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FEEDING RELATIONSHIPS AMONG SPECIES OF *NOTROPIS* (PISCES: CYPRINIDAE) IN A WISCONSIN STREAM[1]

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Abstract. The relationship between spatial preference and diet in four species of the genus *Notropis* (Pisces: Cyprinidae) was investigated in Roxbury Creek, a small stream in southern Wisconsin. Characteristic spatial distributions for each species were determined from frequency of catch in unbaited minnow traps set at varying heights and locations in the pools of the stream. Data for the year 1966–67 indicate that two species, *Notropis atherinoides* and *N. spilopterus* are common in midwater. *Notropis dorsalis* is most frequently found near the bottom and shows a strong preference for the upstream edge of pools. *Notropis stramineus* is also found most often near the bottom but within the pools themselves. The spatial distributions of aquatic invertebrates, the major prey of *Notropis* in the pools of Roxbury Creek, were also investigated. Data gathered from drift and bottom samples taken in eight sampling periods during 1970–71 suggest a separation between the relatively sedentary bottom fauna, composed of oligochaetes, isopods, several genera of chironomids, tipulids, and trichopterans; and the drift fauna, composed of copepods, chironomids of the subfamily Orthocladiinae, ephemeropterans, and terrestrial arthropods. Certain genera, including the ubiquitous *Gammarus* were found commonly in both drift and benthic samples. Indices of similarity between pool benthos and drift ranged between 7% and 59%. Data on food habits of *Notropis* gathered from stomach content analysis of fishes collected over the same period indicate that 73% of the invertebrate genera present are utilized by *Notropis* species in Roxbury Creek. Considerable overlap exists in the invertebrate genera chosen by the four species (69%–84%), and strong overall correlations between species are found in the importance of various orders of aquatic invertebrates in the diet. Differences in food habits relate principally to differences in space utilization. Midwater species tend to feed on drifting chironomids, copepods, terrestrials, and other animals found in the water column. Bottom-dwelling fishes feed on benthic genera of chironomids, tipulids, oligochaetes, and other organisms found commonly in pool substrates. It is concluded that spatial rather than taxonomic considerations are the chief determinants of prey selection in these four species, and that this pattern of resource subdivision acts to reduce competition in sympatric, syntopic populations of these fishes. Data from other Wisconsin streams, from aquarium observations, and from literature review suggest that multispecific assemblages of mutually responsive species like the ones in Roxbury Creek are common in *Notropis*.

Key words: Benthos; Chironomidae; competition; Cyprinidae; drift; invertebrates; Notropis; *predation; schooling; similarity indices; streams.*

INTRODUCTION

This paper attempts to describe the invertebrate fauna of a small Wisconsin stream and to analyze the pattern of exploitation of this resource by four species of the cyprinid genus *Notropis.*

The partitioning of food resources among closely related species touches on at least two important kinds of ecological interactions: predation and competition. The food-gathering adaptations of a predator must to some degree represent an evolutionary response to the habits of its prey. These adaptations may be influenced as well by the continued presence of other predators feeding on the same resource. Which of the two is more significant in determining the ultimate survival of a species is difficult to specify. It seems reasonable to assume, however in the case of relatively unspecialized predators, that pressures from others at the same trophic level could be of greater importance in determining the composition of the diet than would be the habits of animals actually eaten.

Competition has been defined as "the demand typically at the same time of more than one organism for the same resources of the environment in excess of immediate supply" (Larkin 1956:330). It might be better here to employ the term "potentially competitive" for the relationship among these fishes. To establish competition one must first determine whether the resource sought by the species involved is in fact limiting. In the present study this determination could not be made. Attention is focused rather on the ways in which these different species exploit their common supply of food. It is assumed that if this resource were or ever became limiting, a reasonable prediction could be made as to the outcome of the subsequent competitive process.

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Other questions of importance to the nature of potentially competitive interactions may be suggested: how long, for example, have the species been in contact; how intimate is their association; how extensive geographically is the region of overlap? Such questions touch on the significance of the relationship rather than on its functioning. The interactions of animals only casually or sporadically in contact are clearly less interesting than those of more deeply involved species. In *Notropis*, a very large genus of freshwater fishes, syntopic populations are commonly encountered. Whether the resulting contacts are, as a rule, sufficiently well developed to exert strong selective pressures on participating species can only be guessed at. Nevertheless, examples of this apparently widespread process would seem to be of interest.

In analyzing resource utilization among these four species, I hypothesized that partitioning of the food supply is largely a result of the partitioning of space in areas mutually inhabited, rather than of the active selection of different prey types by the fishes. To test this hypothesis I attempted to describe the spatial distribution both of the invertebrate fauna and of the fishes that prey upon these invertebrates, and then to relate the resulting overlaps in distribution to the diet of each of the four species: *Notropis atherinoides*, the emerald shiner; *N. dorsalis*, the bigmouth shiner; *N. spilopterus*, the spotfin shiner; and *N. stramineus*, the sand shiner.

STUDY AREA

Roxbury Creek, arising in northwestern Dane County and entering the Wisconsin River just west of Sauk City, is about 11 km long. Only the lower 1.6 km was investigated in this study. The upper 9.6 km are dry most of the year, as a result of marshland drainage near the town of Roxbury. The lower portion, however, is fed by springs and flows permanently along the edge of a deep forest; the water is clear, the bottom unsilted. Only at flood stage, mainly in spring, does silt-laden runoff enter the stream from agricultural land bordering the upper reaches. Roxbury Creek enters an undammed portion of the Wisconsin where the river is sand bottomed and free flowing.

The stream is narrow, averaging somewhat less than 4 m in width, and shallow, rarely exceeding 1 m in the deepest pools. Current is gentle, 7.5–20 cm/s in pools, although up to 30 cm/s over shallow areas. During floods, velocities of 52 cm/s have been found.

Originating in springs and flowing through shady woodland, Roxbury Creek is a cool stream, with maximum temperature of about 20° C in midsummer. Its lower reaches remains ice-free in winter. Data on other physical and chemical characteristics of the stream may be found in Poff and Threinen (1962).

The substrate is composed principally of sand interspersed with small patches of gravel. Pools are covered with organic detritus mixed with sand and silt.

Sandy streams, subject to mass movements of bottom material, are generally uniform, but rather unstable environments. In Roxbury Creek, however, the stream bed is partitioned into relatively permanent pools and shallows, largely because the creek interacts with the adjacent forest. Trees, undermined and toppled across the stream, or still standing with their trunks and roots extending into the channel, form semipermanent dams all along Roxbury Creek. In time of flood the scouring water excavates pools behind these obstructions. During normal flow silt, mud, and organic matter are deposited, creating conditions suitable for the rich development of animal life. As Nilsen and Larrimore have noted (1973), fallen trees may themselves serve as substrate for the development of invertebrate communities. The long, shallow, sandy stretches form relatively barren connections between these pockets of biological activity. Similar patterns have developed along most of the small tributaries flowing through the forested bottomland of the lower Wisconsin River.

The growth of aquatic plants appears to be inhibited by the shade of the forest canopy. Rooted aquatics, for example, are absent from wooded portions of Roxbury Creek, although waterweed (*Elodea canadensis*) grows abundantly in unshaded upstream reaches. As a consequence, leaf fall and the fruits and flowers of forest trees become the main source of organic matter on which stream life depends. This aspect of woodland stream ecology has been discussed by Hynes (1960), Elton (1966), Minshall (1967), Mackay (1969), and Cummins et al. (1973). The fauna of the stream, ultimately dependent on leaf fall, is largely confined to the pools, where most of this detritus eventually accumulates.

In spite of the stabilizing presence of fallen trees, the pools in Roxbury Creek are sometimes buried by shifting sands. Although most are eventually reexcavated, the life of any pool is of limited duration, and the animal populations inhabiting it are subject to periodic decimation or displacement.

Between 20 and 30 pools, of various sizes but of similar morphology, may be found at any one time along the 1.6 km of permanent flow in Roxbury Creek. The stations selected for study were representative of conditions in most of these pools, and to a large extent reflect conditions in other small sandy tributaries of the lower Wisconsin River.

INTRODUCTION TO THE ECOLOGY OF *NOTROPIS*

The fish fauna of Roxbury Creek is composed of about 30 species belonging to eight families (Table 1). Most of the species are rare; many, particularly the larger piscivorous fishes, must be considered stragglers from the Wisconsin River only about 1.6 km downstream. Among the exceptions are four species of the cyprinid genus *Notropis*: the emerald shiner, *N. atherinoides*; the bigmouth shiner, *N. dorsalis*; the spotfin shiner, *N. spilopterus*; and the sand shiner, *N. stramineus*. Vast numbers of these four species may often be found in the small pools of Roxbury Creek. The two other species of *Notropis* collected from Roxbury Creek were less common. Schools of *N. atherinoides* often harbored small numbers of *N. blennius*. *Notropis cornutus* was collected only once.

Notropis is the largest genus of freshwater fishes in North America; 97 species have been described (Blair et al. 1968). The genus is thought to be of monophyletic origin (Bailey, *pers. comm.*), but has been divided into a varying number of subgenera, usually nine, by different authors (summarized in Jordan and Evermann 1896). Only a few of these subgenera, particularly *Cyprinella*, exhaustively treated by Gibbs (1957*a*, *b*) and the subgenus *Notropis* (Snelson 1968), have received detailed examination.

Originally the genus was restricted to North America east of the Rocky Mountains, but introductions have been made on the West Coast (Blair et al. 1968, Branson 1968). In general, the greatest number of species occur in the Mississippi-Missouri drainage, with lesser numbers to the east and west. Many endemic species have been reported from streams emptying directly into the Atlantic in the Southeastern states (Gibbs 1957*a*, Howell and Williams 1971). Eighteen species are recorded from Wisconsin (Johnson and Becker 1970).

Morphology

Notropis appear generally silvery, with a dark lateral band in some species. As in other cyprinids the jaws are toothless, but pharyngeal teeth in one or two rows are found. The teeth are usually sharp-pointed, hooked, with narrow grinding surfaces (Jordan and Evermann 1896), suggesting a carnivorous diet.

Several other morphological features also appear to be correlated with the food habits of these fishes. Among these is the color of the peritoneum, usually silvery, but black in one herbivorous species, *N. mekistocholas* (Snelson 1971). Similarly, the intestinal tract is short and S-shaped in carnivorous species, but long and coiled in herbivorous types (Snelson 1971). The size, shape, and location of the mouth is useful both in the identification and in the ecological characterization of members of this genus (Hubbs 1941).

TABLE 1. Fish fauna of Roxbury Creek

Taxon	Common name
Catostomidae	
Carpoides sp.	Carpsucker
Catostomus commersonni (Lacepede).	White sucker
Cyprinidae	
Cyprinus carpio Linnaeus	Carp
Campostoma anomalum (Agassiz)	Stoneroller
Rhinichthys atratulus (Hermann)	Blacknose dace
Nocomis bigutatta (Kirtland)	Hornyhead chub
Semotilus atromaculatus (Mitchell)	Creek chub
Chrosomus erythrogaster (Rafinesque)	Southern redbelly dace
Clinostomus elongatus (Kirtland)	Redside dace
Notemigonus chroysoleucas (Mitchell)	Golden shiner
Pimephales notatus (Rafinesque)	Bluntnose minnow
Pimephales promelas Rafinesque	Fathead minnow
Hybognathus hankinsoni Hubbs	Brassy minnow
Notropis cornutus (Mitchell)	Common shiner
Notropis atherinoides Rafinesque	Emerald shiner
Notropis spilopterus (Cope)	Spotfin shiner
Notropis blennius (Girard)	River shiner
Notropis stramineus (Cope)	Sand shiner
Notropis dorsalis (Agassiz)	Bigmouth shiner
Ictaluridae	
Ictalurus natalis (LeSueur)	Yellow bullhead
Ictalurus melas (Rafinesque)	Black bullhead
Umbridae	
Umbra limi (Kirtland)	Central mudminnow
Esocidae	
Esox americanus LeSueur	Grass pickerel
Percidae	
Perca flavescens (Mitchell)	Yellow perch
Percina maculata (Girard)	Blackside darter
Etheostoma nigrum Rafinesque	Johnny darter
Centrarchidae	
Micropterus salmoides (Lacepede)	Largemouth bass
Lepomis macrochirus Rafinesque	Bluegill
Gasterosteidae	
Culaea inconstans (Kirtland)	Brook stickleback

Each of the four species in Roxbury Creek belongs to a different subgenus (Jordan and Evermann 1896). Thus, within the genus the four are not closely related. Subgeneric differences, however, are relatively slight in comparison with the similarities uniting this taxonomically difficult group.

Notropis atherinoides, subgenus (*Notropis*), is somewhat compressed laterally and is the most slender of the four species. It has a short snout and a terminal, oblique mouth; the eye is large. In Roxbury Creek *N. atherinoides* ranged from 30 to 80 mm in standard length.

Notropis spilopterus, subgenus (*Cyprinella*), is similarly compressed, but has a deeper body. The mouth is also oblique and terminal; the snout acute. Standard lengths of Roxbury Creek specimens ranged from 29 to 71 mm.

Notropis stramineus, subgenus (*Alburnops*), is rather stout in comparison to *N. spilopterus* and *N. atherinoides*. The mouth is subterminal and only slightly oblique; the snout is blunt. The eyes are lateral. In Roxbury Creek *N. stramineus* ranged from 28 to 56 mm in standard length.

Notropis dorsalis, subgenus (*Hudsonius*), is compressed dorsoventrally. The head particularly is long and flattened. The mouth is ventral, horizontal rather than oblique, and large. The eyes have a somewhat greater dorsal field than those of the other three species. Standard lengths of *N. dorsalis* in Roxbury Creek ranged from 31 to 60 mm.

All four species are silvery and lack lateral bands. Both *N. dorsalis* and *N. stramineus*, however, have iridescent gold dashes along the dorsal midline behind the dorsal fin, a characteristic facilitating recognition in the field. All species possess short S-shaped digestive tracts and silvery peritoneums.

It appears that these four species form a series with respect to body shape. *Notropis atherinoides* and *N. spilopterus* are both laterally compressed. *Notropis stramineus* with its robust, uncompressed body lies midway between these two and the dorsoventrally compressed *N. dorsalis*. A parallel series exists with respect to the location of the mouth. *Notropis atherinoides* and *N. spilopterus* have terminally placed, oblique mouths, whereas the mouth of *N. stramineus* is subterminal and only slightly oblique; *N. dorsalis* has a ventral, horizontal mouth.

The relationship of characters such as these to habitat has been discussed by Hubbs (1941) and Keast and Webb (1966). Hubbs, in an illuminating paper dealing with three of these species—*N. atherinoides*, *N. stramineus*, and *N. dorsalis*—suggests that dorsoventral flattening and ventral mouths are associated with bottom-dwelling, bottom-feeding habits. while lateral compression together with terminal mouth placement generally implies a free-swimming mode of existence.

Habitat

The ranges of the four species broadly overlap, especially in the upper Mississippi Valley: southwestern Wisconsin, southern Minnesota, Illinois, Iowa, northern Missouri, and northwestern Kansas Distributional data may be found in Trautman (1957) and Hubbs and Lagler (1958).

Notropis atherinoides, which has the most extensive range of the four species, characteristically inhabits larger bodies of water, the great rivers and lakes (Trautman 1957, Cross 1967, Pfleiger 1971). Although the emerald shiner is found most often in midwater (Trautman 1957), Cross (1967) suggests a preference for sand bottoms. The species is common to abundant in the larger lakes of Wisconsin as well as in the lower Wisconsin and Mississippi rivers (Johnson and Becker 1970).

Although characteristic of large rivers, emerald shiners often ascend small tributaries, particularly in fall and spring (Trautman 1957). This movement may be influenced by temperature differences between the river or lake and the tributary stream (Campbell and MacCrimmon 1970).

Notropis dorsalis is a characteristic inhabitant of streams in the prairie regions. Its present distribution has in fact been correlated with a previous advance of prairie in the last xerothermic period. The small isolated populations of *N. dorsalis* in the east, the subspecies *N. d. keimi* is thought to be a relict of this earlier, drier time (Trautman 1957).

It is generally agreed that *N. dorsalis* reaches maximum abundance in the smaller sand-bottomed streams, and is less common in the larger rivers (Simon 1946, Cross 1967, Pfleiger 1971). Starrett (1950*a*), however, considered *N. dorsalis* the third most abundant minnow in the Des Moines River, a stream 125–200 ft in width. Here *N. dorsalis* was sometimes collected over recently covered sandbars, suggesting an ability to make use of newly formed habitats. In Wisconsin, Johnson and Becker (1970) report *N. dorsalis* to be common in sandy streams of medium size in the Mississippi drainage.

Both *N. spilopterus* and *N. stramineus* appear to prefer streams of moderate size and seem generally less rigorous in their choice of habitat.

Notropis spilopterus is found in streams of all sizes in Missouri (Pfleiger 1971), but appears in other regions to prefer medium- to large-sized rivers (Starrett 1950*a*, Johnson and Becker 1970). The spotfin is found over rubble and gravel bottoms (Cross 1967, Pfleiger 1971) but is more commonly reported over sand (Hankinson 1930, Greene 1935, Becker 1966). In southwestern Wisconsin *N. spilopterus* is most common in streams with sand bottoms.

Notropis stramineus, a species characteristic of prairie regions, also appears capable of living successfully in a broad range of habitats. Medium-sized streams, however, contain the largest populations (Starrett 1950*a*, Trautman 1957, Pfleiger 1971). *Notropis stramineus* is found most often over sand.

This survey suggests that, paralleling differences in morphology among these four species, there is a gradient of preference for habitat as well. *Notropis atherinoides* is most abundant in the largest rivers and lakes; *N. spilopterus* and *N. stramineus*, found in streams of all sizes, most characteristically inhabits streams of moderate size; *N. dorsalis* reaches maximum abundance in the smaller streams.

The preference of *N. stramineus* and *N. dorsalis* for sandy substrates is mentioned by many observers. Less clear are the substrate requirements of *N. atherinoides* and *N. spilopterus*, although they are often found over sand. All four species live most successfully in streams and rivers of slow-to-moderate current.

Associations among species of Notropis

Notropis species show a strong tendency to school. Frequently the large aggregations found in open water contain several species. An examination of collections housed at the University of Wisconsin Zoological Museum and of notes from the University of Wisconsin Field Zoology course filed in the museum suggests that multispecific assemblages of *Notropis* are common. Of 291 collections in which at least one species of *Notropis* was present, over 60% contained two or more species. About one-third of the collections contained three or more, and 26 collections were composed of five or more species of *Notropis*. The number of species, of course, generally increases with the size of the stream and the intensity of sampling, the latter detail usually not quantified by collectors. Nevertheless, it appears that positive associations among species in this genus do occur frequently. The co-occurrence of *Notropis* species is also suggested by the data of Breder and Crawford (1922), Snelson (1968, 1971, 1973), Davis and Louder (1971), Howell and Williams (1971), F. B. Cross (*pers. comm.*), and W. L. Pfleiger (*pers. comm.*), among others.

It is not possible to conclude from information gathered principally by seining that real interactions among species are taking place in such assemblages. Observations made in aquaria, however, suggest that *Notropis* species are mutually responsive, individuals of one species readily following those of another. By and large, fishes of several species held in aquaria act as a single school. In experiments involving three *Notropis* species, pairs either of the same or of different species were observed for evidence of schooling behavior in 114-liter aquaria (Table 2). The total length of time that one fish followed, swam parallel to, or turned simultaneously with the other served as the measure of such behavior during 10-min observation periods.

TABLE 2. Schooling behavior of *Notropis*. Each pair of fishes was observed for 10 min. The total length of time that parallel swimming, following, or simultaneous turning occurred served as the measure of schooling behavior

Species	Number of pairs observed	Mean schooling time (min) (± 95% limits)
N. dorsalis	10	8.8 ± 0.7
N. stramineus	8	7.3 ± 1.7
N. spilopterus	11	6.0 ± 1.7
N. dorsalis–N. stramineus	8	7.2 ± 1.5
N. dorsalis–N. spilopterus	10	6.7 ± 1.6
N. spilopterus–N. stramineus	11	4.6 ± 1.5

Notropis dorsalis was the most responsive of the three species both to conspecifics and heterospecifics, whereas *N. spilopterus* schooled least often. In general, fishes showed less interest in members of other species than of their own. The strength of this interest, however, was roughly proportional to the responsiveness shown to conspecifics. Congeneric pairs including *N. dorsalis*, for example, schooled more frequently than congeneric pairs including *N. spilopterus*.

Collections made in regions of sympatry suggest that association among these species occurs with fair regularity. Cross (1967) finds *N. dorsalis* and *N. stramineus* common associates in Kansas streams. In Canada, where *N. dorsalis* has recently been reported for the first time, Fedoruk (1971) lists *N. stramineus* as a common associate. Similar observations have been made by Pfleiger (*pers. comm.*), who often finds these species together, along with *Notropis lutrensis* and *N. umbratilis*. Starrett (1950*a*) comments that *N. stramineus* and *N. dorsalis* commonly associate with *N. spilopterus* in the Des Moines River.

Trautman (1957) mentions large aggregations of *N. atherinoides* and *N. volucellus* in the Ohio River. In the Wisconsin River, *N. atherinoides* often appears in collections with *N. volucellus*, *N. blennius*, and *N. spilopterus*.

It is in the small- to moderate-sized tributaries of the lower Wisconsin River that we find the association among these four species most highly developed. At least three and usually all four species are found together in parts of Duck and Prentice creeks (Columbia County), Roxbury Creek, and a small unnamed creek west of Roxbury Creek (T9N, R6E, S22, Dane County), Honey Creek (Sauk County) Gran Crae Creek (Crawford County), and the Big Green River, (Grant County). These streams are

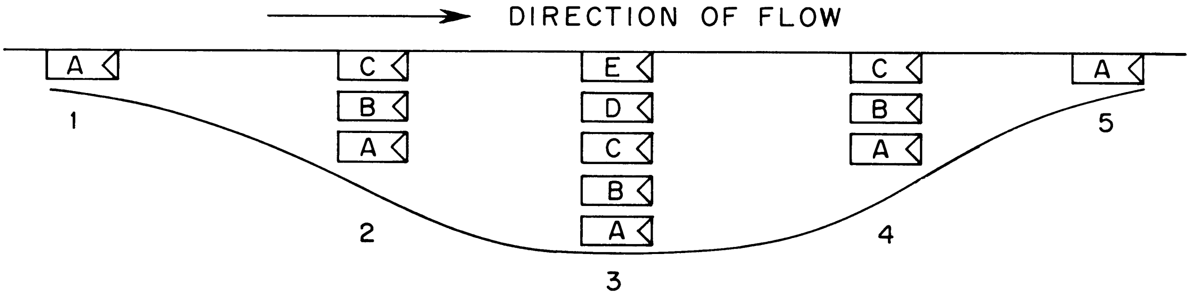

FIG. 1. Arrangement of fish traps in longitudinal section through an idealized pool.

tributaries of the lower Wisconsin. The four species have also been reported together from many collections made in the Wisconsin River itself (Becker 1966).

The ecological significance of this information is not easy to assess. The association of these four species is most frequently encountered in small sandy tributaries of large rivers, a kind of habitat repeated with some regularity along the lower Wisconsin. Such areas, because of their proximity to large rivers, tend to be invaded by species common in the rivers. *Notropis atherinoides* in particular has a propensity for such movements. Because these streams are relatively small and have sand bottoms, they are capable of supporting such species as *N. dorsalis* which prefer such habitats. In this sense, streams like Roxbury Creek are analogous to the "edge habitats" of terrestrial ecology, the importance of the associations among animals living there being directly related to the stability of the habitat and to the frequency with which it recurs.

Each species seems to have morphological adaptations, particularly in mouth location and body shape, sufficiently different to permit coexistence. Moreover, these characters vary from species to species in a regular way. The co-occurrence of four species differing from one another in this fashion strongly suggests an association going beyond chance. Nevertheless, in view of their rather distant relationship within the genus, these animals would seem more likely to be preadapted for coexistence rather than molded by mutual interaction into a functioning unit. The fact that each species reaches maximum abundance in habitats slightly different from those most favorable to the others also suggests that the regular variation in morphological features, however advantageous to their continued coexistence, is not the result of a long history of mutual contact.

Regardless of the interpretation we place on the character of the relationship, it is a fact that year after year large populations of these four *Notropis* species can be found living together in the pools of small Wisconsin streams.

SPATIAL AND TEMPORAL DISTRIBUTION OF FISHES IN ROXBURY CREEK

Methods

Data on the spatial distribution of *Notropis atherinoides*, *N. dorsalis*, *N. spilopterus* and *N. stramineus* were collected for 1 yr (fall 1966 to fall 1967) from six pools in Roxbury Creek. Unbaited fish traps were placed at specified depths and locations within each of the pools. The capture of individuals of a certain species in a trap was considered evidence that the individuals were swimming in the area of the trap. Characteristic spatial distributions for each species were derived from the relative frequency of capture in traps set at different depths or in different locations.

Rectangular traps made of one-fourth in. hardware cloth, 50 cm wide, 12.5 cm high and 30.5 cm long, with a single round opening facing downstream were arranged in a vertical series 5 cm apart. Traps were attached at the proper heights to a frame set permanently in the stream bottom. Changes in water level were compensated for by the addition or removal of the topmost trap. The others remained fixed relative to the bottom and to each other.

Series of traps were placed in five different locations in each pool: the upstream edge, the downstream edge, the deepest part of the pool, and two locations of intermediate depth, one upstream, the other downstream from the deepest point. The arrangement of traps in an idealized pool is shown in Fig. 1. Traps placed at the downstream edge of the pools were ineffective in capturing fishes and are not considered in further calculations. Although the distributions of fishes in traps set at intermediate depths are consistent with distributions determined from traps set at the deepest point, there is no unambiguous way to combine these sets of data. In the discussion of vertical distribution, data are used only from traps set in the water column at the deepest point. Basic data on the arrangement of fishes in the pool is expressed as the relative frequency of capture along two axes: a longitudinal one, from the head of the pool through

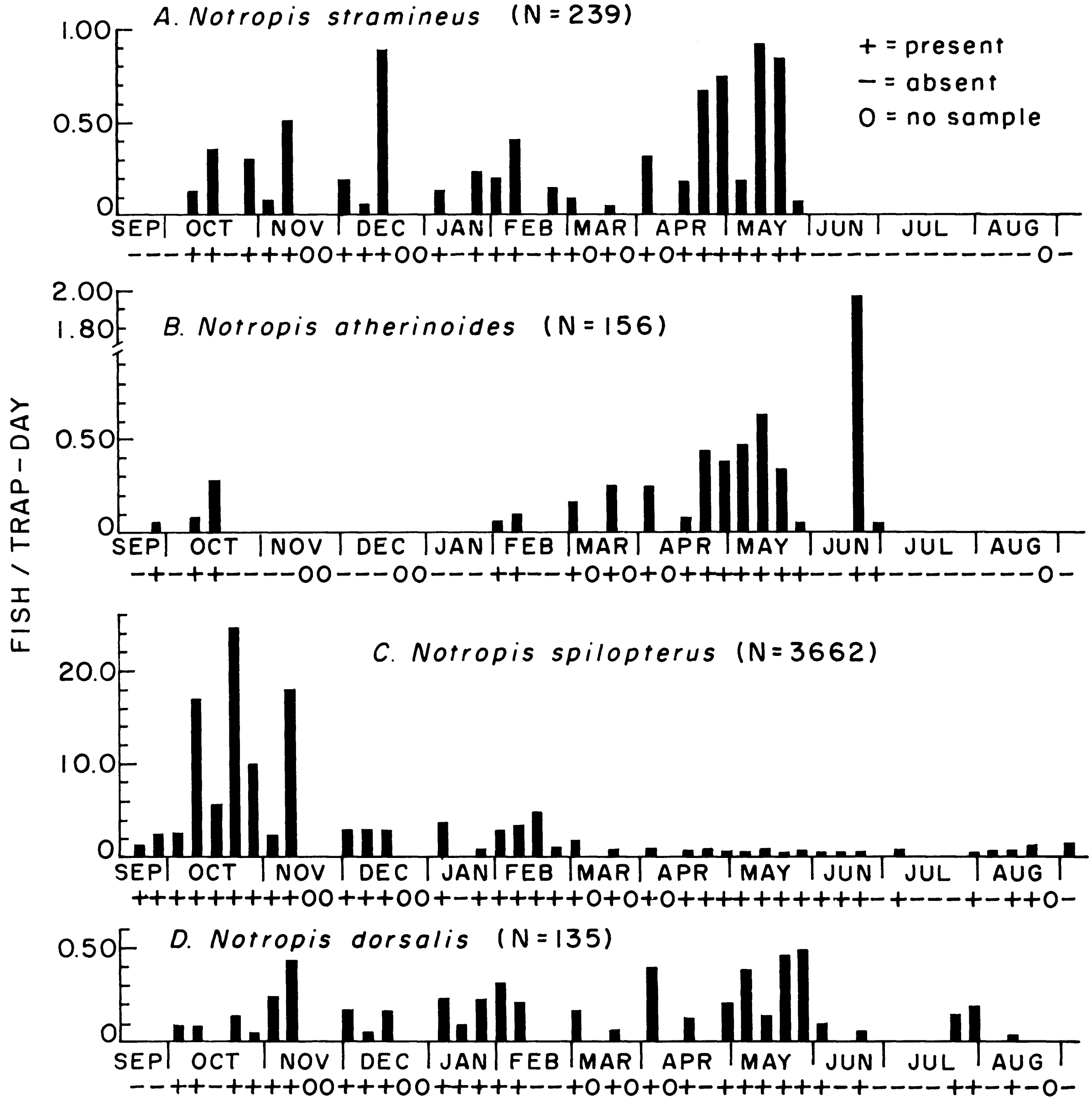

FIG. 2. Seasonal distribution of *Notropis* as indicated by weekly trapping returns. Data are expressed as numbers of fish per trap day. The number of trap days in any week is equal to the product of the number of traps set and the number of occasions traps were examined during that week. In data on presence, "+" below the x-axis indicates the presence of fishes; "–" indicates that no fishes of that species were trapped; "0" indicates that samples were not taken during that week. NOTE: Scale on y-axis differs among species.

the pool proper, and a vertical one, depth of capture within the pool.

Only two pools were trapped at any given time during the study. From time to time pools became unsuitable for further trapping, usually as a result of lowering water levels, filling-in of the pools, or the disappearance of fishes. Traps were examined and reset at dawn and dusk 2 days each week in each pool for the entire year. Fish were removed from the traps, identified, counted, and returned to the stream. Numbers of fish caught during the day or at night are considered suggestive of activity patterns among the four species.

Information on seasonal distribution is derived principally from trap records in 1966–67 and from visual observation throughout the years 1966–71. During this period pools were also sampled with a 15-ft, one-fourth in. mesh nylon seine. Although

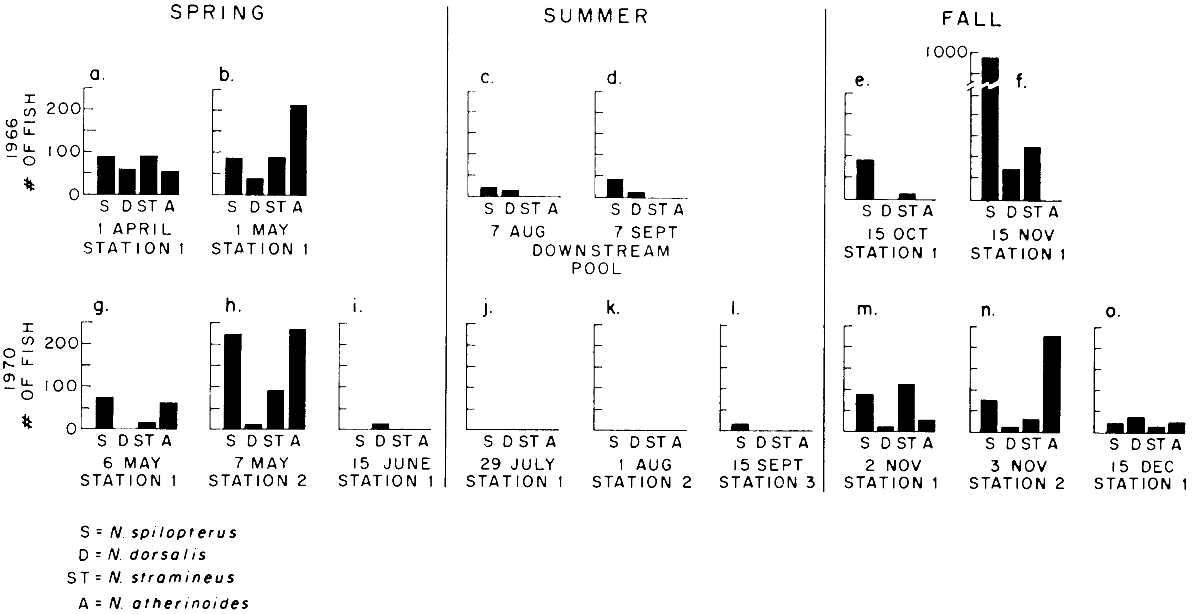

FIG. 3. Seasonal distribution of *Notropis* as indicated by seine collections. In general, 3 seine hauls were made in each pool. Collections in 1966 were taken from Station 1 or from a pool downstream from Station 1. In 1970, collections were taken from Stations 1 and 2 with the exception of collections made on September 15 at Station 3.

the number of seine hauls was not fixed in advance, three passes through a pool was generally sufficient to obtain a quantitatively representative sample.

In an attempt to determine whether the same fish were continually reappearing in the traps, fish were marked by fin-clipping for several weeks both in 1966 and in 1967. On 4 April 1966, 302 individuals representing all four species in roughly equal numbers were marked. Only 3% were recaptured on May 7 of that year. No significant differences in percentage recapture among species were noted. In the spring of 1967, 205 individuals were marked. During the following 3 mo of weekly trapping not one marked *Notropis* was recovered. The data suggest that repeated trapping of the same individuals has little effect on the data. The possibility that fin-removal had serious ill effects on fishes was discounted: aquarium-held animals showed no adverse response to such treatment. Pools were seined periodically during the course of trapping to insure that each species was secured in reasonable proportion to its abundance in the pools as measured by the sum of the frequency of capture in all traps.

Results

Seasonal distribution.—Seasonal changes in the numbers of *Notropis* in Roxbury Creek result primarily from periodic movement of fishes to and from the Wisconsin River. Significant upstream migration of most species occurs in both fall and spring (Fig. 2). Summer populations, on the other hand, are low, suggesting downstream migration in late spring. In winter, populations vary from species to species, although in 1966–67 the numbers declined overall.

The abundance of fishes in the stream is also related to annual variation in the size of river populations, information difficult to obtain with accuracy. Seasonal patterns are probably best expressed, therefore, by data on presence—whether a species occurred at all in a sample—and not by the number

TABLE 3. Results of Runs Test applied to seasonal distribution of *Notropis*. A run is defined as a succession of identical symbols that are followed and preceded by different symbols or no symbols. For large samples a good approximation to the sampling distribution of r (the number of runs) is the normal distribution with

$$\mu_r = \frac{2n_1n_2}{n_1+n_2} + 1 \text{ and } \sigma_r = \sqrt{\frac{2n_1n_2(2n_1n_2 - n_1 - n_2)}{(n_1+n_2)^2(n_1+n_2-1)}}$$

where n_1 = number of elements of one kind and n_2 = number of elements of the other kind (Siegel 1956).

Species	Weeks present (n_1)	Weeks absent (n_2)	Runs	Z	p
N. stramineus	23	19	9	−4.07	$<.01$
N. atherinoides	17	25	11	−3.28	$<.01$
N. spilopterus	37	5	7	0.63	NS at .01
N. dorsalis	28	14	15	−1.66	NS at .01

actually caught (Fig. 2). Data on the presence of species in weekly trapping periods during 1966–67 were tested for significance by the Runs test (Table 3), which distinguishes two types of ordered sequence from the random. Distributions with significantly fewer runs than would be expected by chance imply the action of long-term or seasonal factors (Siegel 1956); distributions with a large number of runs suggest the influence of short-term or cyclic phenomena (MacArthur 1958). *Notropis stramineus* and *N. atherinoides* illustrate the former alternative, the seasonal influence being most strikingly expressed in summer, when neither species was collected from Roxbury Creek. This same pattern was noted also in 1966 and in 1970 (Fig. 3 c, d, j, k, l). *Notropis stramineus*, although trapped in varying numbers, occurred with considerable regularity during the rest of the year. *Notropis atherinoides* appeared more erratically. In the fall and winter of 1966, huge schools occupied the lower reaches of Roxbury Creek, but failed to move upstream into the pools under study. In the fall of 1970, however, *N. atherinoides* was common in these same upstream locations (Fig. 3 m, n, o).

The seasonal distributions of both *N. spilopterus* and *N. dorsalis* were random in 1966–67 (Table 3). *Notropis spilopterus*, while showing striking variation in abundance, was present throughout most of the year. The enormous numbers that moved into Roxbury Creek in the fall of 1966 (Fig. 3 f) were gradually reduced during the remainder of the year until late summer 1967, when the slight indication of future increase was noted (Fig. 2). In fall 1970, upstream migration was less marked than in 1966, but spring populations appeared somewhat larger (Fig. 3 g, h).

Small populations of *N. dorsalis*, generally the least common of the four species, persisted in Roxbury Creek throughout 1966–67 (Fig. 2 d). Even in summer, when other species populations were reduced, a few *N. dorsalis* were collected (Fig. 2 d, Fig. 3 c, d). The regular occurrence of this species in 1966–67 suggests the possibility of a small resident population.

June to August is thought to be the main breeding period of these fishes in the north central states (Starrett 1951). In view of their absence from Roxbury Creek during the summer months, it appears unlikely that any of the four species, with the possible exception of *N. dorsalis*, breeds in the stream. Starrett's excellent analysis of the effect of water levels on breeding success (also Moore 1944) suggests that recruitment is not directly dependent on events in the stream, but rather is determined by conditions in the river.

Nevertheless, periods of abundance in tributary streams, occuring as they generally do in spring and fall, may well be significant to the overall success of these fishes in the lower Wisconsin River. High populations are found in Roxbury Creek throughout the spring, presumably a period of intense feeding before spawning, and again in fall and early winter when food resources appear to be considerably reduced.

Diel activity.—If the number of fishes actually caught in a trap period can be considered a measure of their general activity level during that period, then from the relative numbers of each species caught during the day or the night, we can obtain some information on diel patterns of activity in these fishes.

Notropis dorsalis ($n = 76$, $\chi^2 < .01$) and *N. atherinoides* ($n = 143$, $\chi^2 < .01$) were trapped more frequently at night in Roxbury pools; *N. spilopterus*, on the other hand, was trapped more often during the day ($n = 2{,}686$, $\chi^2 < .01$). No difference is apparent in the behavior of *N. stramineus* ($n = 209$, $\chi^2 > .05$).

All species showed a tendency to appear in "exposed" traps at night. These traps—located in shallow water or near the surface in deeper water—caught relatively more fishes of all species at night than during the day. Increased immunity from terrestrial predators, and the presence of emerging insect larvae may contribute to this. An analogous movement of *N. spilopterus* into shallow water at night in the Des Moines River has been noted by Starrett (1951). Nighttime activity in *N. atherinoides* has been described by Trautman (1957) and Campbell and MacCrimmon (1970).

These data should nevertheless be interpreted with caution. It is not clear, for example, why fish enter unbaited minnow traps at all, nor is it known precisely when in the course of a day's or night's trapping the majority of the animals are caught. Turning on a light in a darkened aquarium room, one invariably finds all four species resting quietly on the bottom. It is only after several minutes of highly disorganized movement that the sluggish fishes resume their normal patterns of behavior. It would seem more probable, therefore, that nighttime capture is an indication of crepuscular rather than truly nocturnal activity.

Spatial distribution.—Seining data, trapping data, and visual observation indicate that in Roxbury Creek *Notropis* species are found almost without exception in the pools, those deposition areas whose morphology has already been discussed. Some preliminary general comments, based on field observations, may help to orient the reader about the spatial distribution in these pools.

At times of peak population in the stream, not only the relatively permanent pools, but also marginal areas—pockets formed behind small branches and troughs connecting pool to pool—are occupied by fishes. Rarely are fish seen swimming over the bare, sandy stretches between pools, and even then they are usually moving from one pool to another. During such times they take advantage of ripples in the sand bottom, resting briefly on the lee sides and darting rapidly from one ripple to another. Only once was a species found to remain for any length of time in such an area. Several *N. dorsalis* were observed by flashlight on an evening in March 1969 moving slowly over these sandy stretches, remaining stationary behind a sand ripple for short periods, then moving on unhurriedly to another. The propensity of *N. dorsalis* for sand flats has been mentioned by Hubbs and Walker (1942).

In the pools fish remain in loose aggregations facing the current. This orientation is usually very precise; it occurs not only in the channel, where most of the fishes are found, but also outside the main thread of the current in eddies near the bank. Very often subsurface eddies can be detected only by the orientation of fishes to the circular pattern of water flow. Fish do not maintain themselves in a stationary position in the channel, but characteristically swim upstream a short distance, then drift backward a similar distance and repeat their forward movement.

It is possible, by careful observation, to distinguish different species in the pools, principally by the breadth of the dorsal aspect and by the nature of the middorsal stripe. Overt interactions between individual fishes of the same or different species are not common. If the fishes remain in species-specific schools this is not apparent from streamside observation.

Sometimes fishes are seen close to or actually feeding on the bottom, but in general the aggregation is well dispersed in the water column, and directional feeding movements are rarely noted.

From time to time small groups break off from the main mass of fishes in a pool and begin hesitantly to move upstream. The slightest disturbance sends them racing back to the pool. Movements upstream generally follow troughs at the bank edge of the stream. The fish move in a long line, several abreast. Very infrequently does a broad wave of fishes move out over wide stretches of sand.

Although it is difficult to generalize from field observations made on shy animals in an environment often rendered opaque by shifting light conditions, the dominant impression conveyed by these animals to an observer is one of patient waiting. For long periods individual fishes, always oriented into the current, may move only short distances upstream and downstream, apparently neither feeding nor interacting with their fellows. The purpose of trapping these animals, then, was to determine if, within this assemblage structured seemingly only by the direction of current flow, subpatterns of spatial preference among the four species could be detected.

TABLE 4. Results of Kolmogorov-Smirnov one-sample test comparing expected and observed cumulative frequency of capture of *Notropis* at different depths and locations

Frequency of capture	*Notropis atherinoides* Trap depth					
Cumulative percentage	A	B	C	D	E	F
Expected	16.7%	33.4%	50.1%	66.8%	83.5%	100.0%
Observed	20.3%	63.7%	84.0%	96.4%	100.0%	100.0%
|O–E|	3.6%	30.3%	33.9%	29.6%	16.6%	. . .

$N = 123$

$D = (\max |O-E|) = .339$

$p = < .01$

Cumulative percentage	Trap location 1	2	3	4
Expected	25%	50%	75%	100%
Observed	23%	30%	85%	100%
|O–E|	2%	20%	10%	. . .

$N = 156$

$D = .200$

$p < .01$

	Depth			Location		
Species	*N*	*D*	*p*	*N*	*D*	*p*
N. atherinoides	123	.339	< .01	156	.200	< .01
N. dorsalis	47	.564	< .01	135	.300	< .01
N. spilopterus	2,252	.035	< .01	3,662	.160	< .01
N. stramineus	132	.478	< .01	239	.220	< .01

Spatial preferences were measured along two axes. Data averaged from all traps at locations 1, 2, 3 and 4 (Fig. 1) measure preferences among the species along a longitudinal axis, from the head of a pool, or shallows region, through the pool itself. Data from traps positioned in the deepest part of a pool, location 3, measure preferences in a vertical direction, the height above the bottom at which fishes of each species are most commonly found.

Deteriorating conditions sometimes necessitated the transfer of traps from one pool to another. As a result, data from some pools, principally those trapped for short periods of time, are less than complete. In order to describe the characteristic spatial distributions of the four species, therefore, I combined data from each of the six pools. (Complete data on the distribution of species in each pool are included in Appendices I, II, and III.)

Comparisons between the distribution of individual species and hypothetical random distributions

TABLE 5. Results of Kolmogorov-Smirnov two-sample test comparing observed cumulative frequency of capture of pairs of *Notropis* species at different trap depths and locations

Cumulative percentage	Trap depth A	B	C	D	E	F
N. atherinoides (123)	20.3%	63.7%	84.0%	96.4%	100.0%	100.0%
N. dorsalis (47)	73.1%	88.4%	97.3%	100.0%	100.0%	100.0%
D	52.8%	14.7%	13.3%	3.6%	. . .	. . .

$$\chi_2^2 df = 4D^2\ \eta_1\eta_2/\eta_1\eta_2 = 4(.528)^2\ (123)(47)/123 + 47 = 38.0$$

$$P < .01$$

Species pair	Depth D	Depth χ_2^2df	Depth *P*	Location D	Location χ_2^2df	Location *P*
N. atherinoides–N. dorsalis	.528	38.0	$< .01$	.420	28.6	$< .01$
N. atherinoides–N. spilopterus	.491	$>$ 110.0	$< .01$	.140	12.0	$< .01$
N. atherinoides–N. stramineus	.442	50.0	$< .01$	.260	25.0	$< .01$
N. dorsalis–N. spilopterus	.738	100.0	$< .01$	.380	56.0	$< .01$
N. dorsalis–N. stramineus	.093	0.09	$> .50$	.340	39.0	$< .01$
N. spilopterus–N. stramineus	.645	$>$ 210.0	$< .01$	.120	11.2	$< .01$

(equal numbers at each trap location or depth) were tested for significance by the Kolmogorov-Smirnov one-sample test (Table 4). This test compares observed and expected cumulative frequency distributions. The point at which the two distributions show the greatest divergence is determined. Reference to the sampling distribution indicates whether such a large divergence is likely on the basis of chance. Differences between pairs of species in spatial distribution along both longitudinal and vertical axes were tested by the Kolmogorov-Smirnov two-sample test (Table 5). Observed distribution of all species differed from expected at 0.01 level. No seasonal differences in the spatial preferences of any species could be detected.

Vertical axis (Fig. 4).—Both *N. dorsalis* and *N. stramineus* were found most often in traps on the bottom (A-level). No significant differences in the vertical distribution of these two species was found (Table 5). *Notropis stramineus*, trapped with greater frequency in midwater, nevertheless appeared less rigidly committed to a benthic existence than did *N. dorsalis*. *Notropis atherinoides* and *N. spilopterus*, on the other hand, were more commonly collected in midwater traps than on the bottom. The latter species in particular demonstrated a clear preference for midwater. The data on the distribution of *N. atherinoides*, whose midwater and surface-dwelling habits have been mentioned by both Trautman (1957) and Cross (1967), must be interpreted cautiously. This species appeared in numbers in Roxbury Creek only in spring, and even then its presence was spotty. Almost 40% of all *N. atherinoides*, for example, were captured in a single trap on the morning of 12 June 1967. This event, possibly reflecting some form of contagious behavior in a strongly aggregating species, affects data on the distribution of *N. atherinoides* to a disproportionate degree.

Longitudinal axis (Fig. 4).—Trapping data indicate a strong preference in *N. dorsalis* for shallow-water areas upstream from the pools (location 1), a preference previously suggested by Hubbs and Walker (1942) and Starrett (1950*a*). The other three species were more commonly trapped within the pool itself (locations 2, 3, 4).

Subpatterns reflecting spatial preference among the four species do apparently exist within the superficially undifferentiated assemblages of fishes in the pools of Roxbury Creek. A possible morphological basis for maintaining particular spatial patterns, involving the relative size of the swim bladder, has been suggested for species in the cyprinid genus *Rhinichthys* (Gee and Northcote 1963, Gee and Maclean 1972). Of the four, *N. dorsalis* is most likely to be found near the bottom and in shallow water. *Notropis stramineus* is likewise most common near the bottom, but exhibits a preference for the pool itself rather than shallow water. Both *N. spilopterus* and *N. atherinoides* appear to be midwater inhabitants in the pools, with the former tending to occur nearer the water surface. Reports on the surface-dwelling habits of *N. atherinoides* (Trautman 1957) cast some doubt on the reality of this difference.

It would be of interest to know whether the spatial distribution of one species changes in the presence or absence of others. Alterations of this kind in the habits of fishes, called "interactive segregation," have been discussed by Nillson (1967), who suggested that the presence of other species with similar habits may tend to restrict the distribution or otherwise modify the habits of a particular species. Traps are not a well-researched sampling tool how-

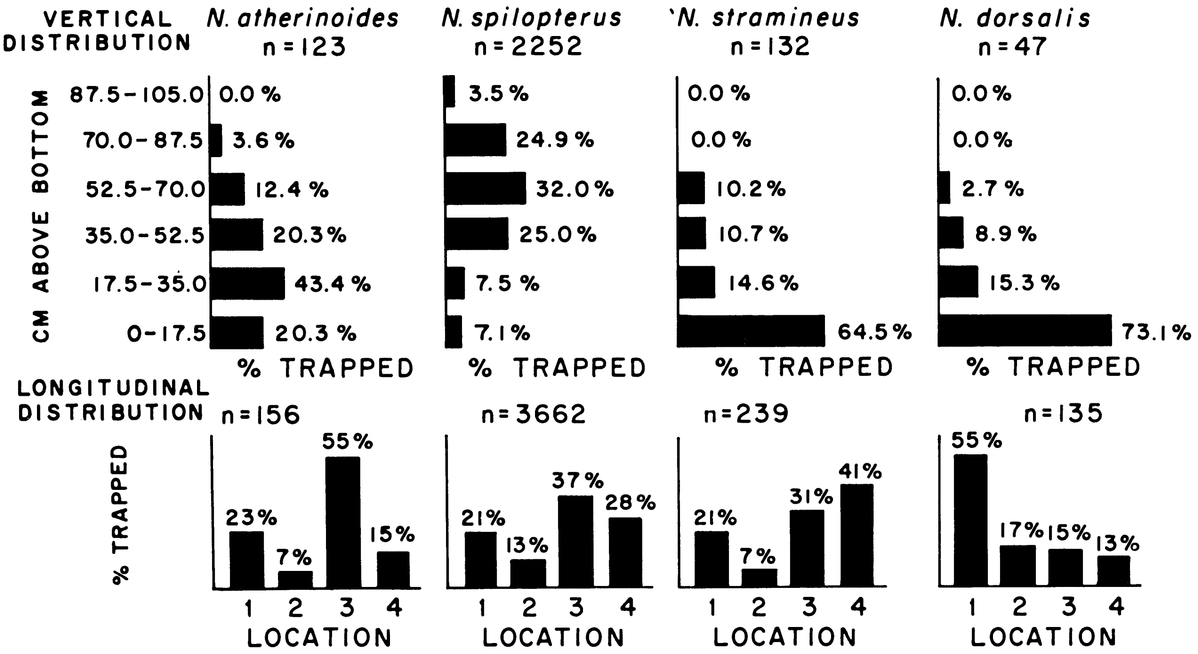

FIG. 4. Longitudinal and vertical distribution of *Notropis* in Roxbury Creek pools. Vertical distributions represent percentage frequency of capture in traps set at location 3.

ever, and their low efficiency makes one cautious. What data do exist suggest that the presence of a particular species does not significantly affect the spatial distribution of others.

THE INVERTEBRATE FAUNA OF ROXBURY CREEK

Only one of many kinds of spatial pattern in the invertebrate fauna, the principal food resource of *Notropis* in these pools, was examined in this study: the abundance of different forms in the drift and in the benthos of pools sampled in 1970–71.

Sampling sites

Two pools were chosen as permanent sampling stations in May 1970. Station 1, about 11 m long and 2 m wide, lies behind a buried tree trunk (Fig. 5). Water depth at the pool center averaged 54 cm in 1970–71. Leaf detritus is the principal component of the substrate. The upstream shallows of Station 1, which averaged 15 cm deep over this period, has sediments of gravel and sand covered by silt.

Station 2, about 1.5 km downstream, is a somewhat smaller pool, but it approximates Station 1 in average depth. The pool has formed behind a large fallen tree. During high water increased flow over the trunk scours and deepens the pool; during normal flow, deposition occurs. Bark fragments, presumably from the tree trunk, litter the substrate. The upstream shallows of Station 2 is composed primarily of sand and the fauna is correspondingly reduced.

Station 2 is frequently buried by shifting sand. On one such occasion, coinciding with the September 1970 sampling period, samples were taken at Station 3, a pool of similar size about 25 m downstream. Here deep deposits of silt formed the pool substrate, and bark fragments were uncommon. By October, Station 2 had been reexcavated with large amounts of organic matter being quickly deposited, and sampling was resumed in this pool.

Methods

Sampling plan.—Stations were sampled during eight 1-wk sampling periods spaced regularly throughout 1970–71. In February one station was not sampled because of bad weather. Both drift and benthic samples were taken in each sampling period. Fish, when present, were collected for analysis of stomach contents. The following 4-day sequence was followed at each station:

day 1: drift sample
day 2: collection of fishes
day 3: drift sample
day 4: benthic sample.

The two drift samples were designed to estimate the impact of feeding fishes on the composition of the drift. In practice the number of fishes was either so great that it was impossible to remove a significant number, or so few that their effect on the drifting fauna was negligible.

Since the quantity of drift varies with a diel as well as a seasonal cycle (Waters 1962, Elliott 1967,

FIG. 5. Roxbury Creek, November 1970. View is of Station 1 in an upstream direction. Branch extending from buried trunk, which forms upstream edge of pool, can be seen in center of photograph.

Holt and Waters 1967, Bishop and Hynes 1969), three different time periods were established for the sampling of drift:

1) 3 h before sunrise to 3 h after sunrise;
2) 3 h before midday to 3 h after midday;
3) 3 h before sunset to 3 h after sunset.

The length of sampling periods was determined from experimental evidence on the digestion rates of fishes in aquaria. The remains of simuliid larvae fed to 24 *Notropis* of several species held in aquaria at 20° C were recognizable in gut contents up to 6 h after feeding. Somewhat slower rates would be expected with more heavily chitinized prey (Molnar et al. 1966) or at cooler water temperatures (Windell 1967).

Collection and analysis of drift samples.—Drift nets were made of 423 μm nylon monofilament attached at the mouth to brass frames of length 50.8 cm and width 17.8 cm. Each net thus sampled an area of 910 cm^2. Depth of the net to the collecting tube was 43.2 cm. Nets were drained from the rear through plastic tubes sewn onto the net fabric. When nets were in use, tubes were sealed with metal clamps.

Nets were set in vertical series in a wooden frame, a procedure designed to examine the possibility of vertical stratification in the drift fauna. The number of nets used depended on the depth of the stream at the point sampled.

In general, the sampler was located in the channel, at approximately the deepest part of a pool. To minimize disturbance, the sampler was placed in the stream from a platform extending from bank to bank.

During a 6-h sampling period, four samples of 20 min each, separated by 90-min intervals, were taken, a total of 80 min of sampling.

Current measurements were made with a Price pattern pygmy current meter with a cup width of three-fourths in., sensitive to velocities 0.03–3.4 m/s. Such measurements, taken at 9-cm intervals from substrate to surface, permitted calculations of the total volume of water passing through each net.

Drift samples were preserved in 2% Formalin

TABLE 6. The invertebrate fauna of Station 1. Numbers in parentheses refer to percentages of the total fauna collected in a sampling period. Benthic percentages represent an average of pool and shallows samples

Taxon	May 5–7		June 16–18		July 31		November 4–6		December 16–18		February 3–5	
	Drift %	Benthos %	Drift %	Benthos %	Drift %	Benthos %	Drift %	Benthos %	Drift %	Benthos %	Drift %	Benthos %
Oligochaeta												
Enchytraeidae							0.9(+)					
Tubificidae												
Limnodrilus				3.4(2.8)		3.8(3.1)		2.8(2.7)				
Others		0.2(0.2)		1.7(1.5)		5.8(5.6)		1.7(1.6)			1.5(+)	
Total Oligochaeta		0.2(0.2)		5.1(4.3)		9.6(8.7)	0.9(+)	4.5(4.3)				
Copepoda												
Cyclopoida												
Eucyclops	3.9(1.4)	0.1(0.1)	8.2(1.4)		0.3(0.1)		11.5(0.5)					
Paracyclops	3.1(1.1)		0.4(0.1)				3.1(0.1)					
Tropocyclops	1.1(0.4)		2.6(0.4)		0.3(0.1)		2.0(0.1)					
Undetermined	10.7(3.7)		1.7(0.3)				6.8(0.2)					
Harpacticoida	3.0(1.0)							0.6(0.6)		+(+)		
Total Copepoda	21.8(7.6)	0.1(0.1)	12.9(2.2)		0.6(0.2)		23.4(0.9)	0.6(0.6)				
Ostracoda									2.8(+)			
Isopoda												
Asellus	0.1(0.1)	1.5(1.0)				0.3(0.2)		0.9(0.9)		0.1(0.1)		0.1(0.1)
Amphipoda												
Gammarus	30.6(10.8)	39.7(25.6)	5.2(0.9)	1.7(1.5)	83.6(18.5)	4.8(3.7)	24.1(0.9)	1.5(1.4)	2.8(+)	3.2(3.2)	14.7(0.3)	4.7(4.6)
Ephemeroptera												
Baetis	2.4(0.9)		19.0(3.3)		0.5(0.1)		2.0(0.1)					
Hemiptera	0.4(0.2)		2.2(0.4)									
Coleoptera	0.5(0.2)											
Neuroptera												
Sialis		0.8(0.5)			0.3(0.1)	1.3(1.0)	0.9(+)	4.2(4.0)		0.5(0.5)		0.9(0.9)
Trichoptera												
Hydropsyche	0.7(0.3)	1.3(0.9)	6.1(1.0)	0.9(0.7)	1.5(0.3)							
Platycentropus	0.2(0.1)											
Pycnopsyche		0.5(0.3)		6.0(0.5)		1.2(0.9)		0.2(0.2)	5.5(+)			
Limnephilidae						0.3(0.2)	1.8(0.1)					
Diptera												
Tipulidae												
Dicranota				7.0(5.8)	0.3(0.1)	0.3(0.2)				0.1(0.1)		0.2(0.2)
Hexatoma		0.5(0.3)		1.7(1.5)		0.3(0.2)		0.2(0.2)				
Tipula										0.1(0.1)	1.5(+)	
Tipulidae A								1.1(1.0)				3.0(2.9)
Ceratopogonidae	0.6(0.2)		0.4(0.1)					0.2(0.2)		0.1(0.1)		
Chironomidae: larvae												
Tanypodinae	0.7(0.3)	0.1(0.1)			0.3(0.1)		1.9(0.1)	0.4(0.4)		0.1(0.1)		0.2(0.2)
Diamesinae				12.2(10.1)				0.2(0.2)		0.2(0.2)		0.1(0.1)
Orthocladiinae												
Brillia	0.1(0.1)		0.9(0.2)				1.9(0.1)	0.7(0.7)		+(+)		
Corynoneura	0.5(0.2)		3.0(0.5)		1.0(0.2)		15.0(0.6)		27.8(0.1)		59.9(1.2)	
Cricotopus	1.9(0.7)											
Nanocladius	2.6(0.9)		5.6(1.0)		1.0(0.2)		1.9(0.1)		2.8(+)		1.9(+)	
Psectrocladius	0.3(0.1)						0.9(+)		2.8(+)		2.9(0.1)	
Thiemaniella	0.3(0.1)		12.6(2.2)		1.0(0.2)				5.5(+)		4.9(0.1)	
Undetermined	2.1(0.7)	0.5(0.3)	3.0(0.5)	0.9(0.7)			3.9(0.2)	0.2(0.2)	27.8(0.1)	+(+)		
Total Orthocladiinae	7.8(2.8)	0.5(0.3)	26.1(4.4)	0.9(0.7)	3.0(0.6)		23.6(1.0)	0.9(0.9)	66.7(0.2)	0.1(0.1)	69.6(1.4)	

TABLE 6. (continued)

Taxon	May 5–7		June 16–18		July 31		November 4–6		December 16–18		February 3–5	
	Drift %	Benthos %	Drift %	Benthos %	Drift %	Benthos %	Drift %	Benthos %	Drift %	Benthos %	Drift %	Benthos %
Tanytarsini												
Micropsectra	23.9(8.4)	26.8(17.3)	0.9(0.1)	45.6(38.1)	1.0(0.2)	78.5(60.0)	10.6(0.4)	80.4(77.2)	11.0(+)	92.3(92.1)	4.4(0.1)	83.9(82.0)
Chironomini												
Cryptochironomus						0.3(0.2)		0.4(0.4)		0.1(0.1)		0.2(0.2)
Microtendipes	0.1(0.1)	1.9(1.2)			0.3(0.1)	0.3(0.2)		0.2(0.2)		0.1(0.1)		
Paratendipes	0.4(0.2)	20.6(13.3)				0.6(0.5)				1.9(1.9)	4.4(0.1)	5.9(5.8)
Polypedilum I	1.9(0.7)		5.2(0.9)		0.5(0.1)		4.7(0.2)	2.4(2.3)				
Stictochironomus				13.0(11.6)		1.3(1.0)		0.5(0.4)			1.5(+)	
Total Chironomini	2.4(1.0)	22.5(14.5)	5.2(0.9)	13.0(11.6)	0.8(0.2)	2.5(1.9)	4.7(0.2)	3.5(3.3)		2.1(2.1)	6.9(0.1)	6.1(6.0)
Chironomidae: pupae	2.8(1.0)	4.7(3.0)	0.9(0.1)	3.4(2.8)	1.0(0.2)		1.1(+)					
Simuliidae	0.2(0.1)				0.3(0.1)							
Tabanidae		0.5(0.3)	0.4(0.1)			0.6(0.4)		0.6(0.6)		0.6(0.5)		0.1(0.1)
Diptera: undet. larvae					0.5(0.2)		1.1(+)	0.2(0.2)				0.4(0.4)
Acari		0.5(0.3)										
Hygrobates			0.6(0.1)	0.6(0.4)								
Lebertia				1.1(0.8)				0.6(0.6)				
Sperchonopsis			1.1(0.2)									
Terrestrials												
Collembola	0.3(0.1)		0.9(0.1)		0.3(0.1)				2.8(+)			
Thysanoptera			1.3(0.2)		0.5(0.1)				2.8(+)			
Hemiptera			1.7(0.3)		0.8(0.2)							
Homoptera			3.0(0.5)		0.3(0.1)		0.9(+)					
Coleoptera	0.2(0.1)		1.7(0.3)		0.3(0.1)							
Diptera	4.1(1.6)		4.3(0.7)		2.4(0.4)		0.9(+)		5.6(+)			
Hymenoptera	0.3(0.1)		1.7(0.3)		1.0(0.2)							
Arachnida	0.5(0.2)		1.7(0.3)	1.7(1.5)	1.2(0.3)							
Others			2.6(0.4)				1.9(0.1)					
Total terrestrials	5.4(2.1)		19.8(3.1)	1.7(1.5)	6.9(1.7)		3.7(0.2)		11.2(+)			

during the summer months; 70% ethanol was used in subfreezing temperatures.

In the laboratory the volume of each drift sample was recorded, filtered through 125 μm silk bolting to remove silt, and examined under a dissecting microscope. Animals were removed and identified. Subsampling was necessary when the volume of detritus in a sample was particularly great. From a gridded petri dish 40-in.-square sections were chosen by random processes. Animals present in the chosen sections were removed, identified, and counted. By this method one-fifth of the total sample was examined.

The number of animals in a drift sample is expressed as drift density, following the definition of Waters (1969).

For comparisons among drift samples taken on different days or at different depths, the 80-min cumulative samples were converted, by a correction factor, to the estimated 6-h values. For comparison with bottom samples, the method of Elliott (1967) was followed. The resulting formula estimates the quantity of drift passing over a strip of bottom 1 m wide in 6 h: $(t'/t)\ (N) \div w$, where $t =$ actual sampling time, $t' = 6$ h, $N =$ number of animals caught in time t, and $w =$ width of drift nets.

Collection and analysis of benthic samples.—The difficulty of taking accurate and comprehensive bottom samples in streams is well known. A review of the problems involved is given by Hynes (1970). Some of these include (1) the choice of proper equipment for the substrate to be sampled (Cummins 1962, Southwood 1968), (2) the sometimes uneven or clustered distribution of animals in the benthos (Mottley et al. 1938, Gaufin et al. 1956), and (3) the number of samples necessary for statistical reliability (Gaufin et al. 1956, Needham and Usinger 1956, Cummins 1962, Ulfstrand 1968). Because of the relatively uniform nature of pool substrates and the small size of the pools themselves, these problems were considered of secondary importance, especially in relation to the potentially deleterious effects of removing large quantities of substrate.

Benthic samples were taken with a D-frame aquatic net of width 30.5 cm and mesh size 20 threads in., scraped over bottom sediments for a distance of 30.5 cm. The net penetrated and allowed sifting of bottom sediments in this stream to approximately 1–3 cm. Although the mesh size of the benthic sampler was somewhat greater than that of the drift nets, no significant difference was found in the size of organisms captured.

During each sampling period two benthic samples were taken along the midline of the pool: one in shallow water near the upstream edge of the pool, the other in deep water near the pool center.

Samples were measured volumetrically, fixed in 2% Formalin, washed through 125 μm silk bolting, treated with $CaCl_2$ to separate animals and organic material from sand and gravel (Anderson 1959, Hynes 1970), and then examined under suitable magnification. Subsampling, using the method described previously, was often necessary to process the large volume of material.

Definitions.—Definitions of several terms that will be used throughout may help to clarify the subsequent discussions:

1) *Drift fauna.* Waters (1965, 1969) recognized three types of drift phenomena: behavioral, constant, and catastrophic. In this study no distinction is made among these types. The drift fauna is operationally defined as those animals collected by nets placed in the pool facing upstream. The question of whether the animals collected are actually moving downstream is left open. The definition can apply equally well to pool inhabitants making brief nondirectional excursions into the water column from the benthos.
2) *Pool fauna.* Those animals collected from the benthos along longitudinal transects run through the center of each pool.
3) *Shallows fauna.* Those animals collected from the benthos along longitudinal transects run through areas just upstream from the heads of pools. These areas are best defined by their spatial relationship to the pools. They differ from one another, sometimes markedly, in bottom type and current speed.

For purposes of comparing elements of the fauna with one another several measures of relative abundance will be used:

1) *Percentage of the total fauna*: the portion that a species composes of the total number of animals collected during a single sampling period, including both drift and benthic samples The calculations necessary to convert numbers of animals per volume of water sampled to number per area of substrate have been discussed earlier.
2) *Percentage of the drift, pool, shallows, or benthic fauna*: the proportion that a species makes up of one of these four kinds of samples taken in a pool during a single sampling period. Benthic samples are averages of the sum of pool and shallow samples.

RESULTS

Sixty-three kinds of invertebrates were collected from the three pools sampled in Roxbury Creek. Quantitative data were obtained on 55 of these. The monthly faunal composition of each pool appears in Tables 6–8. Certain elements of the fauna

TABLE 7. The invertebrate fauna of Station 2. Numbers in parentheses refer to percentages of the total fauna collected in a sampling period. Benthic percentages represent an average of pool and shallows samples.

Taxon	5–7 May		1 August		4–6 November	
	Drift %	Benthos %	Drift %	Benthos %	Drift %	Benthos %
Oligochaeta						
Enchytraeidae	0.3(0.1)				6.2(2.4)	6.1(4.0)
Tubificidae						
Limnodrilus		1.1(0.9)		7.7(1.8)	0.4(0.2)	54.4(35.5)
Ilyodrilus				0.4(0.1)		2.5(1.6)
Others	2.9(0.4)				3.5(1.2)	2.7(1.6)
Total Oligochaeta	2.9(0.5)	1.1(0.9)		8.1(1.9)	10.1(3.8)	65.7(42.7)
Copepoda						
Cyclopoida						
Cyclops	0.3(0.1)				2.7(0.9)	0.2(0.2)
Eucyclops					4.4(1.5)	0.2(0.2)
Macrocyclops	0.6(0.1)		0.1(0.1)		1.3(0.5)	
Undetermined	2.4(0.3)				1.7(0.7)	
Harpacticoida						
Total Copepoda	3.3(0.6)		0.1(0.1)		10.1(3.6)	0.4(0.4)
Isopoda						
Asellus	3.7(0.5)	15.4(12.9)	0.1(0.1)	10.4(2.4)		
Amphipoda						
Gammarus	63.5(10.0)	8.1(6.8)	96.3(73.8)	33.3(7.8)	32.4(11.2)	6.7(4.3)
Ephemeroptera						
Baetis	2.1(0.3)		0.8(0.6)			
Hemiptera	2.1(0.3)					
Coleoptera	0.6(0.2)		+(+)		0.4(0.2)	
Trichoptera						
Hydropsyche			0.1(0.1)			
Platycentropus		0.1(0.1)		1.2(0.3)	0.4(0.2)	
Pycnopsyche	1.4(0.3)	3.3(2.8)		1.5(0.4)	3.1(1.1)	1.8(1.2)
Limnephilidae: undet.			0.2(0.2)			
Diptera						
Tipulidae						
Hexatoma						0.2(0.2)
Prionocera				0.4(0.1)		
Undetermined					0.9(0.3)	
Dixidae			+(+)			
Chironomidae						
Tanypodinae	0.9(0.1)	0.5(0.4)	0.3(0.2)	1.5(0.4)	0.9(0.3)	0.2(0.2)
Diamesinae				0.8(0.2)		0.7(0.4)
Orthocladiinae						
Brillia				0.8(0.2)	0.9(0.3)	
Corynoneura			0.4(0.3)	0.4(0.1)	4.9(1.7)	
Cricotopus	0.6(0.1)					
Nanocladius	0.6(0.1)		+(+)		1.3(0.5)	
Psectrocladius	0.6(0.1)		+(+)		0.9(0.3)	
Thiemaniella			0.1(0.1)			
Undetermined	0.3(0.1)				2.2(0.8)	
Total Orthocladiinae	2.1(0.4)		0.6(0.5)	1.2(0.3)	10.2(3.6)	
Tanytarsini						
Micropsectra	2.1(0.4)	2.8(2.3)		21.5(5.1)	12.8(4.5)	3.9(2.5)
Chironomini						
Paratendipes	6.7(0.8)	68.7(57.6)		13.5(3.1)		
Polypedilum I	1.9(0.4)	0.1(0.1)	0.1(0.1)	2.7(0.6)	11.9(4.2)	9.1(5.9)
Polypedilum II						10.1(6.6)
Stictochironomus				0.4(0.1)		0.9(0.6)
Total Chironomini	8.6(1.2)	68.8(57.7)	0.1(0.1)	16.6(3.8)	11.9(4.2)	20.1(13.1)
Chironomidae: undet.	1.1(0.1)		0.1(0.1)		2.6(0.9)	
Chironomidae: pupae	0.6(0.1)		+(+)	0.4(0.1)	0.9(0.3)	
Undetermined Diptera			0.1(0.1)			
Terrestrials						
Collembola	0.3(0.1)				1.3(0.5)	
Hemiptera			0.1(0.1)			
Homoptera			0.2(0.2)	0.4(0.1)		
Coleoptera	0.3(0.1)		0.4(0.1)	0.4(0.2)		
Diptera	1.5(0.2)		0.2(0.2)			
Lepidoptera	0.3(0.1)					
Hymenoptera	0.6(0.1)		0.1(0.1)			
Others	2.4(0.4)		+(+)	1.6(0.4)	1.2(0.6)	
Total terrestrials	5.4(1.0)		0.6(0.6)	2.4(0.6)	2.9(1.3)	

TABLE 8. The invertebrate fauna of Station 3. Numbers in parentheses refer to percentages of the total fauna collected in a sampling period. Benthic percentages represent an average of pool and shallows samples

Taxon	17–19 September Drift %	 Benthos %
Oligochaeta		
Enchytraeidae	1.7(0.4)	
Tubificidae		
Ilyodrilus		24.5(18.8)
Limnodrilus		36.1(27.7)
Total Oligochaeta	1.7(0.4)	60.6(46.5)
Copepoda		
Cyclopoida		
Cyclops	0.7(0.2)	
Eucyclops	0.7(0.2)	
Paracyclops	0.3(0.1)	
Total Copepoda	1.7(0.5)	
Isopoda		
Asellus		1.3(1.0)
Amphipoda		
Gammarus	11.1(2.4)	17.3(14.1)
Ephemeroptera		
Baetis	7.8(1.7)	
Coleoptera	0.6(0.1)	
Neuroptera		
Sialis		3.9(3.0)
Trichoptera		
Limnephilidae: undet.	2.4(0.5)	
Ptilostomis	0.4(0.1)	1.3(1.0)
Diptera		
Tipulidae		
Dicranota	0.3(0.1)	
Dixidae	2.0(0.4)	
Ceratopogonidae	0.3(0.1)	1.1(0.9)
Chironomidae: larvae		
Orthocladiinae		
Corynoneura	6.7(1.4)	
Nanocladius	0.7(0.2)	
Psectrocladius	0.7(0.2)	
Thiemaniella	2.7(0.6)	
Undetermined	2.4(0.5)	
Total Orthocladiinae	13.2(2.9)	
Tanytarsini		
Micropsectra	4.0(1.2)	11.6(8.9)
Chironomini		
Chironomus		0.6(0.4)
Paratendipes		0.6(0.4)
Polypedilum I	1.0(0.2)	
Undetermined Chironomidae	1.0(0.2)	
Chironomidae: pupae	3.0(0.7)	1.7(1.3)
Simuliidae	0.3(0.1)	
Undetermined Diptera	2.0(0.4)	
Acari		
Hygrobates	0.3(0.1)	
Terrestrials		
Collembola	2.0(0.4)	
Thysanoptera	0.7(0.2)	
Homoptera	16.5(4.5)	
Hemiptera	1.4(0.3)	
Coleoptera	3.1(0.6)	
Diptera	11.8(2.7)	
Hymenoptera	6.4(1.4)	
Arachnida	3.3(0.8)	
Others	1.0(0.3)	
Total terrestrials	46.2(11.2)	

TABLE 9. Habitat classification of the invertebrate fauna based on the total number of individuals of each taxa collected. Data from the three sampling stations have been combined. N = total number collected

Taxon	N	% in drift	% in benthos
		Drift fauna	
Baetis	490	100.0	0.0
Dixa	6	100.0	0.0
Simulium	9	100.0	0.0
Cricotopus	136	100.0	0.0
Nanocladius	279	100.0	0.0
Psectrocladius	64	100.0	0.0
Cyclopoid copepods	1513	99.6	0.4
Corynoneura	269	97.4	2.6
Thiemaniella	90	94.8	5.2
		Indeterminate fauna	
Gammarus	8242	72.0	28.0
Polypedilum I	96	54.8	45.2
Enchytraeidae	165	54.6	45.4
Chironomid pupae	128	52.6	47.4
Aquatic Acari	8	50.0	50.0
Brillia	50	32.0	68.0
Pentaneura	46	30.6	69.4
		Benthic fauna	
Pycnopsyche	129	15.3	84.7
Microtendipes	45	9.0	91.0
Prodiamesa	37	5.9	94.1
Paratendipes	1280	5.9	94.1
Sialis	180	4.9	95.1
Stictochironomus	74	4.7	95.3
Cryptochironomus	49	4.5	95.5
Ilyodrilus	407	4.4	95.6
Micropsectra	12,359	3.7	96.3
Chrysops	39	3.6	96.4
Asellus	534	3.5	96.5
Dicranota	118	3.4	96.6
Limnodrilus	1504	2.3	97.7
Peloscolex	8	0.0	100.0
Polypedilum II	58	0.0	100.0
Tipulidae "A"	350	0.0	100.0
Hexatoma	39	0.0	100.0

show distributions restricted either to the benthos of the pools or to the drift. Others, including some of the more abundant genera, were found both in the drift and on benthic substrates. The relative numbers of the more common organisms collected in either of these two habitats appear in Table 9.

The drift fauna

Animals characteristic of the drift were derived mainly from three taxonomic groups: cyclopoid copepods; chironomid larvae, principally genera in the subfamily Orthocladiinae; and ephemeropteran nymphs of the genus *Baetis*. Terrestrial invertebrates also contributed significantly to the drift, particularly in warmer months. Other dipteran larvae, including representatives of such families as the Simuliidae and the Dixidae were restricted to the drift as well, but were present in very small numbers.

With few exceptions cyclopoid copepods, including at least five genera, were found only in the drift.

Since most of the genera collected are considered benthic forms (Hutchinson 1967), it is possible that they actually inhabit small backwaters, enclaves protected from the main stream of the current, and are washed periodically into the drift. The Cyclopoida were absent from collections in December and February.

Harpacticoid copepods, generally benthic in distribution, were collected in small numbers from both pool and shallows sediments, as well as from the drift.

Members of the chironomid subfamily Orthocladiinae were collected almost exclusively from the drift. At Station 1 orthoclads constituted an average of 32.5% of the drift fauna and were the most abundant drifting forms in December and February samples. The genera *Corynoneura*, *Cricotopus*, two species of *Nanocladius* (*Eukeifferilla*), *Psectrocladius*, and *Thiemaniella* were found only in drift samples at Station 1. *Brillia* and some undetermined genera were infrequently recorded from bottom samples, mainly in the shallows. At Station 2, where reduced numbers of the same genera were present, *Brillia* and a few *Corynoneura* alone appeared in benthic samples. The rest were restricted to the drift. The four genera of Orthocladiinae found at Station 3 were all collected from the drift, where they constituted over 13% of the fauna.

The distribution of the Orthocladiinae is an example of how pools can act as catch basins for elements of the stream fauna not normally part of the pool benthos. The Orthocladiinae are the chironomids most characteristic of running water (Lehmann 1971). They are often abundant in aquatic moss (Percival and Whitehead 1929, Hynes 1961, Elgmork and Saether 1970), in gravel patches, and on higher aquatic plants (Lindegaard-Petersen 1972), habitats for the most part absent from the pools of Roxbury Creek. Many species do not build cases, but move about freely, increasing the probability of being carried away by stream currents. Oliver (1971) suggests that early instars of certain forms are in fact planktonic and that a pelagic habitat may be indicated for some species of *Corynoneura*.

Although *Elodea* beds in the unshaded portion of Roxbury Creek harbor large populations of Orthocladiinae, they are at considerable distance from the pools sampled. A more likely source of drifting forms are the small gravel patches found at varying distances upstream from each of the pools. A similar origin is suggested for the few blackfly larvae (*Simulium*) which also drifted through the pools.

The Ephemeroptera were represented by small nymphs of an undetermined species of *Baetis*. This organism was present only in the warmer months, when it averaged over 4% of the drift fauna. It was never collected from bottom samples in any of the pools. In gravel patches, however, and in *Elodea* beds *Baetis brunniecolor*, *B. flavistriga*, and *B. vagans* were collected. Presumably individuals drifting through the pools were representative of one or more of these species.

Terrestrial invertebrates, either floating on the water's surface or carried close to it, composed significant portions of the drift in warmer months. Infrequently, drowned organisms of terrestrial origin were collected from bottom sediments. Adult diptera—particularly the families Chironomidae, Mycetophilidae, Sciaridae, and Dolichopodidae, often encountered along stream margins (Thomas 1962)—were the most common nonaquatic animals in the drift. Collembola were also frequently collected. Terrestrial Coleoptera, especially the family Staphylinidae, were generally more abundant than their aquatic counterparts. Homoptera (particularly Aphididae) and Hymenoptera of the superfamily Chalcidoidea were also taken in the drift. Spiders were present in low numbers.

Among the other groups characteristic of the drift were oligochaetes of the families Aelosomatidae and Naididae. A diverse and abundant fauna consisting of the genera *Aelosoma*, *Amphichaeta*, *Chaetogaster*, *Nais*, *Ophidonais* and *Pristina* were recorded mainly from the drift in all pools. Once it became clear that their remains could not be identified with certainty from the stomach contents of fishes, quantitative estimates of their abundance were discontinued.

Published reports, as well as collections from other parts of Roxbury Creek indicate that most elements of the drifting fauna spend considerable time on benthic substrates of one kind or another. *Simulium* and *Baetis*, for example, clearly do occur elsewhere, on gravel deposits or in other benthic habitats. In the pools of Roxbury Creek, however, they are largely confined to the drift, where they serve as one of the main food resources for *Notropis*.

The benthic fauna

A somewhat more varied fauna inhabited the benthos of pools in Roxbury Creek. Several major taxonomic groups, including the Diptera, Trichoptera, and Oligochaeta, comprised the bulk of the animals encountered. Isopods and neuropterans, somewhat less abundant, were also characteristically benthic in distribution.

The Chironomidae (order Diptera) contributed the greatest number of individuals to the benthic fauna. Larvae of the tribe Tanytarsini, primarily species of *Micropsectra*, were especially abundant. At Station 1, *Micropsectra* composed an average of 60% of the benthic fauna, generally increasing from midspring to winter (Table 6). Somewhat smaller populations were found at Stations 2 and 3.

Micropsectra was also found in the drift, but in relatively insignificant numbers (Table 9). In May, when large numbers were apparently drifting (Table 6), most were found in samples containing mats of an unidentified blue-green alga. These mats, probably benthic in origin, floated downstream in the early evening of both sampling periods. High metabolic activity resulting in the release of gas bubbles by these plants has been suggested as an explanation (Minckley 1963). Algal mats also contained large numbers of cyclopoid and harpacticoid copepods and oligochaetes of the family Naididae.

Benthic assemblages dominated by *Micropsectra* have been reported from Europe (Lindegaard-Petersen 1972). Mackay (1969) found this genus common in detritus in a woodland Quebec stream. Where populations are high, the cases of *Micropsectra*, which are usually made of sand and detritus (Chutter 1969), may form thick layers on the substrate (Lindegaard-Petersen 1972).

Genera included in the tribe Chironomini (family Chironomidae) were also largely benthic. Chironomini, all of which build cases, generally burrow more deeply into the substrate than do other chironomid groups (Oliver 1971). *Paratendipes*, the most abundant form, showed definite seasonal trends. Populations were highest in May. In November, the genus was absent from both pools (Tables 6, 7). Of the two species of *Polypedilum* one showed a strong tendency to drift. The other was restricted to benthic samples (Table 7). Members of this genus are said to feed on water-soaked wood (Hynes 1970). This may account for their somewhat greater abundance at Station 2, where bark fragments were common. The other genera, *Cryptochironomus*, *Microtendipes*, and *Stictochironomus*, were rarely found in the drift.

The Tipulidae were also primarily benthic inhabitants in Roxbury Creek. Of the five genera reported, only *Tipula*, which grows up to 60 mm in length, drifted to any extent. The appearance of these large, dark larvae, writhing vigorously as they are carried downstream over long stretches of bare sand, is a characteristic winter scene in Roxbury Creek. The other genera were overwhelmingly benthic in distribution. *Dicranota* was restricted mostly to the shallow water benthic samples of Station 1, and constituted one of the distinctive elements of the shallows fauna (Table 6).

Four genera of Trichoptera, referable to the families Hydropsychidae, Limnephilidae, and Phryganeidae, were collected. *Pycnopsyche*, a limnephilid that builds cases of sticks, leaves, and sometimes stones, and whose ecology has been exhaustively treated by Cummins (1964) and Mackay and Kalff (1973) was a common inhabitant of the benthos in all pools. Mature larvae were sometimes collected in drift nets (Station 1, December), but since these animals have a propensity for climbing—they were often found crawling on the outside of the nets—it is not clear whether they were in fact drifting. Early-instar limnephilids did, however, drift in late summer and fall, behavior reported also by Elliott (1967) and Bishop and Hynes (1969).

The Hydropsychidae, net-spinning Trichoptera, were represented by a single species, *Hydropsyche slossonae*, smaller individuals of which drifted through Stations 1 and 2 during May, June, and August. Mature larvae were collected only from the shallow-water benthos of Station 1.

Of the benthic oligochaetes, most common was the tubificid *Limnodrilus*, which appeared in benthic samples in all pools from May to November. *Limnodrilus* made up over half the benthic fauna of Station 2 in November (Table 7), and was present in appreciable numbers in both May and August. A second tubificid genus, *Ilyodrilus*, was common at both Stations 2 and 3 (Tables 7, 8).

Several other animals drifting infrequently were the carnivorous alder-fly *Sialis* and the isopod *Asellus intermedius*. *Sialis*, over 95% of which were collected from the benthos (Table 9), is characteristic of depositing substrates (Hynes [1960]; for a discussion of food habits see Woodrum and Tarter [1973]). A similar habitat is suggested for *Asellus* (Hynes 1960), which was found in greatest abundance at Station 2 (Table 7). *Asellus* was not collected from the drift at either Station 1 or Station 3.

Indeterminate fauna

Of the organisms that could not be easily designated as either drifting or benthic, the amphipod *Gammarus pseudolimnaeus* was by far the most important. *Gammarus* was common in every available habitat in Roxbury Creek, and formed a substantial part of the fauna in all three pools. The large populations of this species may well be correlated with the high dissolved solid concentrations in Roxbury Creek (Poff and Threinen 1962, Macan 1963, Minshall and Kuehne 1969).

Although this mobile species was abundant in drift and benthos, its apparently contagious distribution made accurate estimation of numbers extremely difficult. Greater numbers of *Gammarus* appeared to drift in evening and morning, however, than in the daytime. Diel periodicity is a well-known characteristic of *Gammarus* populations (Waters 1962).

Other organisms present more or less equally in drift and benthos were pupae of the family Chironomidae, whose generic identification was not attempted, but which appeared frequently in both spring and summer samples. Enchytraeid oligochaetes, apparently benthic, showed a propensity to drift in the November sampling period at Station 2 (Table 7).

Drifting aquatic mites were found only in daytime samples. This tendency has been noted also by Moon (1940), Elliott (1967), and Bishop and Hynes (1969). Only three individuals of the mite *Lebertia* were collected at Station 1, all in shallow-water benthic samples. They comprised, together with *Dicranota* and *Hydropsyche*, one of the distinctive faunal elements of this region.

Distribution of drift in vertical strata of the water column

One aim of this study was to examine the possibility of vertical stratification in the drift fauna. At normal stream flow, three nets arranged in vertical series were employed. Although certain animals were restricted to the drift, no recognizable pattern of vertical stratification could be detected. Similar results were obtained by Waters (1965) and Ulfstrand (1968).

Similarities between drift and benthic faunas

Considering that most organisms encountered in Roxbury Creek were more common either in the drift or in the benthos, and that relatively few had indeterminate distributions, one might reasonably expect little similarity between drift and benthic faunas in any one sampling period. To a high degree this expectation is confirmed by percentage of similarity calculations (Table 10). Only in May, when large numbers of the benthic genus *Micropsectra* were trapped in drifting mats of algae, did the percentage of similarity between drift and benthic samples rise above 35%. The average similarity for 10 sets of samples was only 25%.

Paired drift samples, on the other hand, showed consistently high overlap. Only in December, when few animals drifted, did the percentage of similarity dip below 60%. The average for 7 sets of comparisons was over 66%, suggesting that the composition of the drift remains relatively constant during a period of several days at least.

The degree of similarity between pool and shallows samples varied among pools. At Station 1, where the shallows grade gently into the pool and where similar bottom sediments are found, the average degree of overlap was high (67.6%). At Station 2, where sandy shallows drop abruptly into a detritus-filled pool, the degree of similarity was low.

Previous studies have emphasized comparisons between drift and those benthic substrates from which the drift had presumably originated (Elliott and Minshall 1968). In such situations overall similarity in faunal composition is expected. The drift organisms considered here, however, originate primarily in regions other than the pools sampled—in gravel patches, beds of aquatic plants, protected backwaters, and the surrounding terrestrial environment. They float above a relatively sedentary bottom fauna, only the most common and active constituents of which ever venture from the substrate. The separation between drift and benthic faunas is not, of course, complete. Overlap appears extensive, however, only when benthic populations are high.

TABLE 10. Percentage of similarity comparisons between drift and benthos. Percentage of similarity values Southwood 1968, Cox 1972.) are based on a comparison of the percentage of individuals in a genus or other taxonomic category shared between samples: $S = 2w/a + b$ where w = the sum of the lower of two percentage values for genera shared by the two samples, a = sum of all values for the first sample, and b = sum of all values for the second sample

	% Similarity		
Sample	Paired drift	Pool benthos vs. shallows benthos	Drift vs. benthos[a]
Station 1: May	69.2	25.0	59.2
Station 1: June	66.1	48.8	12.4
Station 1: July	...	82.6	7.1
Station 1: November	63.4	81.7	17.5
Station 1: December	35.7	81.1	14.6
Station 1: February	...	84.3	15.3
Station 2: May	71.4	4.7	24.7
Station 2: August	...	35.9	34.6
Station 2: November	70.1	50.6	33.8
Station 3: September	69.2	47.7	28.4

[a] Average of pool and shallows samples

FOOD HABITS OF *NOTROPIS* SPECIES IN ROXBURY CREEK

This report on the food habits of the fishes emphasizes the effect of spatial patterns on composition of the diet. The components of the invertebrate fauna differ not only in their distribution but also in other characteristics—size, ease of capture, palatability—whose importance is difficult to assess. Nevertheless, I suggest that availability in the sense of spatial proximity, largely determines the choice by these fishes of particular prey.

The influence of spatial factors on diet has been pointed out by a number of biologists investigating the food habits of fishes (Nillson 1957, Ivlev 1961, Thomas 1962, Maitland 1965, Keast 1965, 1966, Mann and Orr 1969).

Closely related to the analysis of spatial preference as a means of structuring predator-prey interactions are the twin problems of competition and coexistence. The limits of the resource for which the four species of fish may be competing, and the time dimension in which such interactions may be taking place have not been considered in this study. However, I have examined the pattern of resource subdivision operating in this system, and attempted to determine whether differences in spatial distribution do in fact satisfactorily explain observed differences in diet.

Freshwater fishes often show considerable flexibility in prey selection. Differences in diet among sympatric species, rather than being qualitative, may involve no more than differences in the proportion of the same items eaten by several species (Forbes 1878, Hartley 1948, Larkin 1956, Weatherly 1963). Previous studies of the four species under consideration (Boessel 1937, Starrett 1950*b*, Pfleiger 1960, Minckley 1963, Campbell and MacCrimmon 1970) reported that strong preferences for particular prey are not apparent; instead a variety of invertebrates are used as food, suggesting that habitat and abundance may chiefly determine food habits.

Methods

Fishes were collected from pools on the day following the first of the two sets of drift samples. Collections were made at the end of the period reserved for drift sampling with a 15-ft, one-fourth in. mesh, nylon seine. Although the number of seine hauls was not fixed in advance, samples of fish taken from each pool in general reflect relative population sizes. In order to prevent regurgitation, fishes were killed in MS-222 (Sandoz Pharmaceuticals), an anesthetic for ectothermic vertebrates, and then fixed in 10% Formalin. After being washed, samples were placed in 70% ethanol for permanent storage.

In the laboratory the standard length of each specimen was recorded. In the analysis of food habits, the entire digestive tract was utilized. Contents were first examined under a dissecting microscope and larger items were removed and identified. The remainder was placed on a microscope slide, mounted in Hoyer's solution, then examined under a compound microscope. I determined percentage composition of the diet by counting the number of organisms of each type found in the digestive tract. Supplementary estimates of the volume of different prey types as well as of plant material and detritus were made by the "points method" (Hynes 1950), which assigns numbers (1, 2, 4, 8, 16) to items in the digestive tract based on their relative volume. The degree of fullness of the tract is also ranked on a point scale of 0 (empty) to 20 (full). Estimates were made visually. When large numbers of fish were collected, I selected a random sample of approximately 50 specimens for analysis of food habits.

TABLE 11. Utilization of the invertebrate fauna by *Notropis*.

Prey species	*N. atherinoides*	*N. dorsalis*	*N. spilopterus*	*N. stramineus*
Anacaena			+	
Dixa			+	
Macrocyclops			+	
Ostracoda			+	
Platycentropus			+	
Pycnopsyche			+	
Stictochironomus				+
Asellus			+	+
Cyclops		+	+	
Dicranota		+	+	
Psectrocladius	+		+	
Thiemaniella	+		+	
Acari	+	+		+
Baetis	+	+	+	
Brillia	+	+	+	
Corynoneura	+	+	+	
Cryptochironomus	+		+	+
Hexatoma		+	+	+
Microtendipes	+	+	+	
Naididae	+	+		+
Nanocladius sp. 1	+		+	+
Paracyclops	+	+	+	
Paratendipes	+	+		+
Simulium	+		+	+
Tropocyclops		+	+	+
Micropsectra	+	+	+	+
Chironomidae pupae	+	+	+	+
Cricotopus	+	+	+	+
Enchytraeidae	+	+	+	+
Eucyclops	+	+	+	+
Gammarus	+	+	+	+
Harpacticoida	+	+	+	+
Hydropsyche	+	+	+	+
Ilyodrilus	+	+	+	+
Limnodrilus	+	+	+	+
Nanocladius sp. 2	+	+	+	+
Palpomyia	+	+	+	+
Pentaneura	+	+	+	+
Polypedilum	+	+	+	+
Prodiamesa	+	+	+	+
Terrestrials				
Collembola	+		+	
Thysanoptera	+		+	
Homoptera	+	+	+	
Hemiptera	+		+	
Coleoptera	+		+	
Trichoptera	+			
Lepidoptera	+		+	
Diptera	+	+	+	+
Hymenoptera	+			
Arachnida			+	

Not eaten

Agabus
Chironomus
Chrysops
Corixidae
Dubiraphia
Haliplus
Lumbriculidae
Peloscolex
Peltodytes
Prionocera
Procladius
Ptilostomis
Sialis
Tipula
"Tipulidae A"

Results

Taxonomic considerations.—Of the 55 kinds of aquatic invertebrates for which quantitative data were available, 40, or about 73% of the available fauna, were eaten by at least one species of *Notropis* (Table 11).

The pattern of exploitation suggests an absence of rare, burrowing, or particularly large animals in the diet, with a preference instead for common, accessible, and moderate-sized organisms. The animals preyed upon by three and four species of *Notropis*, for example, were generally among the most abundant in the fauna. All were of an easily ingestible size. Larval chironomid genera were heavily utilized by all species.

In some cases, the absence of a genus from the diet of fishes appears to reflect chance factors—difficulty in identification or rarity—rather than any peculiarity distinguishing it from others in the same family or order. For example, in the case of the cyclopoid copepods the most abundant genus, *Eucyclops*, was eaten by all species, whereas the least common (and incidentally most difficult to identify from fragmented exoskeletons), *Macrocyclops* and *Cyclops*, were eaten by one and two species of fish, respectively.

Of the aquatic animals eaten by at least one species of *Notropis*, 25, or 62.5% were eaten by *N. stramineus*, 27 or 67.5% by *N. dorsalis*, 28 or 70% by *N. atherinoides*, and 36 or 90.0% by *N. spilopterus*. The coefficient of community (Cox 1972) expressing percentage overlap in terms of presence indicates strong similarities among the four species in the choice of aquatic prey (Table 12). Terrestrial representatives of 10 orders of arthropods were eaten. Here, however, distinct differences in utilization are apparent (Table 12). *Notropis atherinoides* and *N. spilopterus*, dwelling in midwater or near the surface, prey on a much wider variety of terrestrials than do the largely benthic *N. dorsalis* and *N. stramineus*. Differences in utilization of terrestrials thus appear to reflect habitat differences among species.

TABLE 12. Percentage similarity comparisons among diets of *Notropis* based on presence.

Aquatic prey

Species	Percentage similarity to *N. dorsalis*	 *N. spilopterus*	 *N. stramineus*
N. atherinoides	84%	80%	77%
N. dorsalis	. . .	78%	75%
N. spilopterus	. . .	. . .	69%

Terrestrial prey

	Percentage similarity to *N. dorsalis*	 *N. spilopterus*	 *N. stramineus*
N. atherinoides	36%	82%	20%
N. dorsalis	. . .	40%	67%
N. spilopterus	. . .	. . .	12%

TABLE 13. Results of Spearman Rank Correlation Test. Coefficient (r_s) indicates degree of correlation among *Notropis* species in the importance of various taxa in the diet. *N* refers to the number of categories employed in constructing the test for each sample. Categories used are invertebrate taxa at the ordinal level. Terrestrial invertebrates are included as a single category. Asterisk means r_s value is significant at .05 level.

Species pair	Correlation (r_s) coefficient	Probability
Station 1: May ($N = 9$)		
N. atherinoides–N. spilopterus	.715	*
N. atherinoides–N. stramineus	.760	*
N. spilopterus–N. stramineus	.556	ns
Station 2: May ($N = 10$)		
N. atherinoides–N. dorsalis	.660	*
N. atherinoides–N. spilopterus	.715	*
N. atherinoides–N. stramineus	.560	ns
N. dorsalis–N. spilopterus	.739	*
N. dorsalis–N. stramineus	.805	*
N. spilopterus–N. stramineus	.520	*
Station 1: November ($N = 7$)		
N. atherinoides–N. dorsalis	.540	ns
N. atherinoides–N. spilopterus	.807	*
N. dorsalis–N. spilopterus	.778	*
Station 2: November ($N = 8$)		
N. atherinoides–N. spilopterus	.842	*
N. atherinoides–N. stramineus	.550	ns
N. spilopterus–N. stramineus	.470	ns
Station 1: December ($N = 6$)		
N. atherinoides–N. dorsalis	.872	*
N. atherinoides–N. spilopterus	.872	*
N. atherinoides–N. stramineus	.872	*
N. dorsalis–N. spilopterus	.872	*
N. dorsalis–N. stramineus	1.000	*
N. spilopterus–N. stramineus	.872	*
Yearly average ($N = 11$)		
N. atherinoides–N. dorsalis	.920	*
N. atherinoides–N. spilopterus	.852	*
N. atherinoides–N. stramineus	.702	*
N. dorsalis–N. spilopterus	.938	*
N. dorsalis–N. stramineus	.834	*
N. spilopterus–N. stramineus	.758	*

Although most of the invertebrates in Roxbury Creek are considered edible by *Notropis*, it is not clear from these comparisons whether they are eaten contemporaneously by the different species, or whether any similarity exists in the extent of utilization. I therefore used the Spearman Rank Correlation Coefficient (Siegel 1956) to assess the degree of correspondence among the four species in the choice of invertebrate prey (Table 13). Each order of invertebrates was assigned a rank (1, 2, 3, etc.) reflecting its proportion of the diet. Because many kinds of animals were not eaten in any one sampling period, it was not possible to carry out this test on taxonomic categories of rank lower than order. Terrestrial organisms, not a properly constituted taxonomic category, are included in these calculations. Correlations among species of fishes based on the importance of different orders in the diet were then made and tested for significance. The correlation coefficient was applied to each of five sampling periods in which more than one species of fish was collected.

Of the 21 possible comparisons between species pairs, 16 showed correlations significant at the .05 level. All comparisons between the pairs *N. spilopterus–N. atherinoides*, *N. spilopterus–N. dorsalis*, and *N. dorsalis–N. stramineus* were significantly correlated. At the ordinal level at least, reasonable similarity in the degree to which various taxa are preyed upon appears to exist. Correspondence in the timing of utilization among fishes is also indicated.

Relationships between diet and the distribution of the invertebrate fauna.—Within most of the higher invertebrate taxa, particularly the abundant Diptera, differences are distinct in the spatial distributions of various families and genera. In order to explore the significance of such patterns in determining prey selection, I used two measures that clarify the relationship between habitat and diet:

1) The percentage of similarity (Southwood 1968, Cox 1972) between the drift and benthic faunas and the diet of each species was calculated. Relative degrees of similarity between drift-diet and benthos-diet comparisons indicate in a broad way where fishes were feeding (Fig. 6).
2) In each sampling period, invertebrates collected were placed in one of six defined habitat categories. The percentage that each of these categories made up of the diet of fishes collected in the same sampling period was determined (Fig. 7, 8). The categories are:

Terrestrial. Terrestrial invertebrates, found mostly on or near the water's surface.

Autochthonous drift. Aquatic organisms found only in the drift.

90% drift. Organisms of which 90%–99% of all individuals were collected in the drift.

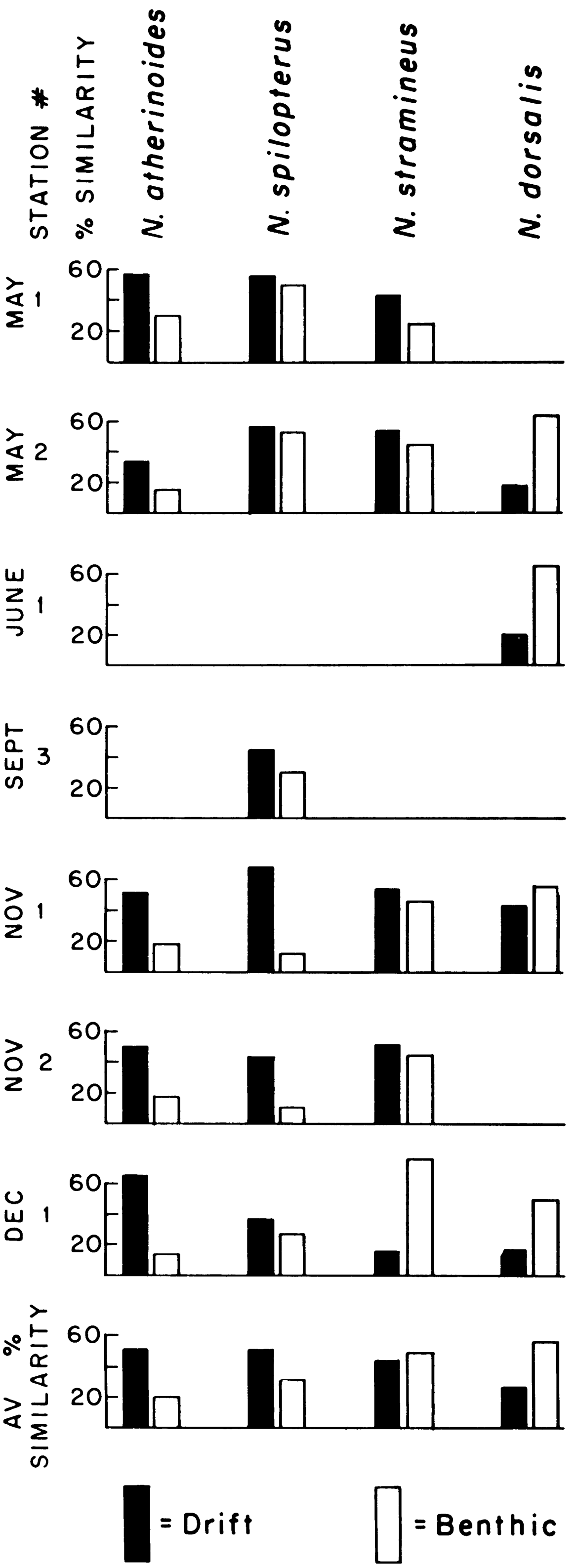

FIG. 6. Percentages of similarity between diets of fishes and drift and benthic faunas. Shaded bars represent percentage similarity between diet and drift fauna; unshaded bars represent percentage similarity between diet and benthic fauna. Absence of a figure indicates species was either absent during that sampling period or was feeding primarily on non-animal foods.

Indeterminate. Organisms of which less than 90% were found either in the drift or in benthic samples.

90% benthic. Organisms of which 90%–99% of all individuals were collected in benthic samples.

Benthic. Organisms found only in the benthos.

These measures do not, of course, exhaust the information available from an examination of digestive tract contents. Certain other trends, particularly seasonal variation in prey selection, are given in a brief description of each species' food habits which precedes the analysis based on spatial considerations. The numbers and kinds of *Notropis* collected in each sampling period are listed in Table 14.

Notropis atherinoides, present in spring and fall samples, preyed consistently on three principal groups of organisms: larval chironomids, copepods, and terrestrial invertebrates. Of the chironomids, Orthocladiinae were by far the most important, particularly in November and December when they averaged nearly 50% of the diet. The abundant benthic form *Micropsectra* was eaten in quantity only in May, when large numbers of smaller individuals were drifting. Terrestrials were consumed most frequently in the warmer months, tending to decrease in importance in fall samples.

Percentage of similarity measures (Fig. 6) indicate strong overall resemblances between the composition of the drift and the diet of *N. atherinoides* in each of five sample periods in which this species was present.

A similar pattern emerges from a consideration of the habitat classification of prey (Fig. 7, 8). Drifting organisms are consistently abundant, while purely benthic forms are largely absent from the diet.

Notropis spilopterus, although feeding on a wider variety of organisms, otherwise showed definite similarities in prey choice to *N. atherinoides*. Orthoclad chironomids were utilized heavily in November and December, and terrestrials assumed prominence in the warmer months. *Notropis spilopterus* also consumed large numbers of the amphipod *Gammarus pseudolimnaeus*, particularly in May, when young individuals were common. This species tended to feed on somewhat larger organisms than were eaten by *N. atherinoides*. These included, in one case, a terrestrial oligochaete 23 mm in length, and, in another, a sizable *Pycnopsyche*. Copepods and other smaller forms, however, were also taken in numbers, most notably in December.

These trends are reflected in the similarity index (Fig. 6), which shows, for all sampling periods, greater dietary resemblances to the drift than to the benthic fauna. Like *N. atherinoides*, the midwater dwelling *N. spilopterus* utilizes primarily drifting foods.

TABLE 14. Numbers and sizes of *Notropis* collected for food habit analysis.

Species	No. collected	No. examined	No. empty	Mean size (mm)	Range (mm)
Station 1. (May 6) evening					
N. atherinoides	62	53	6	33.4	24–44
N. spilopterus	72	49	1	47.2	30–61
N. stramineus	11	10	0	34.1	30–38
Station 2. (May 7) morning					
N. atherinoides	243	36	0	44.0	26–46
N. dorsalis	1	1	0	40.0	. . .
N. spilopterus	222	52	14	47.9	32–60
N. stramineus	99	50	10	40.3	27–51
Station 1. (Jun 17) day					
N. dorsalis	10	10	0	54.9	51–59
N. spilopterus	3	3	3	50.7	46–60
Station 3. (Sep 19) day					
N. spilopterus	19	19	6	37.8	30–63
Station 1. (Nov 2) evening					
N. atherinoides	38	38	10	48.0	37–65
N. dorsalis	7	6	1	40.3	36–45
N. spilopterus	92	91	24	40.3	29–60
N. stramineus	105	16	0	46.4	39–51
Station 2. (Nov 3) morning					
N. atherinoides	232	79	40	47.0	37–64
N. dorsalis	2	2	0	38.5	37–40
N. spilopterus	76	76	21	42.8	33–58
N. stramineus	27	27	0	46.4	33–54
Station 1. (Dec 17) day					
N. atherinoides	21	21	5	46.7	36–53
N. dorsalis	41	33	1	35.7	31–40
N. spilopterus	23	23	5	38.7	32–50
N. stramineus	7	7	1	40.7	28–51

Figures 7 and 8 suggest that, along with drifting forms, organisms of indeterminate origin are also of significance to *N. spilopterus*. This appears to be an expression of the large numbers of *Gammarus* consumed, principally during the May and September sampling periods. Benthic inhabitants, with few exceptions, were not common in *N. spilopterus*' diet.

Notropis stramineus showed greater variability in food habits than did other species, thereby increasing the difficulty of interpreting dietary trends. In November samples at Station 1, for instance, *N. stramineus* fed almost entirely on detritus. In samples taken the following day at Station 2, the *N. stramineus* collected had been preying vigorously on enchytraeid worms, an otherwise minor element in the fauna apparently active at this time of year. In

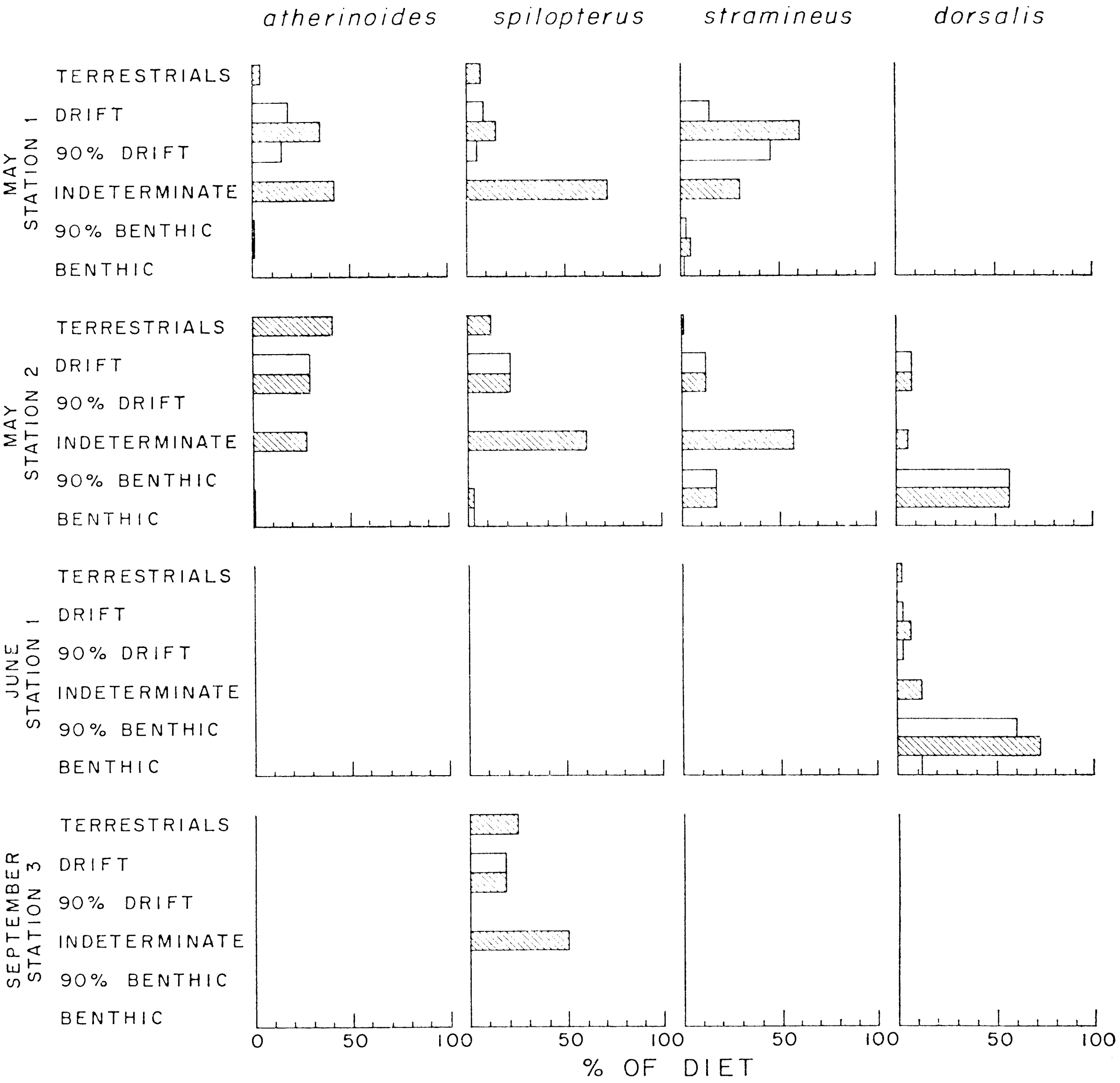

FIG. 7. Percentages of each of six habitat categories in the diets of *Notropis* species collected in May, June and September. Unshaded bars represent drift, 90% drift, benthic, and 90% benthic categories. Shaded bars represent terrestrials, indeterminate, and sum of drift–90% drift and benthic–90% benthic categories, respectively.

other samples copepods, *Gammarus* and larval chironomids assumed dominance. Of this latter group *Micropsectra* and such other benthic forms as *Paratendipes* and *Stictochironomus* greatly outnumbered orthoclads in the diet. Terrestrials were infrequently taken.

These ambiguities are reflected in Fig. 6, which suggests approximately equal similarity of diet to drift and benthic faunas in most sampling periods. Not surprisingly organisms of indeterminate origin were heavily utilized (Fig. 7, 8), but at various times drifting forms (Station 1, May) or benthic organisms (Station 1, December) predominated. Benthic components of the invertebrate fauna were generally more significant to *N. stramineus* than to either *N. atherinoides* or *N. spilopterus*, a fact consonant with the spatial distribution and morphology of this species.

The diet of *Notropis dorsalis* showed much greater consistency than that of *N. stramineus*. Larval chironomids, particularly *Micropsectra*, were important in all sampling periods. At Station 2 in May, however, when *Paratendipes* was abundant in the benthos, this organism replaced *Micropsectra* as

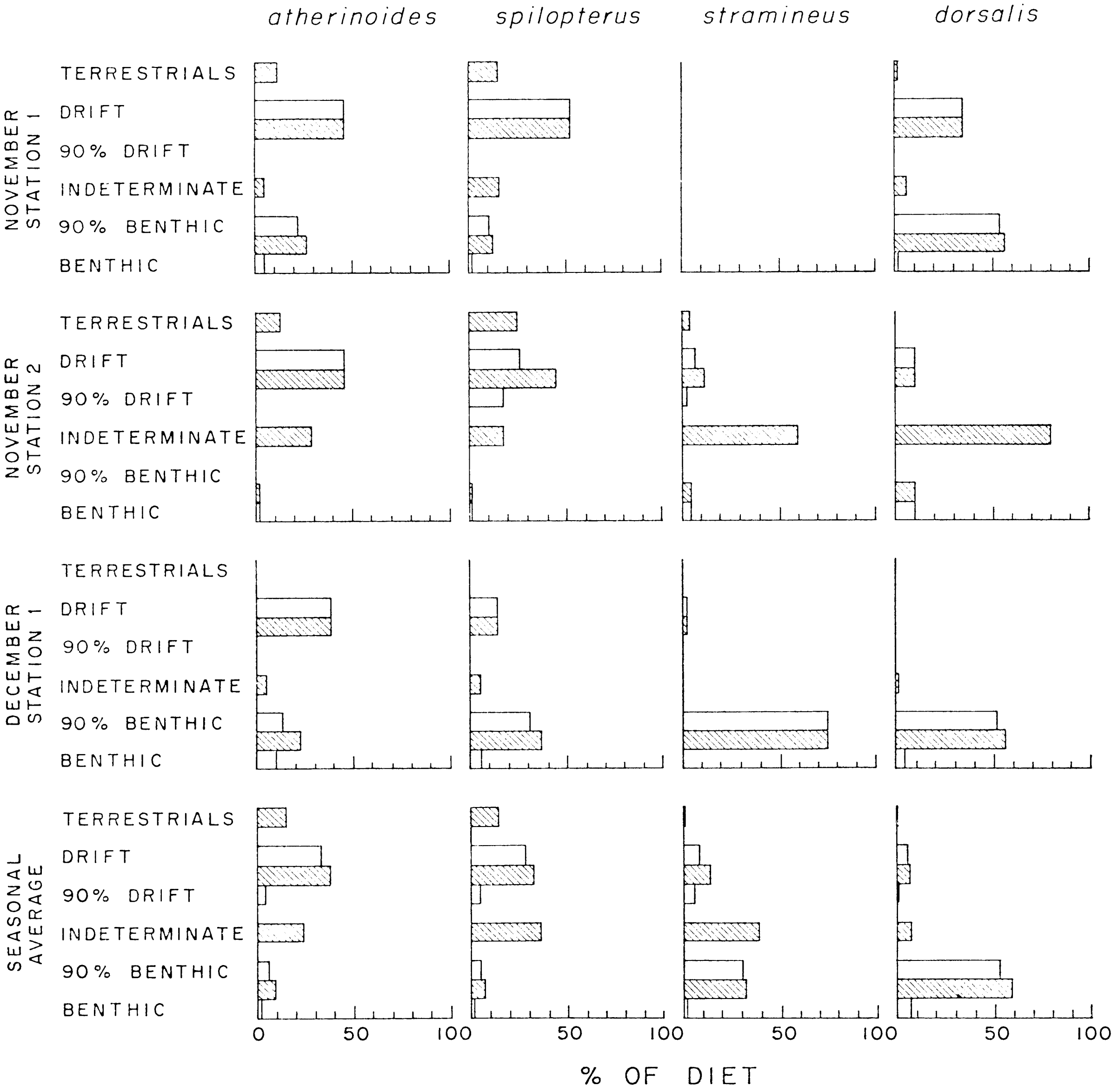

FIG. 8. Percentages of each of six habitat categories in the diets of *Notropis* species collected in November and December, and a seasonal summary. Unshaded bars represent drift, 90% drift, benthic, and 90% benthic categories. Shaded bars represent terrestrials, indeterminate, and sum of drift–90% drift and benthic–90% benthic categories, respectively.

the most common prey taken. Orthoclad chironomids and terrestrials were largely absent from the diet, but copepods appeared in numbers in the December sample. The apparent preference of *N. dorsalis* for shallow-water areas upstream from the pools is expressed by the frequent presence of *Hydropsyche* and *Dicranota*, and on one occasion the mite *Lebertia*—all organisms collected primarily from the shallows—in the diet of this species.

In all sampling periods the diet of *N. dorsalis* consisted more of benthic fauna than of drift (Fig. 6); and in all sampling periods, with the exception of Station 2 in November when few *N. dorsalis* were collected, animals of primarily benthic origin predominated (Fig. 7, 8).

Discussion

Significant correlations were found among all species pairs in the relative importance of various taxonomic categories in the diet (Table 13). Larval Diptera were, on the average, the most important constituents in the diets of all four *Notropis* species throughout the year.

The percentages of similarity between diet and faunal compositions (Table 13) suggest a broad similarity between diet and drift in *N. atherinoides* and *N. spilopterus*, both midwater inhabitants, and an equally strong agreement between diet and the composition of the benthos in the bottom-dwelling *N. dorsalis*. The diet of *N. stramineus* showed approximately equal similarity to drift and benthos, a result not unexpected on the basis of the spatial distributions and feeding behavior of this species.

Notropis atherinoides and *N. spilopterus* utilized terrestrial and drifting organisms to a much greater extent than did either *N. dorsalis* or *N. stramineus*. The latter two species preyed more heavily on benthic elements of the fauna (Fig. 12). In general the utilization of animals of different habitat categories also followed closely the direction expected from a consideration of the independently derived spatial distributions of the four species.

Emphasis in the preceding analysis has been placed on the importance to predators of the proximity of their prey. Because the food habits of each of the four species of *Notropis* are so varied, specialization adapting these fishes to the capture of particular kinds of prey is probably not the chief mechanism by which potential competition is avoided. The apparently stable spatial preferences among the four suggest rather that adaptations allowing fishes to live in particular regions of a pool and to feed on whatever prey is available are more important in permitting coexistence.

In some cases, where the distribution and location of major elements of the invertebrate fauna cannot be determined with certainty—spring and summer sampling periods, for example, when normally benthic forms are active in the drift—the diets of the fishes are correspondingly difficult to interpret. In other situations the relationship between habitat and diet are much clearer. In December, for example, chironomid larvae were the chief prey of all four species. *Notropis atherinoides* and *N. spilopterus*, however, fed on genera restricted almost exclusively to the drift; *N. stramineus* and *N. dorsalis* concentrated on the dominant benthic genus. Every chironomid genus except very rare or cryptic forms is consumed to some extent by each *Notropis* species. The differences in proportions eaten, however, are important, and these generally reflect differences in spatial distribution among the fishes. In the preceding example, bottom-dwelling *Notropis* fed on benthic chironomids; *Notropis* swimming in midwater fed on drifting forms. The same kinds of differences can be seen in the utilization of other invertebrate prey such as terrestrials, Ephemeroptera, other Diptera, particularly the Tipulidae, and at certain times Isopoda and Copepoda.

Within this broad framework, there is a good deal of flexibility. *Notropis atherinoides*, which regularly feeds in midwater or near the surface, for instance, may at one time concentrate heavily on terrestrial insects. In another pool, or in a different sampling period this same species, faced with a potential prey fauna of similar composition, may utilize copepods or drifting chironomid larvae. The factors underlying these shifts in diet—whether they include the presence of *N. spilopterus* feeding in the same regions, or local conditions undetected by sampling—are not easily ascertained. The fact that only one collection of fishes was made in each sample period may account for some of this variability.

Drift-feeding fishes, especially *N. atherinoides*, prey on animals derived largely from sources other than the pools themselves. Events affecting the abundance or resident invertebrates in the pools, therefore, have relatively slight impact on drift-feeders. Bottom-dwelling fishes, especially *N. dorsalis*, are clearly dependent on prey populations produced in the pools. To the extent that fishes are feeding on prey faunas derived from different sources, they cannot compete, regardless of the similarity in prey species chosen.

Notropis spilopterus, living in midwater and preying upon drifting animals, differs from the drift-feeding *N. atherinoides* in several ways. The former appears less firmly committed to drift foods. Several invertebrates important in the diet of *N. spilopterus*, *Gammarus* in particular, are found commonly in both drift and benthos. A greater variety of prey types is used by *N. spilopterus* than by *N. atherinoides*, and there is often a size difference in prey chosen. *Notropis spilopterus* tends to feed on larger items—Trichoptera, *Gammarus*, *Baetis*—while *N. atherinoides* favors the smaller—copepods and chironomids.

Competition between these two species is a distinct possibility in winter, when the variety and abundance of the drifting fauna are severely reduced. Both species in this season heavily utilize the limited numbers of chironomid larvae and Copepoda available in the water column, although many individuals do not feed at all.

Notropis stramineus, which inhabits benthic regions of the pools, differs in several ways from the bottom-dwelling *N. dorsalis*. There is a strong suggestion, both from the kinds of prey species chosen and from the mode of feeding as observed in aquaria, that for *N. stramineus* drifting forms, albeit not surface drift, are as important as benthic fauna. Excepting a propensity for copepods in fall and winter, *N. dorsalis* preys almost exclusively on the benthic fauna. The tendency of this species to occupy shallow areas upstream from the pools is expressed by the frequent presence in the diet of several invertebrates—*Hydropsyche*, *Dicranota*, *Lebertia*—largely restricted to these regions. The importance to *N. stramineus* of detritus and algae, which may in fact be removed from the drift, also tends to separate the two species. Detrital remains in *N. dorsalis* are very often simply the cases of the chironomid larvae on which this species preys.

CONCLUSION

Implied throughout the preceding discussion has been a comparison between possible approaches open to species of *Notropis* in searching for, pursuing, and devouring prey. The alternatives appear to be these:

1) Predators are adapted to the capture of specific kinds of prey. They frequent certain places because their prey generally reside there.
2) Predators are adapted to particular habitats, to regions in which they function most effectively. In these regions they prey indiscriminately on whatever animals of a suitable size are available.

MacArthur and Levins (1964) and Hutchinson (1965) have discussed an analogous set of alternatives. The first, which Hutchinson calls "morphological adaptations" for predation, implies that predators adapted to the capture of different prey types can inhabit the same space. The second, "behavioral adaptations" implies that predators are spatially separated and hence can prey on the same kinds of animals without competing.

From an analysis of the spatial distributions of predators and their prey and from an examination of the diet of the predators, I conclude that the second alternative is much the more compelling explanation for the continued coexistence of four species of *Notropis* in Roxbury Creek. It appears, further, that predatory styles conforming to this general pattern are more likely to develop as a result of selective pressures from other predators utilizing the same food supply than from the habits of the animals preyed upon. The effects of such an approach do, however, have implications for the prey fauna, the degree of impact on different species being roughly proportional to the extent of spatial overlap with the predators. For example, the larval forms of certain Chironomidae, the Orthocladinae, are preyed upon to a much greater extent than might be expected from a consideration of their numbers. This seems to be because their spatial distributions are generally congruent with those of the most abundant predators.

Concerning relationships among the predators themselves, I have presented evidence that they occur together in other Wisconsin streams and over wide areas of their range. These species tend to associate in edge habitats: small, sandy streams tributary to large rivers. Such habitats are sufficiently common in southwestern Wisconsin and in the upper Mississippi Valley generally to arouse our interest in the nature of the relationship. On the other hand, these fishes are not so intimately associated, nor have they such an identity of habitat requirements to permit the conclusion that they have evolved together. Nor is there evidence that the geographic range of any one species has been affected by the presence or absence of the others. It is more likely that the morphological and behavioral characteristics permitting these species to coexist in Roxbury Creek—and these, I have suggested, center on spatial partitioning—are preadaptations allowing these species to coexist wherever they are found together but not demanding a coevolutionary origin.

In the genus *Notropis*, where association among species is sufficiently widespread to treat this particular combination as an example of a more general trend, it is of interest to examine another possible reason for the existence of these groups.

The tendency of *Notropis* to live in large aggregations, and the observations that these four species are mutually responsive in aquarium settings suggest one explanation. Such aggregations may provide protection to individuals from their own predators, although the functions of schools are not well understood (Keenleyside 1955, Shaw 1962, Etkin 1964, Shaw 1970). In natural habitats large schools composed of a single species might be more cohesive than multispecific groups, but competition for food among its members would presumably be more severe. In multispecific schools like the ones considered here, each species may have spatial preferences and hence food habits somewhat distinct from the others. In such groups, at least some of the advantages of schooling are preserved, while the disadvantage of intense intraspecific competition for food are partially avoided. The effectiveness of multispecific aggregations depends ultimately, however, on maintaining in each species a balance between selective forces that tend to preserve morphological and behavioral similarities, thus insuring mutual responsiveness, and selective forces acting in an opposite direction, serving to minimize competition.

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APPENDIX I
SUMMARY: TRAPPING DATA FROM ROXBURY CREEK, ALL POOLS

Trap depth	Number trapped: *N. atherinoides*	*N. dorsalis*	*N. spilopterus*	*N. stramineus*
Pool: Rox I (Station 1)				
F	0	0	0	0
E	0	0	2	0
D	2	0	16	1
C	4	2	44	2
B	2	1	49	1
A	6	7	25	23
Pool: Rox II				
F	...	...	...	...
E	0	0	209	0
D	1	0	715	7
C	1	1	644	10
B	1	4	147	14
A	2	4	168	8
Pool: Rox III				
F	0	0	5	0
E	1	0	42	0
D	0	1	5	0
C	0	0	2	0
B	0	0	3	0
A	0	0	0	1
Pool: Rox IV				
F	...	...	...	...
E	...	...	...	...
D	...	...	...	...
C	1	1	33	2
B	0	0	6	0
A	0	1	7	0
Pool: Rox V				
F	...	...	...	...
E	1	0	1	0
D	10	0	26	3
C	21	0	6	0
B	52	2	12	4
A	19	24	16	57
Pool: Rox VI				
F	...	...	...	...
E	0	0	64	0
D	0	0	5	0
C	0	0	0	0
B	0	0	0	0
A	0	0	0	0

APPENDIX II
SPATIAL DISTRIBUTION: NUMBER OF TRAP-DAYS

Depth		Location 1	2	3	4
35″–42″	F	...	...	6	...
28″–35″	E	...	...	54	...
21″–28″	D	...	...	101	...
14″–21″	C	...	91	123	50
7″–14″	B	...	93	122	82
0″– 7″	A	123	96	128	84

APPENDIX III
SPATIAL DISTRIBUTION: NUMBER OF FISH

N. atherinoides

Depth	Location 1	2	3	4
F	...	...	0	...
E	...	...	2	...
D	...	...	13	...
C	...	2	26	0
B	...	0	55	1
A	12	6	27	12

N. dorsalis

Depth	Location 1	2	3	4
F	...	...	0	...
E	...	...	0	...
D	...	...	1	...
C	...	0	4	0
B	...	1	7	0
A	41	29	35	17

N. spilopterus

Depth	Location 1	2	3	4
F	...	...	5	...
E	...	...	318	...
D	...	...	767	...
C	...	256	729	329
B	...	56	217	111
A	294	108	216	256

N. stramineus

Depth	Location 1	2	3	4
F	...	...	0	...
E	...	...	0	...
D	...	...	11	...
C	...	1	14	10
B	...	3	19	3
A	20	12	88	58

PLATE I. Some widespread *Anolis* species of the western Caribbean. Top-left: *A. carolinensis* ♂ from Crooked, a two-species island; top-right: *A. carolinensis* ♂ from Bimini, brown phase (the same animal can turn bright green); middle-left: small *A. carolinensis* from a tiny one-species island off the west coast of Acklins Island. Notice convergence in general appearance to *A. sagrei* (bottom-left); middle-center: *A. carolinensis* ♂ from Acklins, a one-species island; middle-right: *A. carolinensis* ♀ (green phase) from Bimini, a four-species island; bottom-left: small *A. sagrei* from Crooked; bottom-center: *A. carolinensis* ♂ (green phase) from Bimini, a four-species island; bottom-right: adult *A. distichus* from Bimini.