# TROPHIC DIVERSITY AND FOOD PARTITIONING AMONG FISHES ASSOCIATED WITH AQUATIC MACROPHYTE PATCHES

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## ABSTRACT

Contents of 573 stomachs were examined for five fish species (largemouth bass, yellow perch, warmouth, bluegill, and pumpkinseed) collected among macrophyte patches. Trophic diversities and food overlap coefficients were calculated so that competitive interactions could be identified for further study. The largemouth bass, the bluegill, and the pumpkinseed were classed as food specialists and had low food overlap coefficients between them. There appeared to be little competition between the largemouth bass and either the bluegill or the pumpkinseed, but some competition between the bluegill and pumpkinseed may have existed for caddisflies. The yellow perch and the warmouth had high food overlap coefficients with each other as well as with other species and both exhibited a large trophic diversity. They were classified as food generalists.

## INTRODUCTION

The purpose of this study was to examine competitive interactions among five species of fishes (the largemouth bass, *Micropterus salmoides;* the yellow perch, *Perca flavescens;* the warmouth, *Lepomis gulosus;* the bluegill, *Lepomis macrochirus;* and the pumpkinseed, *Lepomis gibbosus*) in shallow aquatic macrophyte patches in a glacial lake in northern Illinois.

One aspect investigated was trophic diversity which is the diversity of prey species taken by each predator species (Hurtubia, 1973). Trophic diversity as calculated by Hurtubia (1973) can be used to determine niche breadth which is directly related to competition theory (Horn, 1966). To gain further insight into the competitive interactions, food overlap and population size of fishes were also measured.

For the five species investigated, neither trophic diversity nor population size of fish using aquatic macrophyte patches has ever been measured. With the exception of data on the bluegill and the pumpkinseed (Keast, 1978 and Werner and Hall, 1979) there is little information on food overlap between these species.

## STUDY AREA

Cedar Lake is a glacial lake located in the town of Lake Villa, Illinois. A dam built on the south side of the lake resulted in an increased surface area, approximately 114 hectares. An island is situated between the recently formed northwest portion and the original basin. During the summer. the northwestern portion, most of which has a depth of less than 2 m, is choked with macrophytes. The original basin is considerably deeper (13 m) and has scattered macrophyte patches of varying sizes along the shoreline. This is where the fish samples were collected. A hard sand bottom lies between these patches.

## METHODS

At approximately weekly intervals from May to October, fish were collected by seine from macrophyte patches in the shallow water and particularly in the largest macrophyte bed which had a surface area in July and August of approximately $500m^2$, and the macrophytes were primarily species of *Potamogeton*. Most collections were made between 0900-1100 and 1600-1800 hrs; there was no apparent difference in stomach contents between collection times. Fish were preserved in formalin and returned to the laboratory where they were identified, weighed, and measured. The numbers of stomachs examined for each species were: the largemouth bass, 98: the yellow perch, 91: the warmouth, 21: bluegill, 224; and the pumpkinseed, 139. Stomach contents were removed and most food times were identified to genus. Prey organisms were placed into food categories. These categories were used to determine trophic diversity and food overlap coefficients.

In calculating trophic diversity, food overlap coefficients, and niche breadth, each prey item was considered rather than its caloric value. I assumed that fish feed on the most profitable prey per energy expended in search and pursuit of prey (MacArthur and Pianka, 1966). If competition results in a fish species foraging on less desirable or a wider variety of prey, this situation would be more easily discerned by counting each individual organism. The equation used to calculate food overlap coefficients was one used successfully by Pianka (1975). It is

$$a_{jk} = a_{kj} = \frac{\sum_i P_{ij} P_{ik}}{\sqrt{\sum_i P_{ij}^2 P_{ik}^2}}$$

where $a_{jk}$ and $a_{kj}$ are food overlap coefficients between species $j$ and $k$; $P_{ij}$ is the proportion of food type $i$ used by $j$ and $P_{ik}$ is the porportion of food type $i$ used by $k$. Keast (1978), in examining food overlap between the pumpkinseed and the bluegill used the Levin's (1968) equation. The coefficients calculated from the present data are not very different using either equation.

Feeding diversity for each species was calculated by the Brillouin index (Pielou, 1966). The pooled stomach content data for each species were used in this calculation using the following equation:

$$H \text{ (Brillouin index)} = 1/N \log \frac{N!}{\prod_{i=1} N_i!}$$

In this equation, $N_i$ is the number of prey of type $i$ and $N$ is the total number of prey individuals.

The Brillouin index was used to estimate trophic diversity for each predator species (Hurtubia, 1973) and is the most appropriate one for analyzing diversity of collections (Pielou, 1975). A collection is a sample for which there is a complete census (Pielou, 1975). Hurtubia (1973) has shown that the Brillouin index is superior to other indices for determining trophic diversity of predators from stomach contents.

The average (per predator) Brillouin index for each species was calculated by the equation:

$$\bar{H} = 1/Z \sum_{k=1}^{Z} H_k$$

where $H_k$ is the diversity for each stomach and $\bar{H}$ is the average diversity for the fish species.

Trophic diversity was calculated by the procedure outlined by Hurtubia (1973) and Pielou (1966). Each stomach for a particular fish species was treated as an individual sample. The counts for each prey category and the total number of prey were pooled one stomach sample at a time. As these data were pooled one at a time, the diversity as calculated by the equation for the Brillouin index increased until it reached stability at stomach $t$. More data from other stomachs did not appreciably change the accumulated diversity. But data for each sample after $t$ estimated trophic diversity for that species. The formula for calculating this diversity is:

$$h_k = \frac{(N_k H_k - N_{k-1} H_{k-1})}{(N_k - N_{k-1})}$$

where $H_k$ and $H_{k}$-1 are accumulated diversities for stomachs $k$ and $k$-1 $N_k$ and $N_{k-1}$ are the total number of prey types found in $k$ and $k$-$1$ stomachs. The trophic diversity for the predator species of fish is $H'p$. Niche breadth was calculated by dividing the measured trophic diversity, $H'p$, by the maximum possible trophic diversity (Hurtubia, 1973).

Individuals of a species of predator could have similar average diversities ($\bar{H}$) but be foraging on different prey types. A coefficient of similarity was calculated using the formula:

$$CS = \frac{200\ S_{xy}}{S_x + S_x}$$

where $S_x$ and $S_y$ are numbers of prey types in stomachs $x$ and $y$ and $S_{xy}$ is the number of prey types found in both stomachs. A random number of stomachs for each fish species was analyzed to calculate coefficients of similarity. The coefficient is an indicator of how similar the stomach contents of individuals of the same species are.

In July, a capture-recapture analysis of the fish population of the large shallow macrophyte patch was begun. Fish were marked by fin clips and sampling continued at weekly intervals until the end of August. The mean of the Petersen Method estimates (Ricker, 1975) was employed in calculating population sizes.

It was assumed that fish captured in macrophyte beds were feeding there; since the macrcophyte beds contained larger numbers of fish than the areas between them. Seine hauls between macrophyte patches caught 0-4 fish while seine hauls through macrophyte patches caught 30 or more fish. Also, the macrophyte patches contained larger invertebrate populations and some of these inverterbrates cling to vegetation (Connolly, 1981). Other invertebrates were burrowers and sediments in the patches were soft and muddy in contrast to the hard, sandy sediment between patches.

## RESULTS

### Prey Type Categories

Categories used in calculating diversity indices and food overlap coefficients are shown in Table 1. Most categories contain two or more genera. Benthic and plankton samples were taken as part of another study (Connolly, 1981) and identification of organisms from that study corroborated the identification of the stomach contents. The food type categories and organisms in them are shown below.

*Minnows*—the bluntnose minnow (*Pimephales notatus*) and blackchin shiner (*Notropis heterodon*).

*Darters*—the johnny darter (*Etheostoma nigrum*).

*Miscellaneous Fish*—this is a catch-all category for fish which seldom occurred in stomachs and includes the bluegill, the yellow perch, and brook silverside (*Labidesthes sicculus*). This category was not used in calculations of food overlap.

*Large Mayflies*—*Hexagenia* sp.

*Small Mayflies*—*Baetis* sp.

*Crayfish*—*Orconectes virilis*.

*Water Boatmen*—*Trichocorixa* sp.

*Caddisflies*—*Oecetis* sp. and *Polycentropis* sp.

*Amphipods*—*Hyalella azteca* is the only species.

*Cladocerans*—Over 80% were *Ceriodaphnia* sp.

*Chironomids*—*Pseudochironomus richardsoni* and *Endochironomus dirmorphus* comprised 90% of the individuals of this category.

*Tanypodins*—Most were *Tanypus* sp.

*Damselflies*—Most were *Enallagma* sp.

*Snails*—Most were *Arnicola* sp. and *Valvata tricarinate*, but there were other genera as well. This category was particularly difficult because in the pumpkinseed, the shells were often badly broken. The number was determined by counting the number of central portions (vertex) of the snail shells. The vertex was often spared the crushing process of the pharyngeal teeth. If shell particles occurred in stomachs with no vertex, one snail was recorded.

*Bivalves*—*Pisidium* sp. and *Sphaerium* sp.

*Water Mites*—Individuals were not identified to genus.

*Isopods*—*Asellus* sp. is the only genus.

*Miscellaneous Food Items*—This category contains organisms which could not be identified, or whose occurrence in stomach samples was rare. Bluegills had a number of single occurrence organisms and these were a phantom midge. *Chaoborus punctipennis;* a Ceratopogoninae, *Palpomyia* sp.; copepods, *Cyclops* sp.; a cicada, *Magicicada* sp.; a backswimmer, (Notonectidae); a predacious bettle, (Dytiscidae). This category was not used in calculations of food overlap.

## Feeding and Aspects of Foraging

The largemouth bass ranged in size from 10.6 to 24.7 cm. They fed heavily on minnows and darters as well as on some mayflies, water boatmen, and damselflies (Table 1). Their morphology is particularly well adapted for attacking large mobile prey (Nyberg, 1971). Largemouth bass were the most visible of any of the five fish species and were often seen swimming about the macrophytes in small schools of as many as a dozen fish.

The yellow perch ranged in size from 10.9 to 18.9 cm. They also fed heavily on darters as well as on amphipods, mayflies, and water boatment. If a yellow perch successfully captured a darter or minnow, the stomach usually contained few other organisms. In contrast, if neither darter nor minnow was found in the stomachs, a larger number of invertebrate prey was present.

Table 1. Quanitities of food types in the diet of the five fish species.

| Food Organisms | Largemouth Bass | Yellow Perch | Warmouth | Bluegill | Pumpkinseed |
|---|---|---|---|---|---|
| Minnows | 64 | 10 | 1 | 1 | 2 |
| Darters | 149 | 67 | 7 | 1 | 0 |
| Miscellaneous Fish | 3 | 1 | 0 | 0 | 2 |
| Crayfish | 4 | 21 | 2 | 0 | 0 |
| Large Mayflies | 0 | 4 | 9 | 11 | 43 |
| Small Mayflies | 13 | 104 | 2 | 239 | 40 |
| Water Boatmen | 32 | 119 | 1 | 12 | 5 |
| Caddisflies | 5 | 42 | 19 | 1890 | 345 |
| Amphipods | 3 | 450 | 1 | 1037 | 62 |
| Cladocerans | 15 | 5 | 0 | 159 | 1 |
| Chironomids | 1 | 34 | 0 | 1967 | 262 |
| Tanypodins | 1 | 9 | 0 | 80 | 30 |
| Damselflies | 12 | 10 | 2 | 43 | 0 |
| Snails | 5 | 12 | 1 | 79 | 489 |
| Bivalves | 0 | 0 | 1 | 3 | 35 |
| Water Mites | 0 | 1 | 0 | 25 | 0 |
| Isopods | 1 | 1 | 0 | 12 | 0 |
| Misc. Food Items | 1 | 10 | 0 | 18 | 6 |
| Total # Prey | 308 | 900 | 46 | 5577 | 1322 |
| # Fish Sampled | 98 | 91 | 21 | 224 | 139 |
| # Fish With Food | 87 | 73 | 16 | 197 | 109 |

The warmouth ranged in size from 11.1 to 14.5 cm. The warmouth also fed primarily on darters and large invertebrates, particularly *Hexagenia* sp. and caddisflies. They have a large gape compared to other *Lepomis* and tend to be more piscivorous (Larimore, 1957). The warmouth generally occurs in the cover of macrophytes and its coloration may serve to camouflage it from its prey and its predators.

The pumpkinseed ranged in size from 6.8 to 15.7 cm. The pumpkinseed fed on mollusks to a larger extent than any other fish. It is particularly well-adapted for feeding on these organisms since it has large molariform pharyngeal teeth for crushing mollusk shells (Hubbs and Lagler, 1964 and Keast, 1978). The pumpkinseed also fed on mayflies, caddisflies, and chironomids. In contrast to the bluegill, little plant material was found in its stomach.

The bluegill ranged in size from 5.4 to 18.3 cm. The bluegill fed on the smaller invertebrates: chironomids, mayflies, water mites, amphipods, cladocerans, and caddisflies. It also fed on organisms which were rare, such as predacious water beetles, backswimmers, and even stray terrestrial insects. Over 50% of the stomachs contained plant material which consisted of filamentous algae, *Potamogeton* leaves, and sprouting macrophytes. The bluegill appeared to have at least two benthic foraging methods. It either fed on individual organisms or on clumps of vegetation with up to 30 or more organisms attached. In some stomachs, the clumps of invertebrates on *Potamogeton* leaves or sprouts were found intact. The bluegill may use a suction mode of feeding on the "clumps". It has a small mouth and great protusibility of the premaxilla (Keast and Webb, 1966) and a low attack speed (Nyberg, 1971) which would allow this mode of feeding.

## Food Overlap Coefficients

For the largemouth bass, coefficients of food overlap decreased from the yellow perch to the warmouth, to the bluegill, and finally to the pumpkinseed (Table 2). Largemouth bass and yellow perch had a high overlap (0.44) as did the yellow perch and the warmouth (0.44). The latter fish species fed on darters and *Hexagenia* sp. While the overlap coefficient between the largemouth bass and the warmouth was moderate (0.27), largemouth bass predation on darters may have influenced the warmouth and the yellow perch diet by lowering the number of available darters for the yellow perch and the warmouth.

There was also a high coefficient (0.48) between the warmouth and the pumpkinseed. Much of this overlap occurred because both utilize a relatively

Table 2. Food overlap coefficients for five fish species

| Species | Largemouth Bass | Yellow Perch | Warmouth | Bluegill | Pumpkinseed |
|---|---|---|---|---|---|
| Largemouth Bass | 1.00 | 0.44 | 0.27 | 0.11 | 0.03 |
| Perch | 0.44 | 1.00 | 0.44 | 0.26 | 0.11 |
| Warmouth | 0.27 | 0.44 | 1.00 | 0.15 | 0.48 |
| Bluegill | 0.11 | 0.26 | 0.15 | 1.00 | 0.22 |
| Pumpkinseed | 0.03 | 0.11 | 0.48 | 0.22 | 1.00 |

large number of *Hexagenia* sp. The warmouth and the pumpkinseed also fed heavily on caddisflies. The bluegill has only moderate food overlaps with the other four fish species. The bluegill and the perch overlap (0.26) involved principally the amphipods and small mayflies, while the bluegill overlap with the pumpkinseed was mainly due to feeding on caddisflies and chironomids.

## Trophic Diversity

The feeding diversity which is the pooled data for all stomachs for each species should be less than the trophic diversity. An advantage of trophic diversity is that one can estimate trophic diversity without finding all potential prey categories (Lloyd *et al.* 1968). The pumpkinseed had a higher feeding diversity (1.63) than trophic diversity (1.47). Hurturbia (1973) has shown that this can occur when there is specialization in food categories. For the pumpkinseed, this food specialization consisted of snails, caddisflies, and chironomids which made up 37, 26, and 20% of the diet, respectively. The pumpkinseed had the highest individual diversity (0.47) with an average of 12.3 prey individuals per stomach (Table 3). What this signifies is that many of the pumpkinseed were feeding on these 3 food categories and one would expect to find the pumpkinseed stomachs containing these 3 prey categories and one or two other types as well.

The largemouth bass and the bluegill feeding diversities were the same or nearly the same as their trophic diversities (Table 3). Again, these two fish species are food specialists. The largemouth bass had the lowest feeding and trophic diversity and foraged heavily on two prey categories, minnows and darters. Since they feed on large organisms, there were few prey individuals in their stomachs (3.6/stomach). The bluegill specialized in foraging for small prey such as chironomids, caddisflies, and amphipods. It had a high individual feeding diversity (0.45) which was partially due to feeding on "clumps" which contained several different prey types.

The yellow perch had the largest trophic diversity, and foraged on darters and minnows but more often on small invertebrates. Amphipods comprised 50% of the total number of organisms in the yellow perch diet. It had a high trophic diversity because it fed on a large number of prey types and had nearly 4 times as many prey (12.3/stomach) as the largemouth bass. The moderate individual feeding diversity resulted from low individual diversities by those yellow perch feeding on darters and minnows, in contrast, to the higher individual diversities by those feeding on invertebrates.

The warmouth had a high trophic diversity (Table 3). It foraged on several prey categories but its stomachs contain few prey (2.98/stomach). The warmouth fed on prey types which were heavily utilized by three other fish species and this may have resulted in low numbers of prey in the stomachs. With a coefficient of similarity of 0.16, there was little similarity of stomach contents. The high trophic diversity was a result of large variation in prey type by individual warmouth.

Those fish species which specialized on certain prey categories had a smaller niche breadth: the largemouth bass, the bluegill, and the pumpkinseed had nearly the same niche breadth and the smallest niche breadth (Table 3). The yellow perch and the warmouth utilized a larger portion of their maximum feeding niche.

Table 3. Food diversities for five fish species.

| Species | Feeding diversity H | Trophic diversity H'p | Avg. diversity $\underline{H}$ | Coefficient of similarity | Avg. items stomach | Niche breadth |
|---|---|---|---|---|---|---|
| Largemouth Bass | 1.29 | 1.29 | 0.24 | 0.37 | 3.60 | 0.48 |
| Yellow Perch | 1.72 | 2.19 | 0.38 | 0.39 | 12.30 | 0.82 |
| Warmouth | 1.49 | 1.91 | 0.19 | 0.16 | 2.98 | 0.72 |
| Bluegill | 1.53 | 1.59 | 0.45 | 0.46 | 28.30 | 0.60 |
| Pumpkin-seed | 1.63 | 1.47 | 0.47 | 0.31 | 12.30 | 0.55 |

## Fish Population Utilization of Macrophyte Beds

Fish appeared to quickly recolonize macrophyte patches after some had been removed for stomach content analyses. Keast (1978) cited a similar recolonization by the bluegill and the pumpkinseed in Lake Opinicon. Questions arose from this observation on how many fish of each species utilized a macrophyte bed. The largest macrophyte patch was chosen for this part of the investigation since the largest number of fish could be captured from it and consequently a better estimate of population size could be determined than for the small macrophyte beds.

A far greater number of bluegills (1243) utilized this patch than any other species, but only a small portion of that population was present at any one time (Table 4). Few bluegills were recaptured in the main sampling area and only three recaptures were ever obtained from other shallow macrophyte patches. The bluegill may use a number of habitats other than these beds. Keast (1978) found

Table 4. Size of fish populations which utilized the largest macrophyte bed.

| Species | Pop. Size ± S.D. | % of Total Pop. Recap. |
|---|---|---|
| Largemouth Bass | 54.7 ± 5.0 | 55 |
| Yellow Perch | 80.0 ± 27.7 | 14 |
| Warmouth* | 8 | 75 |
| Bluegill | 1243.5 ± 525.3 | 1 |
| Pumpkinseed | 172.2 ± 55.0 | 23 |

that the bluegills preferred macrophyte beds in deeper water and such beds exist in Cedar Lake. The pumpkinseed population (172) utilizing the macrophyte patch was second in size to the bluegill. Unlike the bluegill, the pumpkinseed was often recaptured in the main sampling area and six were recaptured in other shallow macrophyte beds. While the pumpkinseed leaves the main sampling area and probably utilizes other habitat types, it appeared it did so less frequently than did the bluegill. The largemouth bass (55) and the yellow perch (80) populations were nearly the same size but the number of recaptured was very different. Yellow perch probably utilized habitats in cooler water. The warmouth population was small (8) and it was never captured outside the main sampling area and probably used other habitats only to a limited extent.

## DISCUSSION

The largemouth bass, the bluegill, and the pumpkinseed have lower trophic diversities because they specialized on certain food types. There would be virtually no competition between the largemouth bass and either the bluegill or the pumpkinseed with food overlap coefficients of 0.11 and 0.03, respectively. Werner (1977) came to a similar conclusion on the largemouth bass and the bluegill. There was a slightly larger overlap between the pumpkinseed and the bluegill (0.22).

Werner and Hall (1979) felt that the pumpkinseed used vegetative habitats and benthic organisms more efficiently than the bluegill. On the basis of recapture and population estimates, the pumpkinseed remained in the macrophyte beds and there was a small turnover of individuals using the macrophyte patch. Individual bluegills did not stay in a particular habitat for very long. Since the pumpkinseed may be a more efficient benthic feeder (Werner and Hall, 1979), it may reduce the population of a particular prey type so that the less efficient bluegill would leave the weed bed. If exploitative competition such as this exists, it involved possibly only caddisflies. Connolly (1981) found that of 11,069 benthic organisms in shallow waters of Cedar Lake, 64% were snails, and 15% were chironomids but only 1% were caddisflies.

The warmouth may be a habitat specialist rather than a food type specialist. Werner (1977) and Werner and Hall (1977 and 1979) proposed that the green sunfish (*Lepomis cyanellus*) is a food generalist and habitat specialist. Savitz and Janssen (1982) provided some evidence suggesting that the green sunfish is a habitat specialist in order to avoid predation. The warmouth is very similar to the green sunfish in morphology and in their preference for weed beds. There appears to be considerable competition between the warmouth and some of the other fish species.

The yellow perch is similar in that it utilizes a large variety of prey types but probably prefers habitats with cooler water since they have a lower temperature preference than the four other fish species (Magnuson *et al*, 1979). Competition and predation are probably two important forces affecting the warmouth and the perch and only further study can show their relative impacts.

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