]	80.5	6.65
14 Mar 1978	4.325	11.6	13.0	118	11	0	–[a]	65.0	6.61
10 Apr 1978	1.588	19.3	9.8	105	10	3.0	–[a]		6.50
20 Jul 1978	.034	29.0	10.0	127	15	1.0	–[a]		
21 Oct 1978	.008	12.0	10.0	92	8	2.0	–[a]	112.0	
30 Dec 1978		8.0			6	0	–[a]	72.0	
5 May 1979	∿7.000	16.5			23	26.0	22	80.0	
27 Jun 1979	2.985	24.0			36	77.0	20		
8 Aug 1979	.283	25.0			11	4.0	>100	76.0	

[a] Transparency greater than maximum depth

Table 45. Water quality data for sites 61200R, 71300R, and 53300R, Glover Creek.

Date	Discharge (cfs)	Temperature (C)	Dissolved oxygen (mg/l)	Percent saturation	Turbidity (JTU)	Suspended solids (mg/l)	Specific conductance (μmhos/cm)	pH
Site 61200R								
12 Jul 1978	∿0.000	24.5	7.2	85	11	1.0	82.0	
23 Oct 1978	0.002	16.0	9.4	95	13	4.0	95.0	
30 Dec 1978		6.0			6	1.0	54.0	
4 May 1979	1.359	15.0			13	9.0	56.0	
8 Aug 1979	0.085	20.0			11	3.0	66.0	
Site 71300R								
10 Dec 1977	1.395	2.5	14.4	105	19	0	72.5	
12 Jan 1978		1.4	15.4	109	21	0.5	84.0	6.4
Site 53300R								
15 Apr 1978	4.151	19.0	10.9	117	10	3.0		6.5
30 Dec 1978		7.0			10	2.0	67.0	

APPENDIX B

HABITAT SUITABILITY CURVES FOR ADULT LEOPARD DARTERS AND FRY AND SPAWNING STAGES OF SMALLMOUTH BASS

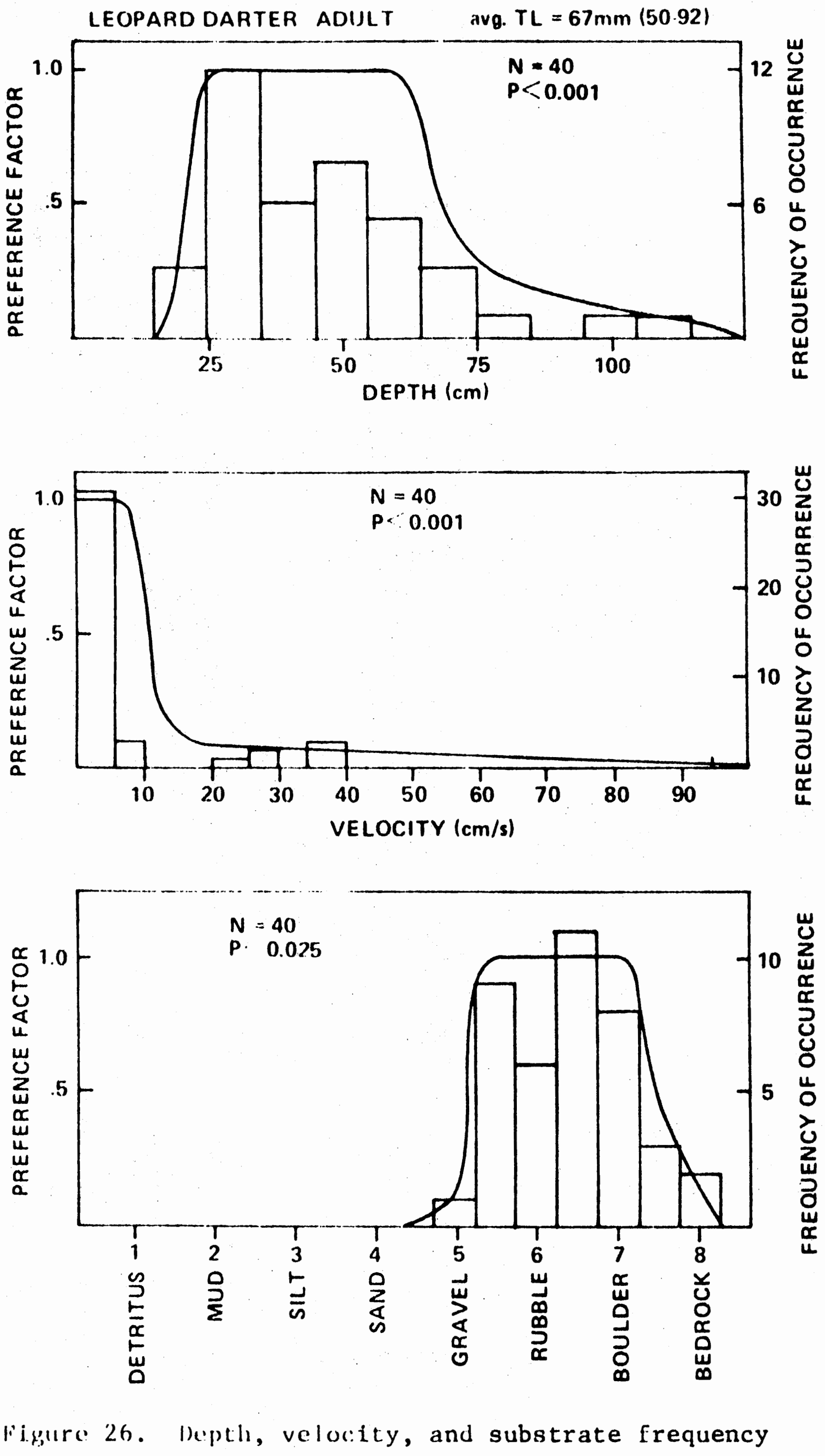

Figure 26. Depth, velocity, and substrate frequency distributions and suitability curves for leopard darters (Orth and Maughan 1980).

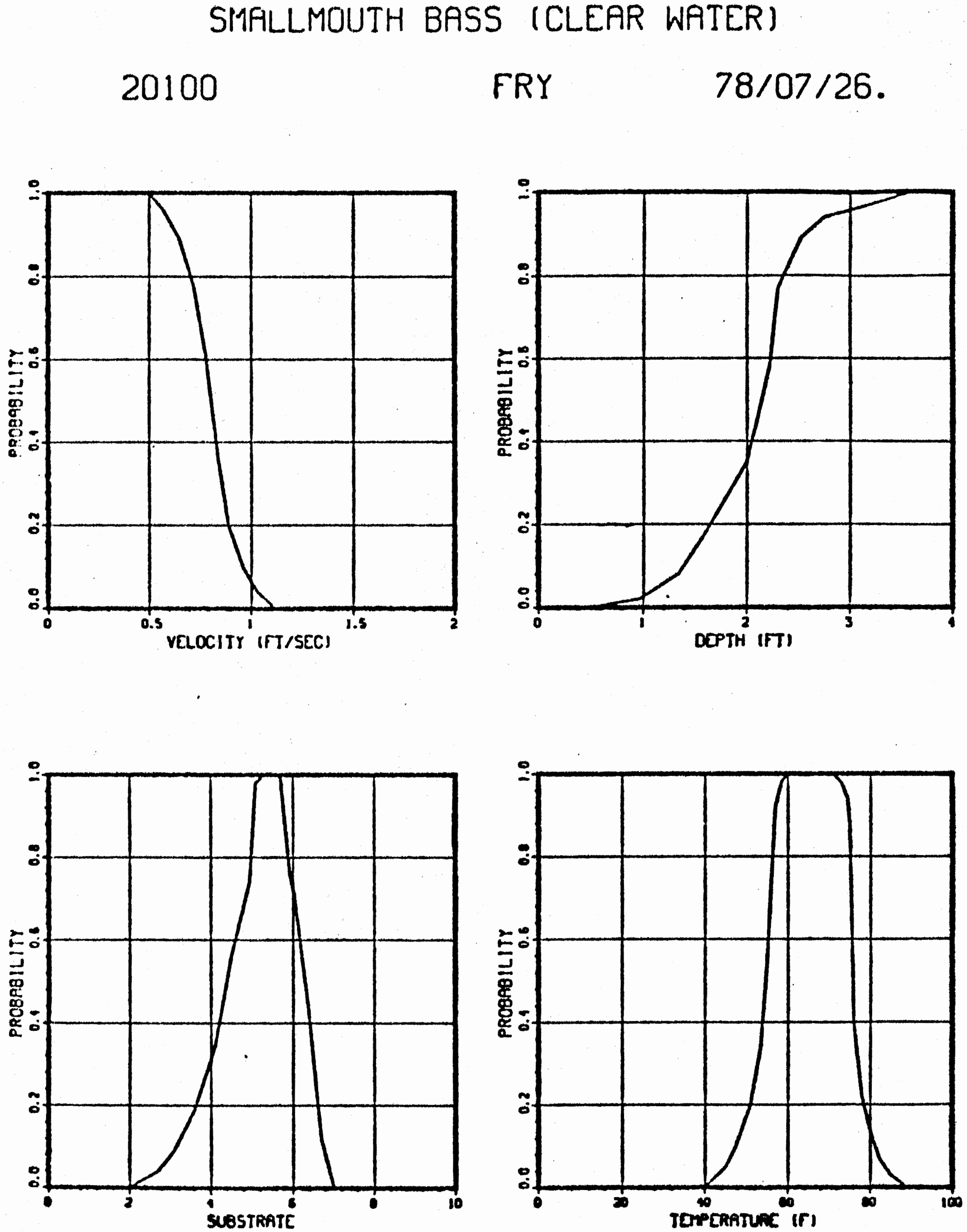

Figure 27. Habitat suitability curves for smallmouth bass fry, developed by Bovee (unpublished, Cooperative Instream Flow Service Group, Fort Collins, Colorado).

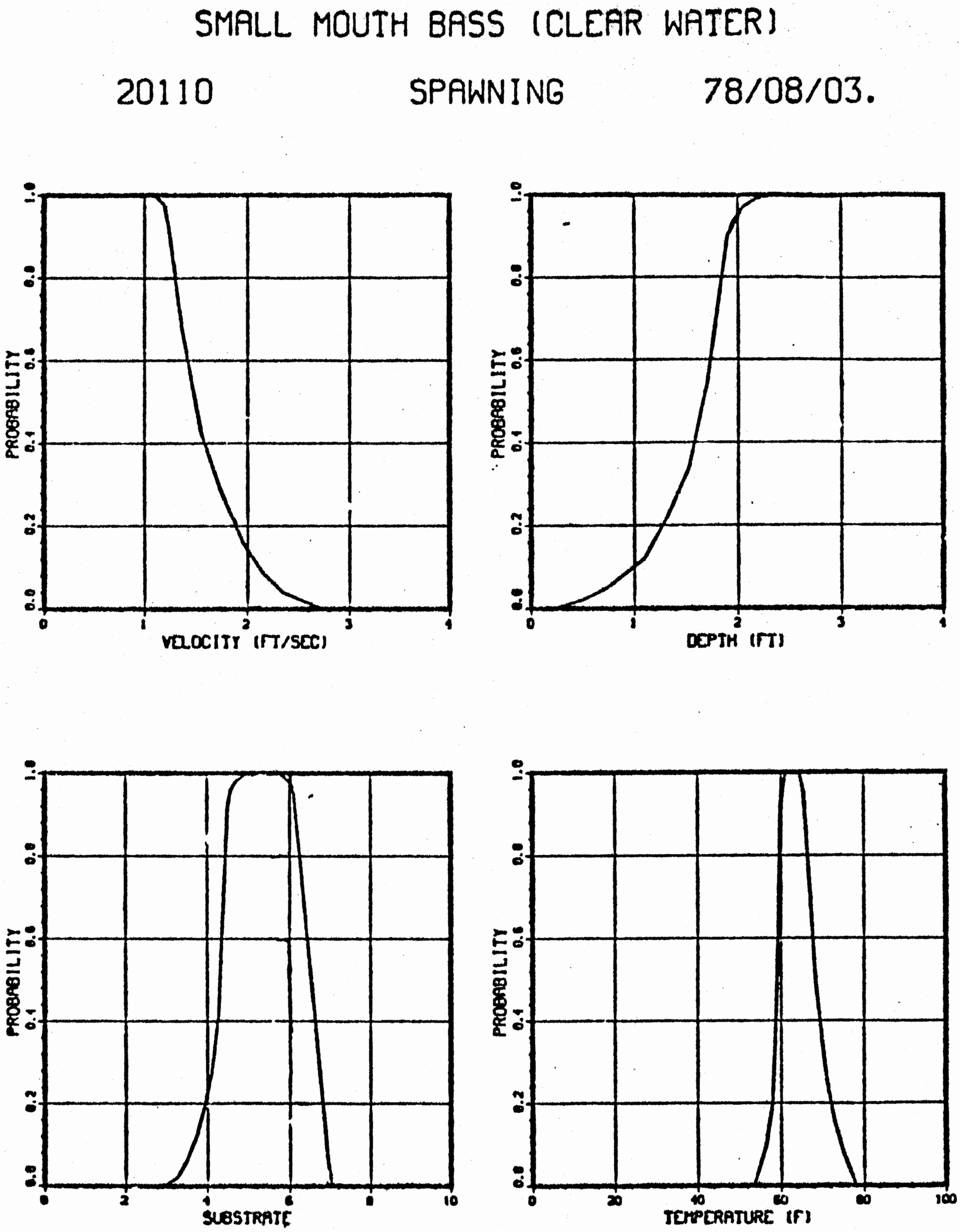

Figure 28. Habitat suitability curves for spawning stage of smallmouth bass, developed by Bovee (unpublished, Cooperative Instream Flow Service Group, Fort Collins, Colorado).

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