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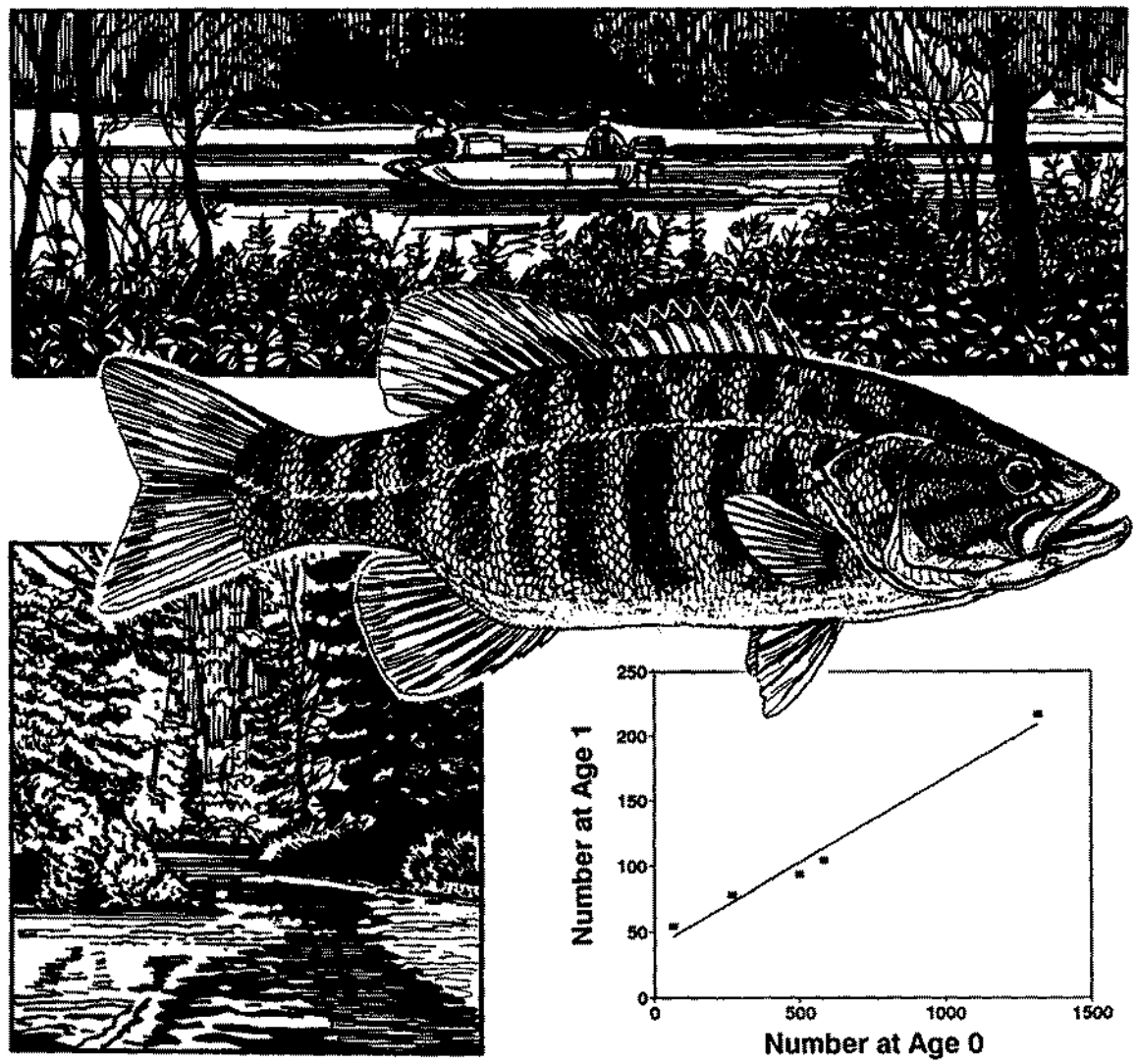
April 1994

Relations Between Habitat Variability and Population Dynamics of Bass in the Huron River, Michigan



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By

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Abstract. One of the assumptions of the Instream Flow Incremental Methodology (IFIM) is that the dynamics of fish populations are directly or indirectly related to habitat availability. Because this assumption has not been successfully tested in coolwater streams, questions arise regarding the validity of the methodology in such streams. The purpose of our study was to determine whether relations existed between habitat availability and population dynamics of smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) in a 16-km reach of the Huron River in southeastern Michigan.

Both species exhibited strong to moderate carryover of year classes from age 0 through age 2, indicating that adult populations were related to factors affecting recruitment. Year-class strength and subsequent numbers of yearling bass were related to the availability of young-of-year habitat during the first growing season for a cohort. Numbers of age-0, age-1, and adult smallmouth bass were related to the average length at age 0 for the cohort. Length at age 0 was associated with young-of-year habitat and thermal regime during the first growing season.

Rock bass populations exhibited similar associations among age classes and habitat variables. Compared to smallmouth bass, the number of age-2 rock bass was associated more closely with their length at age 0 than with year-class strength. Length at age 0 and year-class strength of rock bass were associated with the same habitat variables as those related to age-0 smallmouth bass.

We hypothesize that an energetic mechanism linked thermal regime to length at age 0 and that increased growth resulted in higher survival rates from age 0 to age 1. We also postulate that young-of-year habitat provided protection from predators, higher production of food resources, and increased foraging efficiency. We conclude that the IFIM is a valid methodology for instream flow investigations of coolwater streams. The results of our study support the contention that the dynamics of bass populations are directly or indirectly related to habitat availability in coolwater streams. Our study also revealed

several implications related to the operational application of the IFIM in coolwater streams:

1. Greater emphasis should be placed on the alleviation of habitat impacts to early life history phases of bass.
2. Effects of the thermal regime are important in some coolwater streams even if temperatures remain within nonlethal limits. Degree-day analyses should be routinely included in study plans for applications of the IFIM in coolwater streams.
3. The smallest amount of habitat occurring within or across years is not necessarily the most significant event affecting population dynamics. The timing of extreme events can be as important as their magnitude.
4. Population-related habitat limitations were associated with high flows more often than with low flows (although both occurred). Negotiations that focus only on minimum flows may preclude viable water management options and ignore significant biological events. This finding is particularly relevant to negotiations involving hydropeaking operations.
5. IFIM users are advised to consider the use of binary criteria in place of conventional suitability index curves in microhabitat simulations. Criteria defining the optimal ranges of variables are preferable to broader ranges, and criteria that simply define suitable conditions should be avoided entirely.

Key words: Instream Flow Incremental Methodology, validation, Huron River, smallmouth bass, rock bass, habitat variability, population dynamics.

Introduction

Following the large reservoir and water development era of the mid-twentieth century, North American resource agencies became concerned over the loss of many miles of riverine fish and wildlife resources. This concern was particularly acute in the arid western United States, where water development and appropriation completely dewatered some streams in all but the wettest years. During the 1960's and 1970's, numerous western states enacted legislation designed to protect existing stream resources from future depletions brought about by continued water development. For the most part, these laws sought to identify a specific amount of streamflow, below which further out-of-channel use would be curtailed. The requirement to identify a protected minimum flow resulted in the appearance of a multitude of methods for that purpose (Wesche and Rechard 1980).

By 1976 it became apparent that methods designed to identify minimum flows were inadequate to address all aspects of instream flow problems (Orsborn and Allman 1976; Stalnaker and Arnette 1976). Whereas minimum flows were considered inviolable by biologists making the recommendations, they were often seen as negotiable issues by the decision makers charged with implementing the recommendations. Methods designed for minimum flow analysis were of little use when the instream flow problem entailed negotiated flow regimes or reservoir operations. Because of these inadequacies, the need was expressed for the development of a methodology that could be used to analyze the consequences of a proposed water withdrawal or storage and release operations below federal water projects. Ultimately, this need was manifested in the development of the Instream Flow Incremental Methodology (IFIM; Bovee 1982).

The IFIM was enthusiastically embraced by state and federal resource managers in the western United States, in part because some of its components were similar to methods already in use in many states. Additionally, several studies were conducted during the 1970's and 1980's to determine whether the number or biomass of trout was correlated with measures of habitat derived from the IFIM. The results from these early validation tests in western salmonid streams were encouraging (Nehring 1979; Nickelson et al. 1979; Stalnaker 1979; Wesche 1980; Nehring and Anderson 1983, 1984, 1993; Gowan 1984; Loar et al. 1985; Bovee 1988).

During the 1980's, resource managers increasingly realized that riverine habitats in midwestern and eastern streams were also threatened by water withdrawals, reservoir operations, and power production. Gradually, the IFIM

was adopted for use in eastern streams, primarily because it was considered the state of the art in evaluating instream flow alternatives (Orth 1987).

The decision to move applications of the IFIM into non-salmonid streams of the eastern United States was not universally accepted. During the mid 1980's, a spirited debate was conducted in the professional literature, arguing the merits and demerits of the IFIM in general, and its applicability to coolwater and warmwater species in particular (Granholm et al. 1985; Mathur et al. 1985; Orth and Maughan 1986; Shirvell 1986; Orth 1987; Scott and Shirvell 1987). At the basis of this argument lay a fundamental assumption of the methodology: The dynamics of fish populations are directly or indirectly related to habitat availability in streams. Whereas relations between trout populations and habitat had been successfully tested a number of times in salmonid streams, few such studies had been conducted in streams containing species other than salmonids. Where such studies were completed, the results were often mixed or inconclusive (Orth and Maughan 1982).

The present study was initiated in 1989, at the request of Region 5 of the U.S. Fish and Wildlife Service, to test the validity of the IFIM in a coolwater stream. Our specific objective was to determine how the population dynamics of smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) were related to habitat availability as predicted by the IFIM.

Study Area

Our study area was located in a 16-km reach of the Huron River, in Washtenaw County, Michigan. The upper end of the study area was bounded by the Bell Road Bridge, 24 km upstream from Ann Arbor; the lower boundary was at Delhi Road, 8 km from Ann Arbor (Fig. 1). The drainage of the Huron River above Ann Arbor is a rectangular-shaped area of 190,624 ha; the long axis of the rectangle trends from northeast to southwest. The only significant tributary in the study area is Mill Creek (drainage area 33,670 ha), which enters the Huron River at the town of Dexter.

The Huron River watershed has been shaped and influenced by continental glaciation. Glacial drift, varying in thickness from 30 to 45 m, forms the hills abutting the floodplain throughout the study area. The river channel and floodplain are located in an ancestral spillway channel, formed by meltwater runoff during glacial retreats. There are more than 300 named and 750 unnamed lakes and ponds in the Huron River basin, most of which occur upstream from the study area (Larson et al. 1975).

Southern Michigan has a humid continental climate (Critchfield 1966), moderated by the Great Lakes. Lake effects are most evident during winter and early spring, when weather conditions are similar to those of a maritime climate. Throughout much of the year, frontal systems passing over the Great Lakes provide widespread and relatively uniform rainfall over the entire watershed. These storms often yield abundant rainfall as sustained, steady rains. On the average, 34 thunderstorms occur per year (Larson et al. 1975), usually during late spring and summer.

The Huron River has exhibited large year-to-year and within-year variation in streamflow over the period of record. Runoff events have appeared to follow an approximate 20-year pattern of persistent droughts and wet periods since the early 1900's (Fig. 2). The lowest runoff occurred in 1931 (7.75 cm) and the highest in 1950 (41.68 cm). The highest within-year runoff has normally occurred during late winter and early spring, resulting from a combination of rainfall and snowmelt. Following the spring flood peak, the hydrograph has exhibited a gradual recession to base flows in late summer and early fall. Owing to the profusion of lakes in the system and to the permeable soils of the watershed, precipitation events have been buffered dramatically through surface- and ground-water storage. The recessional limbs of runoff hydrographs for individual storms have been especially gradual, often extending over a period of 5–7 days. The ascending limbs of storm hydrographs have been more pronounced, but runoff peaks have typically lagged precipitation events by 1–2 days.

In addition to the natural lakes in the drainage, there are several control structures upstream from the study area. Nearly all of these dams were constructed for lake elevation control (Knutilla 1972), and they behave much like natural lakes in their influence on the hydrology of the river.

No formal water quality monitoring program has been conducted in the Huron River basin, but spot samples have been collected by the U.S. Geological Survey and the U.S. Army Corps of Engineers (Knutilla 1972). Surface and ground water entering the Huron River are of the calcium-magnesium bicarbonate type and slightly alkaline (pH = 8.1). The high concentrations of calcium and

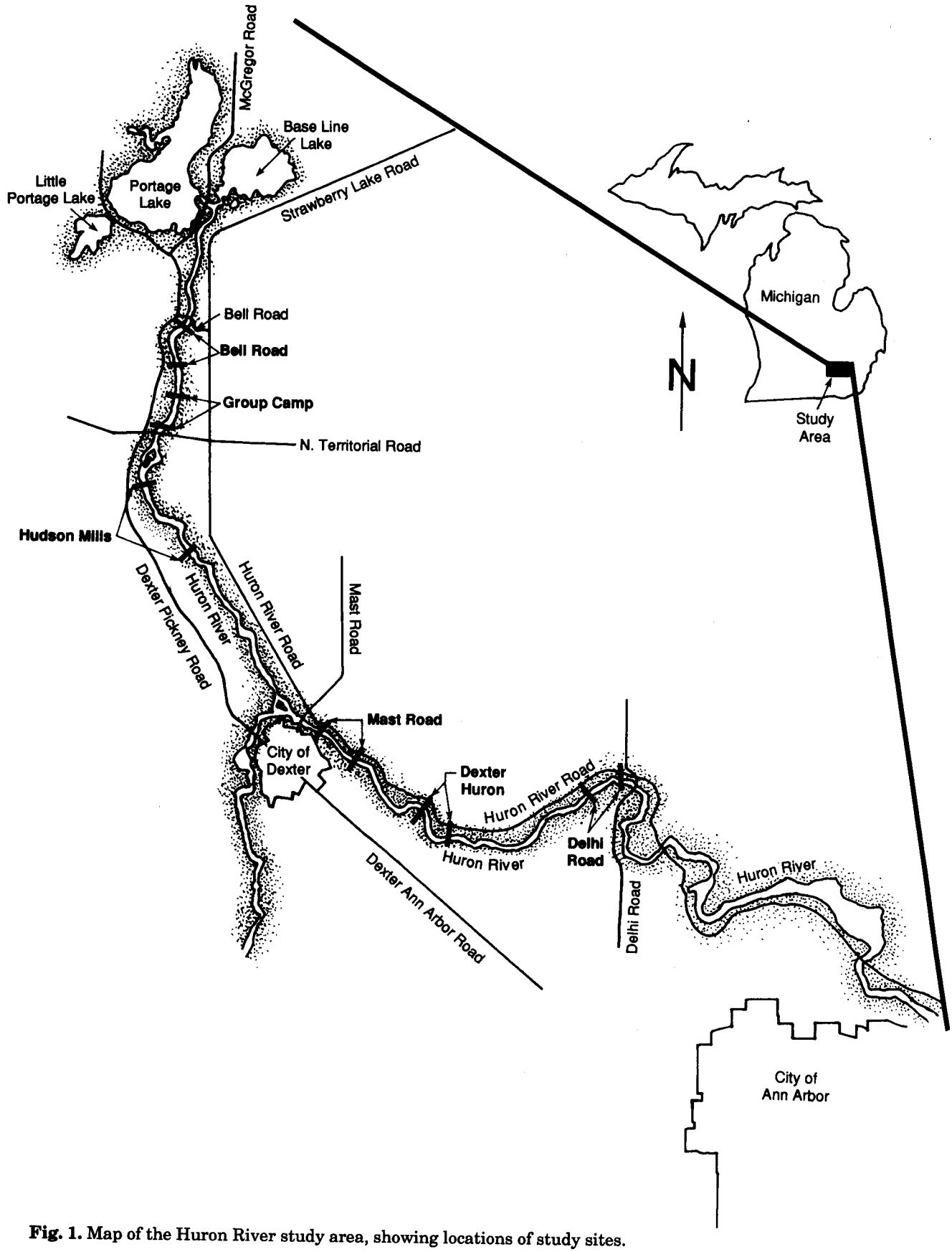

Fig. 1. Map of the Huron River study area, showing locations of study sites.

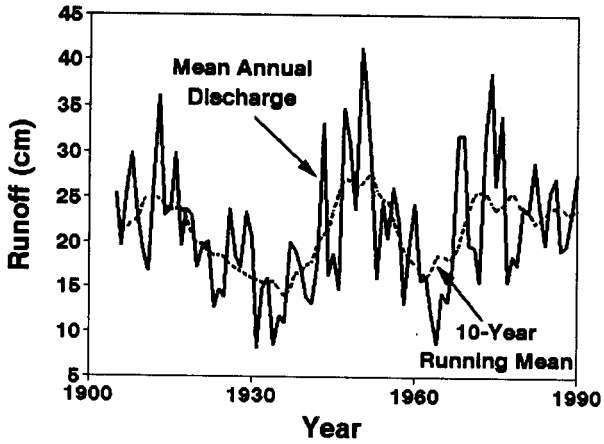

Fig. 2. Mean annual runoff and trends, Huron River at Ann Arbor, Michigan.

magnesium are manifested by extensive marl formation in riffle areas. Bicarbonate concentrations at base flows are approximately 200 mg/L; hardness (measured as $CaCO_3$) ranges from 200 to 225 mg/L. Sulfate concentrations range from 25 to 55 mg/L and chlorides from 27 to 31 mg/L (Larson et al. 1975).

There was little evidence of organic nutrient enrichment during our study. Algal blooms that would have increased turbidity during summer daytime periods were never observed, and turbidity was usually low (1–3 JTU) upstream from the confluence of Mill Creek. Visibility in the Huron River was consistently higher above the confluence with Mill Creek, which Monahan (1991) attributed to suspended matter from agricultural runoff and treated wastewater. Larson et al. (1975) provided evidence that the reduction in visibility could have resulted from color, rather than turbidity. They found little difference in turbidities measured in Mill Creek and the Huron River above the confluence at base flows, but noted that color (measured as platinum-cobalt units) was two to three times higher in Mill Creek.

Extreme temperatures in the Huron River ranged from 0° C to 29.9° C during our study, but average summer temperatures ranged from 18° to 21° C. These temperatures were slightly cooler than optimal for smallmouth bass (Armour 1993) and rock bass (Carlander 1977), but are well within the suitable ranges for both species. Temperatures in the study area were affected by groundwater inflow and the epilimnetic release from Portage and Baseline lakes. The combination of these factors resulted in slightly higher temperatures in the upper reaches of the study area than in downstream portions. Average temperatures at Bell Road were 0.96° C higher than at Delhi Road during summer and 0.25° C higher during winter. The slight elevation in winter temperatures prevented the formation of sheet ice in the upstream reaches, whereas continuous ice cover was common in the lower reaches.

The Huron River is a heavily used recreational stream, owing to its proximity to the Detroit and Ann Arbor metropolitan areas. Canoeing and fishing are popular activities along the length of the study area, and public access is ensured by the Metropolitan Parks system. With the exception of a few private inholdings and the corporate limits of the town of Dexter, the entire study area was within the Metro Park system.

General Experimental Design

In 1983, the Michigan Fisheries Research Institute (Department of Natural Resources) initiated a study on the Huron River to evaluate the effects of catch and release regulations on smallmouth bass and rock bass populations. The study was divided into control and treatment sections, upstream and downstream from Mill Creek. Harvest was allowed in the control section above Mill Creek, whereas catch and release regulations were enforced in the downstream treatment section. Beginning in fall 1983, the investigators established six permanent sampling stations between Bell and Delhi roads (Fig. 1). Population estimates have been made and age and growth data taken in late September or early October every year since then.

The area selected by the Fisheries Research Institute was an ideal experimental setting for an investigation of resident fish populations because it was essentially a closed system. Upstream egress of fish from the study area was blocked by the dams at Portage and Baseline lakes. Access from downstream areas was obstructed by an abandoned mill dam at Delhi Road, and emigration of fish into Mill Creek was inhibited by an impoundment near Dexter. Movement of fish within the study area was unrestricted, with the possible exception of a small rapids near North Territorial Road.

We used the data provided by the Fisheries Research Institute to develop cohort tables for each age group and year class of smallmouth bass and rock bass at each of our study sites. These

estimates were averaged across sites to develop cohort tables to represent the population dynamics of smallmouth bass and rock bass within the whole study area. The cohort tables enabled us to determine the relative strengths of year classes over time, to evaluate the effects of strong and weak year classes on adult population size, and to examine the possible causes and effects of differential growth rates from year to year.

Time series of microhabitat availability (Bovee 1982) were developed for each life stage at three of the sites established by the Fisheries Research Institute. Microhabitat time series for individual sites were combined to produce life-stage-specific habitat time series for the entire study area, corresponding to the same period of record as for the cohort tables. The microhabitat time series were used to extract information on the amount of microhabitat available to the target species during individual or multiple intervals of time through the period of record for the study.

A time series of temperatures, similar to the microhabitat time series, was synthesized from an empirical multiple regression model. Predicted temperatures were used to estimate the starting dates for reproductive and early life history phases and to calculate degree-day accumulations.

Statistical analyses were conducted to test for associations among microhabitat availability, temperature regime, and various population metrics, such as year-class strength, adult population, and growth rates. We also tested for various biological relations, such as those between growth rates and recruitment, and between recruitment and adult population size. Negative associations between species that might indicate effects of competition or predation were also examined.

Habitat Simulations and Metrics

The purpose of our habitat and temperature simulations was to determine microhabitat availability and thermal regime in our study area for the period of record, 1981–89. A multi-step procedure was employed to link outputs from component models of the IFIM (Fig. 3). Habitat suitability criteria were developed from empirical habitat-use data to determine the relative quality of different ranges of microhabitat variables for individual life stages of bass. The habitat suitability criteria and site-specific data on channel configuration, structure, and hydraulics were combined in the Physical Habitat

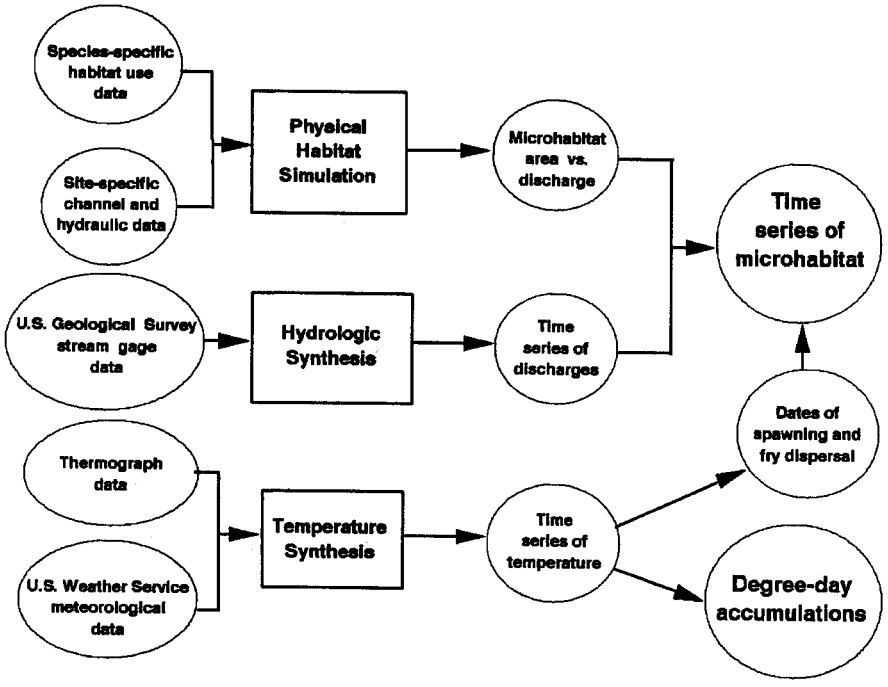

Fig. 3. Schematic diagram of component models and linkages used to determine microhabitat availability and thermal regime in the Huron River.

Simulation System (PHABSIM) to relate microhabitat availability and discharge. Information from the temperature simulations was used to estimate the dates of peak spawning activities and dispersal of fry from the nests. These dates delineated the time periods for the evaluation of habitat for spawning and young-of-year in the habitat time series. Additionally, predicted temperatures were used to calculate accumulated degree-days during the growing season, for subsequent analysis of relations between temperature regime, growth rates, and first-year survival. A hydrologic time series was synthesized from U.S. Geological Survey gaging station data, to determine the amount of discharge occurring in the river at weekly time steps throughout the period of record. The hydrologic time series served as input to the microhabitat time series model and the temperature model. The microhabitat time series model was used to calculate the amount of microhabitat available to each life stage at each time step in the period of record.

Physical Habitat Simulations

Habitat Suitability Criteria

Habitat suitability criteria were developed for four life stages of smallmouth bass and rock bass: spawning, young-of-year, juvenile, and adult. Spawning was defined by the presence of a nest containing eggs or black fry, guarded by an adult smallmouth bass or rock bass. Young-of-year criteria were developed for smallmouth bass less than 11 cm total length (TL) and for rock bass less than 6 cm TL after they had dispersed from the nest. Juvenile smallmouth bass were defined as individuals between 12 and 19 cm TL and adult smallmouth bass as individuals larger than 20 cm TL. Juvenile rock bass were defined as individuals between 7 and 10 cm TL and adult rock bass as individuals larger than 11 cm TL. Criteria were also stratified by winter, spring, and summer seasons, and the summer criteria were divided diurnally and nocturnally. Winter was defined as the period from 1 November to 30 March and summer from 1 June to 31 October. The spring stratification corresponded to the spawning period and was defined differently each year depending on the temperature.

Data on microhabitat use were collected primarily by surface observation, using teams of divers (snorkel and SCUBA), although electrofishing and radiotelemetry were also used for some of the criteria (Monahan 1991). When fish were observed, their locations were marked, and pertinent microhabitat data were collected when the sampling effort was completed. Microhabitat variables measured included depth, mean column velocity, nose velocity (measured 6 cm above the streambed), adjacent velocity (the nearest velocity that was discernibly faster than the mean column velocity at the fish location), distance to adjacent velocity, cover type, distance to cover, dominant particle size, and percent embeddedness of the substrate.

Three different sets of binary criteria for depth and velocity were developed for each life stage and temporal stratification following Bovee (1986). We chose to use a binary format for our criteria because it produced an output from PHABSIM in units of actual microhabitat area within a quality classification (e.g., optimal vs. usable). This approach allowed us to evaluate the relative importance of microhabitat quality in explaining variability in bass populations.

The narrowest range we delineated for any variable was the interval encompassing the central 50% of the locations occupied by a life stage. This interval was defined as the optimal range. A broader variable range, defined as usable, encompassed the central 75% of the occupied locations. The broadest variable range, termed the suitable range, encompassed the central 95% of the occupied locations. For continuous variables (e.g., depth, mean column velocity), we used nonparametric tolerance limits (Bovee 1986) to establish classification boundaries. Where sample sizes were insufficient to apply nonparametric tolerance limits, binary criteria were developed by plotting histograms of occupied locations. Optimal, usable, and suitable ranges were estimated from the histograms, loosely following the same definitions as for the nonparametric tolerance limits.

Cover was classified according to size, function, and complexity. A numerical channel index code was developed to assign a number to each cover type (Table 1). Optimal cover types were defined as those that were used most frequently and accounted for 50% to 75% of the observations. Cover types that accounted for 75% to 95% of the observations were defined as usable. If a cover type was used at all, regardless of how infrequently, it was considered suitable. We indicated the combination of gravel substrate in association with each cover type by adding 10 to the channel index code where such combinations existed (Table 1).

During the course of the study, we observed that riffles and clean cobble substrates were rarities in

Table 1. Channel index codes and descriptions used in the development of habitat suitability criteria for Huron River smallmouth bass and rock bass.

Number code	Description	Example
1	No cover	
2	Small velocity shelter	Cobble or boulder protruding 15–30 cm above streambed
3	Medium velocity shelter	Boulder or tree stump protruding 30–60 cm above streambed
4	Large velocity shelter	Boulder or tree stump protruding more than 60 cm above streambed
5	Small complex	Emergent water willow or other vegetation providing visual isolation and velocity shelter
6	Large compound	One or two large suspended logs providing overhead cover, but minimal velocity shelter
7	Large complex	Log jam or snag providing abundant visual isolation and velocity shelter
8	Near-shore complex	Rootwads and undercut banks providing hiding refuge, visual isolation, and velocity shelter
9	Small compound	Small submerged logs and branches providing limited visual isolation or velocity shelter
10	Unused code	
11	No cover	Suitable spawning gravel with no cover present
12	Small velocity shelter	Small boulder with spawning gravel
13	Medium velocity shelter	Medium boulder or stump with spawning gravel
14	Large velocity shelter	Large boulder or stump with spawning gravel
15	Small complex	Emergent vegetation with spawning gravel
16	Large compound	Large suspended logs with spawning gravel
17	Large complex	Log jam or snag with spawning gravel
18	Near-shore complex	Root wad or undercut bank with spawning gravel
19	Small compound	Submerged branches with spawning gravel

the Huron River. This observation led us to hypothesize that riffles might be important food-producing areas and could have an indirect influence on bass populations. Although we did not have the resources to conduct a detailed analysis of trophic level relations, we were able to investigate the availability of riffle microhabitat in the study area.

We defined riffle microhabitat from habitat suitability criteria obtained from Culp and Homa (1991). Although these criteria originated from Idaho, we felt that they adequately represented the combinations of depth, velocity, and substrate generally associated with riffles in small streams. We recoded the channel indexes from the criteria to make them compatible with the cover and substrate data collected in the Huron River. In the original criteria, no rating was provided for woody debris or emergent vegetation. In streams with sandy main channel sediments, Smock et al. (1985) found vegetation to be a highly productive substrate type. Accordingly, we assigned a high suitability rating to woody debris and emergent vegetation.

Microhabitat Data Collection

Our selection of study sites was influenced by two somewhat conflicting goals. First, we wanted to establish study sites that would allow us to describe the microhabitat in the entire study area for the time series analysis. Second, to examine relations between habitat availability and bass distributions, it was advantageous for our study sites to correspond with those of the Fisheries Research Institute.

Prior to establishing study sites, we conducted several reconnaissance trips through the study area by canoe. We classified mesohabitat types according to the techniques described by Morhardt et al. (1983) and marked the transitions from one mesohabitat type to another on a 7 1/2-minute topographic map. A map wheel was used to determine the length of each mesohabitat unit. These lengths were then used to calculate the percentage of the total study area represented by each mesohabitat type.

Based on our reconnaissance, we decided that the Bell Road, Hudson Mills, and Mast Road sites (Fig. 1) would most effectively meet our needs. The three sites collectively contained most of the common mesohabitat types we had defined, and each site could be classified as being predominantly of a single type. Because the three sites differed substantially in slope, channel configuration, and distribution of substrate and cover, they could also be used to examine spatial relations between habitat and fish distributions. Deep pools were not represented in any of the sites, but these were extremely rare in the Huron River. From habitat mapping, we estimated that Bell Road represented only about 3% of the total study area, but nearly 100% of the riffle habitat type. The Hudson Mills site depicted the shallow runs that occupied 35% of the study area. Mast Road represented deep runs and shallow pools, accounting for 62% of the study area.

Upper and lower boundaries were established to delineate each study site. The lower boundary of each study site was determined by locating the nearest downstream hydraulic control, a feature of the channel that created a backwater effect in the upstream direction. In the Huron River, hydraulic controls usually took the form of short, low-gradient riffles or the upper ends of island complexes. The upper boundaries to the study sites corresponded to those of the sampling stations established by the Fisheries Research Institute.

Sites were subdivided into longitudinal "cells" for subsequent transect placement. Our goal in establishing stream cells was to identify specific microhabitat features as they were distributed longitudinally along the river. The presence or absence of cover, changes in channel cross section, and slope were common delimiters of cells; a transect was established at the center of each stream cell. Horizontal surveys were conducted on all cell boundaries and transects to draw a scale planimetric map of each site (Figs. 4–6). We used the maps to determine the distance represented by each transect for later entry as reach lengths to the hydraulic models in PHABSIM.

Elevation control was maintained through the use of multiple permanent benchmarks (lag bolts or railroad spikes driven into trees). At each site, a primary benchmark was assigned an arbitrary elevation of 30.5 m (100.0 ft), and the elevations of all secondary benchmarks were determined by differential leveling. Level loops at all three sites were closed to within 3 mm (0.01 ft) and were periodically rechecked throughout the study period.

Cross-sectional surveys were initiated during low-flow periods, beginning in autumn 1989 and continuing through summer 1990. To accurately simulate overbank discharges, we extended the transects from the headpin on each side, across the floodplain to the toe of the first terrace. At

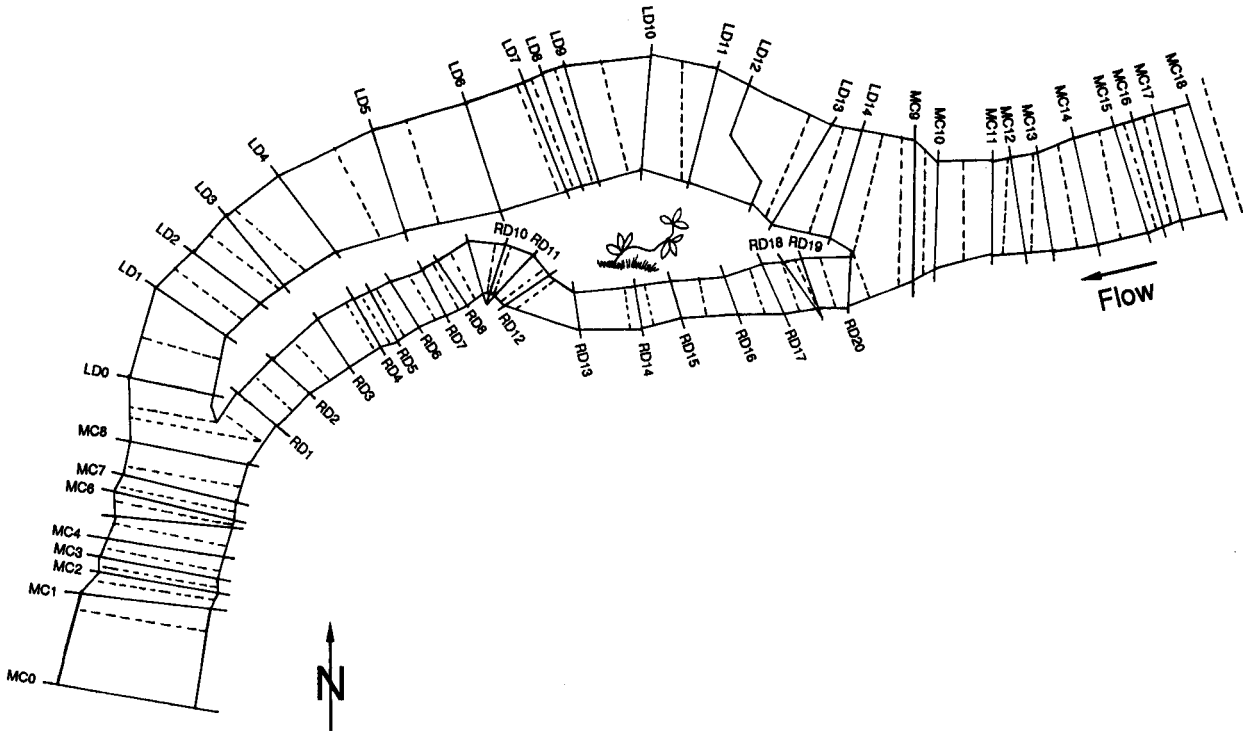

Fig. 4. Scale planimetric map of the Bell Road site. *Solid lines* indicate transects; *dashed lines* indicate longitudinal cell boundaries.

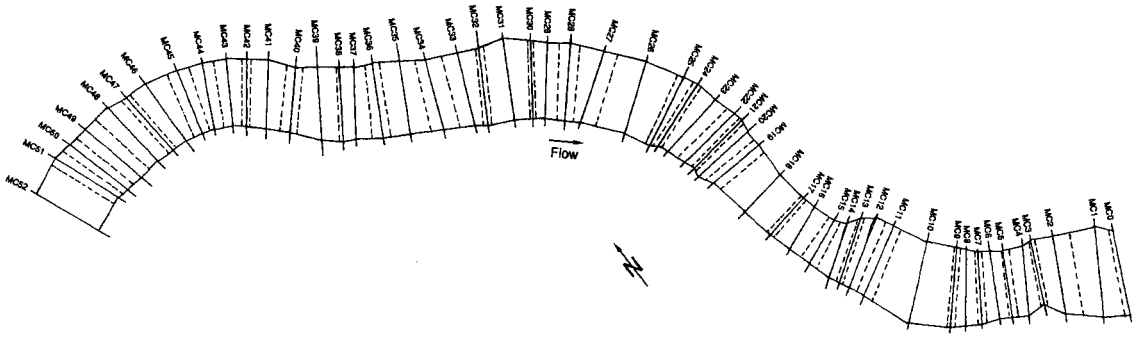

Fig. 5. Scale planimetric map of the Hudson Mills site. *Solid lines* indicate transects; *dashed lines* indicate longitudinal cell boundaries.

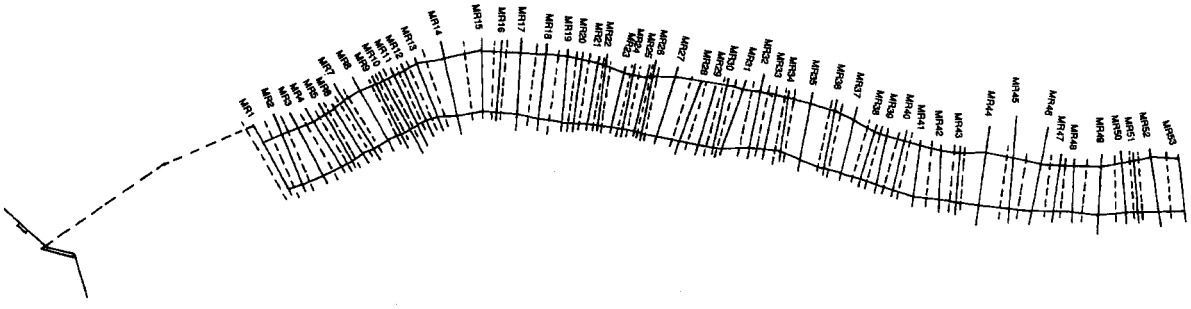

Fig. 6. Scale planimetric map of the Mast Road site. *Solid lines* indicate transects; *dashed lines* indicate longitudinal cell boundaries.

40–50 intervals from the zero point (the toe of the left-side terrace), the following measurements were made:

1. Distance from zero as determined from a measuring tape or by stadia measurements using a level.
2. Ground elevation relative to the primary benchmark, determined by differential leveling.
3. Cover type according to the descriptions in Table 1.
4. Dominant particle size of the substrate (e.g., silt, sand, and subdivisions of gravel, cobble, and boulder).
5. Percent embeddedness of the substrate in sand or finer material, determined to the nearest quartile by visual inspection.

Mean column velocities were measured with either a Price AA or pygmy current meter at each vertical with a depth of 3 cm or greater. Velocity calibration measurements were made at 5.7 m^3/s at Bell Road, 8.8 m^3/s at Hudson Mills, and 11.06 m^3/s at Mast Road. Water surface elevations were measured to the nearest 3 mm on each transect. At Bell Road, the calibration discharges for water surface elevations were 2.1, 5.8, and 9.4 m^3/s. Water surface elevations for Hudson Mills were measured at 2.05, 8.8, and 9.4 m^3/s, and for Mast Road at 3.1, 10.26, 11.06, and 19.34 m^3/s.

We installed and rated two permanent staff gages, one at North Territorial Road, between the Bell Road and Hudson Mills sites, and the other at Mast Road, immediately upstream from the study site. These gages were read before beginning work in the morning, at noon, and before leaving the site in the evening. We also carried along several temporary staff gages, which were installed at convenient locations within each site. These gages were not rated, but were used primarily to monitor changes in stage while we measured water surface profiles. In most instances, we were able to complete the surveys of surface elevations in 4–5 h, and discharges remained steady during the process.

Hydraulic Simulations

The data for each site were organized, checked for errors, and entered into standard input files for the IFG4 hydraulic simulation program (Milhous et al. 1989). Numerical channel index codes corresponding to those in Table 1 were entered into the input files. Although the codes were not used in the hydraulic simulations, they were passed forward by IFG4 to the habitat models.

A multi-stepped procedure, described by Milhous et al. (1989), was used to predict hydraulic conditions at unmeasured discharges (Fig. 7). Water surface elevations were determined for simulated discharges using a "step-backwater" model (WSP). Simulated discharges and water surface elevations were then passed to a second hydraulic simulation program, IFG4, where depths and mean column velocities were computed.

We calibrated predicted water surface elevations to within about 15 mm (0.05 ft) of the measured elevation at the highest calibration discharge. Roughness coefficients were adjusted gradually from transect to transect, increasing or decreasing roughness only when there was physical evidence to justify the change (e.g., a transition from a gravel substrate to cobbles and boulders). The second step in the calibration process was to adjust the channel roughness modifiers to account for the "variable roughness" phenomenon, whereby roughness increases at an approximate exponential rate with reduced discharge (Chow 1959). Appropriate roughness modifiers were found by matching predicted and measured water surface elevations for the lower discharges to within 15 mm. Roughness modifiers were plotted on logarithmic graph paper and fit by least squares. For simulated discharges (production runs) the roughness modifier for each discharge was read from the graph.

While calibrating WSP, we detected variable backwater effects at all three sites. At low discharges, the hydraulic control at the bottom of the site established the backwater effect. At higher discharges, however, a hydraulic control located farther downstream created a backwater that extended over and beyond the at-site (local) control. When this happened, the local control was said to be subordinated by the downstream control. The net effect of this phenomenon was to make the entire rating curve nonlinear, virtually necessitating the use of a step-backwater model, such as WSP.

To conduct simulations of unmeasured discharges, it was necessary to provide WSP with either a starting elevation or energy gradient at the downstream-most transect. Because the subordinated control made it difficult to determine the initial water surface elevation, we used the energy gradient to define the initial conditions for each simulated discharge. The initial energy gradients were about the same for the middle and highest calibration discharges, considerably steeper for the

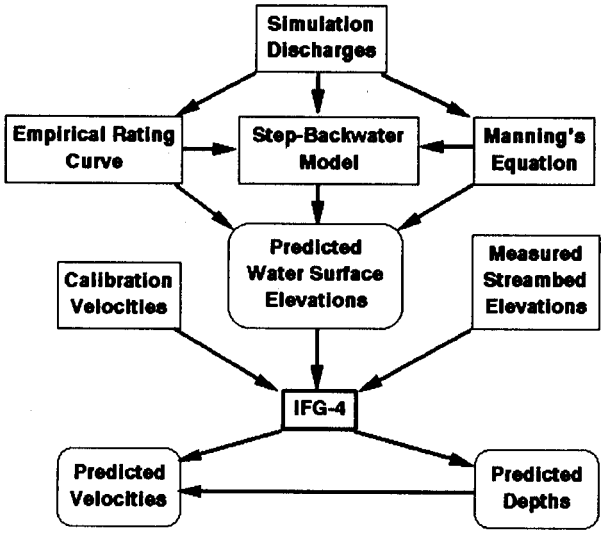

Fig. 7. Multi-step procedures used to predict depths and velocities at unmeasured discharges.

lowest calibration discharge. On the basis of this observation, we made several assumptions with regard to the energy gradient at unmeasured discharges:

1. The energy gradients for discharges less than the lowest calibration discharge were assumed to be the same as the gradient at the lowest calibration discharge.
2. The energy gradients for discharges greater than the highest calibration discharge were assumed to be the same as the gradient at the highest calibration discharge.
3. The energy gradients for discharges between the lowest and middle calibration discharges were assumed to be intermediate to the two calibrated gradients and were estimated by linear interpolation.

The final simulation of the discharges of interest is known as a production run in the parlance of the IFIM. For this study, we simulated streamflows from 0.28 to 85.7 m^3/s to bracket the entire range of discharges that had occurred in the segment over the period of record. For each discharge simulated at Hudson Mills and Mast Road, we entered the starting energy gradient and roughness modifier into the WSP input file. Water surface elevations were predicted by WSP for each simulated discharge, and both were written to the production IFG4 input file. IFG4 was then used to calculate the depths and velocities at each vertical.

At verticals where depths were shallow at the calibration discharge, the measured velocities were often very low, which resulted in the calculation of artificially high values for Manning's n in IFG4. Where we detected inflated values for n, we changed them to match values of nearby verticals with similar cover and substrate characteristics, but in deeper water. In contrast, higher n values were inserted for verticals on forested floodplains to account for the presence of dense vegetation.

The Bell Road site was divided by an island, which required separating the data into four discrete units: the main channel below the island, the main channel above the island, and the left and right side channels. We calibrated each of these units independently and used the procedures described above to develop the production run for the main channel below the island. For the side channels, it was necessary to partition the total discharge according to the portion flowing down each side of the island at each simulated (total) discharge. We had anticipated the need to divide Bell Road into four parts, so during the data collection phase we measured the total and side channel discharges several times. These measurements allowed us to calculate the discharge flowing in the right and left side channels for each of the simulation discharges.

Simulations at Bell Road followed the same general procedures as at the other two sites, with one exception. Instead of using the energy gradient as the starting condition for the side channels, we used the simulated water surface elevations at the uppermost transect in the main channel to calculate starting water surface elevations in the side channels. Similarly, we used the simulated water surface elevations in the larger of the two side channels to determine the starting water surface elevations upstream from the island. This procedure produced much smoother water surface profiles for the total site (and better hydraulic simulations, we think) than if we had treated each component completely independently.

Quality assurance of PHABSIM simulations was conducted by examining model performance over the range of discharges being simulated. Two indicators of model performance were used, the water surface profiles at simulated discharges and plots of the velocity adjustment factor (a coefficient calculated within IFG4 for mass balancing) versus simulated discharge.

Simulated water surface profiles should closely approximate the measured profiles and should typically become more uniform in gradient at higher simulated discharges. At low discharges, the

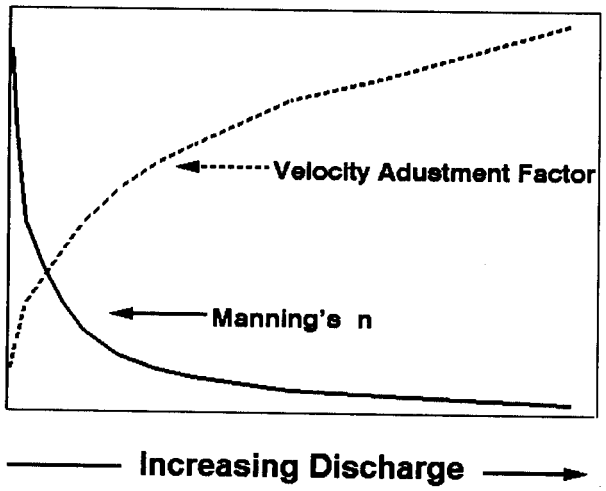

Fig. 8. Theoretical relations between discharge, Manning's n, and velocity adjustment factors.

water surface elevations should become more irregular and follow streambed features more closely. Elevations should logically increase in an upstream direction, with no dips, bumps, or irregularities that are not associated with streambed elevations.

Under normal circumstances, the velocity adjustment factors (VAF's) should look like the inverse of the theoretical relation between Manning's n and discharge (Fig. 8). Velocity adjustment factors should be less than 1.0 at simulated discharges less than the calibration discharge and should increase rapidly to a value of approximately 1.0 at the calibration discharge. At simulation discharges greater than the calibration discharge, velocity adjustment factors should be greater than 1.0 but should increase more slowly than at simulation discharges below the calibration discharge.

Our indicators of model performance adhered well to the aforementioned guidelines, everywhere except in the right side channel of the Bell Road site. Irregularities in the water surface profiles and velocity adjustment factors in this side channel were attributable to a complex variable backwater effect (K. D. Bovee and R. T. Milhous, National Ecology Research Center, Fort Collins, Colorado, unpublished manuscript).

Microhabitat Simulations

We used the HABTAE program (PHABSIM Version II; Milhous et al. 1989) to develop three types of functional relations between discharge and microhabitat for each life stage and time period. The first type was calculated using criteria for optimal microhabitat, the second using criteria for usable microhabitat, and the third using the broadest (suitable) criteria set.Microhabitat simulations for Mast Road and Hudson Mills were conducted using the "whole reach" output from IFG4. For Bell Road, discharge versus microhabitat functions were generated for each of the four individual simulation units. The individual functions were then combined as a weighted total microhabitat and were later synthesized into a single function in a spreadsheet. Weighting factors for the simulation units were determined by dividing the length of each unit by the cumulative length of all the units. The total microhabitat for the combined Bell Road site was calculated by

$$M_{i,j} = \Sigma w_k \times m_{i,j,k} \qquad (1)$$

where

$M_{i,j}$ = total microhabitat, Bell Road site, for habitat stratum (i) and discharge (j);

w_k = weighting factor for simulation unit (k); and

$m_{i,j,k}$ = total microhabitat for habitat stratum (i) at discharge (j) in simulation unit (k).

Synthesis of Thermal Regime

In June 1989, we installed continuous recording digital thermographs at the upper and lower boundaries of the study area. Prior to installation, the instruments were calibrated in a water bath against an ASTM (American Society for Testing and Materials) thermometer. The thermographs were programmed to record water temperature at intervals of 1 h and were removed periodically to download data into ASCII computer files. Recorded temperatures were corrected for each thermograph according to the appropriate calibration equation prior to their use in developing temperature models.

Average weekly water temperatures were synthesized for the period of record using a multi-step process:

1. Hourly temperatures were converted to 7-day averages. Days with fewer than 24 h of continuous data were eliminated from the computations, as were records with fewer than 7 continuous days of data.
2. Average daily air temperatures were estimated for concurrent time periods from maximum and minimum temperatures recorded at a U.S. Weather Service meteorological station on the University of Michigan campus. These data were likewise transformed to weekly averages.

3. Independent, seasonally varied multiple regression models were developed to relate water temperatures at the Delhi Road thermograph with air temperatures and discharges recorded at Ann Arbor.
4. Temperatures at Bell Road were determined by a simple linear correlation with temperatures at Delhi Road.

Three variables were found to be good predictors of water temperatures: the air temperature during a concurrent week, the air temperature during the previous week, and the discharge at Ann Arbor during the concurrent week. Bartholow (1989) determined that water temperature was more sensitive to air temperature than virtually any other variable, explaining the strong relations we found with the concurrent week's air temperature.

The previous week's air temperature was also an important predictor of water temperature, especially during spring and winter. We attributed this phenomenon to the effect of the epilimnial release from Portage and Baseline lakes. The lakes cooled more slowly in fall and warmed more slowly in spring, creating lag periods between thermal inputs and water temperature in the river; the previous week's temperature represented this thermal lag.

Bartholow (1989) also found that water temperature was sensitive to discharge, groundwater inflow, percent shade, and stream width. Shade and stream width were relatively constant throughout the length of the study area, regardless of discharge. In contrast, groundwater inflow was thought to be particularly important during winter and spring. Groundwater inflow and streamflow were highly correlated with precipitation events, so we used the natural logarithm of the discharge as a surrogate for groundwater inflow.

We developed separate models for different seasons because the thermal flux and lag relations change depending on whether the water is warming or cooling (J. Bartholow, National Ecology Research Center, Fort Collins, Colorado, personal communication). Several different seasonal models were developed using different combinations of months. Measured and predicted temperatures were compared for each model to determine which combination resulted in the least overall error.

Quality assurance in temperature modeling was conducted by an evaluation of the dispersion of errors associated with different seasonal models. Although various seasonal models commonly produced similar results, the error dispersions differed in the frequency of large-magnitude errors. Typically, a model might result in a large number of small errors (0–1° C), a smaller frequency of moderate errors (1–2° C), and a few large errors (>2° C). Another model for the same season would result in a slightly lower frequency of small errors, more moderate errors, and fewer or no large errors. When such differences in model performance were apparent, we chose the one that produced the fewest large errors.

The best overall predictions occurred during the winter months, where 94% of the predicted temperatures were within 1° C of the measured temperatures. The poorest overall predictions tended to occur around the periods of equinox, which may have been caused by turnover of the lakes at approximately the same time. During the spring season, only 60% of the predictions were within 1° C of measured temperatures (but 87% were within 1.5° C). To improve model accuracy, the vernal equinox period was combined with the remainder of the spring months and the autumnal equinox period with the summer months. This resulted in a substantial improvement in model accuracy; during summer and early fall, 81% of the predicted temperatures were within 1° C of measured temperatures.

Microhabitat Time Series

Microhabitat time series were developed for each species, life stage, site, and season following the process illustrated in Fig. 9. The ingredients for a microhabitat time series included

1. Site-specific relations between discharge and microhabitat area for each life stage and season to be analyzed. These were obtained from the PHABSIM simulations.
2. Average weekly temperatures from the temperature model, used to identify probable dates for peak spawning activities and the dispersal of fry from nests.
3. Time series of the discharges occurring at each of the study sites over the period of record, aggregated to an appropriate time step.

We decided that the U.S. Geological Survey gaging station records at Ann Arbor could be used as the hydrologic time series for the Mast Road site. The hydrograph for sites upstream from Mill Creek (Hudson Mills and Bell Road) needed to be synthesized, however, because the gaging stations on Mill Creek and the Huron River at Dexter were discontinued in 1976.

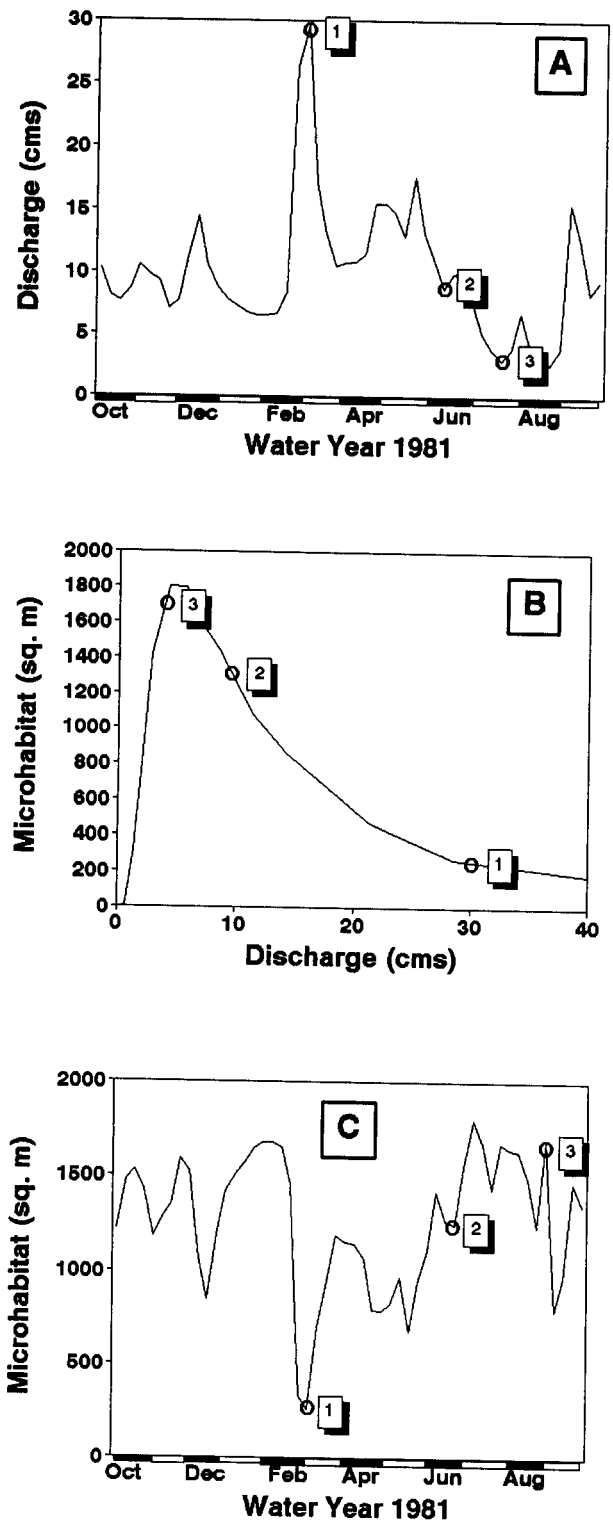

Fig. 9. Development of a habitat time series: (a) an average weekly discharge for a time step is determined from the hydrologic time series, (b) the habitat area corresponding to the discharge is taken from the relation between discharge and habitat area, and (c) the corresponding habitat area is plotted for the same time step.

Although base flows above Mill Creek were virtually the same as those recorded at Ann Arbor, there was considerable disparity at high flows. During snowmelt periods and basinwide precipitation events, discharge at Ann Arbor was consistently higher than discharge at Dexter, reflecting the contribution of Mill Creek. Isolated thunderstorms created discrepancies in this pattern, however, during late spring and summer. If a storm occurred in the watershed above Portage Lake, the streamflow at Dexter was typically about the same as the streamflow at Ann Arbor. In contrast, storms isolated in the Mill Creek drainage resulted in much higher discharges at Ann Arbor than at Dexter. Because the Dexter and Mill Creek gages were both discontinued in 1976, it was necessary to develop a synthetic hydrograph for the 1980–90 water years at the Dexter gage.

Several factors were considered in the selection of an appropriate averaging period (time step) in our time series analysis. Generally speaking, time steps should be sufficiently large to reduce the amount of data to be processed, but small enough to avoid masking biologically significant events. Daily flow records revealed that stream discharge tended to rise and fall rather uniformly over 3–7-day periods following individual storm events. There was good correspondence between discharges averaged over 5–7 d and the average daily discharges occurring within the averaging period. Therefore, we chose a 7-day averaging period primarily for convenience in reducing the volume of data to be processed.

A two-station model was developed to account for variable precipitation patterns in the Mill Creek drainage (Karunanithi et al. 1994). This model incorporated discharges recorded for the Huron River at Hamburg (upstream from the study area) and at Ann Arbor as independent variables, with the discharge at Dexter as the dependent variable. Recorded discharges were transformed to natural logarithms, with the resulting model taking the form

$$\ln \mathrm{DXQ} = a + b \ln \mathrm{AAQ} + c \ln \mathrm{HAMQ} \quad (2)$$

where

ln DXQ = the natural logarithm of the discharge measured at Dexter,

ln AAQ = the natural logarithm of the discharge measured at Ann Arbor,

ln HAMQ = the natural logarithm of the discharge measured at Hamburg, and

a, b, and c = regression coefficients.

This equation was calibrated for each month independently from corresponding periods of record for all three gaging stations. A stratified model was developed for some months to better account for localized precipitation and runoff events occurring in the Mill Creek drainage. The rules for stratification varied from month to month but were based on the ratios of discharges at the Ann Arbor and Hamburg gages. When the discharge at Ann Arbor was less than 1.7 to 2.5 times the discharge at Hamburg (depending on the month), we assumed that runoff from Mill Creek was comparable to that of the rest of the Huron River drainage. These data provided the basis for the "normal" runoff model. When the discharge at Ann Arbor was greater than the prescribed ratio for a month, Mill Creek was assumed to have experienced a localized storm event, thereby triggering the use of a second equation. In addition, a single regression model with no stratification was developed for each month.

Measured discharges from 1980 to 1990 at Ann Arbor and Hamburg were used to predict the discharge at the Dexter gage using the stratified and unstratified models. The choice to use one model or the other was determined by evaluating error dispersion and deviation from zero error in comparison to measured discharges at Dexter. Where there was little difference in model accuracy, the unstratified model was chosen for convenience. Where differences were discernible, the model that most accurately predicted extreme events was chosen for the time step.

Site-specific microhabitat time series were developed using a spreadsheet containing the hydrologic time series and the relation between discharge and microhabitat. For each discharge in the hydrologic time series a corresponding amount of optimal or usable habitat was determined by linear interpolation and entered for the same time step into a separate column in the spreadsheet. Habitat values for inapplicable months (e.g., summer months when winter criteria were used in the habitat simulation) were deleted in each of the spreadsheets. For adults and juveniles, winter was considered to extend from the first week in October to the last week in March and summer from the first week in April to the last week in September. The beginning of the spawning period was defined as when average weekly water temperatures reached 15° C and was assumed to extend 2 weeks beyond peak spawning, defined as when water temperatures reached 19° C (Armour 1993). Young-of-year habitat values were computed for a period starting 1 week after peak spawning and extending through the last week in September.

For each time series, we developed five indexes of habitat availability, representing different perspectives of the habitat time series for each life stage. The average habitat represented an integration of all habitat events occurring over the appropriate portion of the time series. The minimum habitat represented acute, low-habitat events that occurred during a single week within the time period. The minimum of a 5-week running mean for the time period was calculated to depict longer-term habitat shortages. Similarly, we determined 1-week and 5-week maxima to evaluate the effects of periods of abundant habitat. Table 2 contains a list of abbreviations for the habitat metrics we extracted from the microhabitat time series.

The final step in our habitat simulations was to aggregate the habitat metrics for the sites into a single corresponding habitat metric for the entire study area. For the habitat metrics listed in Table 2, the corresponding value for the study area was calculated by

$$H_{total} = (0.03\ H_{BR} + 0.35\ H_{HM} + 0.62\ H_{MR}) \quad (3)$$

where

H_{total} = the weighted average habitat metric for the study area,

H_{BR} = the corresponding habitat metric for Bell Road,

H_{HM} = the corresponding habitat metric for Hudson Mills, and

H_{MR} = the corresponding habitat metric for Mast Road.

The weighting factors for the sites were obtained from the habitat mapping exercise described previously.

Summary of Results

Complete sets of habitat suitability criteria, showing the ranges of optimal, usable, and suitable classifications for all temporal and life stage stratifications, are presented in Tables 3 and 4. With the exception of spawning, smallmouth bass generally occurred in deeper water at comparable life stages than did rock bass (Fig. 10). Within the same species, younger fish tended to occupy shallower water than older fish, and a general shift to shallower water at night was apparent among most of the life stages. In contrast, there seemed to be a movement into deeper water during winter, although the preferred depths were considerably less than the maximum depths available.

Table 2. Abbreviations and descriptions of habitat metrics generated from microhabitat time series. The same abbreviations apply to smallmouth bass and rock bass.

Habitat metric	Description
SPMIN	1-week minimum spawning habitat
SPMAX	1-week maximum spawning habitat
SPAVG	Average spawning habitat from onset to 1-week after peak
SPMIN5	5-week minimum spawning habitat
SPMAX5	5-week maximum spawning habitat
YSDMIN	1-week minimum young-of-year habitat, summer daytime
YSDMAX	1-week maximum young-of-year habitat, summer daytime
YSDAVG	Average growing season young-of-year habitat, summer daytime
YSDMIN5	5-week minimum young-of-year habitat, summer daytime
YSDMAX5	5-week maximum young-of-year habitat, summer daytime
YSNMIN	1-week minimum young-of-year habitat, summer night
YSNMAX	1-week maximum young-of-year habitat, summer night
YSNAVG	Average growing season young-of-year habitat, summer night
YSNMIN5	5-week minimum young-of-year habitat, summer night
YSNMAX5	5-week maximum young-of-year habitat, summer night
JSDMIN	1-week minimum juvenile habitat, summer daytime
JSDMAX	1-week maximum juvenile habitat, summer daytime
JSDAVG	Average growing season juvenile habitat, summer daytime
JSDMIN5	5-week minimum juvenile habitat, summer daytime
JSDMAX5	5-week maximum juvenile habitat, summer daytime
JSNMIN	1-week minimum juvenile habitat, summer night
JSNMAX	1-week maximum juvenile habitat, summer night
JSNAVG	Average growing season juvenile habitat, summer night
JSNMIN5	5-week minimum juvenile habitat, summer night
JSNMAX5	5-week maximum juvenile habitat, summer night
ASDMIN	1-week minimum adult habitat, summer daytime
ASDMAX	1-week maximum adult habitat, summer daytime
ASDAVG	Average growing season adult habitat, summer daytime
ASDMIN5	5-week minimum adult habitat, summer daytime
ASDMAX5	5-week maximum adult habitat, summer daytime
ASNMIN	1-week minimum adult habitat, summer night
ASNMAX	1-week maximum adult habitat, summer night
ASNAVG	Average growing season adult habitat, summer night
ASNMIN5	5-week minimum adult habitat, summer night
ASNMAX5	5-week maximum adult habitat, summer night
AWMIN	1-week minimum adult and juvenile habitat, winter
AWMAX	1-week maximum adult and juvenile habitat, winter
AWAVG	Average adult and juvenile habitat, winter
AWMIN5	5-week minimum adult and juvenile habitat, winter
AWMAX5	5-week maximum adult and juvenile habitat, winter
RIFMINA	1-week minimum riffle habitat, annual
RIFMAXA	1-week maximum riffle habitat, annual
RIFAVA	Average riffle habitat, annual
RIFMIN5A	5-week minimum riffle habitat, annual
RIFMAX5A	5-week maximum riffle habitat, annual
RIFINCA	Average of lowest 50% riffle habitat, annual
RIFMINS	1-week minimum riffle habitat, growing season
RIFMAXS	1-week maximum riffle habitat, growing season
RIFAVS	Average riffle habitat, growing season
RIFMIN5S	5-week minimum riffle habitat, growing season
RIFMAX5S	5-week maximum riffle habitat, growing season
RIFINCS	Average of lowest 50% riffle habitat, growing season

Table 3. Habitat suitability criteria for smallmouth bass in the Huron River, Michigan.

	Depth range (cm)			Velocity range (cm/s)			Cover/substrate (code)		
Life stage/time	Optimal	Usable	Suitable	Optimal	Usable	Suitable	Optimal	Usable	Suitable
Adult summer, day	85–150	76–189	43–366	12–43	6–64	0–88	1–19	1–19	1–19
Adult summer, night	46–113	31–153	31–381	5–27	0–43	0–68	5–8/15–18	5–8/15–8	1–19
Juvenile summer, day	70–110	52–153	40–192	23–54	16–62	0–90	1–5/11–15	1–19	1–19
Juvenile summer, night	61–92	61– 92	31–183	0–33	0–43	0–43	2–9/12–19	2–9/12–19	2–9/12–19
Young-of-year summer, day	46–85	34–110	18–186	9–46	5–57	0–75	2–9/12–19	2–9/12–19	1–19
Young-of-year summer, night	21–49	18–58	15–67	0–20	0–20	0–29	5,7,8/ 15,17,18	5,7,8/ 15,17,18	1–19
Adult/juvenile winter	92–153	92–153	92–458	0–15	0–31	0–45	7,8/17,18	7,8/17,18	1–19
Spawning	67–98	55–110	49–116	0–9	0–13	0–19	15,17,18	15,17,18	15,17,18

Smallmouth bass and rock bass of all life stages made extensive use of low velocity areas (Fig. 11). We found that younger fish tended to occupy higher velocities than adults of the same species during daytime. This may have resulted from dietary differences among the various age groups; the younger fish may have been feeding more extensively in riffles and shallow areas of the main channel, which could explain their presence in faster currents. In smallmouth bass, there was a perceptible shift into slower water at night, but the preferred velocity range of rock bass remained fairly stable on a diel basis. The most definitive selection for low velocities occurred during spawning and winter. Both species tended to avoid areas with velocities in excess of 15 cm/s during these time periods and were most commonly found where the velocity was near zero.

Table 4. Habitat suitability criteria for rock bass in the Huron River, Michigan.

	Depth range (cm)			Velocity range (cm/s)			Cover/substrate (code)		
Life stage/time	Optimal	Usable	Suitable	Optimal	Usable	Suitable	Optimal	Usable	Suitable
Adult summer, day	40–82	31–107	18–195	6–21	0–39	0–72	5–8/15–18	2–9/12–19	2–9/12–19
Adult summer, night	43–85	31–100	18–183	5–28	0–37	0–56	2–9/12–19	2–9/12–19	1–19
Juvenile summer, day	34–76	27–82	18–110	0–22	0–31	0–58	5–8/15–18	5–8/15–18	2–9/12–19
Juvenile summer, night	31–67	24–85	15–131	3–25	0–33	0–66	5–8/15–18	2–9/12–19	1–19
Young-of-year summer, day	24–88	24–92	18– 92	0–23	0–34	0–34	5–8/15–18	5–8/15–18	2–9/12–19
Young-of-year summer, night	24–61	18–76	12–110	0–20	0–31	0–51	2–9/12–19	2–9/12–19	1–19
Adult/juvenile winter	76–107	45–153	45–458	0–15	0–15	0–31	5,7,8/ 15,17,18	5,7,8/ 15,17,18	1–19
Spawning	61–122	55–137	49–153	0–20	0–24	0–28	12–19	12–19	12–19

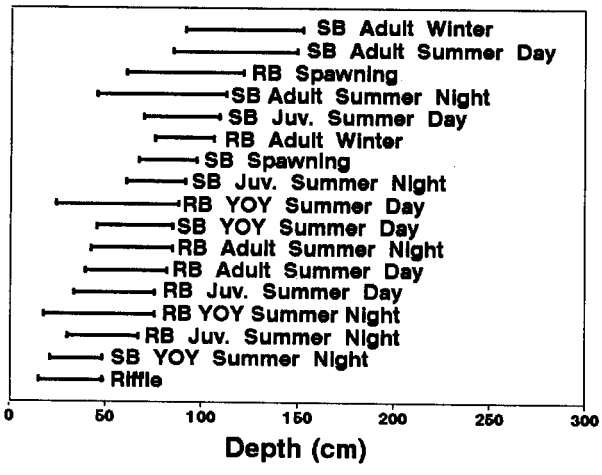

Fig. 10. Descending array of optimal depth ranges for smallmouth bass, rock bass, and riffle microhabitat.

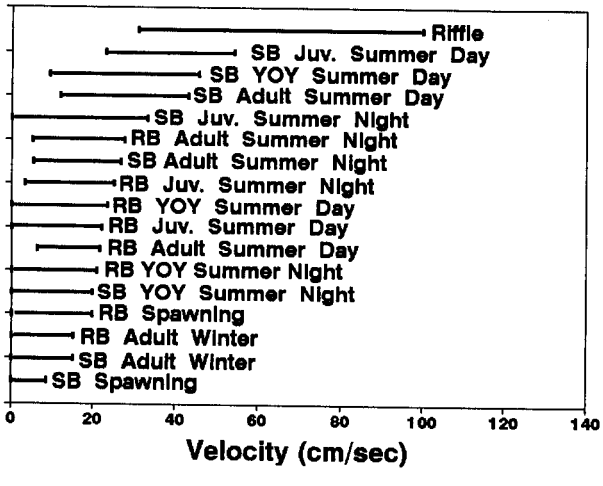

Fig. 11. Descending array of optimal velocity ranges for smallmouth bass, rock bass, and riffle microhabitat.

Some form of cover seemed to be important to all life stages at all times, except for adult smallmouth bass during summer daylight hours (Fig. 12). For some of the life stages, there was little or no selection among cover types (e.g., juvenile and young-of-year smallmouth bass during daytime), although areas with no cover were avoided. At night, however, young-of-year smallmouth bass were highly associated with complex, woody cover types (water willow, undercut banks, and log jams). Rock bass of all sizes always seemed to prefer complex cover types. The most restrictive usage of cover occurred during winter and the spawning period. Log jams and undercut banks were utilized almost exclusively during winter. During spawning, successful nests were always located in areas with a gravel substrate within 1–2 m of some form of complex near-shore cover.

Several trends in microhabitat availability among sites and among temporal and life stage stratifications became apparent from the PHABSIM simulations (Figs. 13 and 14). Optimal microhabitat for all life stages of both fish species tended to increase in a downstream direction. Bell Road generally provided the least microhabitat for any life stage and Mast Road the most. One unique characteristic of the Bell Road site, however, was that the amount of microhabitat was relatively constant at discharges greater than about 3 m^3/s. The consistency of microhabitat at Bell Road (particularly for young-of-year) is attributable to the extensive variable backwater that occurred in the right side channel. The most restricted microhabitats for smallmouth bass were associated with winter and spawning. These microhabitat types were almost nonexistent in the upper river sites and were available in limited supply at Mast Road. Graphical relations between discharge and optimal and usable microhabitat areas for smallmouth bass are contained in Appendix A.

For rock bass, the downstream increase in microhabitat was also apparent, as was the tendency for summer microhabitat to be more plentiful than either winter or spawning microhabitat. Compared with smallmouth bass, microhabitat for young-of-year rock bass was more abundant than for juveniles or adults during summer. Winter and spawning microhabitat for rock bass were limited, but not as severely as for smallmouth bass. As expected, Bell Road provided the largest amount of riffle

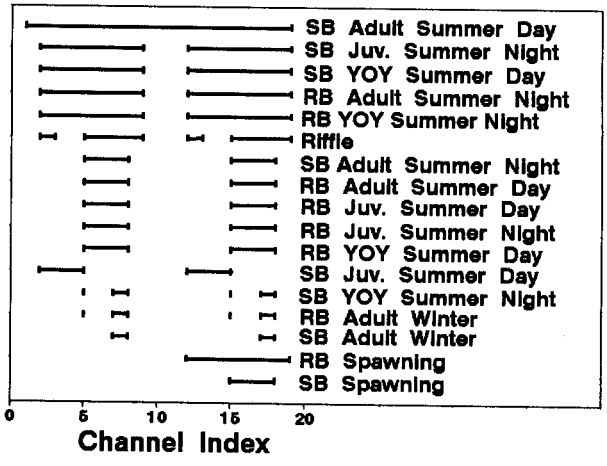

Fig. 12. Optimal cover and substrate classifications for smallmouth bass, rock bass, and riffle microhabitat, arrayed from most general to most specific.

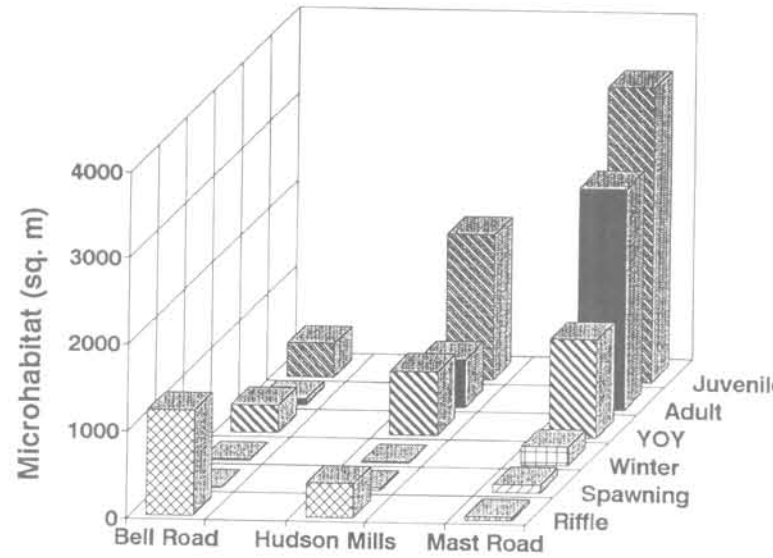

Fig. 13. Average riffle and smallmouth bass habitat availability from 1984 to 1990 at three sites on the Huron River.

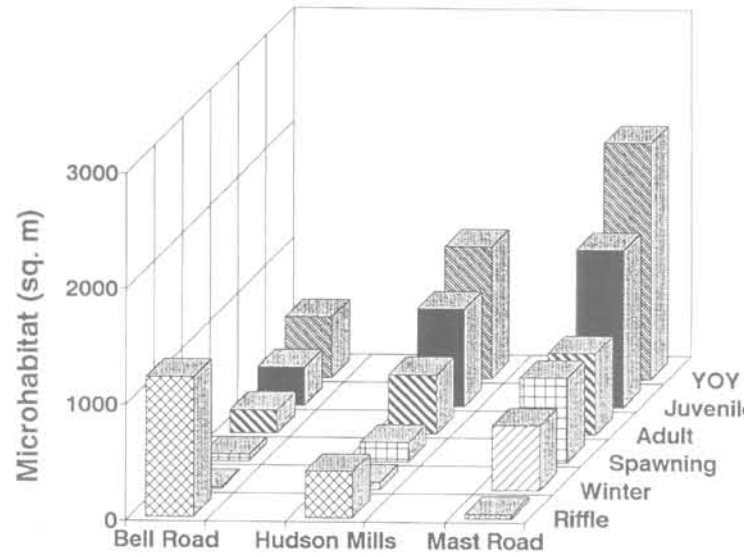

Fig. 14. Average riffle and rock bass habitat availability from 1984 to 1990 at three sites on the Huron River.

microhabitat, compared with the Hudson Mills and Mast Road sites. Graphical relations between discharge and optimal and usable microhabitat areas for rock bass are contained in Appendix B (microhabitat vs. discharge for riffles also).

Degree-day accumulations were calculated for all weeks with average weekly temperatures greater than 10° C, beginning on the estimated date of peak spawning for each year (Table 5 and Appendix C). Generally, there was a shorter lag between the onset of spawning and the spawning peak at Bell Road, reflecting the faster temperature rise in the upper river during late spring. Because the calculation of degree-days began on the date of peak spawning, the length of the growing season was different each year. The disparity in growing season length, however, had relatively little effect on the degree-days accumulated each year. This result indicates that degree-day accumulations depended more on summer air temperatures and discharges than on the dates when water temperatures first warmed up.

Degree-day accumulations were inversely related to summer discharges in the Huron River (Fig. 15). There are several causal mechanisms that can link discharges and summer thermal regimes, but we think the relation is probably coincidental in this instance. At low discharges, a greater pro-

Table 5. Summary of temperature accumulations and estimated dates of spawning activities for smallmouth bass and rock bass in the Huron River.

Year	Site	Degree-days >10° C	Onset spawning (week/month)	Peak spawning (week/month)
1981	Bell Road	1,572	4/May	5/May
1982	Bell Road	1,649	2/May	2/May
1983	Bell Road	1,622	4/May	2/June
1984	Bell Road	1,563	4/May	1/June
1985	Bell Road	1,656	4/April	3/May
1986	Bell Road	1,603	2/May	3/May[a]
1987	Bell Road	1,895	4/April	3/May
1988	Bell Road	1,885	2/May	4/May
1989	Bell Road	1,575	4/May	4/May
1981	Delhi Road	1,361	4/May	1/June
1982	Delhi Road	1,489	2/May	3/May
1983	Delhi Road	1,429	4/May	2/June
1984	Delhi Road	1,417	4/May[a]	1/June
1985	Delhi Road	1,496	4/April	3/May
1986	Delhi Road	1,447	2/May	3/May[a]
1987	Delhi Road	1,689	4/April	4/May
1988	Delhi Road	1,674	2/May	5/May
1989	Delhi Road	1,406	4/May	5/May

[a] Potential spawning interruptions resulting from 2–4° C decrease in temperature.

portion of the total flow is composed of ground water, but this mechanism would tend to cool the water rather than warm it during summer. More likely, the link between discharge and thermal regime is related to the weather. High flow events were usually associated with extended periods of rainfall that accompanied the passage of cold fronts. Characteristically, the weather during these events was cool, cloudy, and not conducive to solar warming. Low flows during summer occurred after extended periods of little or no rainfall, under weather conditions that favored solar warming.

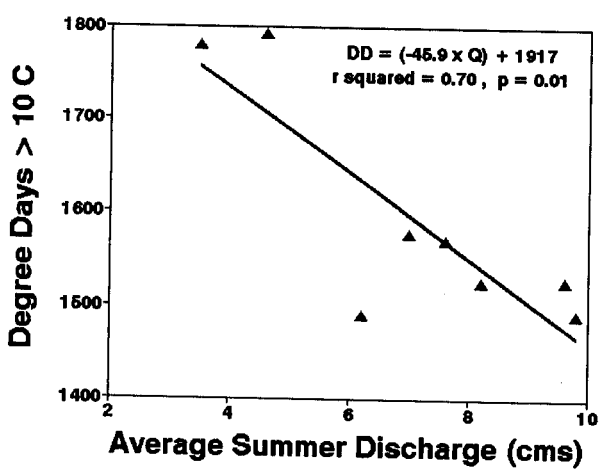

Fig. 15. Relation between degree-day accumulations and average discharges in the Huron River during summer from 1984 to 1990.

Habitat metrics aggregated for the study area from microhabitat time series are contained in Appendix D. Episodes of limited habitat occurred at both ends of the hydrologic spectrum, although most of the habitat minima were associated with high flows (Fig. 16). Excessive velocities in the main channel were primarily responsible for microhabitat reductions that occurred during high flow events. At flood flows, however, large areas of microhabitat became available to some life stages as the floodplain was inundated. The availability of microhabitat was also relatively constant over a wide range of high discharges at Bell Road, a result of the variable backwater effects at this site. These results indicate that island complexes, side channels, and floodplains may provide areas of refuge during floods in the Huron River.

Microhabitat limitations at low discharges occurred primarily through the loss of accessible cover. Virtually all of the complex structure in the Huron River was located near the banks. At low flows, the reduction in water surface elevations resulted in a decrease in depth and surface area, most notably at the edges of the channel. The net result was to make near-shore cover unsuitable or inaccessible to most species and life stages. For life stages that relied heavily on complex, near-shore

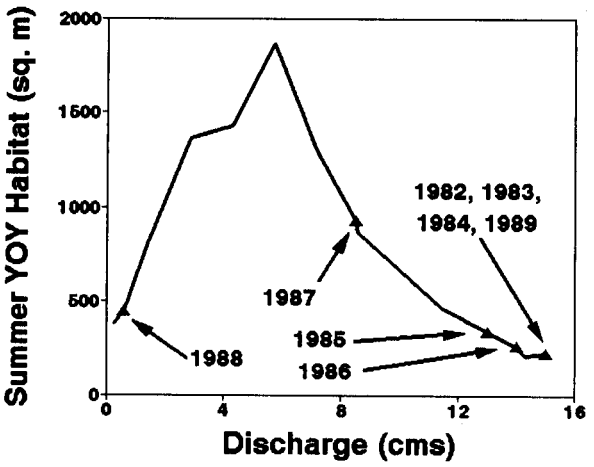

Fig. 16. Relation between discharge and 1-week microhabitat minima for young-of-year smallmouth bass (summer, night) from 1984 to 1990.

cover, the reduction in available microhabitat was significant.

Population Dynamics and Habitat

The goal of our study was to determine whether relations existed between the habitat metrics derived for the Huron River and the populations of smallmouth bass and rock bass that were residents there. Two types of associations were possible in this investigation. The first was a spatial association between the distribution of available habitat and the distribution of bass. The second was a temporal association between independent habitat events and measures of the dynamics of bass populations. Spatial associations have been suggested as successful demonstrations of the validity of the IFIM, but we considered temporal associations to be more biologically relevant. We were particularly interested in reinforcing patterns of relations that might imply causal mechanisms linking habitat dynamics to bass population dynamics.

Hypotheses

We used stepwise regression analysis to test the following hypotheses. For brevity, only the principal null hypotheses are presented here in condensed form (i.e., several related hypotheses are combined into one).

1. H_0: The number of yearling and older bass is unrelated to the number of age-0 bass of the same cohort.
2. H_0: The number of yearling and older bass is unrelated to the average size of age-0 bass of the same cohort.
3. H_0: The number of age-0 bass is unrelated to parent stock density.
4. H_0: The number of age-0 bass is unrelated to the availability of microhabitat for spawning or young-of-year.
5. H_0: The number of age-0 bass is unrelated to accumulated degree-days during the first growing season.
6. H_0: The number of yearling and older bass is unrelated to the availability of microhabitat at age 0 for the same cohort.
7. H_0: The number of yearling and older bass is unrelated to accumulated degree-days during the first growing season.
8. H_0: The size (length) of age-0 bass is unrelated to the availability of young-of-year microhabitat.
9. H_0: The size (length) of age-0 bass is unrelated to accumulated degree-days during the first growing season.
10. H_0: The number of yearling and older bass is unrelated to the availability of microhabitat during the previous winter.
11. H_0: The number of yearling and older bass is unrelated to the availability of juvenile or adult microhabitat during the current summer.
12. H_0: The number of age-0 bass is unrelated to the number of juveniles or adults of the opposite species.

The same tests were performed using optimal and usable habitat time series data to evaluate whether habitat quality was an important determinant of population size. We also used a variety of expressions for the same habitat variable, such as the 1-week minimum as opposed to the 5-week minimum, to determine the relative importance of acute versus chronic habitat limitations.

Development of Population Metrics

Smallmouth bass and rock bass population estimates were determined from data provided by the Michigan Fisheries Research Institute (Department of Natural Resources). Sampling was conducted by two-pass mark and recapture in late September or early October each year, with a barge-mounted electrofishing unit. Streamflow was usually low (3–5 m^3/s) at this time of year, which facilitated sampling efficiency. The exception was in autumn 1986, when high flows (about 25 m^3/s) may have affected sampling.

Table 6. Huron River smallmouth bass population estimates and 95% confidence limits calculated using a modified Peterson estimate.

Site	Sampling year						
	1983	1984	1985	1986	1987	1988	1989
Bell Rd	834 (659–1,079)	300 (171–613)	399 (293–573)	205 (146–321)	448 (293–827)	415 (248–969)	191 (111–475)
Hudson-Mills	Not sampled	129 (80–218)	1,041 (820–1,318)	394 (251–649)	703 (563–903)	775 (529–1,180)	330 (221–511)
Mast Rd	193 (115–340)	141 (87–238)	907 (618–1,441)	Not sampled	1,335 (1,082–1,646)	Not sampled	404 (223–806)
Group-Camp	189 (114–335)	96 (20–96)	192 (138–274)	161 (84–339)	635 (340–1,298)	217 (89–543)	128 (61–295)
Dexter-Huron	Not sampled	156 (106–237)	663 (465–982)	354 (242–540)	1,203 (1,029–1,406)	534 (419–689)	248 (149–439)
Delhi	Not sampled	416 (306–580)	1,440 (1,101–1,876)	898 (723–1,134)	4,415 (3,943–4,944)	2,070 (1,742–2,459)	616 (357–1,155)

We used the unbiased version of the Peterson estimator (Ricker 1975) to calculate the number of fish of each species, at each site, for each year of sampling (Tables 6 and 7):

$$N = \frac{(M+1)\,(C+1)}{(R+1)} \qquad (4)$$

where

N = estimate of the population size at time of marking,
M = number of fish marked in the first sample,
C = total number of fish captured in the second sample, and
R = number of marked fish in the second sample.

Confidence limits (P = 95%) were calculated by treating R as a Poisson variable and obtaining confidence intervals from a nomograph provided by Ricker (1975) for recaptures less that 50. For recaptures greater than 50, we used the formula

$$\mathrm{CI} = \frac{(M+1)\,(C+1)}{(R+1.92+(1.96(R+1)^{1/2}+1))} \qquad (5)$$

to determine the upper and lower confidence limits for R. The upper and lower confidence limits were then added to and subtracted from the estimate obtained from equation 4 to establish 95% confidence intervals about N.

During sampling, all captured fish were measured to the nearest inch. The total number of bass in each size class was tallied, and scales were collected from a variable-sized subsample of fish in each class. For each sample, we multiplied the proportion of the total catch (M + C) in each size class by the proportion of each age class in a

Table 7. Huron River rock bass population estimates and 95% confidence limits calculated using a modified Peterson estimate.

Site	Sampling year						
	1983	1984	1985	1986	1987	1988	1989
Bell Rd	5,713 (4,624–7,052)	6,790 (5,415–8,507)	3,260 (2,561–4,144)	4,172 (2,888–6,257)	6,436 (3,991–10,953)	8,407 (6,798–10,390)	4,664 (3,444–6,458)
Hudson-Mills	Not sampled	1,777 (1,318–2,454)	4,225 (3,076–5,988)	2,406 (1,535–3,972)	2,509 (1,422–4,840)	4,826 (3,154–7,720)	2,959 (2,236–3,999)
Mast Rd	1,330 (952–1,924)	1,197 (804–1,859)	1,663 (1,195–2,384)	Not sampled	1,257 (852–1,932)	Not sampled	1,237 (892–1,766)
Group-Camp	1,692 (1,210–2,079)	1,554 (1,199–2,012)	3,779 (2,792–5,234)	3,944 (3,075–5,053)	4,566 (2,796–7,873)	9,493 (5,887–16,159)	3,277 (2,319–4,792)
Dexter-Huron	Not sampled	686 (306-1,716)	1,051 (429–2,625)	371 (166–889)	553 (167–1,005)	670 (212–1,273)	330 (211–545)
Delhi	Not sampled	1,237 (871–1,820)	2,655 (1,800–4,085)	977 (753–1,269)	1,185 (753–2,017)	5,124 (2,970–9,608)	1,864 (1,467–2,365)

size class. By this procedure, we were able to estimate the proportion of each age class in the total catch.

The number of fish in each age class was determined by multiplying the total population estimate for a site by the proportion of the age class represented in the sample. We used proportional estimation because it resulted in smaller variance than determining a separate estimate for each age class, particularly when there were few recaptures. In addition to numerical age class estimates, average lengths at the end of the first growing season were recorded each year for age-0 smallmouth bass and rock bass at each of the six sites.

The estimated population for each age class was assigned to its corresponding year class by comparing the age of the fish and the sampling year. For example, all 2-year-old fish captured in 1985 were assigned to the 1983 year class. Repeating this procedure for all age classes and sampling years resulted in the development of cohort tables (Tables 8 and 9), which showed the number of fish in each

Table 8. Site-specific cohort tables for smallmouth bass, Huron River.

Year class	Site	Age 0	Age 1	Age 2	Age 3
1980	Bell Rd				0
1981	Bell Rd			31	5
1982	Bell Rd		616	177	30
1983	Bell Rd	186	89	19	3
1984	Bell Rd	33	152	8	0
1985	Bell Rd	202	106	58	19
1986	Bell Rd	91	112	50	8
1987	Bell Rd	274	167	19	5
1988	Bell Rd	179	50	3	
1989	Bell Rd	112	10		
1990	Bell Rd	83			
1980	Group Camp				0
1981	Group Camp			0	13
1982	Group Camp		90	45	20
1983	Group Camp	94	50	36	7
1984	Group Camp	0	4	22	10
1985	Group Camp	137	29	95	5
1986	Group Camp	80	63	22	12
1987	Group Camp	463	7	55	12
1988	Group Camp	166	24	2	
1989	Group Camp	45	21		
1990	Group Camp	170			
1980	Hudson Mills				
1981	Hudson Mills				2
1982	Hudson Mills			44	93
1983	Hudson Mills		41	27	12
1984	Hudson Mills	32	23	8	4
1985	Hudson Mills	892	111	79	59
1986	Hudson Mills	248	79	40	26
1987	Hudson Mills	517	218	78	
1988	Hudson Mills	457	59		
1989	Hudson Mills	140			
1990	Hudson Mills				
1980	Mast Rd				7
1981	Mast Rd			24	0
1982	Mast Rd		101	0	28
1983	Mast Rd	39	4	106	
1984	Mast Rd	137	78		25
1985	Mast Rd	684		44	
1986	Mast Rd		131		32
1987	Mast Rd	1,117		82	
1988	Mast Rd		120		

Table 8. *Continued.*

Year class	Site	Age 0	Age 1	Age 2	Age 3
1989	Mast Rd	113			
1990	Mast Rd				
1980	Dexter-Huron				
1981	Dexter-Huron				0
1982	Dexter-Huron			19	10
1983	Dexter-Huron		16	53	9
1984	Dexter-Huron	121	33	7	0
1985	Dexter-Huron	556	99	24	3
1986	Dexter-Huron	233	48	37	0
1987	Dexter-Huron	1,142	176	79	38
1988	Dexter-Huron	309	109	33	
1989	Dexter-Huron	59	12		
1990	Dexter-Huron	154			
1980	Delhi				
1981	Delhi				27
1982	Delhi			104	96
1983	Delhi		120	115	6
1984	Delhi	149	58	27	31
1985	Delhi	1,137	179	88	60
1986	Delhi	682	88	103	104
1987	Delhi	4,193	517	172	
1988	Delhi	1,386	228		
1989	Delhi	86			
1990	Delhi				

Table 9. Site-specific cohort tables for rock bass, Huron River.

Year class	Site	Age 0	Age 1	Age 2	Age 3
1980	Bell Rd				27
1981	Bell Rd			4,010	1,367
1982	Bell Rd		1,191	1,624	77
1983	Bell Rd	463	2,881	1,806	22
1984	Bell Rd	908	1,345	1,383	90
1985	Bell Rd	59	2,647	843	123
1986	Bell Rd	119	825	972	52
1987	Bell Rd	4,678	5,788	1,653	44
1988	Bell Rd	1,442	2,870	1,241	
1989	Bell Rd	59	1,008		
1990	Bell Rd	37			
1980	Group Camp				396
1981	Group Camp			981	506
1982	Group Camp		220	249	669
1983	Group Camp	101	280	1,398	755
1984	Group Camp	512	1,360	1,498	503
1985	Group Camp	302	1,324	1,735	1,312
1986	Group Camp	552	913	1,803	106
1987	Group Camp	1,370	2,943	3,227	270
1988	Group Camp	3,417	1,573	910	
1989	Group Camp	393	2,649		
1990	Group Camp	4,552			
1980	Hudson Mills				
1981	Hudson Mills				516
1982	Hudson Mills			620	725
1983	Hudson Mills		427	1,983	382
1984	Hudson Mills	200	1,065	785	780
1985	Hudson Mills	450	960	1,353	846
1986	Hudson Mills	248	208	1,529	171

Table 9. *Continued.*

Year class	Site	Age 0	Age 1	Age 2	Age 3
1987	Hudson Mills	135	1,796	958	
1988	Hudson Mills	653	1,536		
1989	Hudson Mills	222			
1990	Hudson Mills				
1980	Mast Rd				332
1981	Mast Rd			683	469
1982	Mast Rd		125	414	183
1983	Mast Rd	77	193	747	
1984	Mast Rd	110	587		257
1985	Mast Rd	107		704	
1986	Mast Rd		197		186
1987	Mast Rd	99		474	
1988	Mast Rd		502		
1989	Mast Rd	60			
1990	Mast Rd				
1980	Dexter-Huron				
1981	Dexter-Huron				181
1982	Dexter-Huron			212	152
1983	Dexter-Huron		96	441	33
1984	Dexter-Huron	137	377	144	121
1985	Dexter-Huron	32	137	188	87
1986	Dexter-Huron	0	77	182	55
1987	Dexter-Huron	166	321	23	32
1988	Dexter-Huron	91	201	20	
1989	Dexter-Huron	76	124		
1990	Dexter-Huron	14			
1980	Delhi				
1981	Delhi				166
1982	Delhi			284	933
1983	Delhi		507	212	70
1984	Delhi	235	1,194	410	900
1985	Delhi	212	391	320	918
1986	Delhi	98	367	1,230	149
1987	Delhi	260	1,793	839	
1988	Delhi	1,178	689		
1989	Delhi	93			
1990	Delhi				

year class, progressing from age 0 to age 3, over the entire sampling period.

We made several assumptions with regard to potential sampling bias that could affect the accuracy of the population estimates and cohort tables. Following Pollack et al. (1990), we assumed that all fish were equally likely to be captured, the population was closed to additions or deletions, and none of the marks was lost. We also assumed that sampling techniques and efficiency were consistent across sites and years, subsamples taken for size-age data were representative of the total sample, and ages determined from scale samples were accurate (e.g., no mistaken or false annuli).

An examination of the cohort tables will reveal that some of these assumptions were violated, particularly in the estimates for rock bass. There is an apparent size-related bias in age-0 and age-1 rock bass because the estimated number of yearlings is commonly larger than the number of age-0 rock bass in the same cohort. Similarly, the number of age-2 rock bass is commonly larger than the number of yearlings in a cohort. Some of the discrepancy may have been due to the small size and difficulty in capture of young-of-year and yearling rock bass (R. Clark, Michigan Fisheries Research Institute, Ann Arbor, personal communication).

We consider the year-class estimates for smallmouth bass to be more accurate than those for

rock bass. The confidence intervals around the population estimates for smallmouth bass were relatively small compared with those for rock bass, and size-related sampling bias is much less evident. Consequently, we have somewhat more confidence in our analysis of relations between habitat and smallmouth bass population dynamics.

For our analysis of temporal relations between habitat and population dynamics, it was necessary to derive cohort tables for the entire study area. The simplest approach would have been to average the number of equal-aged fish in each year class across all of the sites. Unfortunately, this approach was not possible because not all of the sites were sampled every year. Hudson Mills and Delhi Road were not sampled in 1983 or 1990, Dexter-Huron was not sampled in 1983, and Mast Road was sampled every other year from 1986. The population estimate for the study area was changed when estimates from different combinations of sampling sites were in the average. Some of the site-to-site differences in population size were attributable to a spatial correspondence between the amount of habitat at a site and the average number of bass (Figs. 17 and 18).

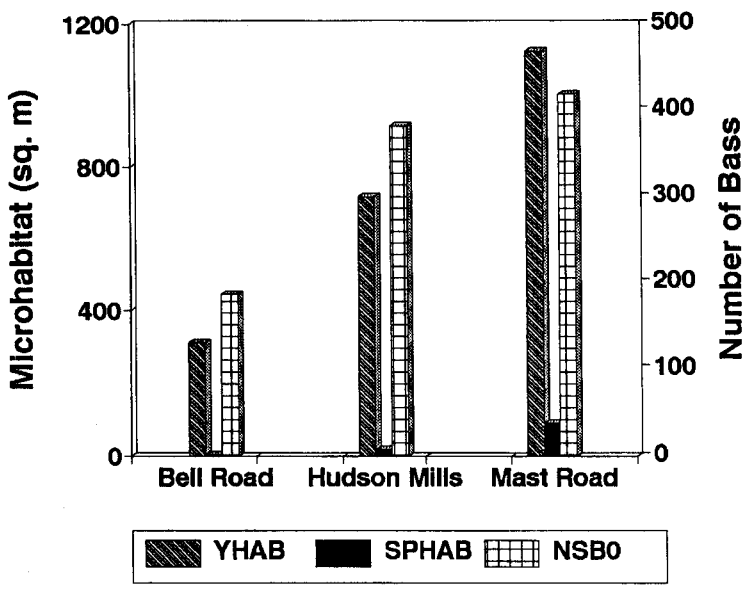

Fig. 17. Correspondence between average amounts of spawning and young-of-year microhabitat with average populations of age-0 smallmouth bass at Bell Road, Hudson Mills, and Mast Road.

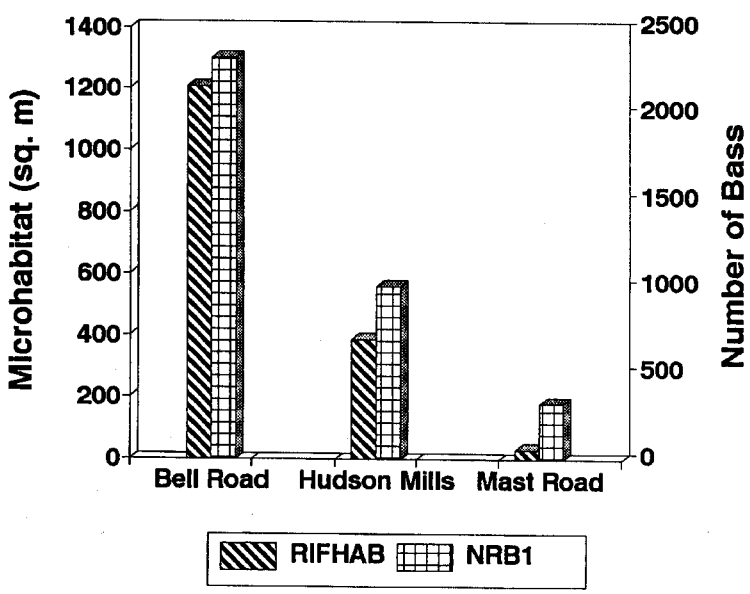

Fig. 18. Correspondence between average amounts of riffle microhabitat with average populations of yearling rock bass at Bell Road, Hudson Mills, and Mast Road.

Table 10. Cohort table for smallmouth bass in the Huron River study area, based on the average estimates from Bell Road, Group Camp, Hudson Mills, Dexter-Huron, and Delhi Road.

Year class	Number at age 0	Number at age 1	Number at age 2	Length at age 0 (mm)
1982			78	
1983		63	50	
1984	67	54	14	76.4
1985	585	105	69	89.0
1986	267	78	50	93.0
1987	1,318	217	81	100.8
1988	499	94		89.2
1989	88			83.8

We developed our study area cohort tables by using the sampling record from 1984 to 1990 and excluding the estimates from Mast Road from the average. This procedure provided us with the longest and most consistent period of record with the largest number of sampling sites. Cohort tables for the study area are presented in Tables 10 and 11 for smallmouth bass and rock bass. The lengths of bass at age-0 listed in these cohort tables also represent an average over the five common sites.

Summary of Results

Year-class Carryover

Numbers of yearling smallmouth bass and rock bass were related to year-class strength at age 0, although the association was stronger in smallmouth bass (Fig. 19). Age-2 smallmouth bass and rock bass were also associated with year-class strength, but the correlations were weaker and less significant than they were for yearlings (Fig. 20). The total population of adult smallmouth bass was also correlated with year-class strength (lagged by 2 years) at about the same significance level as 2-year-olds. These results indicate that carryover of year classes was strong in smallmouth bass populations and moderate in rock bass. The weaker correlations between year-class strength and numbers of age-2 rock bass, however, may reflect the lower accuracy in rock bass population estimates.

Size at Age 0 Versus Numbers of Older Bass

We found that numbers of yearling bass were related to their lengths at the end of the previous growing season, although the correlations were not quite significant (Fig. 21). Numbers of age-2 smallmouth bass and rock bass were also related to their lengths at age 0, at about the same level of significance as for yearlings (Fig. 22). The strongest correlation was between length at age 0 and the total smallmouth bass adult population 2 years later ($r^2 = 0.94$, $P = 0.04$).

Factors Related to Year-class Strength

Numbers of age-0 smallmouth bass were related to the availability of nighttime microhabitat

Table 11. Cohort table for rock bass in the Huron River study area, based on the average estimates from Bell Road, Group Camp, Hudson Mills, Dexter-Huron, and Delhi Road.

Year class	Number at age 0	Number at age 1	Number at age 2	Length at age 0 (mm)
1982			598	
1983		838	1,168	
1984	398	1,068	844	37.8
1985	211	1,092	888	35.2
1986	203	478	1,143	39.0
1987	1,322	2,528	1,340	47.4
1988	1,356	1,374		42.4
1989	169			33.0

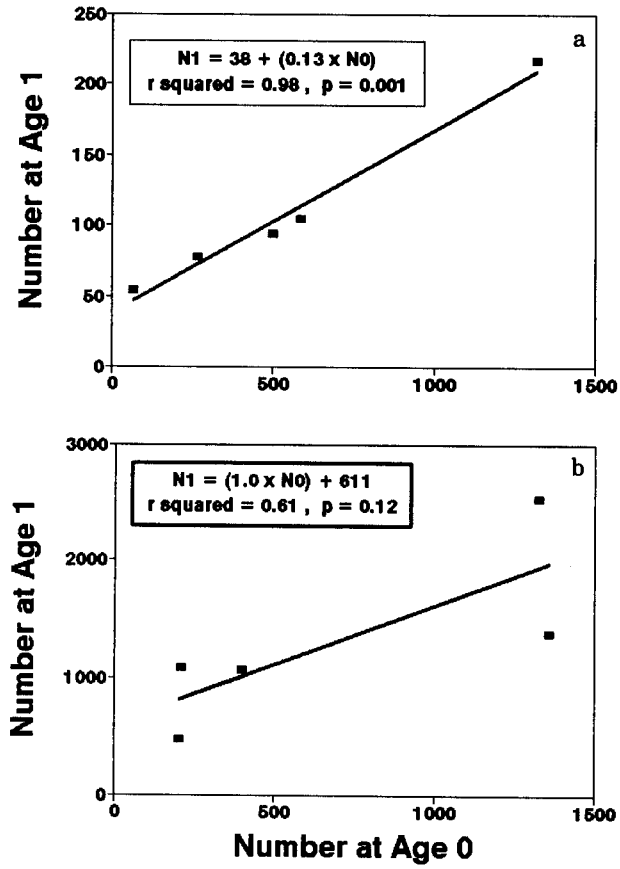

Fig. 19. Relations between year-class strength and the number of yearling bass the following year: (a) smallmouth bass, (b) rock bass.

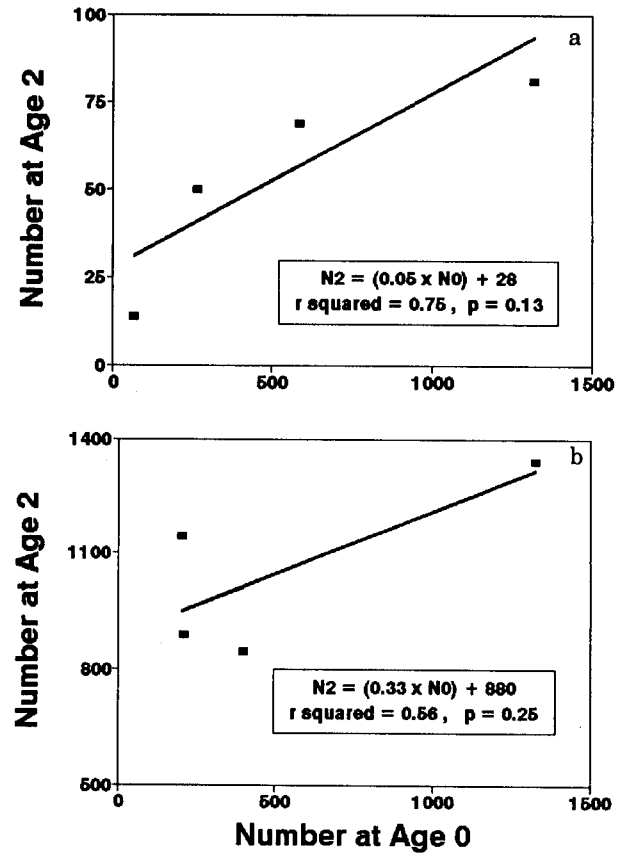

Fig. 20. Relations between year-class strength and the number of 2-year-old bass: (a) smallmouth bass, (b) rock bass.

for young-of-year during summer (Fig. 23a). Year-class strength in rock bass was related to the same variable as for smallmouth bass, although the association was not as strong (Fig. 23b). The most significant correlation between metrics of summer nighttime habitat for young-of-year and year-class strength occurred using the 1-week minimum value (YSNMIN). Year-class strength in smallmouth bass was also related to the average value for young-of-year summer nighttime habitat (YSNAVG), but the correlation was considerably weaker ($r^2 = 0.59$, $P = 0.08$).

Year-class strength in both species was associated with the accumulation of degree-days greater than 10° C (DEGDAY) during the first growing season ($r^2 = 0.66$, $P = 0.05$ for smallmouth bass and $r^2 = 0.91$, $P = 0.003$ for rock bass). There was an appreciable correlation between YSNMIN and DEGDAY ($r^2 = 0.62$, $P = 0.02$), however, indicating that both variables may have been related to similar discharge events.

Year-class strength in smallmouth bass was unrelated to parent stock density, spawning habitat, or daytime young-of-year habitat during summer. In rock bass, a positive but non-significant relation existed between year-class strength and parent stock density ($r^2 = 0.36$, $P = 0.21$); spawning habitat and daytime young-of-year habitat during summer were not related to year-class strength.

Factors Related to First-year Growth

Average lengths of age-0 smallmouth bass and rock bass were related to DEGDAY and to YSNMIN (Figs. 24 and 25) but not to the availability of riffle microhabitat or daytime young-of-year habitat. The lack of a significant relation between riffle habitat and length of age-0 smallmouth bass was somewhat surprising because there was a strong spatial correspondence between these two variables.

In both species, the length at age 0 was positively related to the number at age 0 ($r^2 = 0.67$,

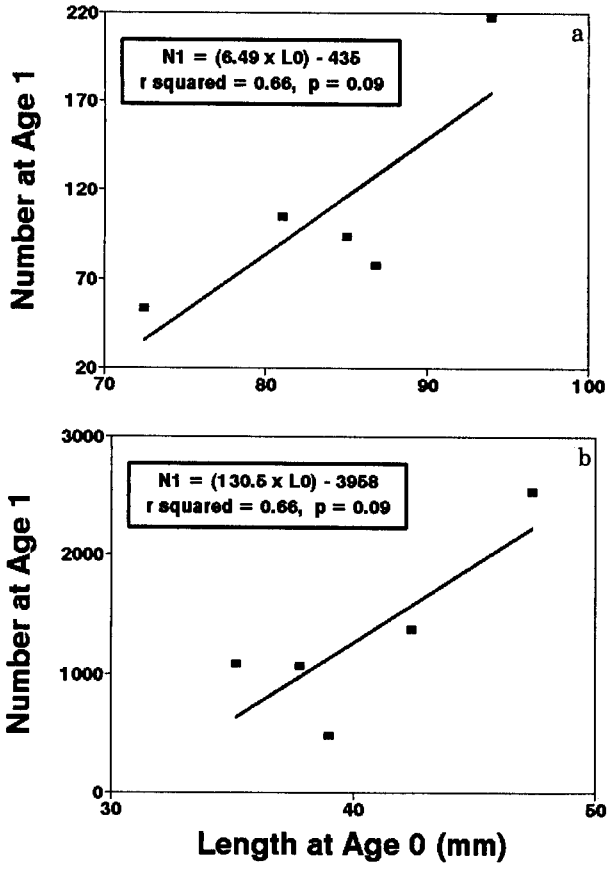

Fig. 21. Relations between length at age 0 and the number of yearling bass the following year: (a) smallmouth bass, (b) rock bass.

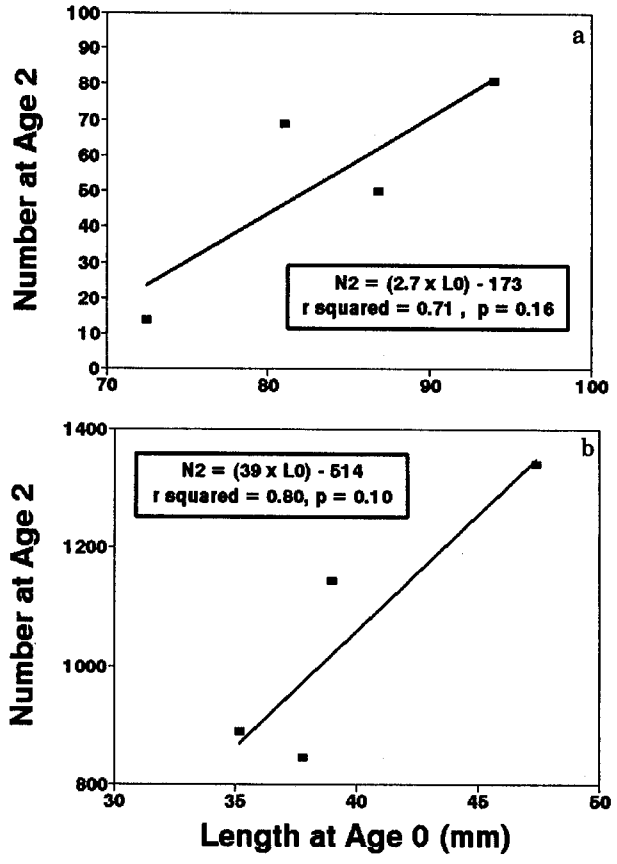

Fig. 22. Relations between length at age 0 and the number of 2-year-old bass: (a) smallmouth bass, (b) rock bass.

$P = 0.05$ for smallmouth bass, $r^2 = 0.77$, $P = 0.02$ for rock bass). Two different connotations are implied by this result. First, survival through the first growing season may have been related to growth rates of age-0 bass. Second, density-dependent inhibition of growth rates, which would have been apparent as a negative relation between numbers and lengths, did not occur.

Microhabitat Versus Numbers of Older Bass

Numbers of yearling smallmouth bass and rock bass were strongly associated with the amount of young-of-year summer nighttime microhabitat (YSNMIN) available at age 0 (Fig. 26). Nearly significant correlations were also obtained between numbers of yearling smallmouth bass and the availability of riffle microhabitat, as represented by the Bell Road site ($r^2 = 0.46$, $P = 0.14$ for smallmouth bass), and degree-day accumulations (DEGDAY) during the first growing season ($r^2 = 0.58$, $P = 0.08$). The correlation between number of yearling rock bass and degree-day accumulation was nearly significant ($r^2 = 0.64$, $P = 0.06$), as was the association between yearling numbers and riffle microhabitat ($r^2 = 0.50$, $P = 0.12$).

Numbers of 2-year-old smallmouth bass were positively but not significantly related to the availability of young-of-year microhabitat YSNMIN) at age 0 ($r^2 = 0.20$, $P = 0.37$). The correlation between numbers of age-2 smallmouth bass and degree-day accumulations (DEGDAY) was nearly significant ($r^2 = 0.49$, $P = 0.12$). Age-2 smallmouth bass numbers were not related to the availability of riffle habitat at age 0, juvenile habitat at age 1, or adult habitat during the current year.

Numbers of age-2 rock bass were moderately related to young-of-year summer nighttime microhabitat at age 0 ($r^2 = 0.39$, $P = 0.18$) but were not related to degree-day accumulation or the availability of riffle habitat at age 0, juvenile habitat at age 1, or adult habitat during the current year.

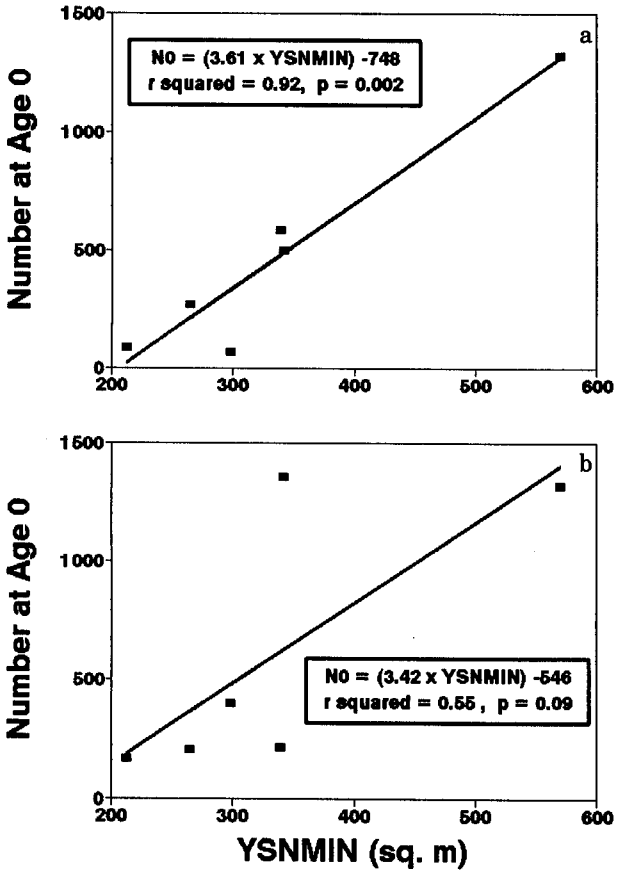

Fig. 23. Relations between minimum summer nighttime microhabitat for young-of-year and the number of age-0 bass: (a) smallmouth bass, (b) rock bass.

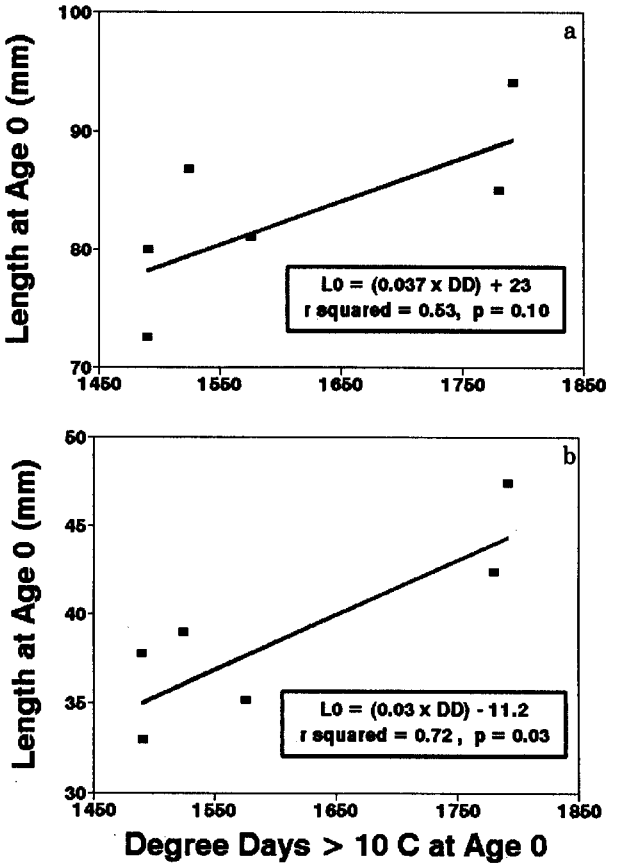

Fig. 24. Relations between length at age 0, (a) degree-day accumulations, and (b) minimum summer nighttime young-of-year habitat for smallmouth bass.

Interspecific Relations

Numbers of age-0 smallmouth bass were positively associated with numbers of age-0 rock bass ($r^2 = 0.56$, $P = 0.09$). Similarly, numbers of smallmouth bass and rock bass at age 1 were highly correlated ($r^2 = 0.82$, $P = 0.014$). These results indicate that strong and weak year classes of the two species tended to coincide.

We found no evidence of population-modifying levels of interspecific competition or predation between the two species. Significant or nearly significant negative correlations between the number of fish in an age class of one species and the number in different age classes of the other species would indicate a competitive or predatory relation between the two. Most of our tests for associations resulted in positive correlations. One negative association was obtained between adult smallmouth bass and age-0 rock bass, but it was non-significant ($r^2 = 0.002$, $P = 0.94$).

Discussion

Mechanisms Relating Habitat and Population Dynamics

Throughout the foregoing analysis, a pattern of connections between habitat and bass population dynamics has emerged. Populations of yearlings and adults were related to the number of age-0 bass produced in a year class and to their size at the end of the first growing season. The number and size of age-0 bass were consistently related to the same two variables, degree-day accumulations (DEGDAY) and nighttime young-of-year microhabitat during summer (YSNMIN). The number and size of age-0 bass were also related to the availability of riffle microhabitat, but the relations with DEGDAY and YSNMIN were stronger and more consistent.

The consistency of the relations among numbers, size, DEGDAY, and YSNMIN was demonstrated when the same two habitat variables were

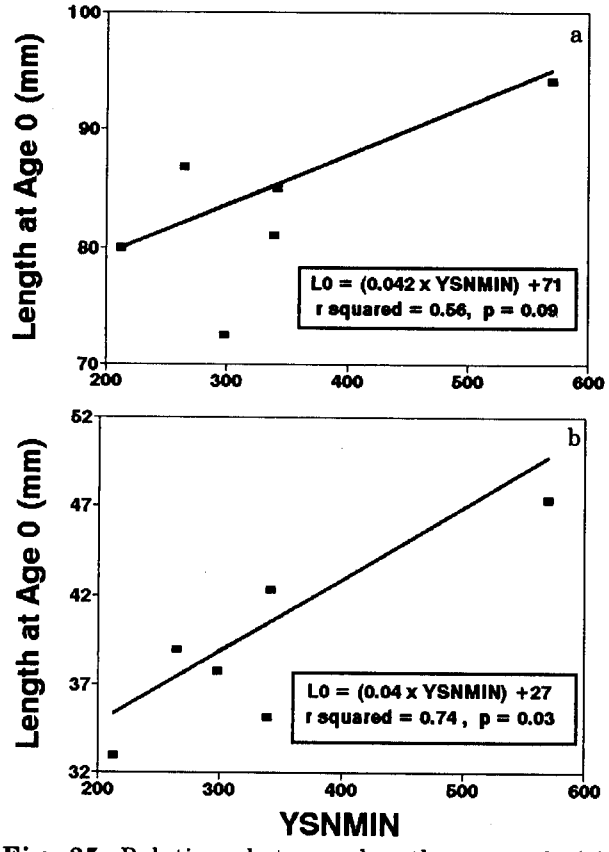

Fig. 25. Relations between length at age 0, (a) degree-day accumulations, and (b) minimum summer nighttime young-of-year habitat for rock bass.

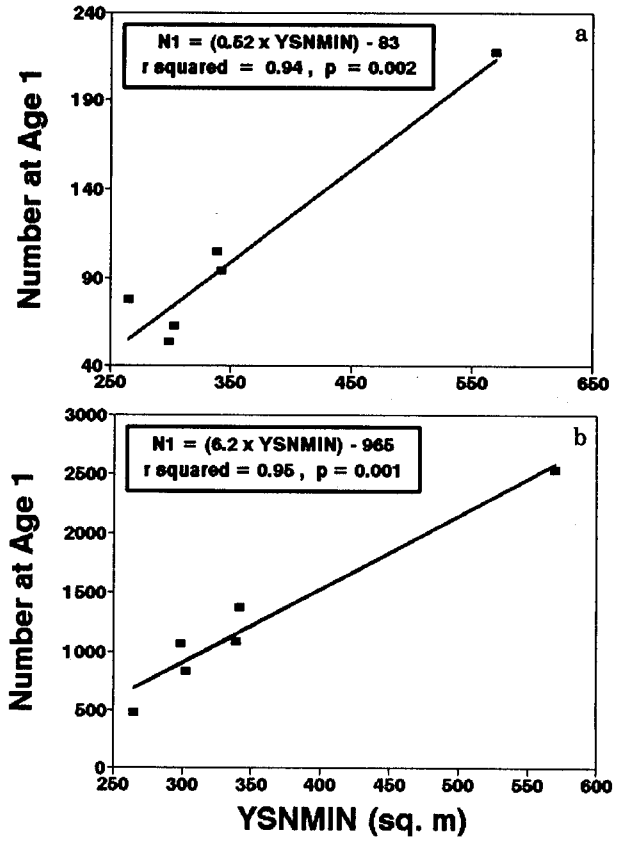

Fig. 26. Relations between minimum summer nighttime microhabitat for young-of-year and the number of yearling bass the following year: (a) smallmouth bass, (b) rock bass.

related to the number of yearlings and 2-year-olds. These results were obtained even though different combinations of years were used in the various analyses. For example, in comparing populations at age 2 with year-class strength at age 0, complete data were available only for year classes 1984–87. The analysis of yearling populations versus YSNMIN (and DEGDAY) included year classes 1983–88. The 1982–87 year classes were used in tests for relations between age-2 bass and habitat variables. Results with this level of consistency would not be expected if the associations were spurious.

One commonly used ecological model of single-species populations is the logistic growth curve (Boughey 1971). The logistic growth model is expressed as

$$dN/dt = rN(1-N/K) \qquad (6)$$

where

N = the number of animals in the population at any given time,

r = the per capita growth rate of the population,

t = the time step, and

K = the maximum size that the population can attain, or carrying capacity.

Solution of equation 6 for different values of N results in an S-shaped curve (Fig. 27). The population growth rate is very low when the population density is very low but increases exponentially at moderate density. The population growth rate slows to zero as the population approaches carrying capacity. A variation of the logistic growth model results in a J-shaped curve, whereby the population overshoots its carrying capacity and subsequently experiences a crash (Boughey 1971). Although neither model is universally typical of all populations, both models serve to explain the postulated state of the smallmouth bass and rock bass populations in the Huron River.

The common characteristic of these population models is that the potential for rapid population growth is maximized when the population is well

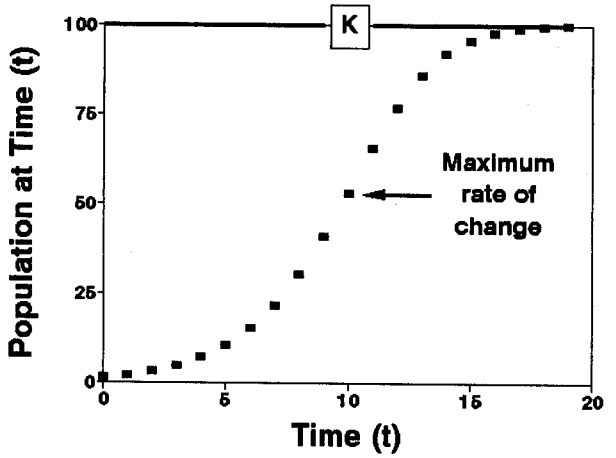

Fig. 27. Illustration of logistic growth curve; population growth is very low when population density is very low or approaches carrying capacity but is exponential at intermediate population density.

below carrying capacity. Given the opportunity, such as the production of a strong year class, the population will increase significantly, provided that no carrying capacity limitation is approached.

We hypothesize four causal mechanisms that might explain the relations found in this study. The first mechanism is the connection between year-class strength and subsequent population size of older bass. Neither species is particularly long-lived in the Huron River (e.g., there were very few smallmouth bass over 3 years old). The short life span of these species implies that continual replenishment of recruits is needed to maintain population size. Adults of both species were harvested in the entire study area prior to 1985, and in the upper segment for the whole period of record. Harvest is equivalent to selective predation on the adults, which could maintain adult populations below carrying capacity. Harvest may also be related to the paucity of old bass in the Huron River. Simple arithmetic and the logistic growth curve explain the rest. If the adult population is well below carrying capacity as we suspect, we would expect the adult population to decline following 1–2 years of poor recruitment and to rebound rapidly following a strong year class. Essentially, this was the response exhibited in smallmouth bass and rock bass populations in the Huron River.

The second mechanism relates size at age-0 and subsequent numbers of older fish. Individuals that gain an early growth advantage may be more likely to recruit to the adult population (Miller et al. 1988; Houde 1989; Luecke et al. 1990; Persson and Diehl 1990). Shuter and Post (1991) found that size of young-of-year smallmouth bass at the outset of winter was an important determinant of survival to age 1. Where winter conditions are sufficiently harsh and prolonged, stored energy is used sooner in smaller fish and can result in mortality from starvation (Armour 1993). Sabo (1993) found that fast-growing larvae were no more likely than smaller larvae to survive to the juvenile stage, but winter conditions in the Huron River were probably more severe than in the Virginia stream he studied. Our study supported the general hypothesis that survival to age 1 was higher for large age-0 fish.

The third mechanism is that degree-day accumulations and size of age-0 bass are linked energetically. Horning and Pearson (1973) found that the growth rate of juvenile smallmouth bass increased asymptotically with temperature, up to a maximum rate at 26° C. Armour (1993) noted that growth could be interrupted or reduced during sudden temperature drops and could even be fatal if the temperature reduction was severe. Degree-day accumulations represented not only temperatures in the Huron River but also the period when temperatures were favorable for growth. During years when the size of age-0 bass was greatest (e.g., 1987 and 1988), temperatures were closer to 26° C during summer, and warmer temperatures tended to prevail later into autumn (Appendix C).

Degree-day accumulations were not synonymous with length of the growing season, defined as the period following fry dispersal. We had anticipated that the growing season would be longer, degree-day accumulations higher, and size of age-0 bass greater when spawning occurred earlier in spring. We found, however, that degree-day accumulations and size of age-0 bass were unrelated to the date of peak spawning activity. These results were similar to the findings of Sabo (1993) in the North Anna River, Virginia.

The fourth mechanism may connect young-of-year summer nighttime microhabitat to numbers and size of age-0 bass. Gilliam and Fraser (1987) proposed that microhabitats selected by fishes tended to simultaneously maximize foraging efficiency and minimize predation risk. When a trade-off was necessary, precedence was usually given to predator avoidance.

Predation can be a significant source of mortality in young-of-year bass, especially in the period immediately following abandonment of the brood site by the guardian male (Neves 1975; Brown 1984). Sabo (1993) noted a dispersal of larval smallmouth

bass to microhabitats with fractured bedrock or large woody debris shortly after the male parents abandoned their broods. He suggested that the association with these cover types by young-of-year smallmouth bass may have been a predator-avoidance mechanism. Although the Huron River contained no fractured bedrock, we observed a similar shift to complex, woody cover types.

Numbers of age-0 smallmouth bass and rock bass were related to YSNMIN for smallmouth bass but not for rock bass. The primary differences between summer nighttime microhabitat for smallmouth bass and for rock bass at age 0 was that smallmouth bass were associated with slightly shallower water and utilized complex woody cover types exclusively (Figs. 10–12). Essentially, YSNMIN for smallmouth bass was a subset of YSNMIN for rock bass; both species used the same microhabitat conditions extensively, but rock bass were observed in a wider range of depths and cover types. We propose that YSNMIN for smallmouth bass represented more than the microhabitat favored at night during summer for that life stage alone. We think that the conditions characterizing this habitat type were ideal for predator avoidance, that these conditions were important to both species, and that the habitat type was probably important during daytime hours as well as at night. The combination of shallow water and dense, complex cover would have made maneuvering very difficult for a large predator and would have provided excellent concealment for the young fish; the low velocity would have minimized displacement of the fish into less secure areas.

Sabo (1993) also hypothesized that young-of-year smallmouth bass may have been attracted to these microhabitats for reasons in addition to protection. He observed that when velocities were relatively high, young smallmouth bass were restricted to the bottom of the water column, where they fed primarily on chironomid larvae. Where velocities were slower, larger microcrustaceans and larval insects were more plentiful, and foraging efficiency of small bass was improved. The dense woody cover that characterized young-of-year smallmouth bass habitat in the Huron River may have provided a very productive substrate surface for aquatic invertebrates (Smock et al. 1985). The combination of higher secondary production, lower energy expenditure, and higher foraging efficiency associated with this habitat type may explain the relation between YSNMIN for smallmouth bass and size at age 0 for smallmouth bass and rock bass.

Implications for IFIM Users

Limiting Habitat Assumptions

One of the most serious criticisms of the IFIM has been a lack of evidence that fish populations respond to changes in habitat (Mathur et al. 1985; Shirvell 1986; Scott and Shirvell 1987; Morhardt and Mesick 1988). An implied assumption of virtually all of these critiques has been that adult populations and adult habitat should be related to demonstrate validity of the methodology. Whether by intention or by default, the presumed association between adult habitat and adult population size has often been adopted in operational applications of the IFIM as well. This choice has resulted in a focus on adult habitat as the primary decision variable when alternatives were formulated and evaluated.

A recurring theme of this study has been that habitat bottlenecks were primarily related to recruitment and associated habitat types. Bovee (1988) hypothesized that where recruitment influenced the year-to-year variability in adult populations, habitats critical to early life history phases of a species tended to emerge as habitat bottlenecks. We suspect that associations between fish population dynamics and habitat events that affect early life history phases are probably common phenomena in many streams. Nehring and Anderson (1993) reported similar associations in Colorado trout streams, so we know that our results are not unique to the Huron River or peculiar to bass populations. Our study indicates that much greater emphasis should be placed on the evaluation of habitat during early life history phases of target species.

The focus of many IFIM studies has been on relations between discharge and microhabitat, to the exclusion or subordination of macrohabitat effects (e.g., temperature or water quality). Temperature is often not considered in an analysis unless it becomes lethal for one or more target species. Our results show that temperature is an important environmental variable in coolwater streams, even when it remains within nonlethal tolerances for smallmouth bass and rock bass. The relation between discharge and thermal regime in the Huron River was probably coincidental. Changes in flow regime or reservoir operations associated with operational uses of the IFIM, however, may have more direct effects on temperatures. In coolwater stream

applications of the IFIM, users are advised to include degree-day analyses in study plans. Rather than considering temperature studies as an option, investigators should plan on conducting these studies routinely.

The foregoing recommendation, however, does not mean that temperature analysis will be absolutely necessary in every coolwater application of the IFIM. As Sabo's (1993) studies indicate, thermal regimes and growth rates may be less important in warmer climates than they were in the Huron River. We are simply advising users of the IFIM that during the study planning phase, the first choice should be to include temperature analysis. If the choice is made to forego temperature analysis, the rationale should be justified and documented in the study plan.

Users of the IFIM are also cautioned not to assume that the least abundant habitat types during a year (or even across years) are the most biologically relevant. Following this assumption, recommended flow regimes might be based on a presumed habitat bottleneck that may not be real. Our results indicate that absolute habitat minima were not always important to a population. For example, spawning habitat and adult habitat during winter were consistently in shortest supply in the Huron River (Appendix D) but were never related to population size. In the past, users have attempted to use output from the IFIM to identify potential habitat bottlenecks. This approach is backwards. Users should attempt to identify probable bottlenecks first from whatever population data are available. Then the IFIM should be used to formulate alternatives designed to protect or alleviate the bottlenecks. In the total absence of population data, a reasoned hypothesis is better than nothing. If no bottleneck can be identified, water management alternatives should be developed that equalize the impacts or benefits across all life stages.

Limiting Flow Assumptions

There are two basic approaches to instream flow problems (Trihey and Stalnaker 1985). The first approach, termed standard-setting, typically attempts to identify a minimum flow, below which the aquatic resource will suffer. The second approach incrementally compares habitat availability over a range of discharges covering the entire hydrograph. An assumption inherent in standard-setting methods is that low discharge events are the principal causes of habitat bottlenecks in streams. Although not inherent to incremental methodologies (e.g., the IFIM), the same assumption is commonly made by investigators during the analysis of flow regimes and water management alternatives.

Our results, and those of others (Nehring 1979; Nehring and Anderson 1983, 1984, 1993; Bovee 1988; Lukas 1993), indicate that low flows are not always the cause of habitat bottlenecks. In our study, the availability of young-of-year summer microhabitat (YSNMIN) was associated with high flows more often than with low flows (Fig. 16). Degree-day accumulations (DEGDAY) were lower during years with high summer discharges than in years with low summer discharges (Fig. 15). Users of the IFIM should be aware that habitat limitations commonly occur at both ends of the hydrologic spectrum for a stream. By focusing on low flow events to the exclusion of high flow events, the analyst not only precludes a whole suite of potentially viable management options but also may ignore biologically significant events in the process. This admonition is especially relevant in the negotiation of flow releases associated with hydropeaking operations. In these deliberations, the base flow release is often the most hotly debated issue, but the flow release during generation may have the most serious biological impact.

A temporal dimension may also determine the importance of extreme flow events; the time of the year that an event occurs may be a consideration. For example, high streamflows of approximately the same magnitude occurred in the Huron River in winter, spring, and late summer. High flows during spring and summer were related to population metrics, but high flows during winter were not.

Habitat Quality Implications

When habitat suitability criteria are used in the form of suitability index curves in PHABSIM, the output from the model is weighted usable area (WUA):

$$\mathrm{WUA} = \Sigma\, c_i a_i \qquad (7)$$

where c_i is a composite suitability index ranging from zero to one for each stream cell and a_i is the surface area of the cell. Weighted usable area has been criticized as an index of habitat availability for several reasons (Mathur et al. 1985; Morhardt and Mesick 1988):

1. Calculation of the composite suitability index by multiplying univariate suitabilities for each

variable treats the variables as independent probability functions.
2. Because weighted usable area is an index, it cannot be measured directly.
3. Different estimates of weighted usable area can be obtained by using different methods of aggregating the composite suitability index.
4. Weighted usable area combines elements of habitat quantity and habitat quality. A large area of low-quality habitat can produce the same amount of weighted usable area as a small area of high-quality habitat.

Binary criteria, as used in this study, can obviate virtually all of these criticisms. Binary criteria cannot be mistaken for probability functions, any method of aggregation will produce the same result, and the output is an actual estimate of the amount of habitat available. Furthermore, the rules for developing binary criteria are more restrictive and less subject to interpretation than those for habitat suitability curves (Bovee 1986). Potentially, criteria development could be more easily standardized using the binary format, leading to greater reproducibility. This does not mean, however, that criteria developers are relieved of all judgment. Developers of suitability curves must decide which polynomial or smoothing technique best fits the data. Developers of binary criteria must decide the cutoff points (e.g., central 50%, 75%, or 95%) used to define what is and what is not to be counted as habitat.

Our results indicate that these cutoff points are not trivial decisions. We conducted parallel correlation tests between numbers of age-0 smallmouth bass and YSNMIN, calculating YSNMIN with optimal, usable, and suitable criteria (Table 3) in separate simulations. The strongest correlation was obtained when YSNMIN was calculated with the optimal criteria. When the usable criteria were used to calculate YSNMIN, the r^2 and P values were considerably lower. When we calculated YSNMIN with the suitable criteria, the correlation became nonsignificant (Fig. 28).

We do not advocate a wholesale shift from habitat suitability curves to binary criteria, however, if investigators are more comfortable with the curve format. The work of Nehring and Anderson (1993) was based on habitat suitability curves, which performed well in their study. We do suggest that criteria in binary format can be substituted for habitat suitability curves, often to the betterment of the study. When using the binary format, one should define the limits of the criteria no broader than the limits we used to define "usable" microhabitat (i.e., the central 75% of the sampled population). Preferably, the optimal ranges should be used to define the limits of the criteria.

Validity of IFIM in Coolwater Streams

The primary reason for conducting this study was to determine whether the underlying concepts of the IFIM were valid in a coolwater stream environment. The most critical concept was the assumption that fish population dynamics were directly or indirectly related to the amount of habitat available within a stream. Because of increased species richness and community complexity, a common countervailing argument has been that populations were more likely to be controlled by biotic interactions than by abiotic factors in coolwater streams.

To address the issue of validity, it is first necessary to define what is meant by direct or indirect relations between habitat and fish population dynamics. As demonstrated by this study, habitat has spatial (structural/hydraulic) and temporal (annual/seasonal/hydrologic) components. The simplest test of validity could be defined as an association of habitat and populations on a spatial scale. In this instance, fish distributions should be aligned with areas containing more and better habitat of importance to the species. Although we could not conduct statistical tests for spatial associations, the distribution of smallmouth bass and rock bass seemed to follow a gradient of habitat distribution in the Huron River (Figs. 17 and 18).

Validity could also be expressed as a test of temporal variability. Under this definition, population attributes should change over time in concordance with variations of key habitat attributes. A more demanding test of validity would be to identify habitat bottlenecks, habitat events ultimately linked to life stages other than the one affected directly. Our results indicate multiple linkages among microhabitat, thermal regime, first-year growth, and year-class strength that carry forward to subsequent age classes of smallmouth bass and rock bass. Possible mechanisms by which these linkages may operate to regulate populations were also identified. We do not think that the associations we found were accidental or spurious. We conclude that the IFIM was valid in the Huron River, not simply because these relations existed, but also because they were consistent, explicable, and mechanistically linked.

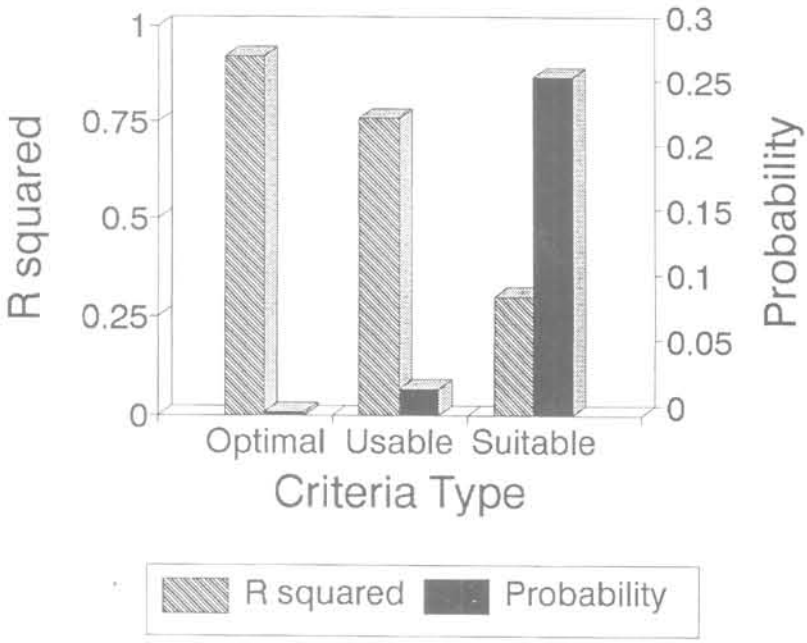

Fig. 28. Effect of the habitat quality classification on correlation strength and significance between YSNMIN and number of age-0 smallmouth bass.

Afterword

Although the purpose of our study was to evaluate the validity of the IFIM in coolwater streams, it was impossible not to draw inferences related specifically to potential land and water use impacts in the Huron River basin. We feel that we owe our insights to the citizens of Washtenaw and Livingston counties, if for no other reason than to repay their cooperation and hospitality.

The Huron River is typical of many streams in southern Michigan. Compared with other streams in the United States, the hydrologic regime of the Huron River is remarkably well buffered, meaning that runoff responds slowly to precipitation events. There are two reasons for this hydrologic response. First, surface storage in this system is very large, owing to the abundance of lakes. Although many of the lakes are actually reservoirs, they are operated as true run-of-river (e.g., instantaneous outflow equals instantaneous inflow) for maintenance of water levels. Second, the high permeability of the soils and large groundwater storage potential of the watershed allow rapid infiltration and storage of precipitation. In essence, the watershed behaves as a huge flood control reservoir.

As we have seen, bass populations in the Huron River responded to the frequency, duration, and magnitude of extreme flow events during the period of record. In our opinion, any human intervention that reduces the buffering capacity of the Huron River watershed will have a deleterious effect on smallmouth bass populations. At present, there are no large-scale water developments threatening to change the hydrologic regime of the Huron River. The watershed, however, is currently experiencing a period of rapid urban growth and development. As more and more of the watershed is developed, drained, and paved, the hydrograph of the Huron River will inevitably become more erratic. The results of such land uses are not only predictable (bass populations will ultimately decline) but also, using the models we developed in this study, quantifiable. The only unknown is how much the hydrograph will change as a result of continued development. We recommend that planners who want to answer this question acquire a good surface runoff model, calibrate it to the Huron River watershed, and simulate different development scenarios to generate predicted streamflow hydrographs. We would gladly share the habitat time series programs developed as part of this study to assess the impact of land development on the bass populations of the Huron River.

Acknowledgments

This study was the result of a cooperative effort involving the U.S. Fish and Wildlife Service, Michigan Department of Natural Resources, and Michigan State University. The most critical information necessary for conducting a study such as this is the biological data needed to develop cohort tables. We thank J. Merna, R. Clark, and R. Lockwood for their efforts in developing the biological data base, and

for their willingness to share it with us. We acknowledge N. Kevern for initiating and implementing the Cooperative Agreement between Michigan State University and the U.S. Fish and Wildlife Service, which allowed us to work together. Convenient, low-cost housing was provided by the University of Michigan, and unrestricted access to our study sites was allowed by the Metropolitan Parks Authority; our thanks to you for your cooperation and assistance. We were truly fortunate to have the services of a stalwart field crew that endured hypothermia, poison ivy, and bodily injury in the completion of this study: T. Cummings, J. Thomas, J. Monahan, and M.G. Black. D. Crawford and J. Shoemaker assisted with graphics, J. Zuboy edited the manuscript, and D. Medellin prepared the manuscript for publication. Our thanks also to V. Lang, K. Mayne, E. Baker, and two anonymous peer reviewers for their comments on earlier drafts of the manuscript.

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Appendix A. Relations Between Discharge and Microhabitat for Smallmouth Bass

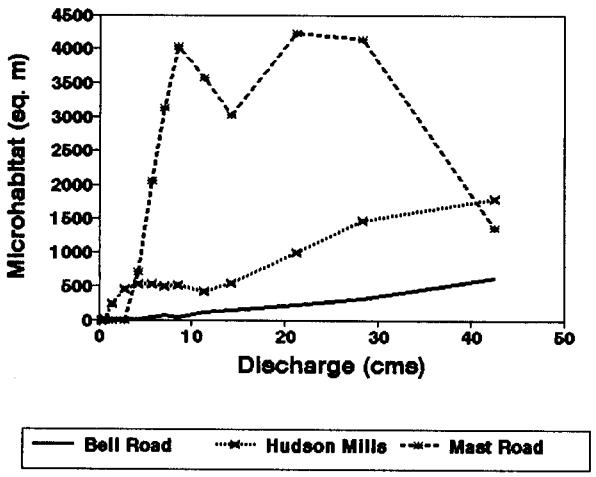
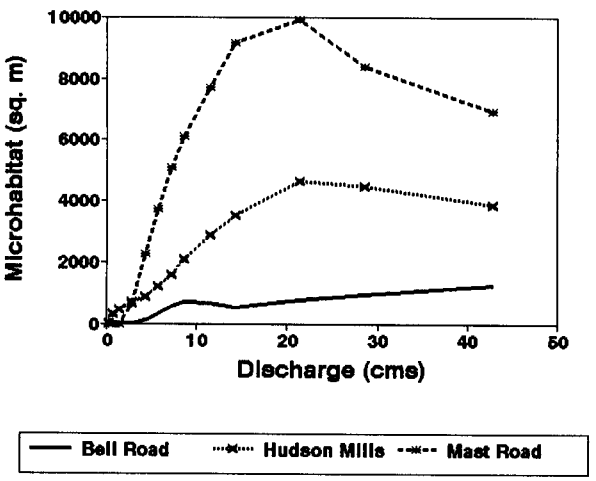


Fig. A1. Optimal microhabitat versus discharge for adult smallmouth bass, summer daytime hours.



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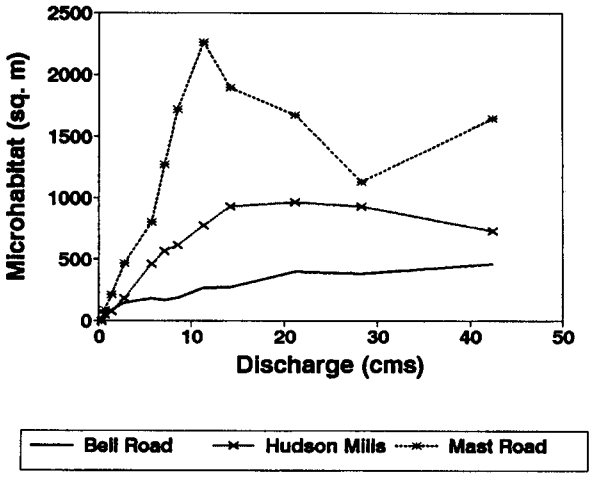

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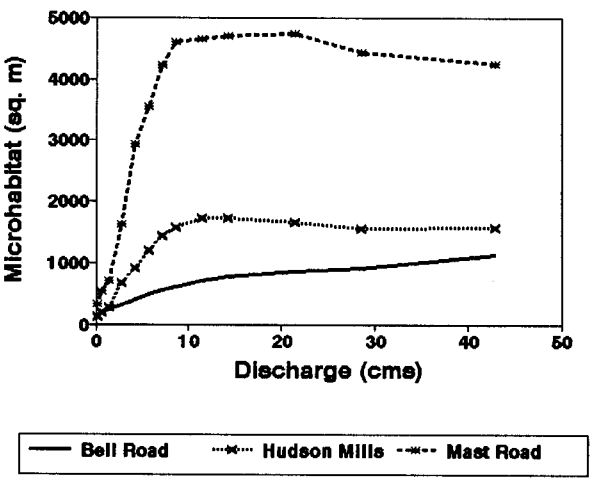

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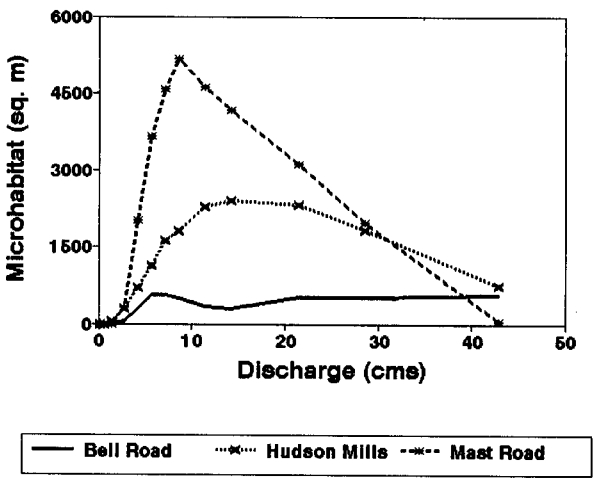

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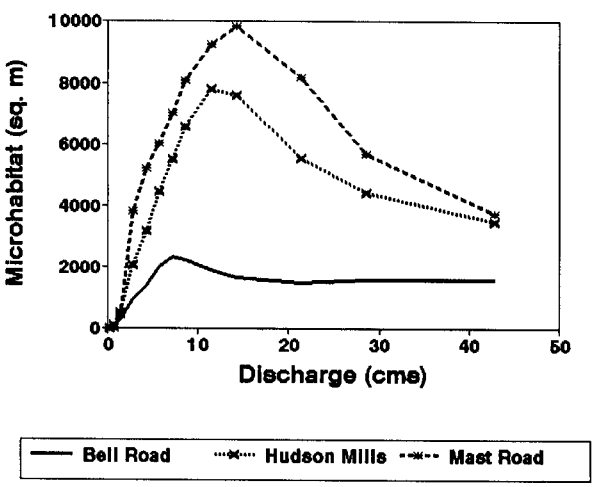


Fig. A6. Usable microhabitat versus discharge for juvenile smallmouth bass, summer daytime hours.

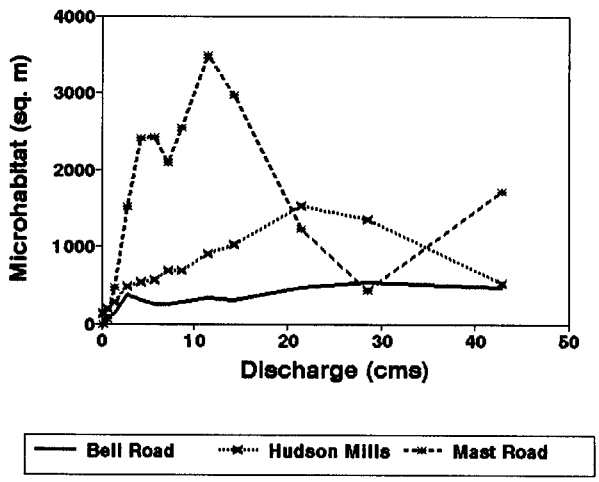


Fig. A7. Optimal microhabitat versus discharge for juvenile smallmouth bass, summer nighttime hours.

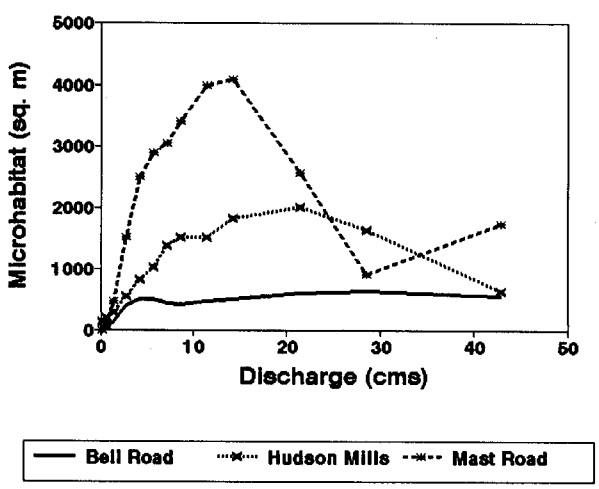


Fig. A8. Usable microhabitat versus discharge for juvenile smallmouth bass, summer nighttime hours.

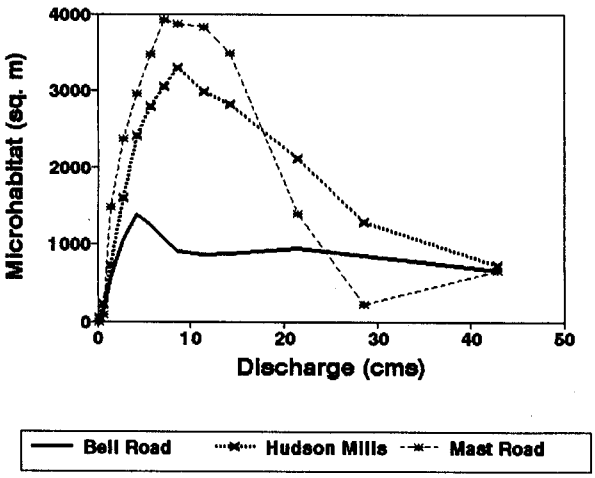


Fig. A9. Optimal microhabitat versus discharge for young-of-year smallmouth bass, summer daytime hours.

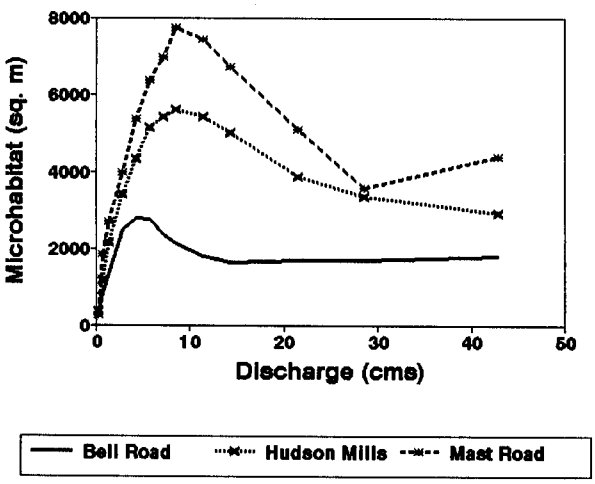


Fig. A10. Usable microhabitat versus discharge for young-of-year smallmouth bass, summer daytime hours.

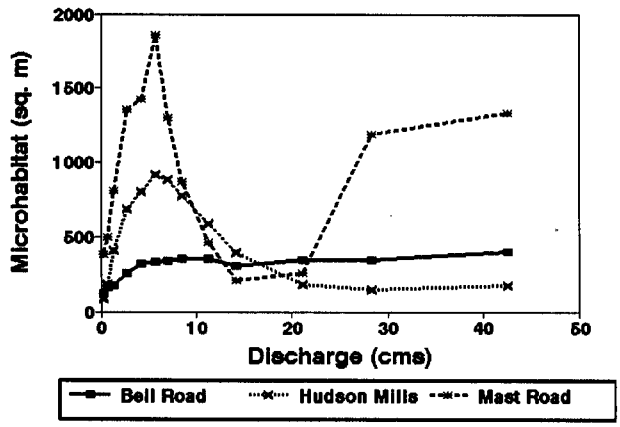


Fig. A11. Optimal microhabitat versus discharge for young-of-year smallmouth bass, summer nighttime hours.

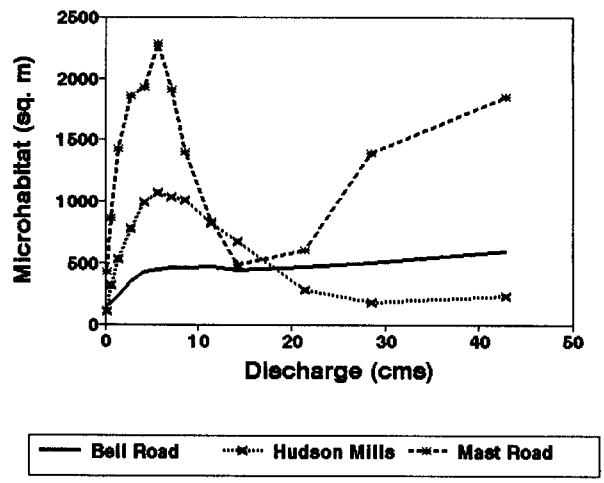


Fig. A12. Usable microhabitat versus discharge for young-of-year smallmouth bass, summer nighttime hours.

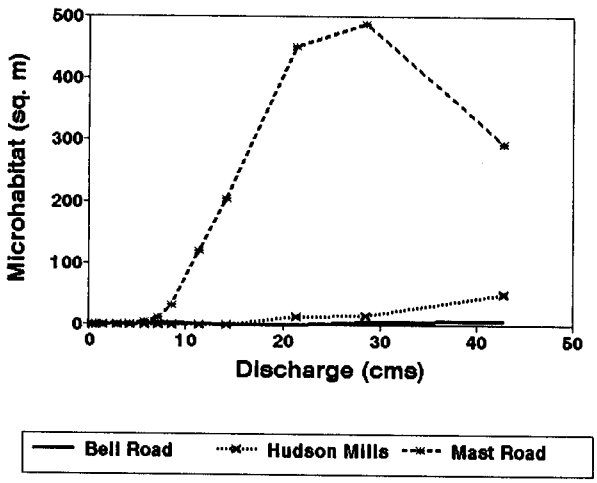


Fig. A13. Optimal microhabitat versus discharge for adult and juvenile smallmouth bass, during winter.

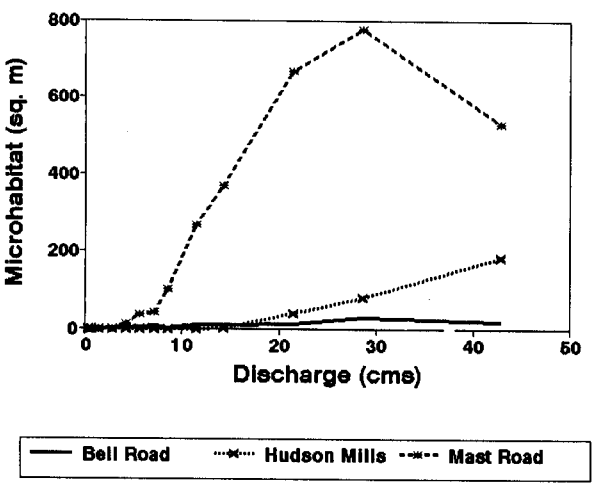


Fig. A14. Usable microhabitat versus discharge for adult and juvenile smallmouth bass, during winter.

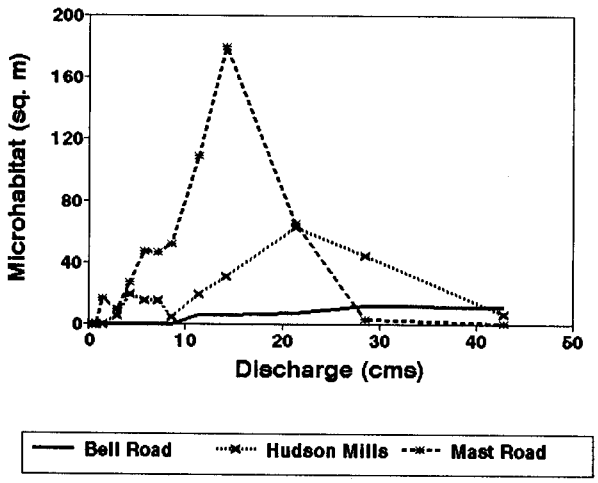


Fig. A15. Optimal microhabitat versus discharge for smallmouth bass spawning.

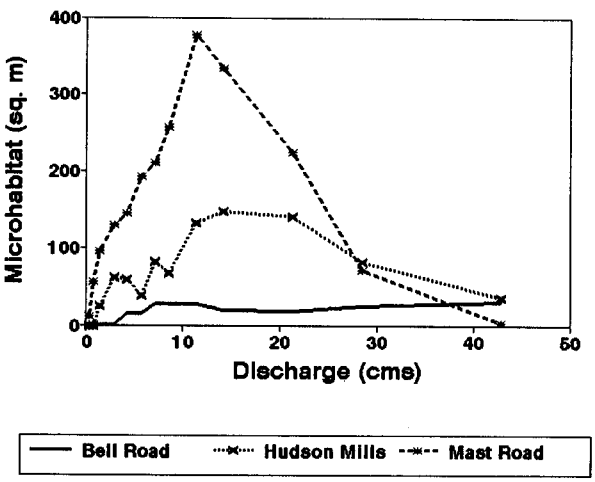


Fig. A16. Usable microhabitat versus discharge for smallmouth bass spawning.

Appendix B. Relations Between Discharge and Microhabitat for Rock Bass and Riffles

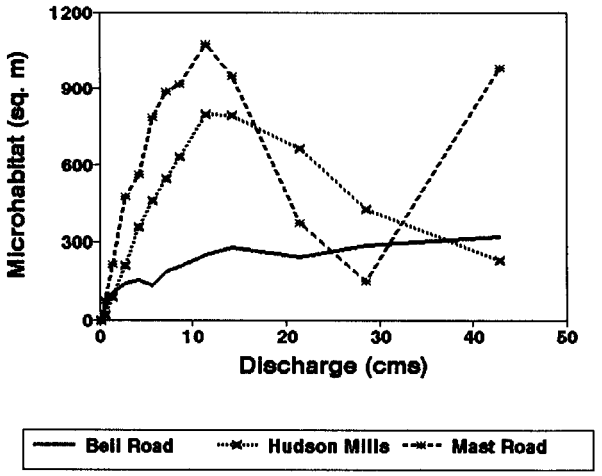
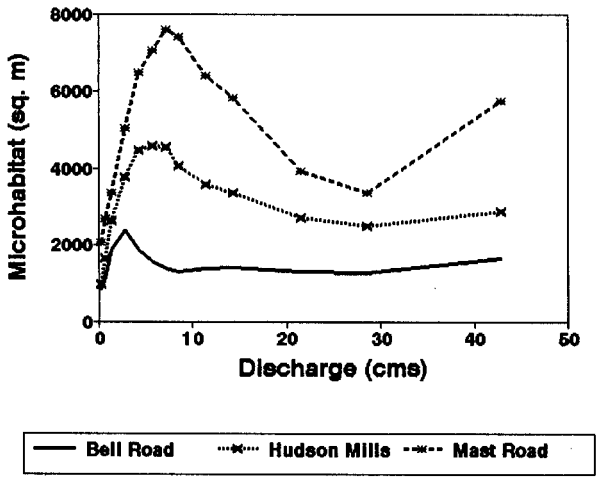


Fig. B1. Optimal microhabitat versus discharge for adult rock bass, summer daytime hours.



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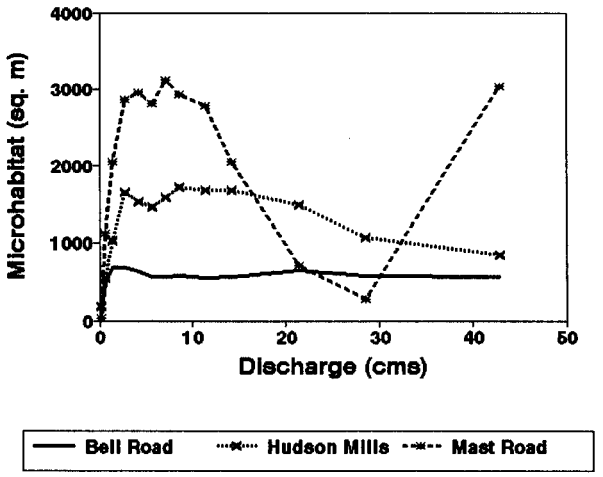
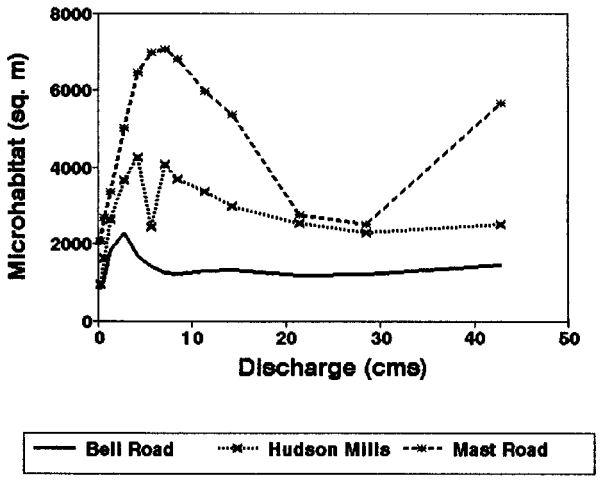


Fig. B3. Optimal microhabitat versus discharge for adult rock bass, summer nighttime hours.



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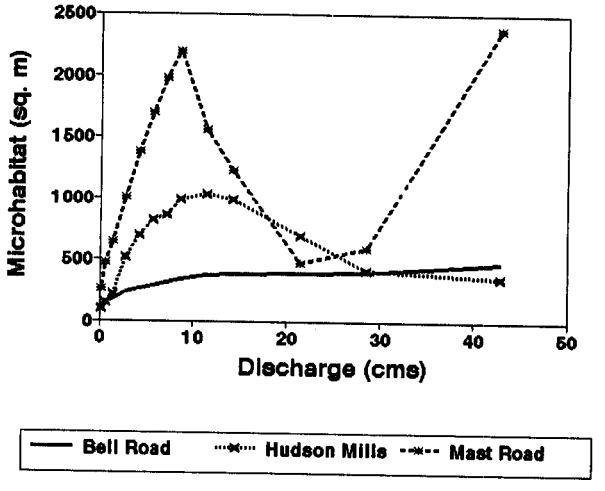

Fig. B5. Optimal microhabitat versus discharge for juvenile rock bass, summer daytime hours.

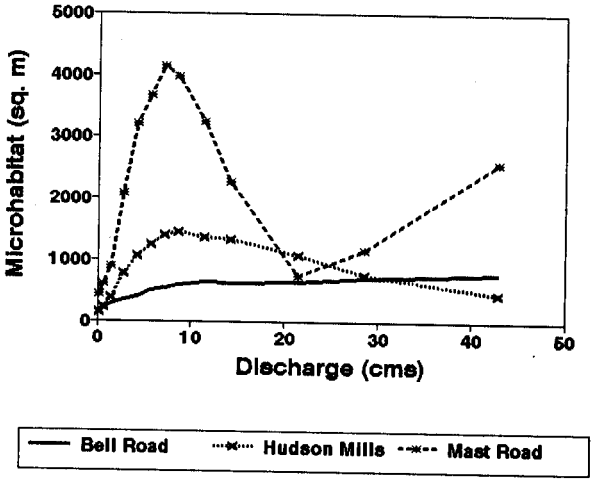

Fig. B6. Usable microhabitat versus discharge for juvenile rock bass, summer daytime hours.

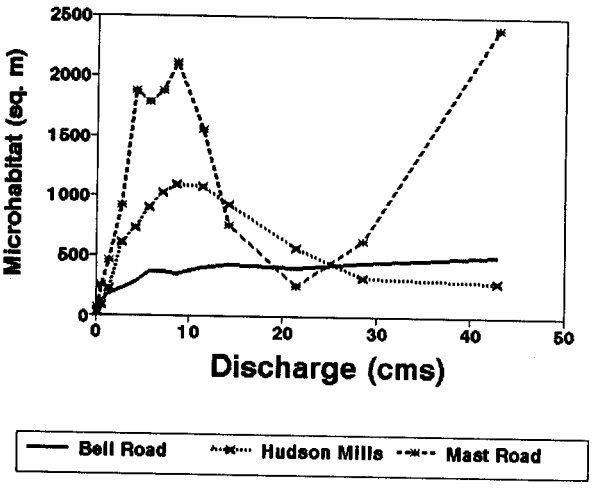

Fig. B7. Optimal microhabitat versus discharge for juvenile rock bass, summer nighttime hours.

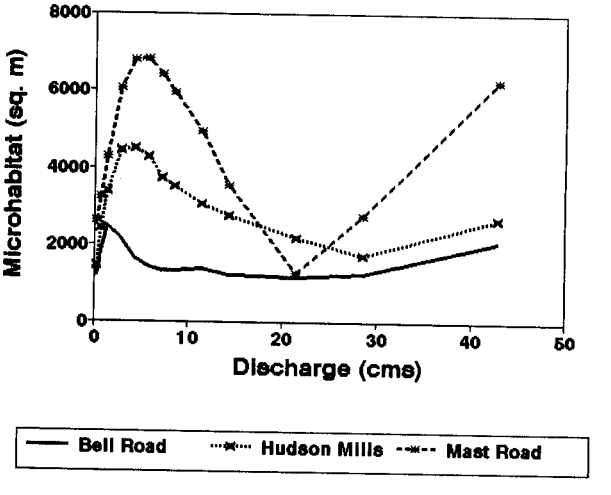

Fig. B8. Usable microhabitat versus discharge for juvenile rock bass, summer nighttime hours.

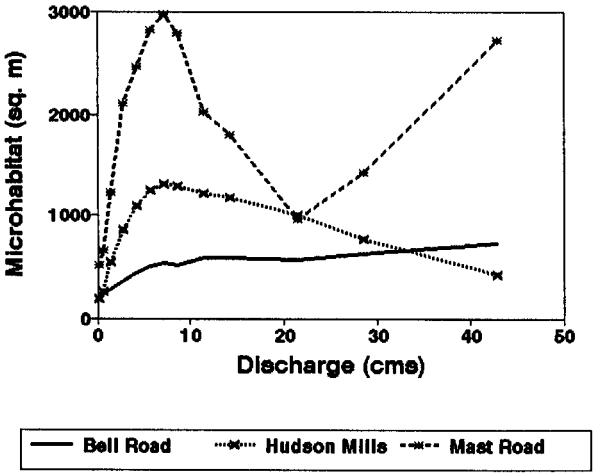

Fig. B9. Optimal microhabitat versus discharge for young-of-year rock bass, summer daytime hours.

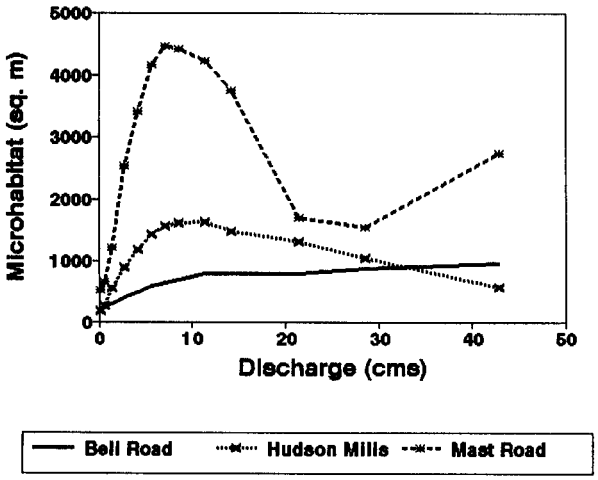

Fig. B10. Usable microhabitat versus discharge for young-of-year rock bass, summer daytime hours.

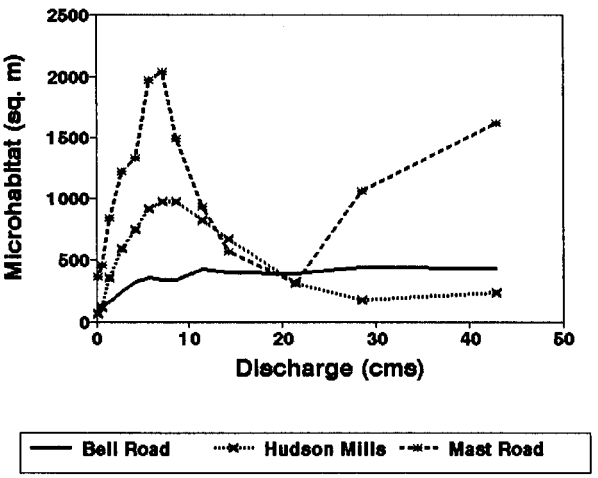

Fig. B11. Optimal microhabitat versus discharge for young-of-year rock bass, summer nighttime hours.

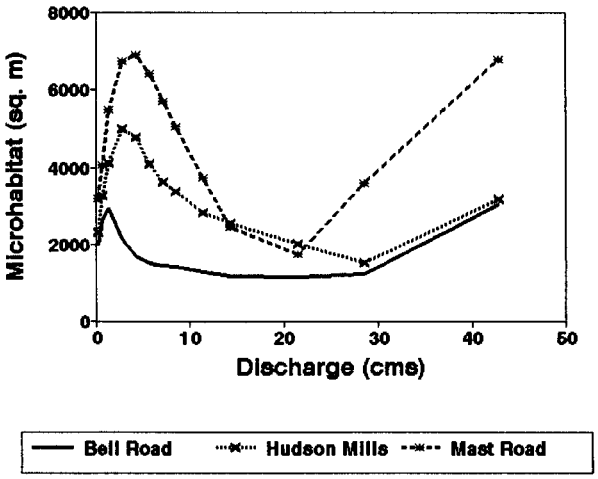

Fig. B12. Usable microhabitat versus discharge for young-of-year rock bass, summer nighttime hours.

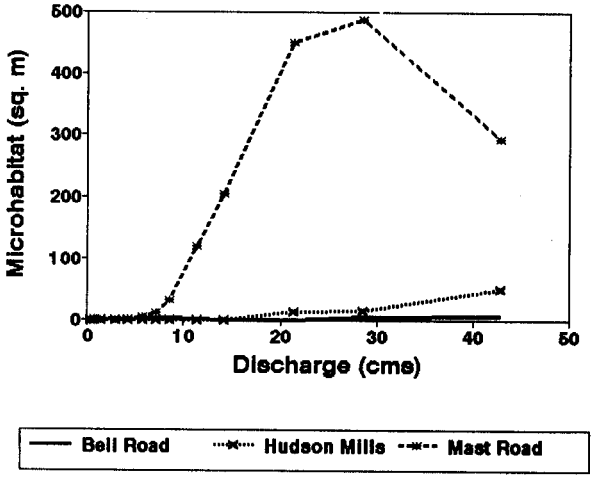

Fig. B13. Optimal microhabitat versus discharge for adult and juvenile rock bass, during winter.

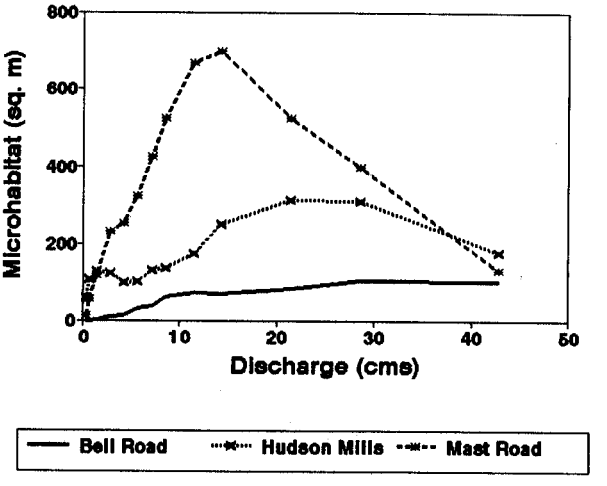

Fig. B15. Optimal microhabitat versus discharge for rock bass spawning.

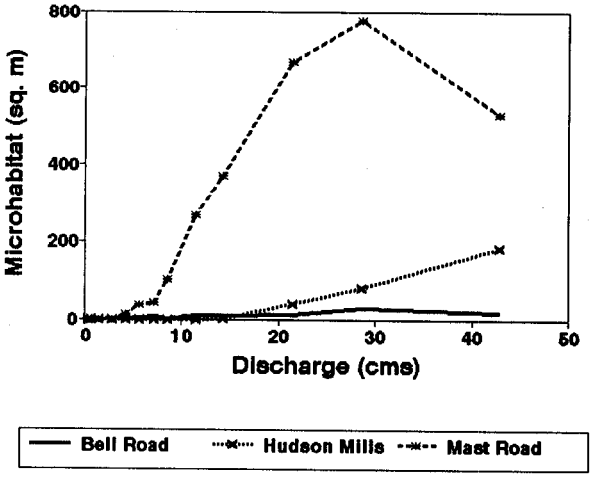

Fig. B14. Usable microhabitat versus discharge for adult and juvenile rock bass, during winter.

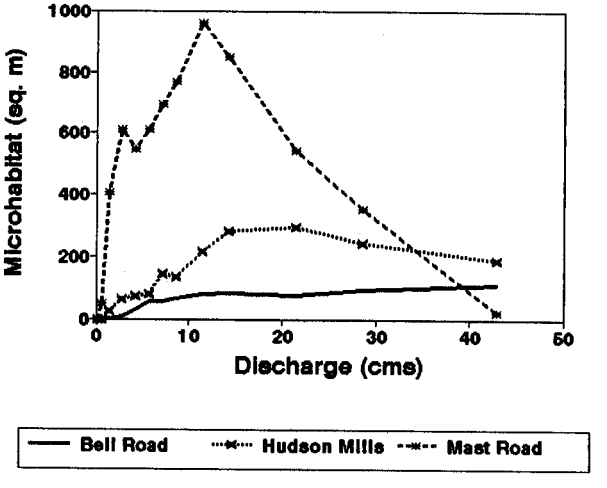

Fig. B16. Usable microhabitat versus discharge for rock bass spawning.

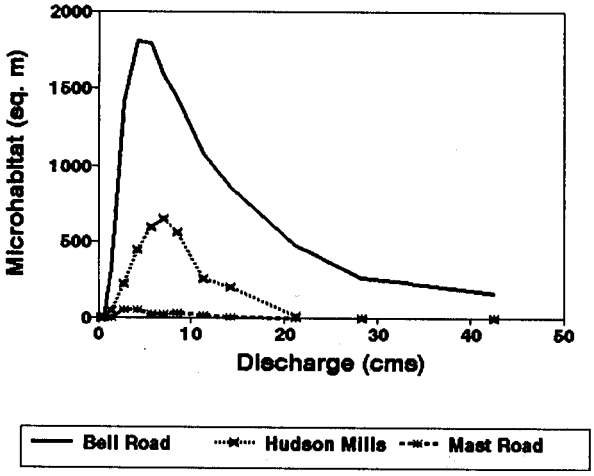

Fig. B17. Optimal microhabitat versus discharge for riffle microhabitat.

Appendix C. Synthesized Temperature Time Series and Hydrographs

Table C.1. Simulated average weekly water temperatures (°C) in the Huron River at Delhi Road.

Month	Week	Water year 1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
October	1	9.9	18.7	17.5	13.6	12.9	15.1	16.3	14.0	14.4	14.7
	2	8.4	16.9	14.9	15.1	13.5	13.5	9.9	9.8	12.6	11.9
	3	7.7	12.4	11.2	15.8	13.8	11.2	11.2	10.5	11.0	12.6
	4	4.9	10.1	10.6	13.6	13.9	13.3	8.8	7.8	13.4	10.4
November	1	5.3	11.4	8.8	9.0	10.5	9.9	9.5	4.2	9.9	10.5
	2	4.7	8.6	8.3	7.5	7.1	7.1	7.3	5.1	7.1	6.7
	3	3.4	3.7	3.3	4.2	6.2	2.1	7.8	6.1	5.6	5.0
	4	0.9	5.2	5.3	1.4	3.5	0.4	4.4	4.4	1.8	5.8
	5	0.8	5.6	3.5	4.3	2.4	1.9	2.9	3.6	1.2	5.3
December	1	1.7	2.1	1.1	1.1	0.1	1.7	1.6	1.5	0.5	1.1
	2	1.3	1.1	0.6	1.7	0.0	0.8	1.6	0.9	0.0	0.5
	3	0.0	0.1	0.0	1.6	0.0	0.5	1.2	1.2	0.0	0.3
	4	0.0	0.9	0.0	0.9	0.0	0.5	0.5	1.5	0.0	0.0
January	1	0.0	0.9	0.0	0.1	0.4	0.0	0.3	0.0	0.0	0.0
	2	0.0	0.0	0.2	0.0	0.3	0.0	0.4	0.0	0.6	0.9
	3	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.5	1.4
	4	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.4	0.6	1.7
	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.1	1.2
February	1	0.0	0.0	0.0	0.0	0.0	0.5	0.2	0.0	0.0	1.5
	2	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	1.7
	3	3.6	0.0	0.9	2.8	1.0	0.7	0.0	0.0	0.0	1.9
	4	4.2	0.0	1.3	1.0	3.6	0.6	0.9	0.4	0.0	1.6
March	1	1.8	0.0	8.2	0.0	3.7	0.0	6.2	2.7	0.0	1.6
	2	2.0	1.3	7.9	0.0	5.3	4.2	3.6	3.3	2.7	5.2
	3	1.5	5.2	3.5	0.7	5.7	5.0	3.9	2.3	2.9	6.0
	4	3.8	4.4	2.1	3.5	7.7	9.1	9.2	6.5	7.3	6.1

Month	Week	Water year 1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
April	1	12.0	3.9	5.1	6.3	8.0	12.4	6.9	11.7	9.9	6.1
	2	13.6	3.3	7.5	8.8	7.3	10.7	9.0	11.6	5.8	6.1
	3	12.7	8.3	6.0	9.1	13.4	10.5	14.6	10.0	8.1	7.6
	4	10.0	12.4	9.4	11.1	18.6	12.0	15.8	10.2	12.1	14.3
May	1	11.3	13.6	12.1	12.9	16.9	13.4	14.3	11.8	12.6	16.9
	2	13.3	16.7	12.4	13.7	17.3	16.5	16.4	15.6	12.4	15.3
	3	13.0	20.7	13.8	14.0	19.0	19.0	18.8	17.5	14.2	14.4
	4	15.9	20.0	16.1	16.9	18.3	15.9	19.3	18.4	18.0	14.7
	5	18.9	19.7	15.2	15.7	18.9	19.1	23.3	21.7	19.7	17.6
June	1	20.2	18.9	15.4	19.4	19.1	20.7	23.8	22.6	20.1	18.5
	2	22.4	19.6	20.6	23.8	18.7	20.2	23.0	22.6	19.7	20.9
	3	22.1	19.5	22.7	23.5	19.1	20.9	24.5	25.0	19.5	22.7
	4	20.5	20.0	23.7	22.8	20.4	21.6	24.3	25.2	21.6	20.6
July	1	22.8	20.8	24.1	23.1	21.9	21.7	23.3	24.4	22.8	24.0
	2	25.8	22.7	23.6	23.3	23.5	22.7	25.8	27.2	23.9	22.7
	3	24.8	24.6	25.7	23.7	23.5	25.0	25.5	28.2	22.9	22.4
	4	22.2	24.3	25.8	24.6	23.2	25.2	26.7	25.4	23.9	23.2
	5	21.4	23.4	24.6	24.3	22.6	24.3	27.1	26.9	24.1	23.6
August	1	22.8	23.4	24.5	24.9	22.8	22.7	24.6	27.2	21.7	21.4
	2	22.5	21.6	22.5	24.4	22.5	21.5	25.1	27.3	21.5	22.5
	3	20.9	20.9	24.0	21.7	20.5	21.8	22.5	23.4	21.3	21.0
	4	21.7	19.4	25.5	21.3	20.9	18.5	19.0	19.4	22.1	24.0
September	1	21.2	19.2	24.3	19.3	23.7	18.0	18.4	18.3	21.6	23.0
	2	21.2	21.2	21.9	19.5	20.8	18.0	20.0	18.3	22.1	22.1
	3	17.0	17.4	20.5	17.6	18.8	17.6	19.8	18.7	18.3	17.2
	4	14.9	15.5	16.0	16.7	16.8	22.2	18.2	17.9	16.6	15.6

Table C.2. Simulated average weekly water temperatures (° C) in the Huron River at Bell Road.

Month	Week	Water year 1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
October	1	10.3	19.7	18.4	14.3	13.5	15.8	17.1	14.6	15.1	15.4
	2	8.7	17.8	15.7	15.8	14.1	14.2	10.3	10.2	13.2	12.4
	3	7.9	12.9	11.7	16.6	14.4	11.7	11.7	10.9	11.5	13.2
	4	4.9	10.5	11.0	14.3	14.5	13.9	9.1	8.1	14.1	10.8
November	1	5.2	10.7	8.4	8.5	9.9	9.3	9.1	4.2	9.4	9.9
	2	4.6	8.2	7.9	7.2	6.9	6.9	7.0	5.0	6.8	6.5
	3	3.5	3.7	3.4	4.2	6.0	2.3	7.4	6.0	5.5	4.9
	4	1.3	5.1	5.2	1.6	3.6	0.8	4.4	4.4	2.0	5.7
	5	1.1	5.5	3.6	4.3	2.6	2.1	3.0	3.7	1.5	5.2
December	1	1.9	2.3	1.4	1.4	0.5	1.9	1.9	1.8	0.9	1.4
	2	1.6	1.4	0.9	1.9	0.4	1.2	1.9	1.3	0.4	0.9
	3	0.4	0.5	0.4	1.9	0.4	0.8	1.5	1.5	0.4	0.7
	4	0.4	1.2	0.4	1.2	0.4	0.8	0.9	1.8	0.4	0.4
January	1	0.4	1.2	0.4	0.5	0.7	0.4	0.7	0.4	0.4	0.4
	2	0.4	0.4	0.6	0.4	0.6	0.4	0.7	0.4	0.9	1.2
	3	0.4	0.4	0.4	0.4	0.4	0.4	0.7	0.4	0.9	1.7
	4	0.4	0.4	0.4	0.4	0.4	0.9	0.4	0.8	1.0	2.0
	5	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.8	1.4	1.5
February	1	0.4	0.4	0.4	0.4	0.4	0.9	0.6	0.4	0.4	1.7
	2	0.4	0.4	0.4	1.8	0.4	0.4	0.4	0.4	0.4	2.0
	3	3.7	0.4	1.2	2.9	1.3	1.0	0.4	0.4	0.4	2.1
	4	4.2	0.4	1.6	1.3	3.6	1.0	1.2	0.8	0.4	1.8
March	1	2.0	0.4	7.9	0.4	3.7	0.4	6.0	2.9	0.4	1.9
	2	2.2	1.6	7.5	0.4	5.2	4.2	3.7	3.4	2.8	5.1
	3	1.7	5.1	3.6	1.0	5.6	4.9	4.0	2.5	3.1	5.9
	4	3.9	4.4	2.3	3.6	7.4	8.6	8.8	6.2	7.0	5.9

Month	Week	Water year 1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
April	1	12.5	3.8	5.2	6.4	8.2	12.9	7.1	12.3	10.3	6.2
	2	14.3	3.2	7.8	9.1	7.5	11.1	9.3	12.1	5.9	6.2
	3	13.3	8.6	6.1	9.4	14.0	11.0	15.4	10.4	8.4	7.8
	4	10.4	13.0	9.7	11.6	19.6	12.5	16.6	10.6	12.6	15.0
May	1	11.8	14.3	12.7	13.5	17.8	14.0	15.0	12.4	13.1	17.8
	2	13.9	17.6	13.0	14.4	18.2	17.4	17.2	16.4	13.0	16.0
	3	13.6	21.9	14.4	14.7	20.0	20.0	19.9	18.4	14.8	15.1
	4	16.7	21.1	16.9	17.7	19.3	16.7	20.3	19.4	19.0	15.5
	5	20.0	20.8	16.0	16.5	19.9	20.2	24.6	22.9	20.7	18.6
June	1	21.3	19.9	16.2	20.5	20.1	21.8	25.1	23.9	21.2	19.4
	2	23.7	20.7	21.7	25.2	19.7	21.3	24.3	23.9	20.8	22.1
	3	23.4	20.6	24.0	24.9	20.1	22.0	25.9	26.4	20.5	24.0
	4	21.7	21.1	25.0	24.1	21.5	22.8	25.7	26.6	22.8	21.8
July	1	24.1	21.9	25.5	24.4	23.2	22.9	24.6	25.8	24.1	25.4
	2	27.3	24.0	25.0	24.7	24.9	23.9	27.3	28.8	25.3	24.0
	3	26.2	26.0	27.2	25.1	24.9	26.5	27.0	29.9	24.2	23.6
	4	23.4	25.7	27.3	26.0	24.5	26.7	28.3	26.8	25.3	24.5
	5	22.6	24.7	26.0	25.7	23.8	25.7	28.7	28.4	25.5	25.0
August	1	24.1	24.7	25.9	26.3	24.1	24.0	26.0	28.8	22.9	22.6
	2	23.8	22.8	23.8	25.8	23.8	22.7	26.6	28.9	22.7	23.8
	3	22.1	22.1	25.4	22.9	21.7	23.0	23.7	24.7	22.5	22.2
	4	22.9	20.4	26.9	22.5	22.1	19.5	20.0	20.5	23.4	25.4
September	1	22.4	20.2	25.7	20.4	25.1	19.0	19.4	19.3	22.8	24.3
	2	22.4	22.4	23.1	20.6	21.9	18.9	21.1	19.2	23.4	23.3
	3	17.9	18.4	21.6	18.5	19.8	18.5	20.9	19.7	19.3	18.1
	4	15.6	16.3	16.8	17.6	17.7	23.5	19.2	18.9	17.5	16.3

Table C.3. Average weekly discharges in cubic meters per second, Huron River at Ann Arbor.

Month	Week	Water year 1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
October	1	13.7	38.2	5.0	3.6	5.5	6.4	36.9	5.5	7.5	5.9
	2	11.0	26.8	5.2	5.1	6.3	6.8	27.0	5.1	5.7	5.8
	3	10.1	18.4	4.8	6.4	6.2	14.2	20.4	5.5	10.1	6.8
	4	11.6	20.0	4.6	5.9	6.5	18.0	15.1	9.1	12.1	8.1
November	1	12.6	22.2	11.4	6.1	6.7	13.8	14.3	13.1	10.7	8.1
	2	11.4	20.1	17.8	9.1	11.3	17.1	13.7	14.7	28.2	12.9
	3	12.8	16.8	14.7	13.2	17.0	25.8	16.5	12.4	30.7	18.4
	4	10.0	19.3	16.4	14.3	12.2	23.4	12.4	12.2	26.2	21.1
	5	10.5	16.7	17.4	17.0	10.6	27.6	15.3	17.7	18.9	15.0
December	1	16.2	15.4	19.4	15.0	9.3	23.3	19.7	16.7	15.7	12.6
	2	19.8	13.4	15.2	23.0	9.0	19.1	21.3	22.2	12.8	10.3
	3	12.9	12.1	16.5	16.7	10.9	15.4	16.8	28.1	10.0	8.6
	4	10.7	12.3	21.1	13.8	13.1	12.9	14.4	27.3	15.3	8.5
January	1	10.2	13.8	15.7	11.0	27.5	11.9	13.2	18.4	13.0	13.3
	2	9.6	12.5	12.5	8.9	20.1	11.3	12.6	12.8	19.3	17.4
	3	8.7	12.6	10.0	8.6	13.3	13.5	14.2	14.1	14.1	19.0
	4	8.3	11.3	9.0	8.3	11.9	17.7	12.2	17.1	12.0	21.3
	5	8.3	10.0	10.2	7.5	10.9	14.4	12.1	16.9	14.0	18.9
February	1	8.6	11.2	11.2	7.8	6.5	22.3	11.9	18.6	11.9	19.2
	2	11.0	10.2	9.2	21.5	8.3	18.5	11.4	15.3	10.3	21.5
	3	51.9	12.3	13.5	23.3	21.2	25.1	10.0	16.2	9.5	32.6
	4	43.9	12.0	14.0	15.5	67.3	20.0	15.0	15.8	8.9	38.5
March	1	24.9	11.5	17.7	10.2	54.6	20.3	21.8	16.8	8.0	29.6
	2	17.3	52.6	17.6	10.7	46.1	54.1	17.2	25.5	10.8	61.9
	3	13.8	81.0	14.8	32.4	30.1	52.0	14.4	22.6	20.1	42.5
	4	15.6	57.0	22.8	35.7	36.7	35.6	14.2	21.3	20.3	29.1
April	1	15.5	52.1	22.4	23.1	45.0	26.1	16.5	29.4	27.1	27.0
	2	20.0	39.7	30.1	14.7	40.9	18.3	14.2	34.8	20.9	27.7
	3	25.5	31.5	42.3	23.2	28.3	19.3	13.8	20.6	16.8	29.6
	4	23.4	19.9	28.2	24.5	22.6	17.2	11.0	14.3	13.6	30.1
May	1	19.9	13.1	50.7	21.6	14.9	17.0	8.1	12.0	11.3	20.3
	2	19.2	15.8	43.1	14.6	14.9	12.7	6.0	8.9	8.5	17.5
	3	26.6	12.5	24.7	13.4	12.1	10.2	6.6	8.4	8.9	25.7
	4	17.3	10.1	21.9	18.5	8.0	13.3	6.7	6.7	10.3	27.4
	5	16.0	13.7	19.8	34.8	10.4	12.2	5.6	4.4	26.5	18.5
June	1	11.4	17.6	22.4	21.0	13.6	13.3	6.3	3.4	30.1	14.2
	2	13.5	11.2	17.5	10.4	10.9	14.7	4.8	2.0	18.0	12.0
	3	13.0	13.2	9.9	6.7	10.5	15.9	3.7	1.6	26.3	9.4
	4	9.1	14.2	8.9	4.4	7.0	12.6	4.8	1.2	37.5	9.8
July	1	6.5	15.0	8.5	3.8	5.6	10.1	5.1	0.8	22.4	7.7
	2	4.8	10.8	6.0	3.6	6.1	14.3	4.5	0.5	10.0	5.1
	3	3.6	9.6	6.1	3.5	8.0	13.2	4.3	1.8	7.0	5.6
	4	4.8	7.2	5.5	2.7	5.9	7.6	3.1	3.3	8.4	5.5
	5	8.3	7.6	7.7	2.5	5.6	4.9	3.6	2.5	6.2	3.7
August	1	4.9	6.0	6.5	3.5	4.5	6.5	3.3	4.0	4.9	3.4
	2	4.0	4.5	5.6	3.6	5.5	4.8	2.5	4.1	4.6	4.6
	3	3.2	3.7	4.0	2.7	7.1	4.1	5.4	6.0	4.2	9.1
	4	5.1	3.4	3.3	2.0	9.7	5.1	10.8	4.2	5.0	4.9
September	1	22.6	3.9	3.1	2.1	9.2	4.7	6.7	4.0	7.8	8.2
	2	15.7	3.5	2.3	3.3	9.7	5.2	5.9	3.8	11.7	11.7
	3	11.2	5.0	4.4	4.2	5.9	6.3	8.3	4.4	11.8	12.8
	4	13.0	5.1	4.8	5.4	6.5	23.5	6.9	11.0	7.7	11.0

Table C.4. Average weekly discharges in cubic meters per second, Huron River at Dexter.

Month	Week	Water year 1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
October	1	10.2	29.2	4.4	3.0	4.4	5.0	25.1	4.2	5.6	4.8
	2	8.1	22.9	4.3	4.0	4.8	5.6	19.9	4.1	4.7	4.7
	3	7.6	14.6	3.9	5.4	4.8	10.2	14.9	4.5	7.6	5.4
	4	8.6	15.2	3.9	4.9	5.3	14.3	11.7	6.8	9.3	6.5
November	1	10.5	18.3	9.4	5.6	5.7	11.4	12.5	10.9	9.0	6.8
	2	9.7	17.7	15.3	8.2	9.1	14.5	12.8	11.8	18.7	10.2
	3	9.2	15.2	12.4	10.3	14.3	20.6	13.2	10.8	22.1	14.7
	4	7.0	15.5	12.4	11.9	10.4	20.6	9.9	10.1	17.2	16.2
	5	7.6	13.5	13.2	13.1	8.2	22.3	11.9	13.2	14.3	11.6
December	1	11.4	12.2	13.8	11.4	7.8	17.9	13.2	12.0	12.6	10.3
	2	14.3	10.8	12.0	13.7	7.3	14.9	13.8	14.0	9.9	8.4
	3	10.4	10.0	12.6	13.0	8.9	12.3	11.8	17.2	8.2	7.1
	4	8.6	10.1	13.8	10.7	9.8	10.5	11.3	18.3	10.4	6.9
January	1	7.8	10.5	11.1	8.3	16.5	9.9	9.9	12.9	9.4	9.5
	2	7.2	10.9	9.2	7.2	13.0	9.4	9.6	10.3	12.6	11.7
	3	6.7	10.0	8.1	6.9	10.0	10.3	10.4	10.7	9.9	12.2
	4	6.5	9.2	7.3	6.7	9.2	12.7	9.5	11.9	8.6	13.8
	5	6.5	8.7	7.7	6.5	8.5	10.8	9.3	11.4	9.8	12.7
February	1	6.6	10.6	9.1	6.9	7.2	15.6	9.7	13.2	8.9	13.9
	2	8.3	10.4	7.8	12.1	7.5	13.8	9.2	12.1	7.7	15.4
	3	26.1	10.4	10.1	15.8	10.8	15.6	8.2	12.1	7.2	17.3
	4	29.4	10.3	10.6	11.2	40.1	14.0	10.4	11.6	6.7	27.3
March	1	17.0	9.4	13.1	7.8	31.3	13.7	16.1	12.6	6.3	18.5
	2	13.0	27.6	11.1	7.9	31.0	33.2	13.1	19.3	8.3	37.1
	3	10.4	48.1	9.5	19.4	23.1	33.9	11.0	17.2	15.1	32.2
	4	10.7	35.9	13.5	22.9	23.2	26.8	10.7	15.9	13.4	22.2

Month	Week	Water year 1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
April	1	10.8	36.9	14.7	15.1	28.5	19.1	12.0	18.8	17.1	19.6
	2	11.4	30.3	18.2	9.9	27.8	12.3	11.2	22.5	13.4	18.3
	3	15.3	23.8	27.0	13.5	21.4	12.5	9.5	14.1	11.3	19.5
	4	15.4	13.5	21.5	14.8	14.9	11.5	8.4	9.6	10.5	19.9
May	1	14.7	10.1	32.6	15.4	10.9	12.5	6.4	8.7	8.9	15.0
	2	12.7	11.9	33.2	11.0	9.8	9.8	4.8	6.0	6.9	13.5
	3	17.5	9.6	18.6	9.9	9.1	7.9	5.3	5.6	6.8	15.7
	4	13.1	7.9	14.7	11.6	6.7	10.4	5.5	5.3	7.2	20.6
	5	11.0	11.2	13.3	21.0	9.0	9.6	4.9	3.9	15.3	13.9
June	1	8.6	15.3	15.4	14.6	12.9	10.7	5.9	3.3	19.4	11.0
	2	9.8	9.4	13.6	8.2	9.5	12.5	4.4	2.1	13.6	10.0
	3	10.0	10.8	8.2	5.2	9.1	14.2	3.2	1.6	17.4	8.1
	4	7.4	11.6	7.0	3.6	5.7	11.3	4.3	1.2	33.5	8.2
July	1	5.0	11.3	6.6	3.1	4.3	7.7	4.0	0.9	16.8	5.9
	2	3.8	8.7	4.8	2.9	4.7	11.0	3.8	0.6	8.0	4.0
	3	2.9	7.7	4.6	2.8	6.0	9.5	3.5	1.6	5.4	4.3
	4	3.8	5.6	4.2	2.2	4.7	5.9	2.8	2.5	6.5	4.3
	5	6.7	6.8	5.7	2.2	4.5	4.0	3.2	2.2	5.2	3.0
August	1	3.6	4.7	5.0	3.0	3.5	4.7	2.9	2.8	4.1	2.8
	2	3.1	3.5	4.6	3.4	4.2	3.9	2.6	3.3	3.8	3.6
	3	2.6	3.0	3.3	2.3	6.5	3.3	4.2	4.4	3.6	6.2
	4	3.8	3.3	2.9	1.8	8.8	4.1	8.5	3.4	4.0	4.3
September	1	15.4	3.3	2.6	1.9	6.6	3.6	5.2	3.2	6.2	5.7
	2	12.7	3.0	2.1	2.7	7.4	3.9	4.6	3.1	8.0	8.2
	3	8.2	4.0	3.4	3.3	4.5	4.6	5.7	3.3	9.3	9.0
	4	9.2	4.1	3.8	4.0	4.6	15.5	4.9	7.3	6.2	8.0

Appendix D. Habitat Metrics Extracted from Time Series

Table D.1. Habitat metrics (m^2) for smallmouth bass, derived from optimal habitat suitability criteria.

Year	Habitat metric				
	ASDMIN	ASDMAX	ASDAVG	ASDMIN5	ASDMAX5
1981	259	2,883	1,991	1,063	2,839
1982	325	3,088	1,780	484	2,571
1983	119	3,187	1,801	365	2,963
1984	103	2,972	1,344	208	2,694
1985	745	3,140	2,041	1,428	2,594
1986	556	2,915	1,989	929	2,620
1987	145	2,593	1,457	346	2,290
1988	1	2,944	1,094	53	2,542
1989	582	3,186	2,206	1,031	2,757
1990	329	2,933	2,119	875	2,784
	ASNMIN	ASNMAX	ASNAVG	ASNMIN5	ASNMAX5
1981	373	1,742	1,144	610	1,575
1982	396	1,726	1,127	431	1,569
1983	282	1,596	976	389	1,734
1984	229	1,646	814	321	1,419
1985	488	1,700	1,124	664	1,559
1986	453	1,677	1,165	519	1,605
1987	318	1,649	814	393	1,413
1988	45	1,711	668	129	1,442
1989	466	1,740	1,152	561	1,547
1990	391	1,715	1,099	501	1,700
	AWMIN	AWMAX	AWAVG	AWMIN5	AWMAX5
1981	18	297	100	24	232
1982	50	316	148	68	272
1983	1	285	123	16	270
1984	0	291	105	3	249
1985	2	315	106	4	244
1986	4	310	182	94	285
1987	49	303	157	78	215
1988	2	305	166	29	282
1989	2	307	126	40	256
1990	3	308	152	9	301
	JSDMIN	JSDMAX	JSDAVG	JSDMIN5	JSDMAX5
1981	565	4,012	2,662	1,617	3,630
1982	157	3,931	2,548	1,077	3,660
1983	88	4,057	2,153	597	3,695
1984	115	3,827	1,754	415	3,201
1985	211	3,974	2,894	1,439	3,687
1986	1,323	3,875	2,896	1,807	3,620
1987	252	3,972	2,385	756	3,473
1988	0	4,036	1,556	30	3,650
1989	628	4,058	2,819	1,556	3,763
1990	723	3,984	2,665	1,555	3,756

Table D.1. *Continued.*

Year	Habitat metric				
	JSNMIN	JSNMAX	JSNAVG	JSNMIN5	JSNMAX5
1981	551	2,612	1,660	891	2,275
1982	626	2,728	1,833	1,359	2,331
1983	412	2,584	1,482	977	2,066
1984	657	2,527	1,380	1,009	1,855
1985	451	2,626	1,793	1,203	2,348
1986	603	2,564	1,825	993	2,476
1987	975	2,424	1,678	1,316	2,040
1988	89	2,638	1,308	320	2,178
1989	536	2,658	1,634	834	2,279
1990	482	2,650	1,607	640	2,566
	YSDMIN	YSDMAX	YSDAVG	YSDMIN5	YSDMAX5
1981	1,265	3,591	2,950	1,809	3,443
1982	2,143	3,612	3,040	2,391	3,490
1983	1,712	3,592	2,870	2,201	3,394
1984	1,256	3,557	2,305	1,896	3,136
1985	2,624	3,612	3,303	3,010	3,488
1986	1,321	3,576	3,058	1,620	3,411
1987	1,904	3,598	2,865	2,232	3,358
1988	102	3,503	2,007	776	3,402
1989	576	3,580	2,613	1,340	3,408
1990	2,197	3,592	3,135	2,641	3,549
	YSNMIN	YSNMAX	YSNAVG	YSNMIN5	YSNMAX5
1981	271	1,375	860	477	1,176
1982	266	1,404	837	389	1,339
1983	303	1,481	1,079	775	1,308
1984	299	1,426	1,014	856	1,347
1985	339	1,477	1,004	607	1,332
1986	265	1,393	812	302	1,284
1987	570	1,471	1,183	1,005	1,316
1988	342	1,394	941	556	1,224
1989	213	1,359	904	546	1,297
1990	454	1,477	985	537	1,312
	SPMIN	SPMAX	SPAVG	SPMIN5	SPMAX5
1981	70	110	92	58	93
1982	56	112	89	82	90
1983	3	96	49	24	69
1984	4	90	49	24	56
1985	33	116	74	59	103
1986	57	117	94	82	108
1987	30	69	39	26	47
1988	12	43	27	10	38
1989	7	92	48	35	45
1990	33	132	70	31	90

Table D.2. Habitat metrics (m^2) for rock bass, derived from optimal habitat suitability criteria.

Year	Habitat metric				
	ASDMIN	ASDMAX	ASDAVG	ASDMIN5	ASDMAX5
1981	197	953	636	332	884
1982	292	1,052	694	426	887
1983	150	1,028	580	341	833
1984	213	923	505	328	774
1985	196	939	717	527	878
1986	231	931	701	413	905
1987	332	941	620	395	825
1988	35	942	459	128	842
1989	221	953	651	371	879
1990	181	942	618	265	928
	ASNMIN	ASNMAX	ASNAVG	ASNMIN5	ASNMAX5
1981	334	2,477	1,713	743	2,431
1982	683	2,813	2,038	1,248	2,460
1983	263	2,759	1,864	703	2,884
1984	393	2,507	1,754	681	2,430
1985	488	2,588	2,167	1,404	2,437
1986	494	2,509	1,941	1,089	2,446
1987	1,081	2,534	2,196	1,600	2,437
1988	386	2,514	1,835	1,122	2,414
1989	543	2,546	1,897	1,042	2,440
1990	285	2,504	1,804	669	2,421
	AWMIN	AWMAX	AWAVG	AWMIN5	AWMAX5
1981	166	651	336	184	530
1982	201	658	425	298	616
1983	46	599	369	109	556
1984	26	632	299	81	508
1985	79	748	313	107	516
1986	111	653	442	328	587
1987	217	658	436	323	537
1988	63	617	415	164	537
1989	83	620	353	223	540
1990	88	673	366	128	623
	JSDMIN	JSDMAX	JSDAVG	JSDMIN5	JSDMAX5
1981	477	1,718	1,051	588	1,386
1982	518	2,186	1,210	878	1,539
1983	432	2,126	1,139	554	1,559
1984	406	1,555	923	548	1,449
1985	461	1,937	1,337	857	1,547
1986	525	1,650	1,139	704	1,397
1987	749	1,714	1,233	903	1,522
1988	293	1,717	957	432	1,463
1989	451	1,735	1,184	793	1,546
1990	522	1,705	1,104	628	1,504

Table D.2. *Continued.*

Year	Habitat metric				
	JSNMIN	JSNMAX	JSNAVG	JSNMIN5	JSNMAX5
1981	398	1,685	1,017	488	1,513
1982	328	1,673	1,169	763	1,559
1983	294	1,870	1,122	402	1,546
1984	286	1,552	919	438	1,488
1985	321	1,799	1,321	692	1,553
1986	464	1,612	1,092	551	1,612
1987	564	1,681	1,284	950	1,667
1988	143	1,693	997	312	1,501
1989	287	1,703	1,182	733	1,556
1990	408	1,672	1,100	535	1,555
	YSDMIN	YSDMAX	YSDAVG	YSDMIN5	YSDMAX5
1981	950	2,277	1,807	1,341	2,097
1982	1,183	2,310	1,832	1,429	2,167
1983	1,375	2,276	1,987	1,683	2,219
1984	1,198	2,289	1,710	1,486	2,175
1985	1,495	2,316	2,068	1,813	2,235
1986	1,030	2,281	1,802	1,287	2,129
1987	1,492	2,297	1,974	1,698	1,596
1988	465	2,245	1,479	802	2,029
1989	884	2,312	1,820	1,303	2,237
1990	1,492	2,261	1,960	1,601	2,156
	YSNMIN	YSNMAX	YSNAVG	YSNMIN5	YSNMAX5
1981	481	1,596	1,031	671	1,325
1982	493	1,596	1,040	625	1,398
1983	845	1,595	1,248	989	1,520
1984	759	1,603	1,031	896	1,497
1985	637	1,613	1,297	970	1,526
1986	532	1,599	1,013	594	1,363
1987	843	1,608	1,247	999	2,150
1988	299	1,579	888	522	1,263
1989	341	1,614	1,084	702	1,500
1990	673	1,553	1,178	786	1,420
	SPMIN	SPMAX	SPAVG	SPMIN5	SPMAX5
1981	527	658	591	440	589
1982	481	662	587	583	603
1983	322	639	479	384	558
1984	161	671	423	397	472
1985	503	656	583	548	599
1986	529	666	605	579	616
1987	391	505	440	391	451
1988	301	517	401	200	517
1989	278	530	374	278	422
1990	273	668	485	379	581

Table D.3. Habitat metrics (m^2) for smallmouth bass, derived from usable habitat suitability criteria.

Year	Habitat metric				
	ASDMIN	ASDMAX	ASDAVG	ASDMIN5	ASDMAX5
1981	809	6,348	4,438	1,998	6,230
1982	953	6,678	4,101	1,258	5,886
1983	385	6,643	3,815	998	6,407
1984	256	6,499	3,122	6,08	6,090
1985	1,721	6,510	4,062	2,489	5,898
1986	1,475	6,343	4,501	1,910	6,136
1987	468	6,038	2,854	961	5,269
1988	1	6,508	2,308	85	5,603
1989	1,535	6,713	4,413	2,038	5,856
1990	956	6,445	4,304	1,754	6,069
	ASNMIN	ASNMAX	ASNAVG	ASNMIN5	ASNMAX5
1981	1,282	3,292	2,850	2,038	3,278
1982	1,405	3,294	2,726	1635	3,234
1983	863	3,296	2,607	1,415	3,284
1984	694	3,295	2,200	1,064	3,234
1985	1,976	3,282	2,840	2,344	3,220
1986	1,837	3,287	2,869	2,052	3,264
1987	957	3,227	2,358	1,391	3,140
1988	299	3,292	1,898	453	3,200
1989	1,893	3,296	2,903	2,127	3,249
1990	1,399	3,292	2,817	1,907	3,252
	AWMIN	AWMAX	AWAVG	AWMIN5	AWMAX5
1981	59	456	189	72	364
1982	119	487	250	151	412
1983	11	431	212	45	428
1984	4	442	185	19	393
1985	22	489	187	24	403
1986	25	485	296	166	438
1987	118	475	267	167	349
1988	17	483	273	70	439
1989	23	486	222	101	407
1990	23	486	252	36	477
	JSDMIN	JSDMAX	JSDAVG	JSDMIN5	JSDMAX5
1981	2,714	6,903	5,331	3,756	6,717
1982	2,723	6,981	5,115	3,136	6,706
1983	1,725	6,518	4,388	2,772	6,128
1984	1,104	6,919	4,116	2,098	6,234
1985	2,685	6,919	5,111	4,112	6,437
1986	3,354	6,966	5,571	3,660	6,797
1987	2,064	6,941	4,421	2,798	6,401
1988	0	6,966	3,364	323	6,235
1989	2,972	6,922	5,208	3,783	6,356
1990	2,849	6,978	5,088	3,495	6,668

Table D.3. *Continued.*

Year	Habitat metric				
	JSNMIN	JSNMAX	JSNAVG	JSNMIN5	JSNMAX5
1981	982	2,980	2,136	1,539	2,813
1982	860	3,064	2,217	1,539	2,864
1983	716	2,843	1,837	1,269	2,566
1984	662	3,067	1,691	1,038	2,306
1985	751	3,078	2,211	1,566	2,819
1986	1,073	3,018	2,317	1,485	2,911
1987	978	2,868	2,005	1,346	2,638
1988	89	3,056	1,506	320	2,615
1989	817	3,034	2,077	1,244	2,756
1990	784	3,067	2,011	1,063	2,955
	YSDMIN	YSDMAX	YSDAVG	YSDMIN5	YSDMAX5
1981	3,250	5,987	4,865	4,001	5,605
1982	3,449	5,954	4,949	3,749	5,621
1983	2,646	6,009	4,665	3,445	5,586
1984	2,356	5,883	3,708	2,947	4,995
1985	4,196	5,975	5,368	4,841	5,741
1986	3,573	5,892	5,040	3,821	5,577
1987	2,882	5,961	4,545	3,458	5,435
1988	845	5,793	3,294	1,652	5,558
1989	2,708	5,972	4,662	3,519	5,503
1990	3,418	5,974	5,106	4,200	5,842
	YSNMIN	YSNMAX	YSNAVG	YSNMIN5	YSNMAX5
1981	456	1,658	1,125	693	1,481
1982	443	1,697	1,104	3,961	1,625
1983	499	1,749	1,380	1,059	1,609
1984	515	1,701	1,324	1,144	1,646
1985	526	1,746	1,294	859	1,632
1986	442	1,675	1,064	495	1,581
1987	820	1,741	1,491	1,321	1,612
1988	490	1,688	1,244	847	1,530
1989	412	1,662	1,166	762	1,596
1990	657	1,746	1,272	761	1,602
	SPMIN	SPMAX	SPAVG	SPMIN5	SPMAX5
1981	179	244	212	177	228
1982	195	232	213	201	221
1983	5	215	141	80	195
1984	28	234	144	107	174
1985	124	239	191	178	223
1986	194	238	218	208	228
1987	120	232	148	109	173
1988	72	175	122	62	157
1989	44	228	134	99	120
1990	147	250	200	127	219

Table D.4. Habitat metrics (m^2) for rock bass, derived from usable habitat suitability criteria.

Year	Habitat metric				
	ASDMIN	ASDMAX	ASDAVG	ASDMIN5	ASDMAX5
1981	3,267	6,269	4,865	3,562	5,781
1982	3,344	6,377	5,182	4,185	6,068
1983	3,005	6,332	4,913	3,527	6,154
1984	3,258	6,297	4,585	3,803	6,098
1985	2988	6,376	5,509	4,033	6,162
1986	3,239	6,331	5,125	3,818	5,896
1987	4,185	6,340	5,612	4,831	6,200
1988	2,069	6,306	4,636	2,779	5,945
1989	3,094	6,352	5,089	3,620	6,205
1990	3,109	6,330	4,904	3,334	6,000
	ASNMIN	ASNMAX	ASNAVG	ASNMIN5	ASNMAX5
1981	2,436	5,852	4,260	2,795	5,509
1982	2,849	5,982	4,821	3,721	5,737
1983	2,416	5,899	4,487	2,828	5,929
1984	2,577	5,887	4,272	3,099	5,730
1985	2,398	5,918	5,050	3,561	5,724
1986	2,583	5,887	4,706	3,237	5,654
1987	3,703	5,919	5,209	4,533	5,824
1988	2,066	5,870	4,372	2,771	5,499
1989	2,456	5,901	4,550	3,055	5,734
1990	2,465	5,862	4,429	2,712	5,673
	AWMIN	AWMAX	AWAVG	AWMIN5	AWMAX5
1981	915	1,479	1,113	948	1,257
1982	995	1,682	1,196	1,066	1,504
1983	456	1,229	1,028	619	1,193
1984	363	1,265	981	553	1,182
1985	548	1,734	1,052	649	1,403
1986	665	1,490	1,135	979	1,304
1987	985	1,296	1,154	1,089	1,208
1988	503	1,224	1,067	747	1,206
1989	562	1,227	1,068	935	1,202
1990	578	1,616	1,079	740	1,336
	JSDMIN	JSDMAX	JSDAVG	JSDMIN5	JSDMAX5
1981	770	3,007	1,927	979	2,672
1982	846	3,088	2,171	1,470	2,872
1983	696	3,049	1,990	915	2,882
1984	657	3,017	1,706	931	2,829
1985	785	3,090	2,445	1,456	2,907
1986	860	3,048	2,111	1,196	2,739
1987	1,350	3,051	2,423	1,835	2,914
1988	409	3,020	1,803	644	2,740
1989	740	3,074	2,161	1,207	2,937
1990	853	3,044	2,044	1,054	2,825

Table D.4. *Continued.*

Year	Habitat metric				
	JSNMIN	JSNMAX	JSNAVG	JSNMIN5	JSNMAX5
1981	1,869	5,851	3,937	2,066	5,652
1982	1,738	6,036	4,451	2,974	5,846
1983	1,543	5,967	4,390	1,901	5,763
1984	1,628	5,864	4,285	2,275	5,798
1985	1,609	5,856	4,724	2,767	5,751
1986	1,937	5,850	4,128	2,354	5,850
1987	2,821	5,865	5,258	3,860	5,855
1988	1,680	5,848	4,631	3,124	5,771
1989	1,616	5,845	4,186	2,678	5,803
1990	1,777	5,863	4,133	2,236	5,743
	YSDMIN	YSDMAX	YSDAVG	YSDMIN5	YSDMAX5
1981	1,344	3,337	2,738	1,942	3,076
1982	2,038	3,362	2,825	2,300	3,289
1983	1,561	3,337	2,772	2,097	3,202
1984	1,305	3,303	2,210	1,754	3,061
1985	2,573	3,357	3,131	2,858	3,272
1986	1,387	3,353	2,844	1,750	3,113
1987	1,719	3,330	2,713	2,103	4,677
1988	466	3,207	1,887	824	3,180
1989	1,306	3,350	2,653	1,651	3,234
1990	2,111	3,342	2,934	2,573	3,222
	YSNMIN	YSNMAX	YSNAVG	YSNMIN5	YSNMAX5
1981	2,201	6,063	4,538	2,839	5,688
1982	2,213	6,051	4,478	2,735	6,014
1983	3,989	6,075	5,393	4,767	5,924
1984	3,830	6,096	5,683	5,414	5,989
1985	2,661	5,985	4,769	3,690	5,584
1986	2,317	6,045	4,192	2,561	5,904
1987	3,711	6,065	5,565	4,870	4,523
1988	3,426	6,086	5,342	4,284	5,971
1989	2,057	6,035	4,313	2,940	5,814
1990	3,119	6,035	4,928	3,408	5,886
	SPMIN	SPMAX	SPAVG	SPMIN5	SPMAX5
1981	397	504	467	255	465
1982	427	532	475	473	494
1983	332	486	415	280	449
1984	187	492	321	173	321
1985	349	520	461	388	454
1986	431	529	490	448	501
1987	202	349	262	197	274
1988	96	349	202	67	349
1989	323	479	385	313	392
1990	291	531	417	274	455

Table D.5. Habitat metrics (m^2) for riffle microhabitat.

Year	Habitat metric				
	RIFMIN	RIFMAX	RIFAVG	RIFMIN5	RIFMAX5
1981	8	313	184	70	298
1982	0	311	144	6	284
1983	7	314	162	18	290
1984	16	313	165	84	306
1985	5	308	190	11	280
1986	7	301	142	34	271
1987	13	305	180	68	284
1988	2	311	139	20	276
1989	7	313	189	56	294
1990	6	314	158	18	279

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