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Application of Diel Feeding Chronology to Habitat Suitability Analysis of Warmwater Stream Fishes

Thomas J. Kwak

Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108, USA

Michael J. Wiley

School of Natural Resources, University of Michigan, Ann Arbor, MI 48020, USA

and Lewis L. Osborne and R. Weldon Larimore

Center for Aquatic Ecology, Illinois Natural History Survey, Champaign, Il 61820, USA

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Diel feeding chronology and daily ration were determined from stomach or foregut contents of common carp (*Cyprinus carpio*), golden redhorse (*Moxostoma erythrurum*), channel catfish (*Ictalurus punctatus*), smallmouth bass (*Micropterus dolomieu*), and longear sunfish (*Lepomis megalotis*) in the Vermilion River, Illinois. Feeding was highly variable among individuals, hours, and months for each species. Discontinuous feeding was detected in common carp, golden redhorse, and channel catfish. Common carp and the two centrarchid species fed with greatest intensity near sunrise and sunset; golden redhorse and channel catfish feeding was highest at night. Daily ration estimates were higher for fishes with stomachs than those for stomachless species. Microhabitats occupied by fish over the diel period were identified using nondisruptive techniques: direct observation, prepositioned electrofishing, and radiotelemetry. Microhabitat use during high-feeding periods was significantly different ($P \leq 0.10$) than that during low feeding for at least one habitat variable in each species examined. Association with cover also varied between feeding regimes. Our findings suggest that realism of instream flow assessments may be improved if habitat suitability criteria are stratified by feeding regime.

Nous avons déterminé, à partir du contenu des estomacs et de la partie antérieure du tube digestif, la chronologie nycthémérale de l'alimentation et la ration quotidienne de carpes (*Cyprinus carpio*), de suceurs dorés (*Moxostoma erythrurum*), de barbues de rivière (*Ictalurus punctatus*), d'achigans à petite bouche (*Micropterus dolomieu*) et de crapets à longues oreilles (*Lepomis megalotis*) de la rivière Vermilion, en Illinois. L'alimentation de chaque espèce présentait une grande variabilité en fonction des individus, de l'heure et du mois. Une alimentation discontinue a été notée chez les carpes, les suceurs dorés et les barbues de rivière. Les carpes et les deux espèces de centrarchidés s'alimentaient avec le plus d'intensité aux environs du lever et du coucher du soleil tandis que les suceurs dorés et les barbottes de rivière s'alimentaient surtout la nuit. Les rations quotidiennes estimées étaient plus élevées chez les poissons possédant un estomac proprement dit. Les microhabitats occupés par les poissons au cours d'une période nycthémérale ont été déterminés par techniques non perturbatrices: observation directe, pêche électrique à équipement déjà en place et radiotélémétrie. Pour chaque espèce et au moins une variable liée à l'habitat, les microhabitats utilisés pendant les périodes d'alimentation intensive différaient de façon significative ($P \leq 0,10$) de ceux des périodes de faible alimentation. Le facteur d'association avec le couvert variait aussi en fonction des régimes d'alimentation. Nos résultats portent à croire que la stratification par régimes d'alimentation des critères de pertinence de l'habitat pourrait permettre d'accroître l'exactitude de l'évaluation des apports au cours d'eau.

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Little is known of the feeding biology of many warmwater stream fishes, particularly those species of little sport or commercial value. While distinct foraging and resting habitats have been identified for stream salmonids (Gosse and Helm 1982; Fausch 1984), a similar finding has not been well documented in warmwater streams. Nonetheless, predator–prey relationships certainly influence habitat use by warmwater stream fishes (Power and Matthews 1983; Gilliam and Fraser 1987; Gorman 1987; Schlosser 1987). Diel and seasonal changes in habitat use by some species may be attributed to a predator avoidance response, a response to differences in prey availability, or most likely, a complex interaction of both factors (Cerri 1983; Cerri and Fraser 1983). Such variability in activity and habitat use is common in stream fishes and is likely related to predator–prey interactions.

Efforts to determine the effects of flow modifications on stream habitat and biota have yielded a variety of models and techniques (Morhardt 1986), none of which incorporates the feeding dynamics of fishes. Orth (1987) recognized the Instream Flow Incremental Methodology (IFIM), described by Bovee (1982), as state of the art. Although widely used in stream habitat assessment (Reiser et al. 1989), a growing body of evidence indicates the existing habitat assessment techniques, including the IFIM, are problematic when applied to warmwater streams (Gore and Nestler 1988; Osborne et al. 1988; Bain and Boltz 1989). Furthermore, limited predictive abilities

of the IFIM, due mainly to a lack of correlation between estimated available habitat and fish biomass, have led to disagreement on its correct application (Mathur et al. 1985; Orth 1987; Gore and Nestler 1988).

The IFIM incorporates species biology into hydraulic models using univariate functions referred to as probability-of-use, utilization, suitability, or preference curves (Bovee and Cochnauer 1977; Bovee 1986). Orth (1987) offered ecological considerations including energetics, food limitation, and predation risk that may improve biological realism in the development and application of instream flow and habitat models. He noted that the unique features of foraging and resting sites are not adequately described by present habitat suitability functions which do not distinguish between seasons or activities such as feeding. Orth (1987) recommended that habitat variables that describe food availability must be sought and that instream flow assessments include site-specific habitat criteria that reflect the local adaptations of fishes to predators.

In this paper we examine the diel feeding and habitat use for five fish species of a prairie stream and develop a procedure for incorporating feeding dynamics into the development of habitat suitability criteria. As part of this study we (1) determine feeding chronology and daily ration of fishes in the field and distinguish high-feeding and low-feeding intervals of the diel cycle, (2) develop on-site habitat suitability criteria for the same species, and (3) develop distinct habitat suitability criteria by temporally stratifying feeding regime (high or low). Finally, we compare these suitability functions to determine if microhabitat use differs between high- and low-feeding periods and discuss the implications of our findings with regard to habitat suitability analysis.

Study Area

The study was conducted in two adjacent branches of the Vermilion River (Wabash drainage) in east-central Illinois. The Salt Fork and Middle Fork of the Vermilion drainage are fifth- and sixth-order streams (sensu Horton (1945) and Strahler (1957)) and drain approximately 1204 and 1109 km^2, respectively. The watersheds of both streams are primarily agricultural and much of their upper reaches has been channelized to facilitate drainage. The streams drain relatively impermeable soils and receive most of their water from surface and shallow subsurface (field tile) runoff. Detailed descriptions of riparian structure and land use, water quality and temperature, and ecosystem metabolism of the Vermilion drainage basin may be found in Wiley et al. (1990).

Fishes were collected for feeding studies from a 2-km reach of the Salt Fork, located 16 km upstream of its confluence with the Middle Fork. The study reach had a drainage area of 995 km^2 and a mean slope of 0.76 $m \cdot km^{-1}$. Microhabitat use data were collected from fishes found throughout the Salt Fork and Middle Fork drainages, but primarily from locations in the lower reaches of each stream. These areas conformed to a typical sequence of shallow riffles, runs, and deep pools (up to 3 m during base flow). Substrates were predominantly coarse gravel, cobble, and boulders in riffles, coarse sand and fine gravel in runs, and silt–sand mixtures in pools.

Methods

Feeding Chronology

Individuals of five fish species, common carp (*Cyprinus carpio*), golden redhorse (*Moxostoma erythrurum*), channel catfish (*Ictalurus punctatus*), smallmouth bass (*Micropterus dolomieu*), and longear sunfish (*Lepomis megalotis*), were collected for feeding studies over 24-h periods on 8–10 May, 23–24 July, and 22–23 October 1984. Fish were sampled over two 12-h periods during May and over a single 24-h period in July and October. Mean water temperature (and range) during each 24-h experiment was 14.0°C (12.1–15.0) in May, 26.0°C (24.5–28.0) in July, and 11.3°C (10.2–12.5) in October.

Fish were collected with a boat-mounted, boom-type electrofisher, powered by either a 230-V 3000-W, three-phase alternating current (AC) generator or a 240-V direct current (DC) power source (60 $pulses \cdot s^{-1}$). Each 24-h experiment consisted of eight 3-h intervals which included a 2-h collection period followed by 1 h of no collecting to assure an adequate time separation between samples. Subsequent collections were made in an undisturbed stream reach upstream of the previously sampled area.

All fish were measured for total length (± 1 mm TL) and weighed (± 1 g), and all species except smallmouth bass were killed and iced. The entire alimentary canal was removed and fixed in a 10% formalin solution and later preserved in 70% ethanol. Stomach contents of smallmouth bass were removed from live fish in the field using Plexiglas tubes (Van Den Avyle and Roussel 1980) and preserved. The fish were then fin-clipped to avoid resampling and released.

Fish numbers and sizes varied among species, experiments, and sampling intervals (Table 1). All fish included in this study were age 1 or older, based on frequency distributions, limited age determination by scale analysis, and size–age relationships found in the literature (Carlander 1969; Pflieger 1975; Carlander 1977; Smith 1979). In the laboratory, preserved contents were removed from the stomachs of channel catfish and longear sunfish and from the foreguts (anterior one third of the alimentary canal) of common carp and golden redhorse. Contents were drained, blotted, and weighed (± 0.1 mg) on a tared analytical balance. A relative content wet weight (RWW) for each fish was calculated as the stomach or foregut content weight divided by the fish body weight and multiplied by 100.

When the RWW for all species and dates was plotted against fish weight, the maximum RWW values at a given size (weight) displayed an inverse relationship with fish weight (Fig. 1a). Individual species plots for common carp, channel catfish, and smallmouth bass also showed a similar inverse relationship between maximum size-specific RWW values and fish weight (e.g. Fig. 1b). No such negative relationship was detected in golden redhorse or longear sunfish data, which may be a function of the more restricted size range of individuals sampled compared with the other taxa examined (Table 1).

To adjust for bias in RWW associated with size of common carp, channel catfish, and smallmouth bass, we regressed the size-specific maximum RWW for each species against the corresponding fish weight using simple linear regression (e.g. Fig. 1b). A RWW adjusted for fish weight (RWW′) was calculated for each individual fish by incorporating the linear model into the equation

$$(1) \quad \mathrm{RWW}' = \mathrm{RWW} \cdot \frac{a + b\,(W_{50})}{a + b\,(W_i)}$$

where a is the Y intercept and b is the slope of the linear regression of fish weight on maximum RWW, W_{50} is the median fish weight for the species, and W_i is the weight of the individual fish. RWW′ was substituted for RWW in all calculations and plots for common carp, channel catfish, and smallmouth bass. This procedure had a similar effect as analogous methods of

TABLE 1. Summary of results from three diel feeding studies of five fish species in 1984 from the Salt Fork of the Vermilion River, Illinois. Data are sample sizes (±SD), total length (TL) (±SD) and weight (±SD), relative content wet weight (RWW) (±SD), percentage of empty stomachs or foreguts, P-value of F-test in one-way ANOVA to test the effect of time on RWW (temporal continuity of feeding), gastric evacuation rate (R), and daily ration (C_{24}) (±95% confidence limits) expressed as RWW. Mean water temperature (and range) during each 24-h experiment was 14.0°C (12.1–15.0) in May, 26.0°C (24.5–28.0) in July, and 11.3°C (10.2–12.5) in October.

Species and month	Total N	Mean interval N	Mean TL (mm)	Mean weight (g)	Mean RWW ($g \cdot 100\ g^{-1}$)	% empty	F-test P	R (h^{-1})	C_{24} (%)
Common carp									
May	43	5 (±4)	464 (±101)	1567 (±999)	0.10 (±0.13)	25.6	0.0774	0.10	0.23 (±0.10)
July	41	5 (±3)	469 (±90)	1337 (±670)	0.05 (±0.10)	43.9	0.0099	0.25	0.45 (±0.25)
October	32	4 (±3)	506 (±109)	1950 (±1161)	0.34 (±0.25)	6.2	0.0059	0.09	0.74 (±0.18)
Combined	116	14 (±6)	478 (±100)	1592 (±971)	0.15 (±0.20)	26.7	0.2118		
Golden redhorse									
May	74	9 (±1)	320 (±43)	367 (±152)	0.10 (±0.08)	13.5	0.0694	0.15	0.38 (±0.06)
July	66	8 (±2)	316 (±48)	314 (±89)	0.10 (±0.10)	33.3	0.0051	0.13	0.31 (±0.07)
October	78	10 (±1)	332 (±35)	391 (±125)	0.25 (±0.15)	5.1	0.0006	0.20	1.22 (±0.14)
Combined	218	27 (±3)	323 (±42)	360 (±129)	0.16 (±0.14)	16.5	0.0313		
Channel catfish									
May	32	4 (±3)	359 (±81)	460 (±315)	0.34 (±0.47)	18.8	0.0209	0.27	2.53 (±1.31)
July	40	5 (±4)	329 (±66)	325 (±207)	1.04 (±1.47)	17.5	0.2045	0.29	7.73 (±2.70)
October	22	3 (±1)	329 (±93)	351 (±248)	0.39 (±0.32)	9.1	0.9468	0.13	1.23 (±0.58)
Combined	94	12 (±6)	339 (±78)	377 (±262)	0.65 (±1.06)	16.0	0.0095		
Smallmouth bass									
May	10	1 (±1)	236 (±42)	181 (±102)	0.62 (±0.72)	0	0.6206	0.32	5.70 (±4.56)
July	22	3 (±1)	257 (±91)	266 (±246)	0.82 (±1.09)	0	0.3548	0.32	6.05 (±2.56)
October	44	6 (±3)	220 (±62)	171 (±208)	0.63 (±1.00)	20.5	0.9125	0.20	3.17 (±1.74)
Combined	76	10 (±3)	232 (±71)	199 (±211)	0.68 (±0.99)	11.8	0.8020		
Longear sunfish									
May	68	8 (±2)	128 (±18)	53 (±23)	0.72 (±0.98)	8.8	0.8551	0.23	3.81 (±1.34)
July	65	8 (±3)	130 (±20)	54 (±22)	0.66 (±0.97)	13.8	0.1372	0.18	2.93 (±1.14)
October	35	4 (±3)	126 (±18)	50 (±31)	0.49 (±0.77)	31.4	0.7546	0.22	2.00 (±1.02)
Combined	168	21 (±3)	128 (±19)	53 (±24)	0.65 (±0.94)	15.5	0.9366		

adjustment for size proposed by other investigators (Knight and Margraf 1982; Herbold 1986). Differences between RWW and RWW′ in our study, however, were minimal due to the relatively restricted size ranges of fish (e.g. Fig. 1b and 1c).

Mean daily rations (C_{24}) were calculated for each species and date using the method of Elliot and Persson (1978):

$$(2) \quad C_{24} = \sum_{i=1}^{m} \frac{(S_{(i+1)} - S_i e^{-RT})\, RT}{1 - e^{-RT}}$$

where S_i and $S_{(i+1)}$ are the mean RWW of a fish group at the time of successive sampling intervals i and $i+1$, respectively, R is the gastric evacuation rate for the species on that date, T is the time interval between successive samples (T = 3 h), and m is the number of sampling intervals in the 24-h experiment (m = 8).

R was estimated as the slope of the relationship between digestion rate (r) and mean RWW (S_i) of a fish group (Boisclair and Leggett 1985). Because digestion rate is a positive linear

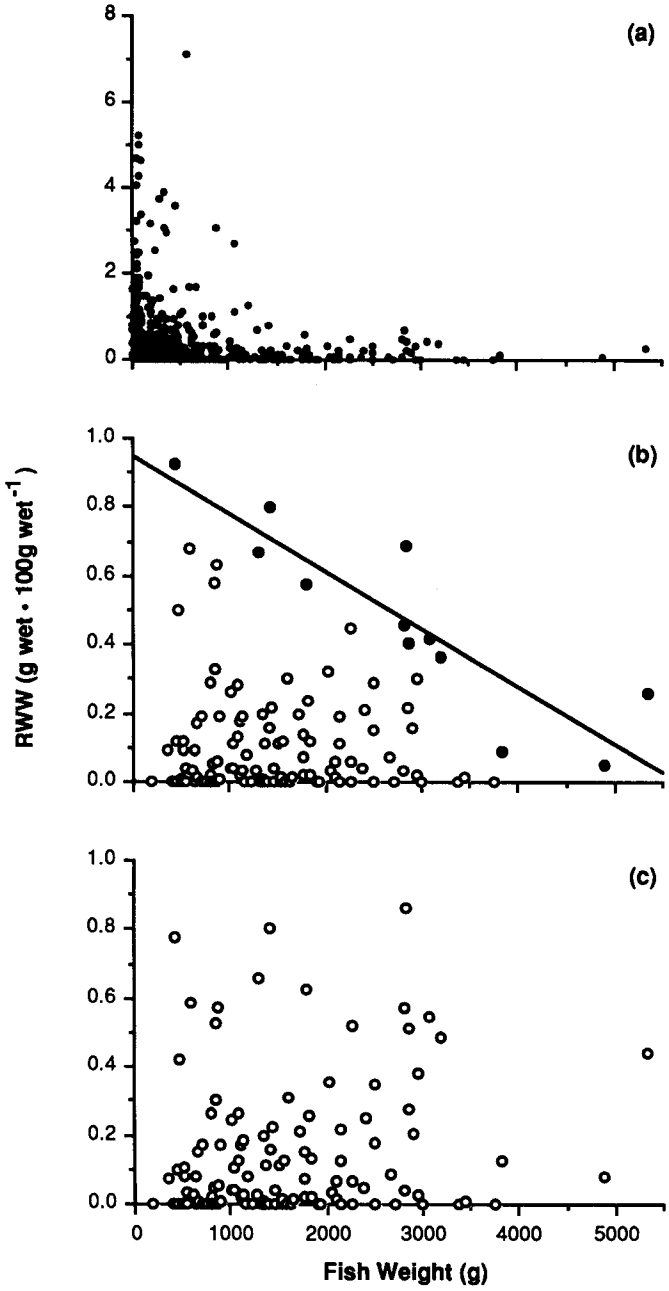

FIG. 1. Plots of relative content wet weight (RWW) versus fish body weight for fishes collected in the Salt Fork of the Vermilion River, Illinois, during three 24-h experiments in 1984. (a) All species plot showing inverse relationship of maximum RWW and fish weight; (b) common carp unadjusted for size showing similar trend; RWW maxima used to derive linear model for adjustment procedure are represented by solid circles; (c) common carp with RWW adjusted for size.

function of fullness that passes through the origin (Elliot 1972), a single observation of that relationship allows the calculation of R. To estimate digestion rate from the decline in stomach or foregut contents, a time of day must be selected during which fish are assumed not to feed. This assumption is best approximated during an interval immediately following a peak in RWW. Thus, species-specific digestion rate r was estimated for each 24-h experiment as

$$(3) \quad r = \frac{S_{(i+1)} - S_{imax}}{T}$$

where S_{imax} is the mean RWW in the interval i of peak mean RWW over the diel period, $S_{(i+1)}$ is the mean RWW from the subsequent sampling interval, and T is the time interval between successive samples (T = 3 h). R was then estimated as digestion rate (r) as a proportion of the peak mean RWW (S_{imax}):

$$(4) \quad R = \frac{r}{S_{imax}}.$$

The reliability of this method to estimate R was verified by Boisclair and Leggett (1985) for yellow perch (*Perca flavescens*); they found no significant differences between results of this method and field-derived estimates of R by sequentially sacrificing fish..

Confidence limits were calculated for daily ration estimates using a proportional error estimate in a fashion similar to Post (1990). A mean time-weighted RWW was calculated for each diel experiment and species, and an estimate of its standard error (s) was calculated as

$$(5) \quad s = \left[\frac{1}{m^2}\left(\sum_{i=1}^{m} \frac{s_i^2}{n_i}\right)\right]^{0.5}$$

where s_i^2 is the variance of the RWW of fish in interval i, n_i is the number of fish sampled in that interval, and m is the number of intervals (m = 8). A proportional error was then calculated by dividing s by the mean time-weighted RWW. The 95% confidence limits are the daily ration estimate ± the product of the daily ration, the proportional error, and the t-score (α = 0.05).

To describe a general feeding chronology for each species, a plot of RWW over time was constructed which incorporated combined data from the three 24-h experiments (Fig. 2). One-way analysis of variance (ANOVA) was used to test temporal feeding continuity as determined by changes in RWW of stomachs or foregut contents over time. Differences among sampling interval means were determined using the Tukey (HSD) multiple comparison test (Zar 1984).

Microhabitat Use

Microhabitats used by stream fishes were identified throughout the diel period and periodically throughout all seasons during 1984–85. Approximately one half of the microhabitat data for channel catfish and smallmouth bass (50 and 55%, respectively) were collected during 1980–81. One-way ANOVA revealed no significant differences ($P > 0.05$) between microhabitat use during 1980–81 and 1984–85 for any habitat variable for these species, which justified including the data from earlier years. Fish were located using a combination of three techniques: direct observation, prepositioned electrofishing, and radiotelemetry (Table 2). These techniques were employed because they locate an undisturbed fish during all hours of the day and in a variety of water conditions. Detailed descriptions and evaluations of these techniques can be found in Larimore and Garrels (1985).

Visual observation of fish from the stream bank was enhanced using polarized glasses or binoculars in daylight and a portable light source (Coleman model 220 lantern with reflector) at night. Observations were usually followed by capturing the fish using a Smith–Root type VII DC backpack electrofisher to confirm species identification and to measure the fish.

Electrodes, constructed of two 3-m strands of 12-gauge, solid-core copper wire, were wired to a two-conductor electrical cable and prepositioned in discrete uniform habitats at least 24 h before sampling. The electrodes were positioned nearly

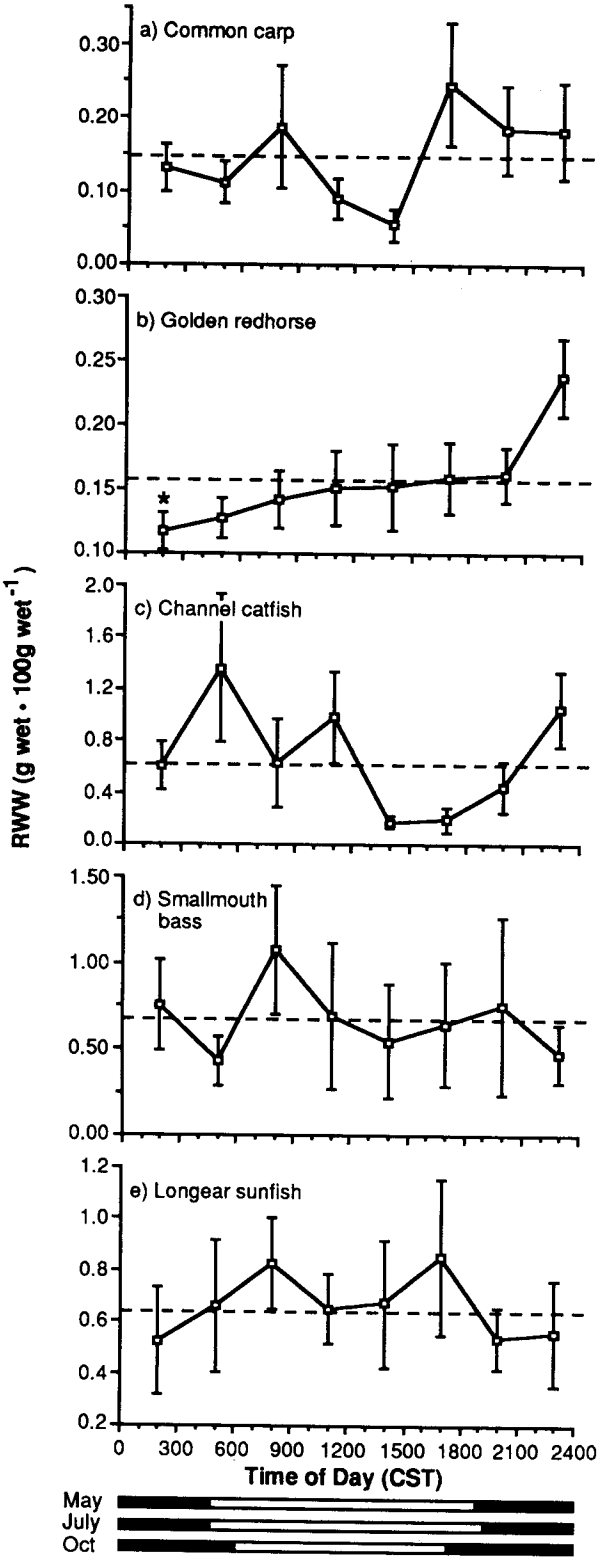

FIG. 2. Diel feeding chronologies of five fishes of the Salt Fork of the Vermilion River, Illinois, as determined from changes in relative content wet weight (mean RWW ± 1 SE) over time. Plots include the combined results from three 24-h experiments conducted in May, July, and October 1984. Asterisk denotes significantly different mean (Tukey HSD, $P < 0.01$) from that of the previous sampling interval. Horizontal broken lines indicate the unweighted (by interval or month) mean RWW for each species. Open and solid portions of bars represent light and dark hours, respectively, during each 24-h experiment. Sample sizes for each experiment are given in Table 1.

parallel to the direction of flow approximately 0.5 m apart, suspended by wooden stakes, and connected by an extension cord to an AC generator (115-V, 1500-W) located at least 20 m from the stream. In sampling, electrodes were activated, stunned fish collected, and physical habitat characteristics within the electric field were quantified (see below). A 24-h recolonization period was allowed before the electrodes were reactivated.

Radiotelemetry involved the use of internal and external radio transmitters. Small, 50-MHz radio transmitters were attached to fish anesthetized with tricaine (MS-222). Transmitters displaced a volume of 10–12 cm^3. Most transmitters were surgically implanted into the body cavities of fish, although some externally attached transmitters were also used. The external transmitter was fixed to a hard plastic saddle roughly molded to fit over the dorsum of a fish. The saddle was adjusted in the field to the individual size and form of a fish. The saddle-mounted transmitter was attached with surgical thread through the dorsum, posterior to the dorsal fin or in a space at the interface of the spinous and soft dorsal fins, where a small portion of fin was clipped. Styrofoam shavings were affixed to approximately adjust the external transmitters to neutral buoyancy. To minimize disorientation and stress, marked fish (numbered Floy anchor tag) were held only until they had recovered from the anesthetic, then released, and subsequently located over a period of several months.

Depth, velocity, substrate, and associated cover were measured after the exact location of a fish was determined by one of the above techniques. Mean column water velocity (0.4 × total depth for depths ≤0.76 m; 0.2 and 0.8 × total depth for depths >0.76 m) and velocity at the stream bottom were determined using a Marsh–McBirney model 201 digital flowmeter. Night collections and turbid conditions precluded the measurement of nose depth or nose velocity (Bovee 1986). Substrate composition was classified by size and texture according to a modified Wentworth particle-size scale (Bovee and Milhous 1978).

Suitability Curves

The diel cycle for each species was partitioned into high-feeding and low-feeding periods whenever RWW fell above or below the unweighted (by interval or month) mean RWW (Table 1) in the combined feeding chronology plots (Fig. 2). Separate suitability curves were constructed from physical measurements associated with sites where fish were located during high- and low-feeding periods. Unweighted measurements of depth and velocity were tabulated and grouped into increments of 0.1 m and 0.1 $m \cdot s^{-1}$, respectively. Substrates were classified into 10 groups ranging in particle size from bedrock to boulder. In observations of mixed substrate, the prevalent class was used. Frequencies of measurements for each variable were normalized to unity, i.e. the modal range of each habitat parameter was assigned a value of 1.0, and frequencies of other intervals were expressed as a proportion of the mode. Utilization, i.e. the relative frequency of observations for each microhabitat variable (Bovee 1986), was plotted for each variable, and a curve was fitted to the data by interpolation. To facilitate a smooth curve, a range of no use between two ranges of a habitat variable used by a species was not incorporated into the curve. Unweighted frequency distributions of microhabitat use for each species during high-feeding and low-feeding periods were compared using the Kolmogorov–Smirnov two-sample test (Sokal and Rohlf 1981) using the same class sizes for habitat variables specified above. Suitability curves and

TABLE 2. Summary of microhabitat use during high-feeding and low-feeding periods by fishes of the Salt Fork and Middle Fork of the Vermilion River, Illinois. Data are total length (TL) (±SD), techniques used to locate fish (DO = direct observation, PE = prepositioned electrofishing, RT = radiotelemetry), sample size (number of locations), mean values (and range) of depth and mean and bottom velocity, substrate particle size range, and D statistic of Kolmogorov–Smirnov two-sample test comparing microhabitat frequency distributions for each habitat variable during high-feeding and low-feeding periods. Results for common carp are not presented according to feeding regime due to low sample size. Significant D values: $^{*}P \leq 0.10$; $^{**}P \leq 0.05$; $^{***}P \leq 0.01$.

Species and feeding intensity	Mean TL (mm)	Techniques	N	Habitat variable: Depth (m)	Mean velocity ($m \cdot s^{-1}$)	Bottom velocity ($m \cdot s^{-1}$)	Substrate
Common carp	418 ± 34	DO	13	0.33 (0.15–0.88)	0.14 (0–0.27)	0.07 (0–0.18)	Silt – fine gravel
Golden redhorse	249 ± 104	DO, PE, RT					
High feeding			9	0.38 (0.18–0.58)	0.18 (0–0.37)	0.04 (0–0.12)	Bedrock – fine gravel
Low feeding			21	0.48 (0.15–1.25)	0.14 (0–0.58)	0.06 (0–0.30)	Bedrock – coarse gravel
D				0.38	0.24	0.10	0.48*
Channel catfish	415 ± 42	RT					
High feeding			74	0.79 (0.15–1.71)	0.08 (0–0.55)	0.01 (0–0.09)	Bedrock – small cobble
Low feeding			43	0.80 (0.46–1.28)	0.07 (0–0.24)	0.01 (0–0.09)	Bedrock – coarse gravel
D				0.26*	0.06	0	0.06
Smallmouth bass	275 ± 53	DO, PE, RT					
High feeding			81	0.57 (0.18–1.25)	0.04 (0–0.58)	0.02 (0–0.12)	Bedrock – small cobble
Low feeding			43	0.54 (0.18–1.25)	0.13 (0–0.70)	0.04 (0–0.43)	Bedrock – boulder
D				0.19	0.32**	0.06	0.22
Longear sunfish	88 ± 17	DO, PE					
High feeding			82	0.40 (0.12–0.85)	0.05 (0–0.40)	0.02 (0–0.24)	Silt – large cobble
Low feeding			18	0.31 (0.21–0.46)	0.04 (0–0.12)	0.01 (0–0.03)	Bedrock – large cobble
D				0.32*	0.10	0.11	0.38**

comparisons of frequency distributions are not presented for common carp due to limited sample sizes (13 locations total).

Results

Feeding Chronology and Daily Ration

Relative stomach or foregut content wet weights (RWW) varied widely among individuals both within and between sampling intervals for each species, and standard deviations were often greater than mean values (Table 1). Mean daily RWW varied among months and species, ranging from 0.05% for common carp in July to 1.04% for channel catfish in the same month. The stomachless species, common carp and golden redhorse, had low combined mean RWW values of 0.15 and 0.16%, respectively, while higher combined means ranging from 0.65 to 0.68% were found in the fishes with stomachs: channel catfish, smallmouth bass, and longear sunfish.

Significant differences in RWW between sampling intervals for a diel experiment ($P < 0.05$) were detected in common carp, golden redhorse, and channel catfish, indicating discontinuous feeding (Table 1). Common carp and golden redhorse both fed discontinuously in the July and October experiments, and channel catfish did so in May. Variation in RWW over time appeared high in general diel plots (data for three diel series combined) for all species (Fig. 2), but feeding was discontinuous ($P < 0.05$) only in golden redhorse and channel catfish when combined data were tested, and golden redhorse feeding (as inferred from RWW) declined signficantly ($P < 0.01$) from 2300 to 0200 Central Standard Time (CST).

Diel feeding chronologies for common carp and the centrarchid species were similar, suggesting peaks in feeding intensity associated with sunrise and sunset (Fig. 2). Feeding was higher during dark hours for common carp compared with daylight hours and was lower at night for longear sunfish. Golden redhorse feeding decreased sharply after a peak at 2300 CST and then progressively increased through the remainder of the diel series. Channel catfish feeding peaked near sunrise (0500 CST) and was generally high during dark and morning hours and was low during the afternoon and near sunset.

The percentage of empty stomachs in each experiment ranged from 0 for smallmouth bass in May and July to 43.9 for common carp in July and showed a general inverse relationship with mean RWW (Table 1). Percentage of empty stomachs was lowest in October for common carp, golden redhorse, and

channel catfish, but was conversely the highest in that month for the two centrarchid species.

Gastric evacuation rates (R) ranged from $0.09 \cdot h^{-1}$ for common carp in October to $0.32 \cdot h^{-1}$ for smallmouth bass in May and July (Table 1). Estimates of R correlated positively with mean water temperature during an experiment for all species except golden redhorse, where the correlation was negative. Daily ration (C_{24}) estimates were higher in species with stomachs compared with those of species without stomachs and ranged from 0.23% for common carp in May to 7.73% for channel catfish in July. Confidence limits for C_{24} were generally near or below $\pm 50\%$ of the estimate for all species except smallmouth bass, where confidence limits were higher, primarily due to low sample sizes.

Microhabitat Use Associated with Feeding

Fish examined occurred in a diversity of habitats as reflected by the variation in quantitative microhabitat measurements for each species (Table 2; Fig. 3 and 4). Common carp and golden redhorse were found in similar shallow habitats with moderate velocities and a restricted range of fine substrates. Channel catfish occurred in a wide range of habitats deeper than those for other species with low velocities over a wide range of bottom materials, but most frequently over silt–clay. Smallmouth bass and longear sunfish habitats were similar areas of shallow to moderate depth, low velocity, and a wide range of substrate sizes. However, ranges of all habitat variables were wider for smallmouth bass than those for longear sunfish.

Microhabitat use frequency distributions during high-feeding and low-feeding periods were significantly different ($P \leq 0.10$) for at least one habitat variable for each species examined (Table 2), indicating differential habitat use during these periods. Differences were detected in substrate for golden redhorse, depth for a channel catfish, mean velocity for smallmouth bass, and depth and substrate for longear sunfish.

Habitat suitability curves provide a descriptive tool to characterize these differences in habitat use associated with feeding (Fig. 3 and 4). Golden redhorse habitat during high-feeding periods was shallower, lower in velocity, and had finer substrates than during low-feeding periods, and ranges used most fequently (modes) associated with each feeding regime were different for depth and substrate (Fig. 3a). Modal use during high-feeding and low-feeding periods was equivalent for all habitat variables for channel catfish, but ranges of depth, mean velocity, and substrate particle size extended higher during high-feeding hours (Fig. 3b). Smallmouth bass used a similar range of depths in each feeding regime, but the modal range during high-feeding hours was 0.2 m deeper than that during low feeding (Fig. 4a). High-feeding habitat for that species was lower in velocity and had a coarser substrate mode than low-feeding habitat, yet areas over boulders were used only during low-feeding hours. Longear sunfish high-feeding habitat was deeper and swifter than that of low-feeding periods, but the modes during the two regimes were identical (Fig. 4b). Modes of substrate use for the two periods were the same, but longear sunfish were found more frequently over gravel substrates during high-feeding times and used areas with bedrock only during low feeding.

Although statistical comparison is not possible for the data on cover associated with habitat used during low-feeding and high-feeding hours, notable differences were found in the proportions of locations with cover between feeding regimes for all species examined (Table 3). Common carp were associated with branch piles or plants at 69% of locations. Golden redhorse used woody structure, large rocks, and root wads in equal proportions, but were associated with cover over twice as often during high-feeding periods. The same three cover types were used by channel catfish, but this species was found using tree roots more frequently than other types of cover. Channel catfish used cover more frequently during low-feeding hours. Smallmouth bass were associated with woody structure, large rocks, and roots in equivalently low proportions during high feeding. The species was found using the same cover during low feeding but much more frequently used large rocks and roots. Longear sunfish and common carp were the only species studied that used live vegetation for cover. Cover in the form of woody structure, rocks, plants, and roots was associated with equivalent proportions of longear sunfish habitat during high-feeding hours. This species was found using cover in 100% of locations during low-feeding hours (nearly twice as often as in high-feeding periods) with woody structure used most frequently. Of the vegetation used as cover, aquatic plants were favored by this fish during low-feeding hours and terrestrial plants during high feeding.

Discussion

Comparison of our feeding results with those of other investigators is limited by differences in methodology and units used to express results. Principal differences in methods to determine feeding patterns include variation in the proportion of the alimentary canal sampled (e.g. stomach or foregut versus entire canal), the method of measuring content weight and fish body weight (wet or dry) and the coincidental expression of those weights as a proportion, and the many variations employed to calculate estimates of gastric evacuation rate (R) and daily ration (C_{24}) (Elliot and Persson 1978; Adams and Breck 1990, and papers cited therein).

Furthermore, interpretation of our results is complicated by variable, unequal, and often relatively low sample sizes. We acknowledge these shortcomings and advise caution in interpretation. Thus, the failure to detect statistically significant trends in data may not lead to a definitive conclusion. For example, significant differences among sampling intervals over the diel period indicate that feeding is discontinuous; however, the absence of significance does not necessarily imply continuous feeding unless sample sizes and variability are sufficient to achieve reasonable test power. Another finding where sample size may influence interpretation is the comparison of habitat descriptions stratified by feeding regime. Channel catfish high-feeding habitat was more diverse (wider ranges in variables) than that during low-feeding hours, but this result is confounded with variation in sample size (Table 2; Fig. 3b). However, the demonstration of the reverse trend (wider variation with lower number of samples) in smallmouth bass (Table 2; Fig. 4a) supports the validity of these results as indicating biological differences in habitat use. Such considerations also led us to consider $P \leq 0.10$ statistically significant for the relatively low sample sizes of frequency distributions compared by the Kolmogorov–Smirnov two-sample test (Table 2). Our utilization curves (Fig. 3 and 4) would probably be smoothed further before using them in an instream flow assessment, but we have minimized smoothing to preserve detail in comparisons.

Measurements of microhabitat use of all species we examined (Table 2) conform well to qualitative habitat descriptions found elsewhere (Scott and Crossman 1973; Pflieger 1975; Smith 1979; Becker 1983), and further discussion is presented according to species.

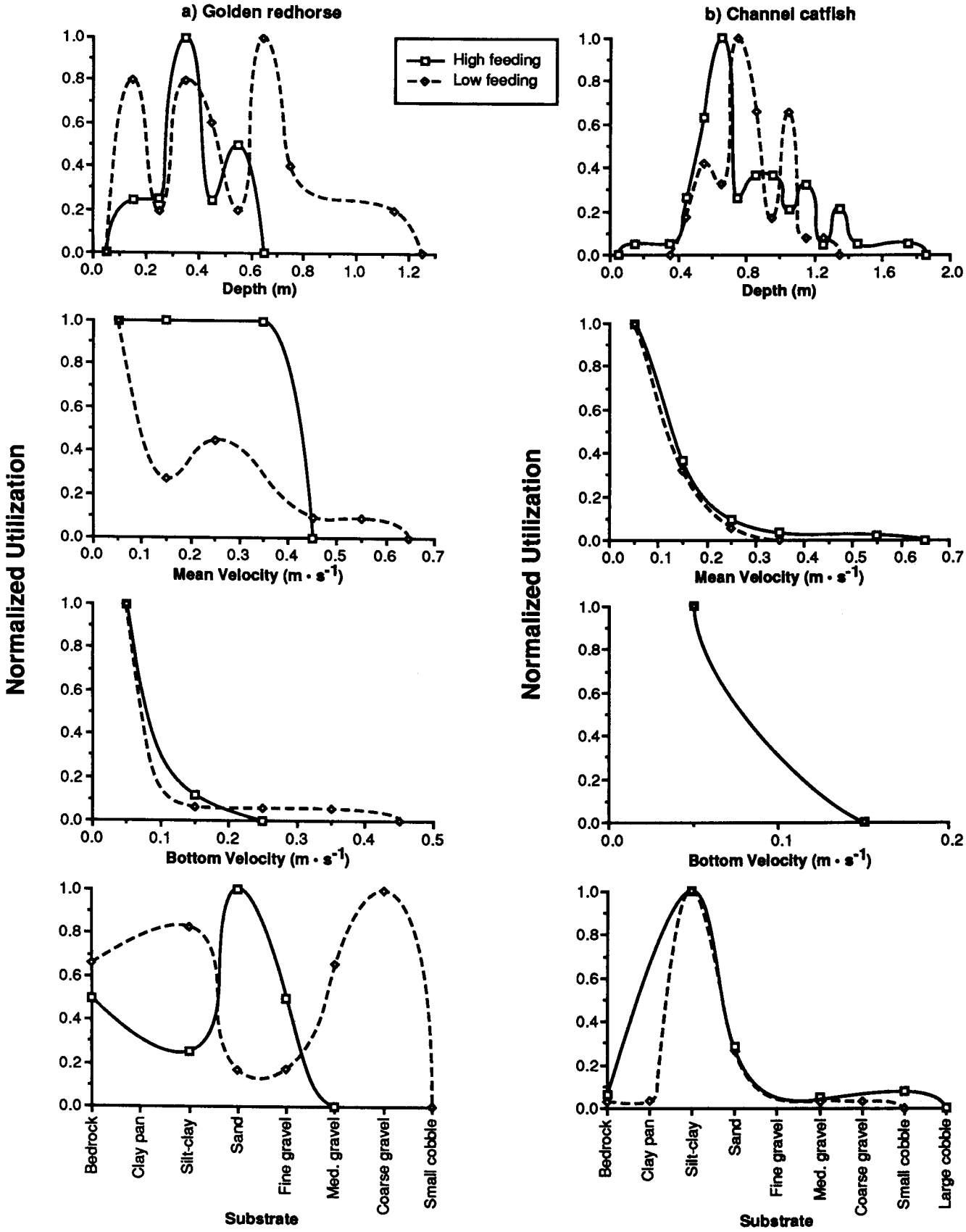

FIG. 3. Microhabitat utilization (frequency of use) curves stratified by feeding regime (high or low) for golden redhorse (left column) and channel catfish (right column) in the Salt Fork and Middle Fork of the Vermilion River, Illinois. Sample sizes (number of locations) are given in Table 3.

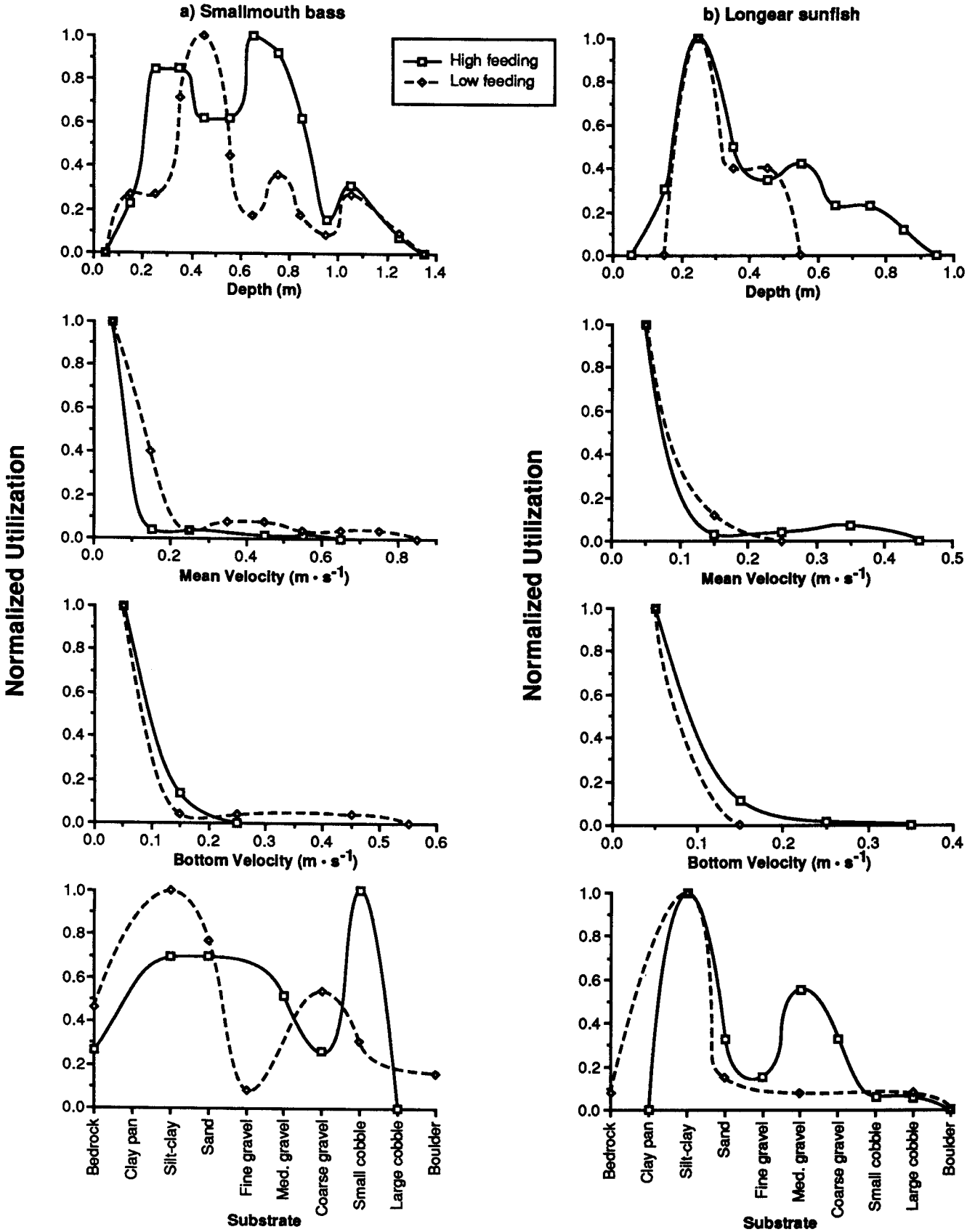

FIG. 4. Microhabitat utilization (frequency of use) curves stratified by feeding regime (high or low) for smallmouth bass (left column) and longear sunfish (right column) in the Salt Fork and Middle Fork of the Vermilion River, Illinois. Sample sizes (number of locations) are given in Table 3.

TABLE 3. Percent by number of microhabitat locations where fishes were associated with cover during high-feeding and low-feeding periods in the Salt Fork and Middle Fork of the Vermilion River, Illinois. Sample sizes are listed in Table 2.

Species and feeding intensity	Cover type					Total
	Woody structure	Large cobble and boulders	Terrestrial plants	Aquatic plants	Root wads	
Golden redhorse						
High feeding	11.1	11.1	0	0	11.1	33.3
Low feeding	4.8	4.8	0	0	4.8	14.3
Channel catfish						
High feeding	8.1	4.1	0	0	28.4	40.5
Low feeding	9.3	4.6	0	0	37.2	51.2
Smallmouth bass						
High feeding	2.5	4.9	0	0	3.7	11.1
Low feeding	4.7	23.3	0	0	18.6	46.5
Longear sunfish						
High feeding	13.4	11.0	13.4	1.2	18.3	57.3
Low feeding	61.1	11.1	0	16.7	11.1	100.0

Common Carp

Statistical analyses of entire gut contents of Mississippi River common carp indicated a uniform pattern of feeding throughout the diel cycle (Garcia and Adelman 1985), in contrast with the discontinuous feeding patterns that we detected in July and October (Table 1). The estimates of R obtained for common carp by Garcia and Adelman (1985) of $0.23–0.27 \cdot h^{-1}$ at 21.5–26.5°C and those found in field studies by other stomachless cyprinid fishes (*Pachychilon pictum, Leuciscus cephalus, Rutilus rubilio*) of $0.22–0.24 \cdot h^{-1}$ at 25°C (Kitchell et al. 1978) are similar to that found in our July experiment for common carp of $0.25 \cdot h^{-1}$ at a mean temperature of 26.0°C. Lower R values similar to those we calculated for the May and October experiments were reported by Garcia and Adelman (1985) at corresponding temperatures. Methodological differences precluded comparison of C_{24} estimates.

In streams, common carp are usually found in deep pools (Pflieger 1975; Becker 1983); however, all but one microhabitat location for common carp in our study were from the channelized agricultural upstream area of the Salt Fork. These occurrences suggest that this highly adaptable species was exploiting this enriched but severe environment of dramatic fluctuations in temperature and oxygen (Wiley et al. 1990) that less tolerant species could not.

Golden Redhorse

We found no other analogous feeding studies of golden redhorse or other members of *Moxostoma* in the literature. Daily food consumption by young white suckers (*Catostomus commersoni*) calculated by Dobie (1972) (8.5–19.0%) was much greater than that of golden redhorse in our study (0.31–1.22). The negative relationship between fish size and C_{24} found by Dobie (1972), however, suggests that the disparate findings between studies are due to size effects.

In accord with the positive relationship found between R and water temperature in four of the five species we studied (Table 1), gastric evacuation rate of many other species has shown a positive exponential relationship to temperature (Elliot and Persson 1978; Adams and Breck 1990, and papers cited therein). The inverse relationship between R of golden redhorse and mean water temperature during each 24-h experiment may indicate a systematic error in methods or could be the result of interseasonal variation in food habits. Golden redhorse R was calculated from intervals during dark hours following a peak in RWW, when no feeding was assumed. We are unable to determine if this assumption was met during the intervals selected, and its violation may account for the unexpected results. Furthermore, behavioral and physiological factors may also have influenced these results, as variation in the size and composition of food items or meal size and frequency can alter digestion rates (Windell 1978; Flowerdew and Grove 1979; Persson 1981; Mills et al. 1984). Ahlgren (1990) found that diet composition of juvenile white suckers in ponds varied significantly with season and with relative availability of food items. The proportion of detritus in white sucker foreguts in that study varied seasonally from 5% in July to 97% in January and February. The food habits of golden redhorse are likely to be equally variable in its dynamic lotic surroundings and could account for the observed variation in digestion from the accepted trend. Considering the equivalent sizes of golden redhorse among experiments (Table 1), size effects probably did not influence estimated R values.

Channel Catfish

In support of the perception of most anglers and the general contention of Pflieger (1975) that channel catfish are inactive during the day and feed at night, Bailey and Harrison (1945) found feeding most active from sunset to midnight, and Davis (1959) also noted nocturnal feeding. Contrary to these conclusions, Mathur (1970) reported feeding greatest during daylight hours, based on mean weights of stomach contents (not expressed as a proportion of fish weight). We also found channel catfish feeding during the day with peaks in feeding near sunrise (0500 CST), midday (1100 CST), and at night (2300 CST), but little feeding occurred through the afternoon (Fig. 2). Channel catfish are omnivorous and opportunistic in their food habits, showing wide variation in diet through the diel period and among seasons (Bailey and Harrison 1945; Mathur 1970).

Our results in comparison with those of these other investigators suggest that the diel feeding chronology of this species is variable as well.

The slightly deeper mode (Fig. 3b) and greater use of cover (Table 3) by channel catfish during low-feeding hours support the habitat aspect of Davis' (1959) findings that adults spend the day in deep holes, under logs or other shelter, and feed in shallow water at night. The wider range of depth and substrate size that we found during high-feeding periods may indicate movement between habitats during these hours. Confirming the finding that channel catfish seldom occur in dense aquatic vegetation (Trautman 1981), woody structure, rocks, and roots were the only forms of cover used by this species in our study.

Smallmouth Bass

Smallmouth bass RWW variation was wide among individuals within a sampling interval; nonetheless, peaks near sunrise and sunset were evident in the feeding chronology (Fig. 2). A similar diel feeding pattern was described by Hubbs and Bailey (1938) and was demonstrated for young smallmouth bass collected in August by Stewart (1978). Laboratory studies also confirmed diurnal feeding (Munther 1970). The daily ration estimate of 4.2%, calculated for young smallmouth (Stewart 1978) using the method of Keast and Welsh (1968), which is considered a minimal estimate, fell within the seasonal range of 3.17–6.05% for juvenile and adult smallmouth bass in our study (Table 1). The ranges of mean RWW of stomach contents (0.36–1.14%) and percent empty stomachs (0–38%) determined in seasonal feeding studies of juvenile and adult largemouth bass (*Micropterus salmoides*) by Cohcran and Adelman (1982) contain the corresponding ranges that we determined for smallmouth bass (0.62–0.82% mean RWW and 0–20.5% empty). However, daily rations that we calculated for smallmouth bass (3.17–6.05%) are slightly higher than those of largemouth bass (1.19–5.58%), due in part to relatively higher R values that we estimated for smallmouth bass. R estimates calculated from mean temperatures during each of our diel experiments using an exponential function derived by Cochran and Adelman (1982) for largemouth bass were 0.07, 0.21, and $0.05 \cdot h^{-1}$ for May, July, and October, respectively, as compared with 0.32, 0.32, and $0.20 \cdot h^{-1}$ calculated in our study. The reasons for the interspecific differences in R may be methodological, behavioral, or physiological as discussed above for golden redhorse.

The habitat use that we determined for smallmouth bass (Fig. 4a) corresponds well with other relationships developed from field observations (Orth et al. 1982; Rankin 1986) and laboratory simulation (Sechnick et al. 1986). Although this species is typically associated with coarse rocky substrates (Reynolds 1965; Munther 1970; Orth et al. 1982; Paragamian 1981; Rankin 1986), Vermilion River smallmouth bass frequently occurred over fine substrates (Fig. 4a). In contrast with laboratory experiments (without prey present) where smallmouth bass showed no substrate preference, habitat choice of stream-dwelling fish was influenced by depth, velocity, and strongly by substrate (Sechnick et al. 1986; Rankin 1986). These disparate findings between laboratory and natural environments suggest that selection for large-diameter substrates by smallmouth bass in a natural stream may be a response to variability in velocity caused by irregular substrates (Hynes 1970; Rankin 1986) or to cover (Rankin 1986; Sechnick et al. 1986), but are most likely due to differences in prey densities (deMarch 1976; Stein 1977; Minshall 1984; Rankin 1986).

High-feeding habitat of smallmouth bass had significantly lower velocities than those found during low feeding (Table 2), a result that supports the characterization of this species feeding in quiet areas along the shoreline (Pflieger 1975). During low-feeding hours, fish occurred in higher velocities, but more frequently used cover, presumably as a shelter from flow (Table 3; Fig. 4a). Other studies also demonstrated the importance of cover as a habitat determinant for smallmouth bass (Munther 1970; Probst et al. 1984; McClendon and Rabeni 1987). While we did not detect a significant difference in substrate selection between feeding regimes of smallmouth bass, the modal substrate classes are distinct (Table 2; Fig. 4a). We found smallmouth bass most frequently over coarse substrates (small cobble) during high-feeding periods, similar to observations by Rankin (1986) of foraging occurring primarily over boulder, rubble, and cobble substrates. Moreover, smallmouth bass habitat use during feeding may be influenced by associations with other species such as suckers (Catostomidae) or turtles (Pflieger 1975; Rankin 1986); however, we are unable to address this relationship.

Longear Sunfish

Feeding studies of longear sunfish are rare, but many have been conducted on other centrarchid species, with studies of bluegill (*Lepomis macrochirus*) being most numerous. Similar to our findings for longear sunfish (Fig. 2), bluegill feeding is primarily diurnal with an occasional nocturnal component (Keast and Welsh 1968; Baumann and Kitchell 1974; Sarker 1977). Studies of other sunfishes including pumpkinseed (*L. gibbosus*) (Keast and Welsh 1968), white crappie (*Pomoxis annularis*) (Childers and Shoemaker 1953; Mathur and Robbins 1971), and black crappie (*P. nigromaculatus*) (Childers and Shoemaker 1953; Keast 1968) found a similar pattern of diurnal feeding, often with peaks near sunrise or sunset. Becker (1983) noted that longear sunfish become inactive at night, but feeding may occur under bright moonlight.

Despite a negative correlation of longear sunfish density in lakes with percent cover, Laughlin and Werner (1980) found highest densities in areas of moderate cover. Longear sunfish in the Vermilion River were strongly associated with cover, particularly during low-feeding periods (Table 3), but utilized the open, deeper, and swifter waters over coarse substrates of the stream channel during feeding. Studies of bluegill suggest that such a pattern of habitat use is a response to the presence of predators and that sunfish sacrifice energy gain for safety (Mittelbach 1986, and papers cited therein).

Longear sunfish in our study showed a decline in mean RWW and daily ration and an increase in the percentage of empty stomachs from May to October (Table 1). The same general decreasing seasonal trend has been observed for longear sunfish (Laughlin and Werner 1980; Angermeier 1985), other sunfishes (Seaburg and Moyle 1964; Kitchell 1970; Angermeier 1985), and six other stream fishes (Angermeier 1985). A marked decline in the abundance of invertebrates through the summer in a small stream within the Vermilion watershed was documented by Angermeier and Carlson (1985). The daily ration estimates of Seaburg and Moyle (1964) for three sunfish species (0.58–2.20%), minimum estimates for bluegill (2.5%) and pumpkinseed (2.6%) of Keast and Welsh (1968), and monthly means for bluegill (0.36–2.31%) of Kitchell (1970) were all generally lower than our estimates for longear sunfish (2.00–3.81%). Our daily ration estimates for longear sunfish are all below maximum daily ration estimates for bluegill at equivalent temperatures (Kitchell 1970), but the daily ration for longear

sunfish in May (3.81%) was equivalent to the maximum for bluegill at 15°C (3.86%). These findings indicate that longear sunfish feed near maximum intensity in May, and similar seasonal feeding trends observed for longer sunfish and other species support the hypothesis that invertebrate availability is near maximum for many fish during spring and early summer and decreases through autumn. Alternate feeding strategies by other species that we studied may account for the absence of a similar trend in those fishes.

Recommendations

The findings of this study demonstrate differences in microhabitat use associated with feeding activity for each species examined. By directly observing brown trout (*Salmo trutta*) occurrence during four different activities (including feeding and resting) during daylight hours, Gosse and Helm (1982) also demonstrated significant differences in microhabitat use among activities for all life stages. Distinct and in some cases significantly different habitat use in certain habitat variables may indicate those proximate environmental cues that fish use to distinguish feeding and resting sites. However, the primary stimulus of microhabitat selection in feeding may not be determined from field data because current velocity and substrate are confounded variables in a natural system (higher velocities are associated with coarser substrates). Furthermore, other studies have demonstrated that fish respond to a composite of habitat conditions rather than to a single habitat variable independently (Bain et al. 1988; Orth and Maughan 1982; Moyle and Baltz 1985), and a recent focus on the complexities of hydraulic stream ecology (Statzner et al. 1988; Heede and Rinne 1990) will likely lead to a more realistic multivariate approach to describing habitat use, availability, and quality.

Our results imply that realism could be improved in instream flow assessments if habitat suitability criteria were stratified by feeding regime; however, difficulties involved in such disaggregations should not be overlooked. Diel feeding chronologies are highly variable, reflecting innate behavioral adaptations, flexible behavioral responses to energetic parameters, and responses to competitors and predators. For example, it is well known that many riverine fishes may move between a foraging site and a nearby cover-associated resting site repeatedly while feeding. This type of habitat use within a feeding interval would not be adequately represented in the type of analysis we have employed here. Even with such difficulties, we found clear distinctions in habitat use associated with feeding, and these differences may appear more extreme if habitat availability were considered. Unlike the Vermilion River drainage, many lowland rivers have well-developed fringing floodplains which greatly increase habitat diversity, and the distinction between feeding and resting habitat may also be more evident in such environments. Although admittedly less precise than directly observing fish behavior, the approach that we have adopted here (temporal stratification) allows the distinction of activity in turbid waters and at night when observations are impossible.

An alternative approach to identify and protect feeding habitat of fish is to develop habitat suitability criteria for prey taxa. Orth (1987) discussed the rationale for including aquatic invertebrates and forage fishes in instream flow assessments, and Statzner et al. (1988) have reviewed a variety of such techniques and studies. While this approach may require less field work than conducting a procedure similar to that in our study, sorting and classifying organisms would be labor-intensive in the laboratory. Distinct suitability criteria would have to be developed for each individual (or dominant) prey taxa, and thus the procedure may be impractical for fishes with diverse or variable food habits. Feeding habitat suitability criteria derived from fish behavior may therefore provide a more realistic composite of optimal prey conditions than those directly obtained for prey. In addition, effort can be reduced if the diel feeding chronology of a fish has revealed a distinct rhythm. In such a case, on-site feeding studies may not be necessary to temporally stratify fish microhabitat use by feeding regime. In a decision between these two approaches, the behavior of both predator and prey must be considered.

Habitat suitability criteria are usually distinguished by species and life stage, and additional stratification by activity or season may also be desirable. Spawning suitability criteria are often developed separately, and our results indicate that distinct criteria for feeding and resting habitat are warranted as well. Gathering frequency data to develop site-specific suitability criteria is costly and labor-intensive and may be limited by economic and logistic constraints. As a pool of data is further stratified, sample size of each suitability function is reduced, and the potential for bias is increased. Bovee and Cochauner (1977) recognized sample size and source of the data in developoment of evaluation criteria for suitability functions, which were classified into one of four classes ranging from "reconnaissance grade," based only on stream descriptions, to "excellent," requiring a minimum of 200 measurements of occurrence. Practical constraints may limit sample size and the degree of stratification allowed and may thus lead to overlooking a critical habitat. For example, further disaggregation of our habitat use data by season would have provided added insight, but was constrained by sample size. Our objectives in this study were to examine microhabitat use associated with diel feeding chronology; however, seasonal patterns should be addressed in other studies.

There are no standardized procedures for stratifying suitability data, but a bimodal or polymodal habitat frequency distribution may indicate that more than one activity is represented and further stratification may be warranted (Bovee 1986). If activity is not considered, the habitat of a critical activity (e.g. feeding or spawning) will be not be adequately represented, and any measurement of central tendency (e.g. mean, median, mode) will be biased toward the predominant activity. The investigator is therefore faced with a subjective decision in balancing sampling bias and realism in determining an optimum level of stratification with limited sample sizes, and fish behavior rather than budgetary concerns should govern this decision. Because most habitat suitability field data are collected during daylight hours, they are variably biased with respect to feeding regime. As a final recommendation, we suggest that when stratification of site-specific suitability data by feeding regime or any other activity is not feasible, field measurements should be collected throughout the diel period under a variety of hydraulic conditions and over several seasons and should include cover associations to minimize bias.

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