Effects of habitat availability on dispersion of a stream cyprinid

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Synopsis

We analyzed temporal changes in the dispersion of the rosyside dace, *Clinostomus funduloides*, (family Cyprinidae) in a headwater stream, to assess the role of habitat availability in promoting fish aggregation. The dace foraged alone and in groups of up to about 25 individuals, and dispersion varied significantly among monthly censuses conducted from May through December. In two of three study pools, dace aggregated during July, October and/or December, but spread out during other months, especially during September when dispersion did not differ significantly from random. Dispersion was not significantly correlated with the total amount of suitable habitat available to foraging dace, but during summer, corresponded to the availability of depositional areas adjacent to rapid currents. Foragers aggregated in eddies or depositional areas during high stream discharge in July, and shifted out of depositional areas when current velocities declined from July to September. During late autumn, however, aggregations formed independently of changes in habitat conditions, and dace dispersion did not vary significantly among months in a third pool. The study suggests that dace dispersion cannot be predicted from the overall availability of suitable habitat as estimated from point measurements of depth and velocity; both the occurrence of a specific habitat feature (i.e., eddies adjacent to high velocity currents) and seasonal differences in behavior more strongly influenced the spatial distribution of foragers.

Introduction

The spatial distribution of foraging stream fish likely mediates their influence on prey stocks or processes such as primary production. For example, widely dispersed foragers may have negligible effects on invertebrates (Allan 1982, Reice 1991), whereas aggregations of fish can strongly affect invertebrate populations in a local area (Gilliam et al. 1989, but see Culp 1986). Similarly, schools of herbivorous fishes can significantly reduce algal standing crop and contribute to spatial variation in stream algae (Power & Matthews 1983, Power et al.

1985). Fish dispersion, however, may depend on interactions with predators (Fraser & Cerri 1982, Power & Matthews 1983, Power et al. 1985, Schlosser 1987, Harvey et al. 1988) and potential competitors (Allan 1986, Gorman 1988), or in the case of group foraging species, on social attraction among foragers (Pitcher 1986). In the absence of strong biotic interactions, the availability of preferred habitat could determine fish dispersion, with decreased habitat availability resulting in greater fish aggregation.

In this study we tested the hypothesis that fish dispersion correlates with habitat availability under

conditions of weak biotic interactions. The rosyside dace, *Clinostomus funduloides*, is not subject to strong predation pressure (Grossman & Freeman 1987) or frequent interactive competition (Freeman & Grossman 1992a) in our headwater stream study sites. Dace feed on drifting invertebrates and may forage solitarily or in groups. Analyses of group dynamics, however, revealed only weak evidence of social attraction (Freeman & Grossman 1992b). We thus hypothesized that forager dispersion primarily depends on the availability of suitable foraging habitat, and we tested for correlations between dace dispersion and total habitat availability. Results demonstrated that the total area of suitable habitat did not influence forager dispersion as strongly as did the occurrence of a specific habitat feature, eddies adjacent to rapid currents.

Study site

Coweeta Creek is a fifth order stream located at the Coweeta Hydrologic Laboratory (U.S.D.A. Forest Service; Macon County, North Carolina), in the southern Appalachian Mountains. The stream drains experimental watersheds (primarily forested) and flows through mixed hardwood forest in the study site area. Detailed site descriptions are provided by Grossman & Freeman (1987) and Swank & Crossley (1987). We periodically mapped dace distributions and quantified habitat availability in three pools in Coweeta Creek: pool 1 (11 m long, 4 to 6 m wide); pool 2 (10 m long, 5 to 6 m wide), located 40 m downstream from pool 1; and pool 3 (16 m long, 3 to 5 m wide), located 190 m downstream from pool 2.

Methods

We mapped fish distributions by slowly snorkeling from the downstream to upstream ends of a pool, monitoring fish activity in each area of the pool for at least two minutes. Monitoring involved recording the number of fish present in a given area (the size of which depended on water clarity) every 15 s, for a total of eight counts. We averaged these eight counts to estimate the number of dace using a given area. Dace did not perceptibly react to a slowly moving snorkeler. Pool surveys normally required 40 to 65 min to complete. We made two surveys of each pool (morning after 09.30 h and afternoon before 16.30 h) to estimate dispersion during a given month, from May to December 1989.

We used these data to map fish distributions in relation to transect lines spaced 1 m apart from the downstream to the upstream ends of each pool. Color-coded spikes driven into the stream bank at the ends of transect lines and in the substrate at meter intervals along transects facilitated mapping. To estimate habitat availability during a given month, we measured water depth and average current velocity at 1 m intervals on every transect. Average current velocity was measured with an electronic velocity meter, with the probe placed at 60% of total depth (where depth exceeded 75 cm, we averaged velocity measurements taken at 20% and 80% depth). Snorkeling surveys and habitat availability measurements were completed within three days of each other.

Using maps of fish distributions, we estimated the average number of dace in each square meter of a pool during a given survey. For each survey we calculated Morisita's index of dispersion (Elliott 1977):

$$I = n \sum_{i=1}^{n} (x_i (x_i - 1))/(\sum_{i=1}^{n} x_i (\sum_{i=1}^{n} x_i - 1)),$$

where n = total # of meter-square quadrats, and x_i = # of dace in quadrat i.

The index equals one when individuals are randomly distributed among quadrats. Values less than one indicate increasingly even distributions, whereas values greater than one indicate increasingly clumped distributions up to a maximum value of n, when all individuals are in one quadrat. Morisita's index is independent of animal abundance and mean density, and therefore, is a good tool for comparing animal dispersion in a given area through time even if abundances change (Elliott 1977). Index values are sensitive to the size of the quadrat relative to the areal extent of animal groups. Values are relatively stable with increasing quadrat size until quadrats become much larger than animal groups, at which point index values decline (Elliott

1977). The quadrat size used in this study, $1 m^2$, is larger than most dace groups, except when large groups form in a particular pool area. In the latter case, quadrat size could be smaller than group size, with the possible effect of increasing index values relative to surveys when fish are dispersed in smaller groups. Thus, changes in group size relative to quadrat size could influence index values in this study. However, this should not affect the general interpretation of results, because values would be lower if fish were more dispersed and inflated if fish formed larger groups.

Using Morisita's index, animal dispersion may be tested for significant departure from random by comparing $I \left(\sum_{i=1}^{n} x_i - 1 \right) + n - \sum_{i=1}^{n} x_i$ to a chi-square distribution with $n - 1$ degrees of freedom (Elliott 1977). We used this procedure to test whether dace dispersion differed significantly from random during each survey.

Further analyses addressed two questions, (1) did dace dispersion in a given pool vary through time and (2) were changes in dispersion related to changes in habitat availability? We evaluated question one by applying Kruskal-Wallis tests to monthly values of Morisita's index calculated separately for each pool. To test for linear relationships between dispersion and habitat characteristics in each pool, we calculated Spearman's rank correlation coefficients between index values and mean depth and mean current velocity. We also estimated the absolute amount of 'suitable' foraging habitat available in a given month by counting the number of transect measurements with depth ≥ 20 cm and velocity ≤ 39 $cm s^{-1}$. These values approximated the lower and upper limits of depth and velocity, respectively, used by dace over two years in another Coweeta Creek study site, which included pool, run and riffle habitat (means ± 2 s.d.'s: 20–91 cm for depth, 0–39 cm s^{-1} for velocity, $n = 245$; Grossman & Freeman unpublished data). We tested for significant correlations between this estimate of habitat availability and dace dispersion. Finally, we tested whether dispersion was linearly correlated with either dace abundance or per capita availability of suitable habitat (estimated by the number of 'suitable' transect measurements divided by dace abundance).

Survey and habitat availability data permitted a test for temporal changes in the depths and velocities used by dace in each pool. To describe habitat use by dace during each survey, we calculated average depth and average velocity measurements for the meter square quadrats containing a given group of foragers. These measurements were weighted by the average number of dace in the area. Nested ANOVA (i.e., replicate surveys nested within months) tested for significant differences in habitat use among months. Critical probability levels were adjusted for multiple comparisons by the Dunn-Sidak procedure (Ury 1976) in all tests in which more than one variable was compared among groups; adjusted probability levels are reported with results.

Results

Dace dispersion

Dace displayed clumped distributions within each pool during all surveys except those conducted in September, when one or both monthly dispersion estimates were not significantly different from values predicted for random dispersion (Table 1). Note, however, that actual spatial dispersion did not appear random in September because dace avoided shallow quadrats at stream margins (Fig. 1–3). Dace actively foraged during all surveys: individuals faced into the current and periodically struck at drifting particles. It is unlikely that dace aggregations resulted from spawning activity. Dace spawn during spring or early summer (Davis 1972), and at Coweeta, dace appear gravid in May and June (Grossman et al. unpublished data). Thus, only the May survey in pool 1 was likely to have been influenced by spawning activity; we did not observe reproductive behavior during any survey. Dace ranged from 5 to 7 cm total length, probably corresponding to ages 1+ and 2+ (Davis 1972).

The largest groups contained 15 to 25 dace, and formed at the upstream end of pool 1 in May, July, October and December, and also in pool 2 during July and October. However, individual dace often changed location and usually were not all in large, discrete groups. Only 50% of counted individuals

were in quadrats with average densities >4 dace (data summed for all surveys). Quadrats with average densities of 1 to 4 dace accounted for 43% of counts of individuals. The remaining 7% of all individuals foraged without another conspecific within 0.5 m and probably foraged solitarily, based on an estimated maximum distance between interacting fish of 5–10 body lengths (Seghers 1981, Pitcher et al. 1983, Helfman 1984).

Dace were not the only drift-feeding fishes present, however, other water-column fishes always were much less abundant than dace and did not measurably affect dace dispersion. Values of Morisita's index were not correlated in any pool with abundances of other cyprinids, young-of-the-year rainbow trout, *Oncorhynchus mykiss*, or older trout (Spearman's correlation coefficients, $p > 0.05$).

Temporal variation in dace dispersion and habitat availability

Dace dispersion differed significantly among months in pools 1 and 2, but not in pool 3 (Table 1). In pool 1, dace became more dispersed from July to September, and then became strongly clumped in December, with relatively low variation between surveys in any given month. Within month variation in pool 2 and especially in pool 3 reduced monthly differences. In pool 2, however, dace again exhibited the greatest dispersion in September and became very clumped in October and December. In both pools 1 and 2, increased dispersion in August and September corresponded to dace foraging in the middle of the pools rather than nearer to one side, as in July (Fig. 1, 2). Fish dispersion in pool 3 did not vary significantly from month to month (Table 1) and at least some dace foraged in the center of the pool during each survey (Fig. 3).

Were changes in dispersion or spatial distribution related to changes in habitat availability? All three pools were deepest and fastest in July, as a result of unusually high rainfall (second wettest July in 55 years at Coweeta). Stream discharge decreased through August and September, and all pools were shallowest, with the slowest current velocities in September (note maximum velocities and extent of

shallow areas, Fig. 1–3). Thus, increased dace dispersion from July to September in pools 1 and 2 (as measured by Morisita's index) corresponded to decreasing average velocities and depths. Similarly, in pool 3, dace were more dispersed along the main current of flow in August and September than in July (Fig. 3). However, the extreme concentration of dace into groups during late autumn (i.e., during December in pool 1 and October in pool 2) did not correspond to large increases in average depths or velocities. As a result, dispersion was not significantly correlated ($p > 0.05$) with average depth or velocity. Temperature, which was the same among pools within measurement error, probably did not directly influence dispersion. Water temperature only varied from 16 to 17° C among the July, August and September censuses, and if lower autumn temperatures (9 to 11° C and 7 to 8° C during the October and December censuses, respectively) elicited greater aggregation by dace, this effect varied among pools.

Correlations between dispersion and the amount of suitable habitat, the amount of suitable habitat per individual, or dace abundance also were non-significant ($p > 0.05$) in all three pools. In fact, pools 1 and 2 contained more suitable habitat when dace

Table 1. Dace dispersion in pools 1, 2 and 3. Morisita's index of dispersion was calculated for two surveys each month. Dispersion differences among months were tested by Kruskal-Wallis (K-W) tests.

Month	Pool 1	Pool 2	Pool 3
May	4.16**	no data	no data
May	5.78**		
July	11.30**	6.38**	10.21**
July	10.88**	7.75**	3.37**
August	6.49**	4.42**	6.55**
August	6.79**	4.06**	9.43**
September	1.25	7.03**	2.81
September	1.42	1.42	10.92**
October	4.54**	22.97**	5.88**
October	8.35**	29.89**	4.67**
December	23.39**	22.10**	no data
December	16.69**	44.66**	
K-W value	10.08	7.31	0.67
probability	< 0.1	< 0.1	> 0.8

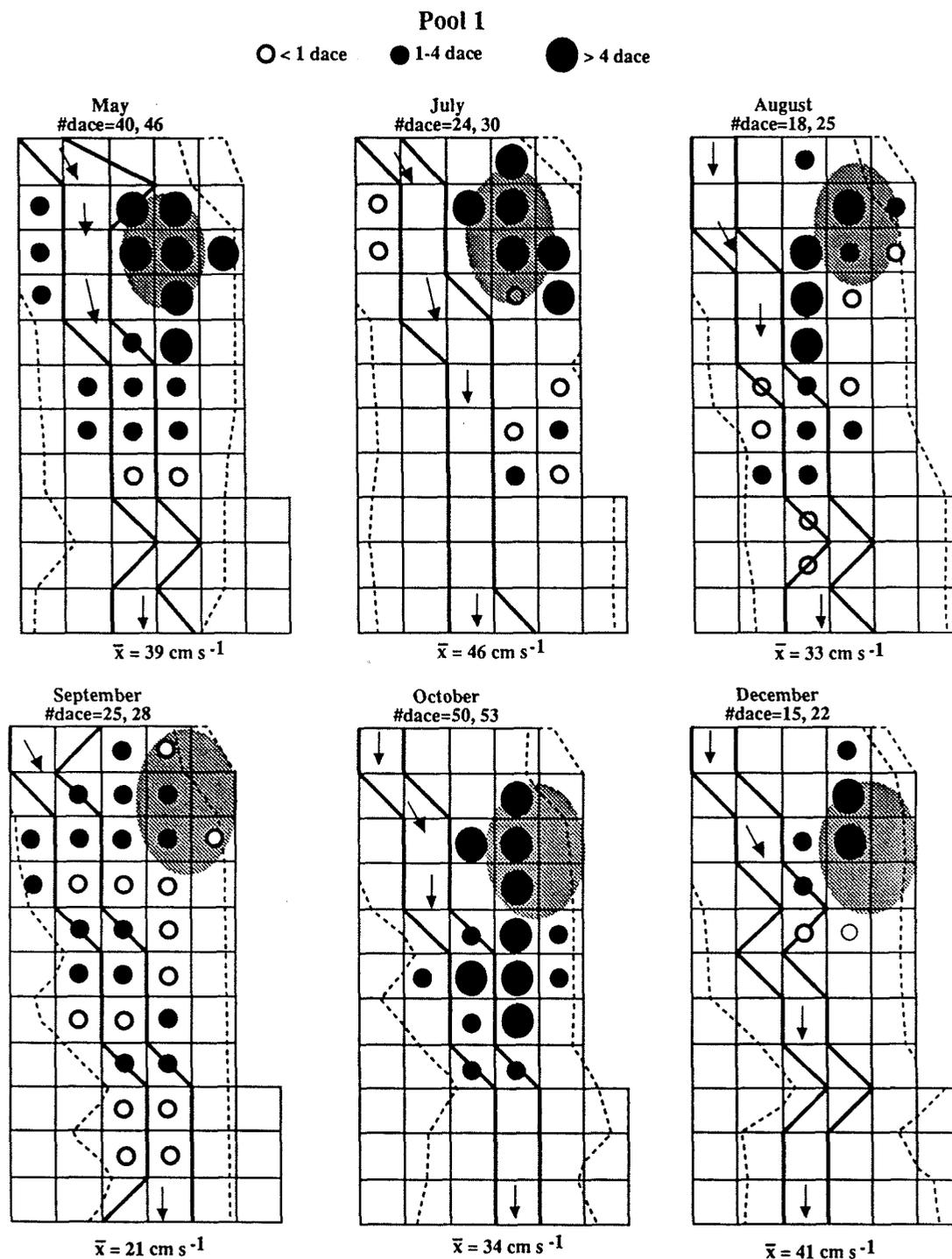** indicates non-random dispersion ($p < 0.01$).

Fig. 1. Dace dispersion in pool 1, May through December 1989. Drawings represent a map of the pool, with each box equal to 1 m². Circles indicate the maximum dace density (in each square meter) observed in either of two surveys in a given month. No dace were observed in empty quadrats. Estimated dace abundances (n's) are shown for the two surveys in each month. Dashed lines delineate shallow (<20 cm) marginal areas. The area of fastest current through the pool is outlined by heavy lines that connect the highest velocity measurements in successive transects; the mean of these maximum velocities is shown below each map. Arrows indicate the direction of flow. The shaded oval represents an eddy (i.e., an area with current directed upstream).
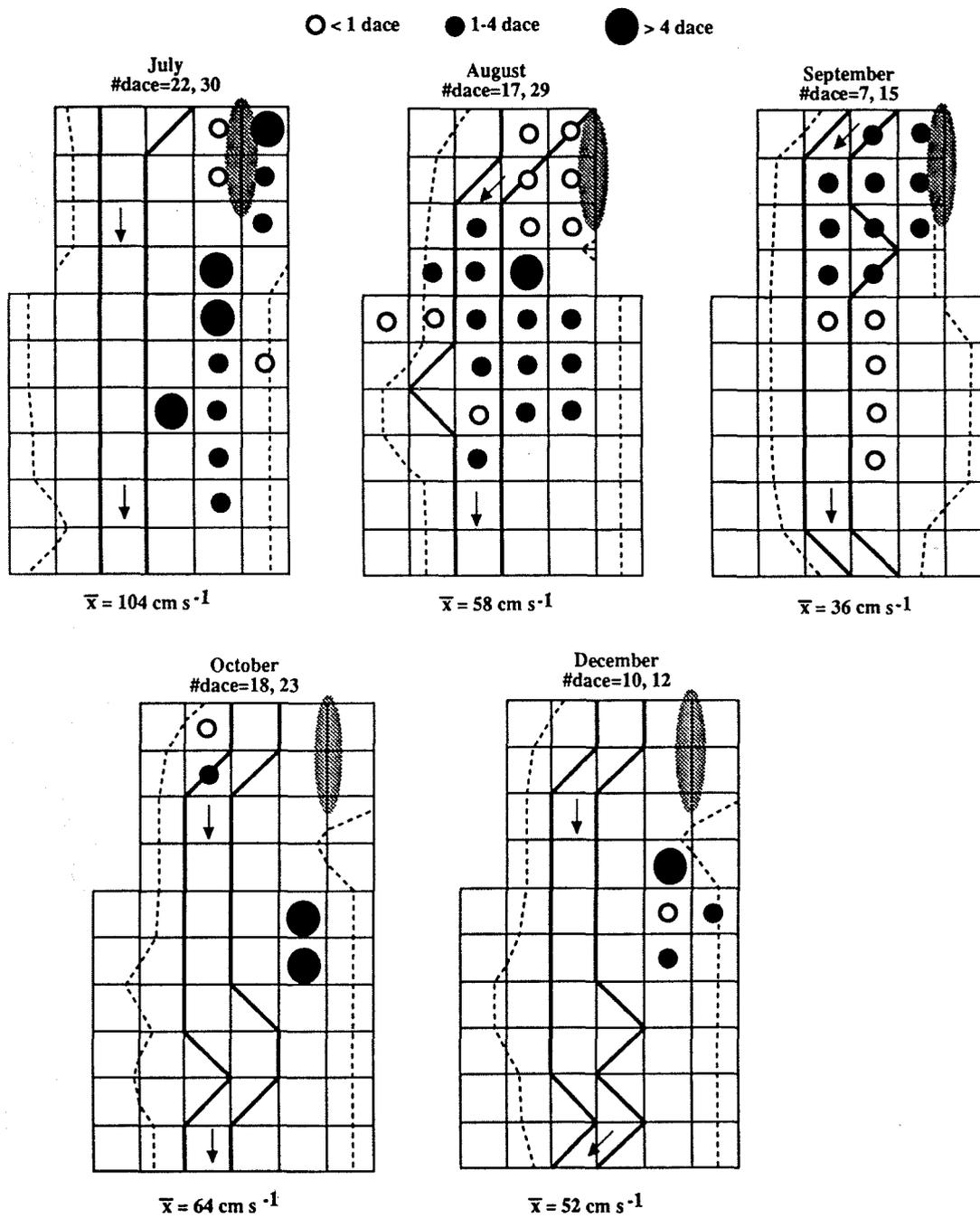
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Pool 2

○ < 1 dace   ● 1-4 dace   ⬤ > 4 dace

July
#dace=22, 30

$\overline{x} = 104$ cm s^{-1}

August
#dace=17, 29

$\overline{x} = 58$ cm s^{-1}

September
#dace=7, 15

$\overline{x} = 36$ cm s^{-1}

October
#dace=18, 23

$\overline{x} = 64$ cm s^{-1}

December
#dace=10, 12

$\overline{x} = 52$ cm s^{-1}

Fig. 2. Dace dispersion in pool 2, July through December 1989. Symbols are the same as in Fig. 1.

Pool 3

O < 1 dace   ● 1-4 dace   ⬤ > 4 dace

| July #dace=11, 21 | August #dace=27, 28 | September #dace=12, 18 | October #dace=39, 40 |

$\bar{x} = 68$ cm s^{-1} $\bar{x} = 45$ cm s^{-1} $\bar{x} = 34$ cm s^{-1} $\bar{x} = 48$ cm s^{-1}
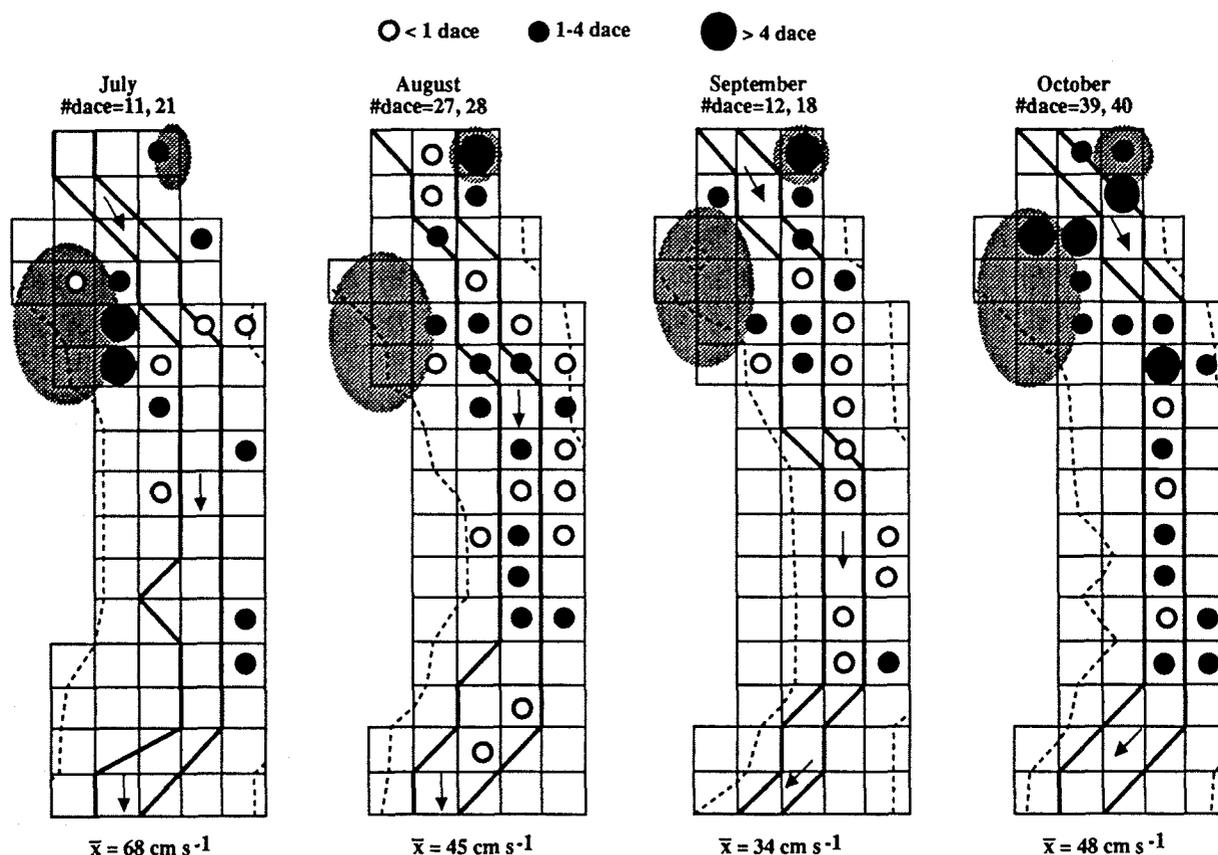
Fig. 3. Dace dispersion in pool 3, July through October 1989. Symbols are the same as in Fig. 1, except that two eddies are indicated by shaded ovals.

were strongly clumped than during some months when foragers were more widely dispersed (e.g., July vs. September in pool 1, October vs. August in pool 2; Table 2). The ratio between available habitat and dace abundance varied both within and among months, but was similar among pools (Kruskal-Wallis comparison among pools for July through October, H= 2.34, df= 2, p> 0.25). Thus, neither temporal changes in dace dispersion nor differences among pools were strongly related to the overall availability (absolute or per dace) of suitable foraging conditions.

Dace aggregation in depositional habitats

The availability of eddy areas near rapid flows may have influenced dace dispersion. In pools 1 and 3, the largest groups of dace foraged in or close to eddies (i.e., depositional areas with some current directed laterally or upstream). Eddies formed near the upstream ends of pools 1 and 3, next to the main inflowing current, with substrates of organic matter deposited over sand. Dace not in eddies primarily foraged in or adjacent to the main current flowing through the pools (Fig. 1, 3). Pool 2 differed in that a smaller eddy formed near the upstream end, and current velocity exceeded that in pools 1 and 3 (especially in July, Fig. 1–3). In pool 2, the largest groups of dace consistently formed immediately

downstream from a boulder (3 m from the head of the pool, Fig. 2) that created a mixing or depositional area in a location with high current velocity. Dace otherwise spread out in or adjacent to the main current of flow, similar to pools 1 and 3.

The potential influence of depositional habitats on dace dispersion could not be detected from habitat use data. Mean depths and velocities for quadrats occupied by dace (weighted by the average number of dace counted in each area) did not differ significantly among months in 5 of 6 comparisons (p> 0.05). Only mean depth occupied by dace in pool 3 differed significantly among months, and actual differences were slight (range of mean depths =48–55 cm). Thus, habitat use data, based on point measurements of depth and velocity, did not reflect shifts in forager distribution relative to depositional areas, as revealed by census maps.

Discussion

The spatial distribution of foraging dace in our headwater study sites varied markedly, both among pools and through time, which could result in differences in how dace affect, for example, concentrations of drifting prey. Despite weak biotic interactions in these sites, dace dispersion was not directly correlated with overall habitat availability, based on point measurements of depth and velocity. Two other factors appeared influential, (1) occurrence of a specific habitat feature (relatively deep eddies next to rapid currents), and (2) increased gregariousness in autumn.

Census data from pools 1 and 2 for July through September suggest that dispersion was influenced by current regimes. Foraging dace were most clumped when discharge and current velocities were highest (in July) and were most widely dispersed when discharge was lowest (in September). These shifts probably resulted from foragers avoiding extremely high velocities in pool centers during July. However, we hypothesize that dace also aggregated in eddies or depositional areas in July because prey availability and foraging success were relatively high in these areas. By foraging in a depositional area adjacent to a rapid, turbulent current, dace held position in relatively low velocities (where capture success is high, Hill & Grossman 1993) and gained access to larger prey carried by the faster current when these prey became entrained in eddy currents. However, as discharge and current velocities decreased, the difference between the rate of prey entrainment in eddies and prey capture success for individuals foraging in the main current probably declined. As a result, foragers became more widely dispersed.

In summary, dace dispersion depended not only on overall habitat conditions, but also on the availability of depositional areas adjacent to high velocity currents. Rinne (1991) similarly observed that spikedace, *Meda fulgida*, were most abundant in deeper, lower velocity areas associated with eddying currents. Thus, frequency distributions of point measurements of depth and velocity may not ade-

Table 2. Temporal variation of the amount of suitable habitat available to foraging dace. Values are absolute habitat availability (the number of transect measurements with depth ≥20 cm and current velocity ≤39 cms⁻¹) and relative habitat availability (the number of suitable transect measurements divided by dace abundance in each of two censuses each month).

Month	Pool 1		Pool 2		Pool 3	
	Absolute	Relative	Absolute	Relative	Absolute	Relative
May	38	0.8, 0.9	no data		no data	
July	44	1.5, 1.8	16	0.5, 0.7	30	1.4, 2.7
August	43	1.7, 2.4	18	1.1, 0.6	40	1.4, 1.5
September	40	1.4, 1.6	31	4.2, 2.0	48	4.0, 2.7
October	35	0.7, 0.7	22	1.0, 1.2	40	1.0, 1.0
December	35	2.3, 1.6	25	2.2, 2.5	no data	

quately quantify habitat availability or requirements for some stream fishes. Rather, measurements at a larger scale (in this case, size and depth of depositional areas, and their proximity to rapid currents) may better represent habitat suitability. For example, differences among pools in dace dispersion did not correspond to variation in habitat availability relative to dace abundance, and most likely reflected differences in the availability of especially profitable foraging areas. The absence of strongly attractive foraging sites in pool 3 (where eddy currents were either small, <1 m^2, or in shallow water near the pool margin) may have contributed to greater variability in forager dispersion at a given water level, and to weaker differences among months. This hypothesis could be tested by comparing fish dispersion between replicated habitat units with similar average depths and velocities but differing in the availability of eddies.

A second factor, independent of habitat availability, influenced dace dispersion during autumn, when foragers became strongly clumped in two pools. Dace foraged in one small area of pool 1 during December, and of pool 2 during October and December, despite habitat conditions similar to August, when foragers were relatively widely dispersed. Analyses of group dynamics (Freeman & Grossman 1992b) also provided evidence of greater attraction among foragers in autumn. However, both the timing and degree of increased grouping varied among pools, suggesting that increased contagion was not a fixed response to lower water temperatures or some other seasonal change.

Elucidating causes of variation in fish dispersion will advance our ability to predict dynamics of interactions among foragers, and between fish populations and their prey and predators. The spatial distribution of foraging stream fishes may vary dramatically in response to changes in habitat composition (e.g., the sizes and arrangements of depositional and erosional areas) and as a result of behavioral changes, whereas the overall availability of suitable habitat may have relatively little influence.

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