CONTEXT-SPECIFIC TROPHIC AND FUNCTIONAL ECOLOGY OF FISHES OF SMALL STREAM ECOSYSTEMS IN THE OUACHITA NATIONAL FOREST

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Abstract—Fish play diverse and important roles in stream ecosystems, but details about ecosystem effects are poorly known for many freshwater fish species. A requisite first step to understanding functional roles of individual species is information on their trophic ecology in the context of particular environmental settings. Stomach contents were analyzed for approximately 1,600 individuals of 21 common fish species (mostly insectivores or omnivores) from four streams in the Ouachita National Forest, Arkansas. Two streams (South Fork Alum Creek and Crooked Creek) were in watersheds with little recent timber harvest and two (Bread Creek and Blaylock Creek) were in watersheds harvested under Forest Service standards and guides. Individual fish species were distinctive in kinds of foods eaten, and were not substitutable for each other in ecosystems. Benthic and water column species differed in diet, but interspecific differences in food consumption were not closely linked to taxonomic similarity. Composition of fish diets were overall 70 to 85 percent similar between harvested and non-harvested watersheds, with dipterans and terrestrial insects the major foods used by all fish assemblages; most individual species had similar diets in different creeks or longitudinally within creeks. Foods eaten per species, multiplied by estimates of fish density from snorkeling and seining surveys, resulted in an order of magnitude prediction of consumption of about 13,000 invertebrate food items per day per 100 m of stream by the local fish assemblage.

INTRODUCTION

Small streams draining the Ouachita National Forest in Arkansas and Oklahoma are inhabited by a large number of native fishes with 117 species known from the Ouachita Highland (Matthews and Robison 1998). These fishes, dominated numerically by minnows (Cyprinidae), suckers (Catostomidae), catfishes (Ictaluridae), topminnows (Fundulidae), sunfishes (Centrarchidae), and darters (Percidae), can be very abundant locally. Thousands of individuals frequently occupy a single pool-riffle complex in these small upland streams. Matthews and Robison (1998) found a modal number of 13 fish species per collection across nearly 200 sites in the Ouachita Mountains, and collection of up to 20 species per site was not unusual. Until the 1980s, little emphasis was placed on the ecological roles of stream fishes, but it is now well known that feeding, nutrient release, and mechanical activities of fishes can have strong and diverse effects in stream ecosystems (Matthews 1998). Beginning with work by Power and Matthews (1983), Power and others (1985), and Grimm (1988), there is clear demonstration that some fish species have strong effects on structural and functional properties of North American stream ecosystems. Expanding the initial work of Power and others (1985), several papers (e.g., Gelwick and Matthews 1992, Gelwick and others 1997, Vaughn and others 1993) demonstrated that a single highly abundant, algivorous species [central stoneroller, *Campostoma anomalum* (Rafinesque)] had direct or indirect effects on at least 20 important structural or functional properties of small stream ecosystems (Matthews 1998). The central stoneroller can cause differences in algal community composition or productivity, uptake and dynamics of organic matter, invertebrate community composition or life history, movement of materials in streams, carbon-nitrogen ratios, and standing crops of bacteria. The species also plays a major role in predator-driven trophic cascades and can alter the manner in which stream ecosystems function overall. The central stoneroller is a highly abundant species in many streams of the Ouachita National Forest where it occurs in schools of up to several thousand and grazes algae vigorously and actively from rock substrates of flowing pools and riffles.

The demonstration that a single common species can change the dynamics of a stream ecosystem, while interesting, falls short of providing managers with information on the overall impacts of fish communities on stream ecosystems. The best assumption from a management view is probably that all fish species in a small stream have the potential to change or influence important dynamics in that stream, such as primary productivity, nutrient relationships, breakdown of particulate organic matter, linking individual pools with each other, or changing algal or invertebrate communities. To demonstrate this concept, (Gido and Matthews, in press), recently tested the hypothesis that a water-column minnow species (red shiner, *Cyprinella lutrensis* Baird and Girard) could have direct or indirect effects on benthic primary productivity. Over one fall and winter, they showed a direct positive relationship between the density of red shiners and primary productivity on artificial substrates in large outdoor experimental streams. However, the red shiners did not cause a decrease in density of benthic stream invertebrates (many of which graze algae). Presumably, the enhancement

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of benthic primary productivity resulted from an increased rate of nutrient transfer from surface or water column invertebrates, a primary food of red shiners, to nutrient limited periphytic algae. Regardless of the mechanism, (Gido and Matthews, in press) provided a clear demonstration that fishes other than strictly benthic species can have major impacts on stream ecosystem processes, including processes in the benthic (stream bed) compartment.

Regionally, good information about ecosystem effects is available for only one species (*Campostoma anomalum*) that is common in Ouachita National Forest streams, out of the more than 200 fish species recorded from Oklahoma and Arkansas. The long-range goal of our research program is to determine effects of a wide range of fish species on ecosystems of small streams, adopting the functional groups approach outlined by Matthews (1998).

The requisite first step to any assessment of the functional effects of a fish species on stream ecosystems is acquiring detailed, context specific information on its food use. That is, what (and how) does a fish eat and what is the specificity or plasticity of its feeding? Does a given species use largely the same food items regardless of its location in a stream, the stream system in which it occurs, its potential competitors for food, or availability of foods? Additionally, there is great need to understand if a particular fish species uses foods most like those of closely related species, and the extent to which species are redundant, or “substitutable” for one another, in an ecosystem. If a fish species feeds consistently regardless of environmental context, broad a priori predictions of its effect in an ecosystem should be possible. If feeding (and functional role) of a fish is more context-specific, focus would shift to more local, site-specific studies of fish communities in order to understand ecosystem dynamics. Managers should bear in mind that the fish community and the ecosystem are intricately linked in two “directions.” It is becoming clear that fish have effects in ecosystems, but it is equally clear that the condition of the ecosystem plays a major role in the kinds and abundances of fish the system can support. Thus, the fish-ecosystem relationship can be considered a feedback loop in which the ecosystem affects the fish and the fish affect the ecosystem. Only by understanding effects of anthropogenic activities on the overall ecosystem, and this link to fishes, can an appreciation be gained of the interlinked roles of man, fish, invertebrates, and stream quality that actually comprises the stream ecosystem at the watershed level.

This study describes a first approximation of the use of foods by a substantial number of stream fish species of the Ouachita National Forest. Food use is examined in the context of stream, season, timber harvest regime, and, for selected species, longitudinal position in the stream. Specifically, general food use is summarized for 21 species in each of two pairs of streams in the upper Little Missouri River drainage and the upper Saline River drainage. Further, similarities and differences in food use are tested among species, two major feeding groups, and taxonomic relatives. Assemblages are examined from the perspective of food use differences among streams and timber harvest regimes. For selected species, intraspecific differences in food use are examined among or within streams and between harvest regimes. Finally, an order of magnitude estimate is calculated to ascertain the potential effects of fish assemblages on the stream invertebrate community.

METHODS AND MATERIALS

Study Area

Stream fish communities were sampled by seining at 24 sites on four dates (November 1989, May 1990, October 1990, May 1991). Six sites each were located in Blaylock and Crooked Creeks (Little Missouri River drainage, northwest of Glenwood, AR), and six each in South Fork Alum and Bread Creeks (Saline River drainage, north of Hot Springs, AR). All sites were on public lands of the Ouachita National Forest (Matthews 1993). Within each of the two river drainages, one creek was considered “harvested” and one, “nonharvested” on the basis of recency of timber harvest within the watershed (Clingenpeel 1994) and unpublished basin area stream survey data (Alan Clingenpeel, Forest Hydrologist, Ouachita National Forest, Box 1270, Hot Springs, AR). At the time of field sampling, about 12 percent of the stands in Blaylock Creek had been harvested in the previous 20 yr, whereas essentially no stands had been harvested in Crooked Creek in that time period. Similarly, about 21 percent of the stands in the Bread Creek watershed had been harvested in the last 20 yr, and no stands had been harvested in South Fork Alum Creek watershed during that period.

At each site, fish were sampled by seining with small seines in all identifiable habitats (e.g., pools, riffles, runs) for approximately 1 to 1.5 hr over about a 200-m stream reach. Each site included multiple pools and riffles, although some of the extreme headwaters sites (particularly in Bread Creek) were sometimes reduced to a series of disconnected pools. All fish were preserved in the field in 10 percent formalin, transported to the University of Oklahoma Biological Station, and later were identified, enumerated, and transferred to 50 percent isopropanol for permanent storage. A summary of the fish collected is provided in Matthews (1993).

Subsequent to fish sampling, the Ouachita Mountain Ecosystem Management Research Project (Southern Research Station) provided funding for assessment of stomach contents of the fishes collected at the 12 sites. Matthews, Miller, and Stewart revisited all study streams and conducted sampling to make a reference collection of all possible benthic invertebrates from the study streams. Invertebrates were sampled qualitatively (i.e., dipnetting, kicknetting, and picking invertebrates from stones). These samples were identified and enumerated primarily by Miller, who holds a Masters of Science degree on distribution and ecology of benthic stream invertebrates. She was assisted in identifications by Dr. David Bass, Central Oklahoma University, an authority on benthic stream invertebrates in the region. Thus, fish stomach content was assessed against the background of a detailed reference collection of invertebrates from the study streams. This allowed creation of a templet for recording contents of individual stomachs that included 65 invertebrate taxa arranged hierarchically so that results could be viewed at the lowest taxonomic categories or aggregated by family, order, etc.

Miller, Stewart, and other technicians (directed by Miller or Matthews) conducted examination of stomach contents of over 2,000 individual fishes. Individual fishes were chosen from across the original field collections and in approximate proportion to the abundance of the fish species in the field (table 1). Each fish was weighed and measured, and eviscerated. The stomach was weighed, opened and thoroughly cleaned of contents, and then re-weighed to obtain weight of total foods. Stomach contents were identified using binocular dissecting microscopes. Eviscerated fish were returned to archival storage at the Biological Station. Data on counts of food items were coded by hand by Miller and others, and the data sheets sent to Warren who directed entry of the data into a relational database. This database was ultimately returned to Cobb who carried out all data manipulations in a spreadsheet format. In the present study, all data were aggregated at the level of order. All food items not in the established taxonomic categories, plus any terrestrial invertebrates (i.e., winged adults presumably taken from the surface) were classified in the category "other." Approximately two thirds of all items categorized as "other" were actually adult terrestrial invertebrates.

Table 1—Numbers of stomachs examined per fish per species and number of individuals of that species surveyed at 12 sites on four creeks in the Ouachita National Forest (1989-1991)[a]

Species	Stomachs	Number observed
Etheostoma radiosum Orangebelly darter	270	1982
Lythrurus umbratilis Redfin shiner	226	1,764
Semotilus atromaculatus Creek chub	185	2,798
Luxilus chrysocephalus Striped shiner	137	1,183
Notropis boops Bigeye shiner	95	704
Fundulus olivaceus Blackspotted topminnow	88	229
Etheostoma blennioides Greenside darter	79	170
Etheostoma collettei Creole darter	72	212
Etheostoma whipplei Redfin darter	67	209
Notropis ortenburgeri Kiamichi shiner	64	321
Lepomis megalotis Longear sunfish	55	425
Labidesthes sicculus Brook silverside	54	57
Fundulus catenatus Northern studfish	31	41
Noturus lachneri Ouachita madtom	31	37
Lepomis cyanellus Green sunfish	25	52
Esox americanus Grass pickerel	24	30
Aphredoderus sayanus Pirate perch	19	19
Hypentelium nigricans Northern hog sucker	14	40
Erimyzon oblongus Creek chubsucker	12	176
Micropterus dolomieui Smallmouth bass	11	44
Ameiurus natalis Yellow bullhead	10	13

[a] All seining and snorkeling observations pooled.

Our analyses are based on 1,589 fish stomachs from field samples in 1989-91. Fish stomachs were distributed among study streams as follows: Saline Drainage, South Fork Alum (non-harvested), 425 stomachs and Bread Creek (harvested), 304 stomachs; Little Missouri Drainage, Crooked Creek (non-harvested), 331 stomachs and Blaylock Creek (harvested), 529 stomachs. Estimates of abundances of the 15 most common species, excluding the central stoneroller, were derived from seining and from supplementary snorkeling observations made at all sites by Gelwick in spring 1991. These abundance estimates were used to extrapolate estimates of effects. Snorkeling observations also were used to derive classifications of species as "benthic" or "surface and water column" species. The central stoneroller, a common species in study streams, was excluded from our analyses because it depends almost exclusively on an algal diet.

Data analyses included calculations of a standard diversity measure (Shannon-Weiner) and a percent similarity index to compare and contrast foods eaten by assemblages and species among streams and between harvest regimes. Determination of overall similarities and differences among species was examined by multivariate clustering and principal components analyses using the NT-SYS computer programs. Our study was aimed at first approximations of food use by fishes in the study streams and required an exploratory approach to data analysis. As such, data analysis is summarized with results so that the method and rationale can be addressed in the context of principal findings.

RESULTS

Stomach contents were represented by 10 to 270 individuals each of 21 common fish species (table 1). The majority of invertebrate taxa recovered from fish stomachs were dipteran (midge) larvae and pupae, which occur on stream substrates, or adult insects that primarily are available to fishes at the water's surface (> 6,000 items represented by dipterans) (fig. 1). Other commonly eaten food items included (in order of abundance in stomachs): Ephemeroptera (mayflies); Trichoptera (caddisflies); Homoptera (true bugs); Arachnoidea (spiders, ticks, and mites); Crustacea (mostly crayfish and excluding microcrustaceans); Coleoptera (beetles); Hymenoptera (ants, wasps, and bees); Lepidoptera (moths and butterflies); microcrustaceans (mostly cladocerans and copeopods); Annelida (segmented worms); Plecoptera (stoneflies); and Nematoda (nematodes). Eight other invertebrate categories occurred frequently enough to be included in the analyses (fig. 1).

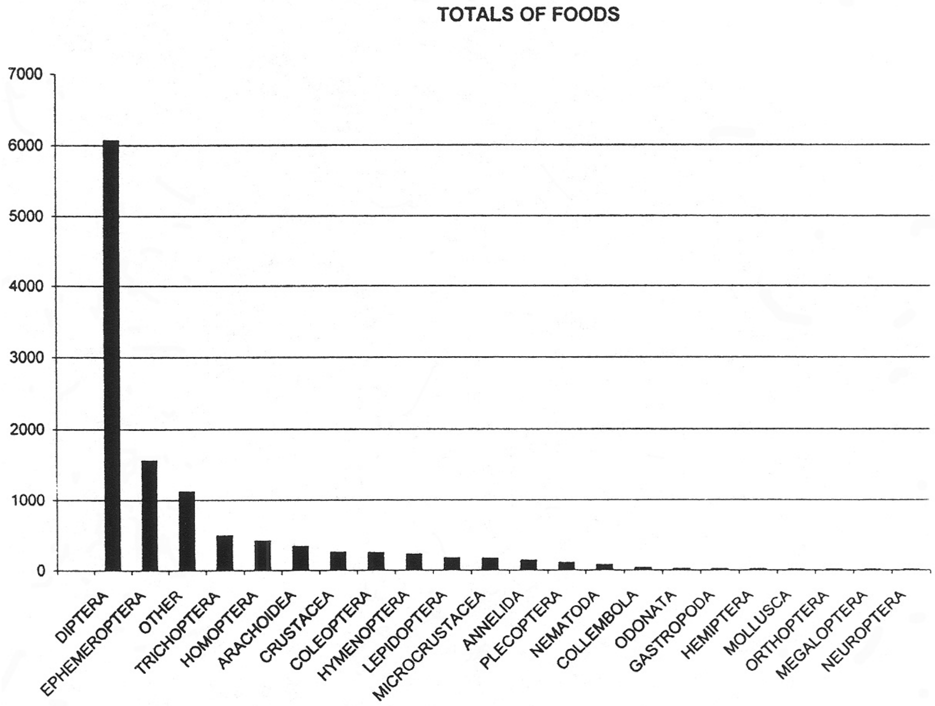

Figure 1—Total number of food items by taxonomic category found in stomachs of 1,589 fishes examined in four streams of the Ouachita National Forest.

A principal components analysis (PCA) was carried out for the 21 most common fish species to determine similarities and differences among species in foods eaten across 18 taxonomic categories of food items (with finer invertebrate categories pooled within orders). In PCA, each food item may be visualized as an individual axis across species that is aggregated with related food items into a lesser number of new or principal component axes (PC Axes), each of which represents original items that were most highly correlated with the new axis (Gauch 1982). The PCA provides a view of similarities and differences in diet by fishes, and in two dimensions, arrays fish species in multivariate space along gradients of foods used by those fishes. The first three PC axes accounted for 49.2 percent of the total variance in food items among the 21 fish species (19.1, 15.6, and 14.5 percent, for PC Axes I, II, and III, respectively). Accounting for nearly half the total variance in food use is a relatively high result for an ecological analysis. To compare fish species with respect to their overall similarities and differences on these "food" axes, two-dimensional scatterplots of fish species scores on PC Axis I versus PC Axis II and PC Axis I versus PC Axis III were used to interpret food use by fishes (figs. 2A and 2B).

PC Axis I separated (fig. 2A, from right to left) fish species with a tendency to eat Homoptera, Annelida, Hymenoptera, or "other" items (two thirds of which were terrestrial) from species that fed less on these categories. PC Axis II (fig. 2A) separated species that fed more on Ephemeroptera, Trichoptera, Lepidoptera, and Nematoda from species that ate less from these groups and more crustaceans. Interpretation of the distribution of fish species along the food axes is facilitated if benthic (bottom living) species are delineated from surface and water column species (fig. 2C). Surface and water column species are almost completely separable in overall diet from benthic species (fig. 2C). Surface and water-column species included: *Luxilus chrysocephalus* Rafinesque; *Lythrurus umbratilis* (Girard); *Fundulus olivaceus* (Storer); *Notropis boops* Gilbert; *Semotilus atromaculatus* (Mitchill); *Labidesthes sicculus* (Cope); *Fundulus catenatus* (Storer); and various sunfish and bass species. Benthic species included: darters such as *Etheostoma blennioides* Rafinesque, *Etheostoma radiosum* (Hubbs and Black), *Etheostoma whipplei* (Girard), and *Etheostoma collettei* Birdsong and Knapp; catfishes like *Noturus lachneri* Taylor and *Amieurus natalis* (Lesuer); and the sucker, *Hypentelium nigricans* (Lesueur). The only exception to this separation in diet is the sucker *Erimyzon oblongus* (Mitchill), which is a mostly benthic species but was grouped on both food use axes with the surface and water column species. Overall, the PCA axes suggest that the benthic species eat more aquatic insect larvae (e.g., mayflies, caddisflies, or moth larvae), whereas the surface and water column species feed more on items of terrestrial origin. Although not surprising, this finding underscores the high diversity in food use by a local fish assemblage. Importantly, the patterns emphasize that food use, which is indicative of potential role in the ecosystem, relates in a predictable fashion to the microhabitat use by each species.

PC Axis III accounted for almost as much variance as did PC Axis II. Thus, it was of interest to examine distribution of fish species on those two axes (figs. 2B and 2D). The two axes did, in fact, provide greater overall separation of species in multivariate diet space with less evidence of outliers. Importantly, use of some of the most common food items,

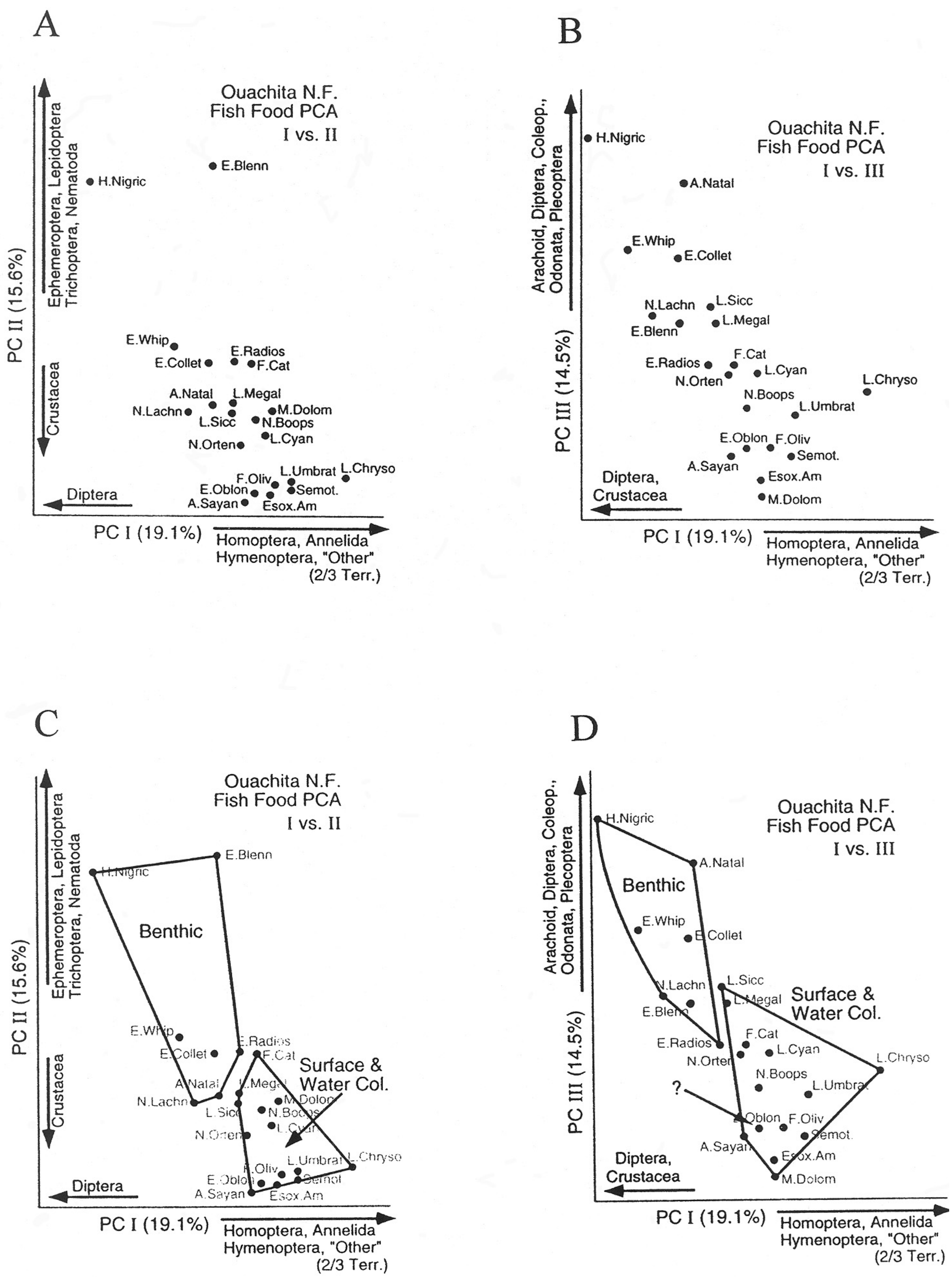

Figure 2—Principal components analysis ordinating fish species on the basis of food use in four streams of the Ouachita National Forest (A). PC Axis I verus PC Axis II; (B). PC Axis I versus PC Axis III; (C). PC Axis I verus PC Axis II, but with benthic and water column species denoted by polygons; (D). PC Axis I versus PC Axis III, but with benthic and water column species denoted by polygons.

including dipterans, was highly associated with PC Axis III. PC Axis III separated species along a gradient of high to low consumption of dipterans, odonates, plecopterans, or coleopterans (upper to lower, respectively, fig. 2B). Again, benthic species (e.g., *Hypentelium nigricans, Amieurus natalis, Etheostoma whipplei, Etheostoma collettei*) fed more on these items than did the surface and water column species. Combination of PC axes II and III provided complete segregation of benthic from surface and water column species on the basis of diet (fig. 2D). Again, *Erimyzon oblongus* was an exception (fig. 2C). It grouped with the surface and water column species in diet in spite of its benthic microhabitat use. The PCA results indicate distinctive separation in diet of most species that coincides with microhabitat use. From this, it is suggested that managers may be able to make rough approximations of trophic roles of fish in stream ecosystems by using the location of fish species in the water column.

Principal component analysis also indicated some correspondence between general food consumption and taxonomic association of species. From the delineation of the three most abundant families (darters, Percidae; minnows, Cyprinidae; sunfishes, Centrarchidae) on the PCA plots (figs. 3A and 3B), it is clear that darters are strongly segregated in diets from the sunfish and minnows. Obviously, this can relate to the differences in microhabitat use. Darters live and feed almost exclusively on the stream bottom predominantly in riffle habitats, and minnows and sunfishes live and feed more in the water column of pools. However, it is equally apparent that there is substantial overlap between minnows and sunfishes in overall diet. Their overlap in diet is logical in that these two families include species that overlap strongly in occurrence in the water column (on the basis of our snorkeling observations), and it is obvious in the field that members of both families will take food items (e.g., adult insects) from the surface of a pool. It would be tempting to conclude that managers could merely sample a stream, determine the family to which a species belonged, or the degree of relatedness between species, and assume some information about the similarities and differences in roles of the species in the ecosystem. This appears not to be the case.

Two triangular similarity matrices were created to more rigorously test the hypothesis that food use among fish species is predictable from taxonomic relatedness. One matrix measured similarity on the basis of overall diet, and the other, taxonomic distances among the species. Similarity in diets for the 21 fish species was assessed by a pair-wise product moment correlation matrix of foods eaten by food category. The diet similarity matrix (data not shown) was summarized by clustering of fish species (fig. 4). Taxonomic distances among species were scored for all possible species pairs using criteria from Douglas and Matthews (1992). Species within the same genus were scored with a taxonomic distance of 1; species in the same family, as 2; species in same order, as 3; and species from different orders, as 4. The resulting taxonomic similarity matrix gave each species pair a score of 1 to 4, depending on the relatedness of the species. If similarities (or differences) in diet among species pairs are associated with taxonomic relatedness, then the two matrices (diet and taxonomic similarity) should match closely. To test the degree of association between the matrices, a Mantel test was performed (Douglas and Matthews 1992) in which one matrix was randomly rearranged 9,999 times, and the degree to which the real matrices match each other was compared to the way the matrices would

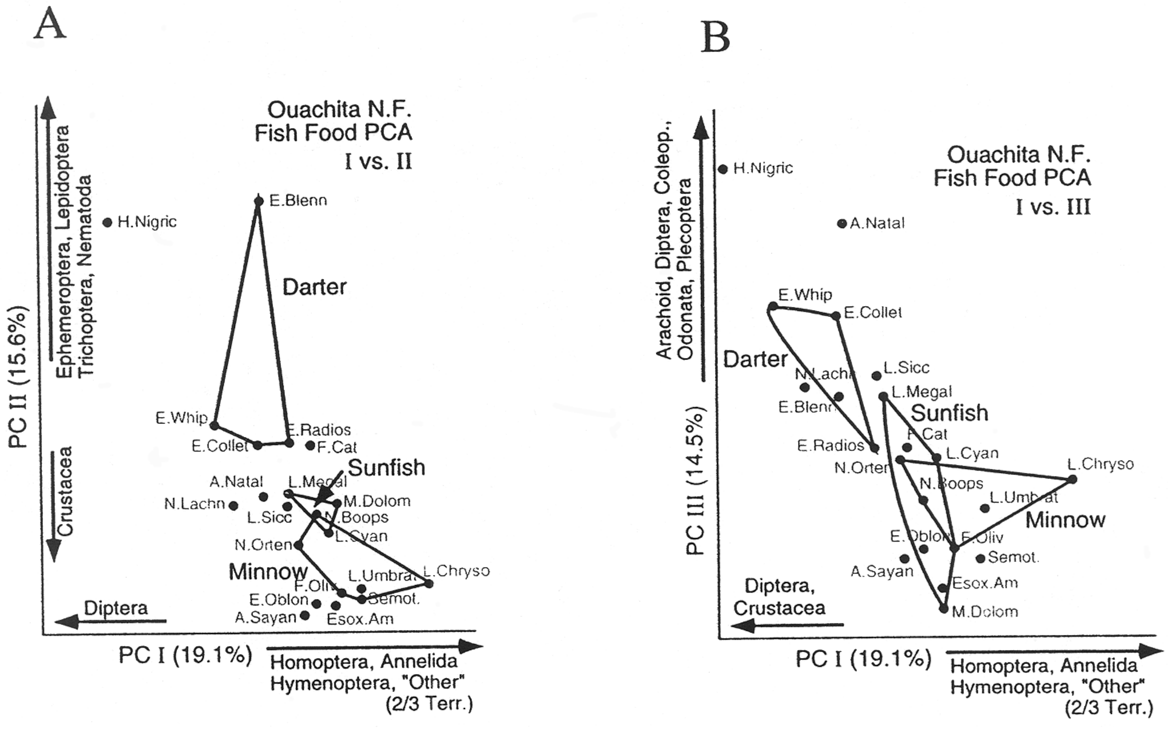

Figure 3—Principal components analysis as in figure 2 but with most abundant families denoted by polygons.

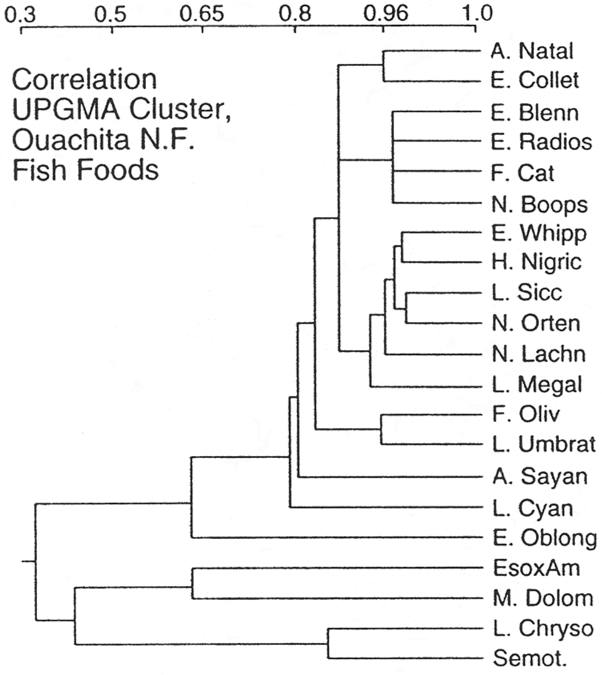

Figure 4—Phenogram based on correlation of food use similarities between 21 common species in four streams of the Ouachita National Forest.

match after being "reshuffled" at random. The Mantel test of the food use and taxonomic similarity matrices was not significant ($P = 0.395$) which signifies the two matrices are not closely or significantly matched in structure. Although there are some general differences in food use by darters versus minnows and sunfishes (explained earlier), there was no statistically detectable correspondence between diet and taxonomic relatedness across all species. Hence, managers could not safely predict trophic similarities among species on the basis of taxonomy alone. Each common species in an ecosystem needs detailed study of diets or their function in that respective system.

The degree of redundancy in a stream fish assemblage or among species within a region is another question of interest. Redundancy implies that closely related species might be so similar in their trophic or functional ecology that one could be substituted for the other. For example, if two closely related species are fully redundant, it would be possible for one to be lost from a system, the other to be introduced, and the system retain all of its original functional properties. In this study, the redundancy hypothesis can be assessed by examining positions of closely related fish species in multivariate food use space (figs. 2A and 2B). The PCA plots indicate some pairs of closely related species are rather similar in diets relative to other species in general (fig. 2B) including the minnows, *Notropis boops* and *Notropis ortenburgeri* Hubbs; the sunfishes, *Lepomis megalotis* (Rafinesque) and *Lepomis cyanellus* Rafinesque; and the minnows, *Luxilus chrysocephalus* and *Lythrurus umbratilis.* Conversely, other taxonomically similar species pairs are broadly separated in multivariate diet space (fig. 2B) including: the darters, *Etheostoma radiosum* and *Etheostoma whipplei*; the suckers, *Hypentelium nigricans* and *Erimyzon oblongus*; the catfishes, *Noturus lachneri* and *Amieurus natalis*; and the topminnows, *Fundulus catenatus* and *Fundulus olivaceus*. Overall, there is no apparent support for the postulate that closely related species pairs

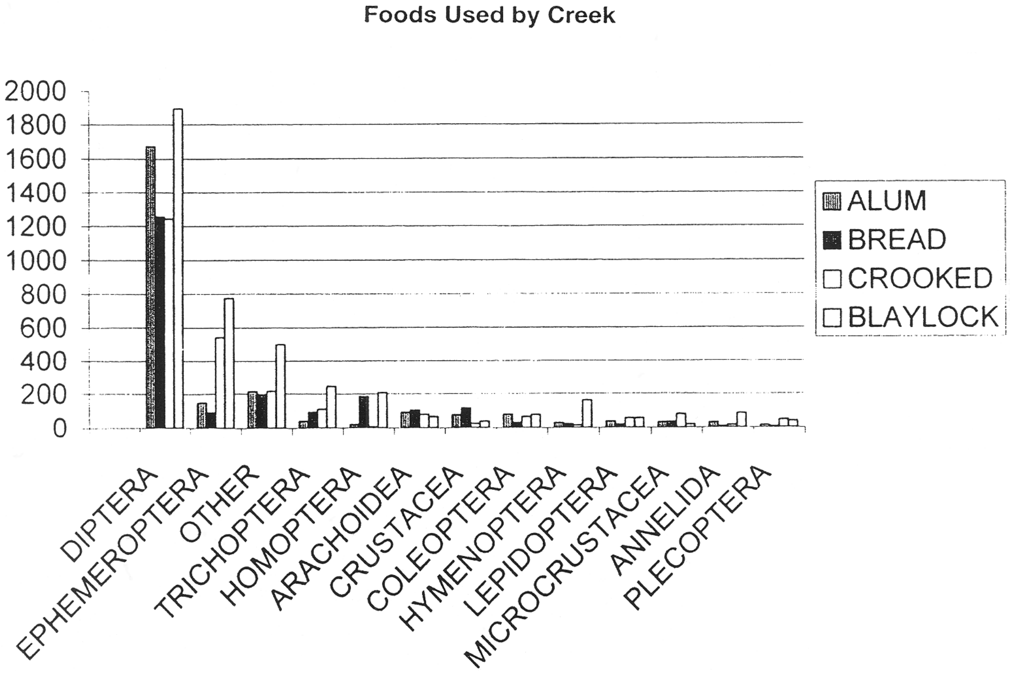

Figure 5—Use of 13 major food categories by fish assemblages across four streams of the Ouachita National Forest. Vertical (Y) axis represents total numbers of each item found an all examined fish stomachs.

are highly similar in diets. They do not in general appear redundant or "substitutable" for each other. For management, this implies intentional or accidental introductions of species are not likely to allow one species to be lost and another gained without potential for trenchant changes in ecosystem function.

Because context-specific diet of fishes influences their potential ecosystem effects, the degree of similarity of trophic effects for fish assemblages in different creeks is another important management consideration. To address this, our entire sample of fish stomach contents was summarized separately in each creek across all four sampling periods (fig. 5). In all four creeks, dipterans dominated in diets of the 21 species (fig. 5), and the "other" category (mostly adult insects) also was important in all creeks. Differences in importance of mayflies (Ephemeroptera) in fish diets appeared to be related to river drainage. Far fewer mayflies were eaten by fish in Alum and Bread Creeks (Saline River drainage) than in Crooked and Blaylock Creeks (Little Missouri drainage). However, mayfly consumption may be related more to typical environmental conditions in the streams than to specific drainage. Alum and Bread Creeks have seasonally intermittent flows (Taylor and others, in press), (Williams and others, in press), whereas Crooked and Blaylock Creeks always exhibited substantial flows during our visits. Persistent flow of the latter streams should favor more consistent availability of mayflies, particularly in riffles (Brown and Brussack 1990) which may dry up periodically in Alum and Bread Creeks. This hypothesis is further supported by the lower occurrence of Trichoptera (caddisflies; also linked to flowing habitats) in diets of fishes in Alum and Bread Creeks than Crooked and Blaylock Creeks (fig. 5). Besides simple taxonomic composition, diversity of diets can reflect breadth of potential impact of a fish assemblage in a stream. However, Shannon-Weiner diversity indices of fish stomach contents (pooled by creek) were not substantially different among creeks, ranging from 1.42 in Alum Creek to 1.81 in Blaylock Creek. Thus, some foods of fishes differed among streams, likely in the context of the environmental setting which influences food availability, but the dominant food item (dipterans) was the same in all four streams.

To assess the degree to which timber harvest or drainage influences overall similarity in fish diets, a Percent Similarity Index (PSI) was calculated for all food items across stomachs in each creek. Within a river drainage, total fish assemblages in harvested and non-harvested creeks showed high similarity in diets. In the Saline drainage, similarity between foods eaten in Alum (non-harvested) and Bread (harvested) Creeks was 85.1 percent. Likewise, the PSI for Crooked (non-harvested) and Blaylock (harvested) Creeks was 71.5 percent. Creeks with similar harvest history, but in different river drainages, also showed high similarity values (harvested, Bread and Blaylock, PSI = 74.5 percent; non-harvested, Alum and Crooked, PSI = 77.0 percent). Thus, there was no evidence that timber harvest histories as defined here influenced similarities or differences in foods eaten by fish assemblages among creeks.

Intraspecific difference in diet is the finest scale of resolution to examine context-specific effects of fishes on stream ecosystems. For selected species, diet was examined to determine if intraspecific differences could be related to timber harvest regime or creeks. For each of the seven most abundant species in our samples, similarity (PSI) was calculated between stomach contents for all individuals in harvested and non-harvested watersheds (within the river drainage where the species was present and/or most abundant, since most species did not occur in all creeks or both drainages). Intraspecific PSI in diet between harvested and non-harvested watersheds was high; five of seven species had PSI values of > 5 percent. Values ranged from a high of 87.8 percent for *Etheostoma radiosum* to as low as 48.0 percent for *Lepomis megalotis*. PSI values for other species were: *Etheostoma whipplei*, 84.7 percent; *Etheostoma collettei*, 81.9 percent; *Semotilus atromaculatus*, 78.5 percent; *Fundulus olivaceus,* 76.2 percent; and *Lythrurus umbratilis,* 63.1 percent. Intraspecific diversity (Shannon-Weiner Index) of diets for these species also was similar in harvested and non-harvested watersheds. There is no compelling evidence from our data set that timber harvest regimes, at the spatio-temporal scale evaluated here, had strong effects on foods consumed by individual fish species. Similarity between streams was highest for the three darter species (*Etheostoma* spp.), which feed primarily on benthic organisms in riffles, and lowest for three species (*Fundulus olivaceus, Lythrurus umbratilis*, and *Lepomis megalotis*) that may feed substantially on surface items (e.g., adult terrestrial insects). It could be speculated that disturbance from timber harvest changes availability of terrestrial insects more than that of riffle dwelling benthic invertebrates, but direct supporting evidence or plausible mechanisms are lacking.

For a single species, patterns were sought in food use within a stream, longitudinally, seasonally, and in regard to harvest regime. The largest sample of stomachs was available for *Etheostoma radiosum*, which is abundant throughout Crooked and Blaylock Creeks. A PCA with raw data standardized within food item was conducted for this species where each sample at a site (Fall 1989; May 1991, when most specimens were available) was ordinated along gradients of the eleven most used food items. PC Axes I and II accounted for 25.7 and 18.0 percent of the variance, respectively, but the results suggested few local patterns in food use. Visual inspection of plots of PC Axis I versus PC Axis II (not shown), revealed no difference in amount of multivariate diet space occupied by *E. radiosum* in either creek but did indicate a slightly greater diet breadth in May than in October. No strong longitudinal patterns in diet were detected. Likewise, diets in extreme headwaters (where few or no other species are present) were not notably different from those at larger, downstream sites.

Fish density and known foods were used to calculate a crude estimate of the number of invertebrates eaten by a local fish assemblage. The estimate is instructive in evaluating direct and indirect impacts fish food consumption may have in these stream ecosystems. In May 1991, Gelwick counted fish by snorkeling while seine sampling was conducted at the 24 field sites. The total counts by seining and snorkeling for the 15 most common species (excluding *Campostoma*) are provided by Matthews (1993). Potential use of invertebrate foods by fish in a 100-m reach of the study streams were estimated for each species as: (individuals/m) x (detection factor) x (food items/stomach) x (feedings/d).

Individuals per meter is the total numbers of a species detected by snorkel or seine (using greatest value) divided by 4800 m of stream sampled (approximately 200 m per site at all 24 sites). A detection factor of four was used to account for undetected individuals. Detection of 25 percent of individuals actually present at a sampling site is reasonable in our judgement, but it is emphasized that an increase or decrease in this factor will drastically change the final estimate. Food items per stomach were based on the average number of items found in stomachs for a species, and feedings per day were estimated as six. Based on food passage times of minnows (Unpublished data. On file with: William Matthews, Professor, University of Oklahoma Biological Station, HC 71 Box 205, Kingston, OK 73439), the observed food items in each stomach were assumed to represent foods ingested in the last two hours before the fish were sampled and for purposes here, represents one feeding. Our use of six feedings per day is derived from studies that show most minnows and darters feed throughout daylight hours (Matthews and others 1982; Surat and others 1982). The resulting product was summed across species, and the sum expressed as invertebrate foods used per 100 m of stream.

Our calculations yielded a crude estimate of 13,144 invertebrate food items consumed by a “typical” fish assemblage (i.e., 15 common species) per 100 m of stream per day. Clearly, this does not reflect reality at any one site but is a very general extrapolation from stomach contents and sites that only broadly represent streams in the Ouachita National Forest. Importantly, even a minor adjustment in assumptions of detection or number of feedings can drastically affect the estimate. However, if 13,000 items per l00 m of stream per day is viewed as an “order of magnitude” estimate, a starting point is established for exploring the degree to which fishes remove invertebrates from these stream systems or the rates of transfer of nutrients from living invertebrates to release in the water column. Exploration of these and similar dynamic rates could be useful in modeling overall trophic effects of fishes in stream ecosystems of the region.

DISCUSSION

Many studies have shown the trophic plasticity of stream fishes, but most also revealed strong relationships between diet and microhabitat use of stream fishes. Mendelson (1975) found, for example, that minnows differed in habitat selection, but fed opportunistically on invertebrates available in those microhabitats. Our findings support the hypothesis of correspondence between microhabitat use by stream fishes and their potential trophic effects within the ecosystem. Importantly, our study also suggests that food use by a species is not fully predictable from taxonomic relationships. We summarize other major findings as follows:

1. Dipterans and terrestrial insects were major food items eaten by fish assemblages in all creeks
2. For 18 major invertebrate food items, individual species were distinctive in feeding habits
3. Major families of fishes were generally distinctive in diets.
4. Similarity in foods eaten was not rigidly related to taxonomic relatedness of species, and closely related species within families are not redundant or substitutable in stream ecosystems.
5. For seven common fish species, diets were 75 percent similar on average between watersheds with little or no timber harvest and those with timber harvest conducted under Forest Service standards and guides in the last 20 yr.
6. Likewise, overall diets were 70 to 85 percent similar between fish assemblages in harvested and non-harvested watersheds.
7. At least one common, widespread species (orangebelly darter) showed little longitudinal or spatial pattern in diets use within a stream.
8. Average food intake by each species, multiplied by estimated densities of the species over all study streams yielded a crude estimate of 13,000 food items eaten per day per 100 m of stream.

Our study produced evidence related to trophic effects of fish in ecosystems. Expanded field and manipulative studies are beginning that ask more detailed questions about functional effects observed from snorkeling observation of feeding, microhabitat use, and behaviors of fishes in these ecosystems. Our goal in the next several years is to expand what is now known about food habits and context to focused experiments linking fish species to stream processes from a functional groups perspective. This experimental approach will eventually incorporate in stream experiments and observations, focused mechanistic experiments, and tests of ecosystem roles of fishes in artificial stream systems.

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