THE COMPARATIVE FEEDING ECOLOGY OF CYPRINID FISHES OF THE CHOCTAWHATCHEE RIVER, FLORIDA

by

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CHAPTER 1

COMPARATIVE FEEDING ECOLOGY OF THE
CHOCTAWHATCHEE RIVER MAIN CHANNEL CYPRINIDS

Introduction

Cyprinid fishes of the genera Notropis and Hybopsis are ubiquitous biological features of North American freshwater systems (Eddy and Underhill 1978). These genera, usually forming multispecies assemblages, are the most abundant and speciose members of the ichthyofauna in Coastal Plain streams and rivers (Douglas 1974, Smith-Vaniz 1968, Swift et al 1986). The abundance and diversity of these fishes in most riverine systems suggests that they probably have important roles in trophic aspects of community structure, both as predators and as prey (Pfliegler 1974). However, except for several studies in small streams, the trophic interrelationships of these fishes have been largely neglected (Campbell 1979, Hubbs 1987).

Studies in smaller systems have indicated that cyprinids exhibit considerable dietary plasticity. Described as "opportunistic", "generalist", and "indiscriminate", the feeding habits of cyprinids generally reflect trends in resource availability more than actual prey preferences (Starrett 1950, Whitaker 1977). Cyprinid stomachs have been shown to include varying amounts of microalgae, detritus, plant seeds, aranaeids, crustaceans, and the larval and adult forms of most types of insects (aquatic and terrestrial), indicating a general trend towards omnivory.

Seasonal and spatial patterns of prey availability appear to explain much of the variation in cyprinid feeding habits (Gillen and Hart 1981, Hoover 1981, Mendelson 1975, Starrett 1950, Whitaker 1977). Angermeier (1985) and Felley and Felley (1987) have shown how cyprinid diets reflect seasonal availability of resources. Allochthonous inputs, such as detritus and terrestrial insects, have been shown to contribute significantly to cyprinid diets (Felley and Felley 1987, see Darnell 1961, Goulding 1980, Lowe-McConnell 1987). Many cyprinids are
able to invade temporarily available habitats, such as inundated floodplains, and make use of unexploited trophic resources contained therein (Finger and Stewart 1987, Ross and Baker 1983). Angermeier and Karr (1987) have suggested that cyprinids' ability to utilize seasonally fluctuating food resources has contributed to their ecological and evolutionary success in lotic environments (see also Wiens 1977, 1984).

Few studies have assessed the relationship between microhabitat preferences and feeding habits for individual species (Sale 1979, but see Mendelson 1975, Schultz and Northcote 1972). Microhabitat preferences and differential patterns of food resource usage have been demonstrated in lotic (riverine) assemblages of cyprinids (Baker and Ross 1981, Felley and Hill 1983, Ross et al. 1987), but usually not simultaneously (but see Felley 1984, Gatz 1979, Mendelson 1975). Mendelson (1975) suggested that cyprinids in a small Wisconsin stream were morphologically adapted for living in particular microhabitats, and randomly consumed whatever prey were available within these areas. Moyle (1973), Werner et al. (1977), Whitaker (1977), Hoover (1981), and Surat et al. (1982) have also demonstrated the relationship between microhabitat specialization and feeding habits. However, they suggested that the observed patterns probably resulted from dynamic (synecological) interactions between the species (e.g., resource partitioning), rather than (autecological) differences in morphology or behavior as suggested by Mendelson (1975, and see Strong 1983, Grossman and Freeman 1987).

Ontogenetic feeding shifts, another possible source of dietary variation, have not been well studied in lotic fish assemblages (but see Angermeier and Karr 1983). Intraspecific variation in feeding habits has been shown to be an important factor in the trophic organization of other fish assemblages: lentic (Osenberg et al 1987, Werner and Hall 1988), estuarine (Chao and Musick 1977, Darnell 1958, Livingston 1982, 1982, Stoner and Livingston 1984), and marine (Ross 1977). Livingston (1982, 1984, 1988) and Stoner and Livingston (1984) have criticized the usage of species-level designations in studies of trophic ecology. They suggest that 'trophic units' (groups of adjacent size classes with similar feeding habits) should be used as the lowest ecological entities (functional units) in feeding studies, because variation in feeding habits
between different-sized individuals of a species is often greater than the variation between similar-sized individuals of different species. The potential role of ontogenetic shifts in the maintenance of age-structured populations is discussed by Keast (1977) and Werner and Gilliam (1984).

This study will describe the feeding habits of cyprinid fishes from the main channel Choctawhatchee River, Florida. In this chapter, I will describe the structure of the main channel fish community, and examine temporal, spatial, intraspecific (ontogenetic), and interspecific sources of dietary variation for the abundant main channel cyprinids.

**Material and Methods**

**Study Area**

The Choctawhatchee River originates in southeastern Alabama and flows ~280 km to the Choctawhatchee Bay in northwestern Florida (Figure 1). Approximately 161 km of the river lies in Florida, draining 3700 km² of rural lands (58.4% forestry and 25.7% agriculture; Florida Rivers Study Committee 1985). The river is a large, meandering, alluvial system, characterized by heavy sediment and nutrient loads, extensive snag (erosional) and shoal (depositional) habitats, low gradient, and an extensive floodplain (Livingston et al. 1988, Wolfe et al. 1988). Water quality in the system is generally good except for heavy sediment loading (probably associated with extensive clear-cutting in the watershed) and some minor point source inputs (FDER 1986). Stream flow (discharge) is highly variable with peaks in the late spring and early summer months (USGS and NFWMD stage records).

**Study Organisms**

Of the eighteen species of minnow-like cyprinids known to occur in the Choctawhatchee Drainage basin (Bailey et al. 1954, Mettee 1970, Swift et al. 1986), only six are considered to be typical of main channel habitats: the silverjaw minnow (*Ericymba buccata*), speckled chub (*Hybopsis aestivalis*), clear chub (*Hybopsis winchelli*), longnose shiner (*Notropis longirostris*),
weed shiner (*Notropis texanus*), and the eastern blacktail shiner (*Notropis venustus cercostigma*, Gibbs 1957). These fishes represent different subgenera, and therefore probably do not share extensive coevolutionary histories within the Choctawhatchee drainage (sensu Mayden 1987, Mendelson 1975). Bailey et al. (1954), Suttkus and Raney (1955), Swift (1970), and Swift et al. (1977, 1986) have discussed biogeographical aspects of the distributions of these fishes.

**Fish Collection and Analysis Methods**

Monthly (3/87-2/88) collections of fishes were made at three main channel monitoring stations as part of an ecological characterization of the Choctawhatchee drainage basin (Livingston et al. 1988). Stations were selected based upon their overall similarity in macrohabitat features (relative amounts of snag and shoal areas), relative longitudinal placement, and seasonal accessibility for sampling. Fishes were collected during daylight hours, using a 10-hp pulsator electrofisher (Smith-Root Model 5.0 GPP) mounted to a 5.25 m fiberglass boat. DC voltage (0 to 1000 volts, 5000 watts, 25 amps) and pulse frequency were adjusted at each station depending on stream conductivity and catch efficiency. Fishes were collected while moving the boat in and out of the shoreline in an upstream direction. Three 200 sec shocks were done on each side of the channel, and an effort was made to sample all major macrohabitat types. Channel size and morphology, heavy discharge, and extensive snags precluded the use of seines and block nets. Electrofishing data from the FGFWFC indicated that electrofishing was a relatively consistent sampling method for the dominant species (including the main channel cyprinids; see Results section). Fishes were preserved immediately in 10% buffered formalin and returned to the laboratory for identification, measurement (mm SL), and trophic analyses. Fishes were not anesthetized prior to preservation because electrofishing appeared to adequately stun them (they did not move after adding formalin). Temporal persistence of community structure was assessed by comparing the concordance (Kendall's W, Sokal and Rohlf 1981) of rank abundances of the dominant species (those species accounting for ≥90% of all fishes collected) over a six year period (data courtesy of G. Bass, FGFWFC). These data also provide
information on electrofishing efficiency. Livingston et al. (1988) provide sampling protocols, physico-chemical collection data, and detailed site descriptions.

**Trophic Analyses**

The stomach (foregut) contents of fishes were pooled into 10 mm SL size-classes (up to 20 individuals for each species, sampling date, and station) and stored in 70% ethanol with rose bengal stain. Dietary analysis of these samples was carried out using the method of Carr and Adams (1973) as modified by Livingston (1982, 1984). Each sample was rinsed with distilled water through a series of nested sieves of decreasing mesh size (425, 250, 150, and 75 µm). The contents of each sieve fraction were identified, enumerated, dried (24 h @ 100 °C) and weighed, and the % dry weight contribution of each prey type calculated. Larger prey items of some fishes were measured (with a micrometer), dried, and weighed without processing through the sieves (for size class analyses, these data were placed in the largest [425 µm] sieve fraction). All analyses were carried out using dry weights (see Wallace 1981 for a discussion of the advantages of using dry weight measures in dietary studies).

Patterns in prey size selection between size classes were graphically determined by comparing the weight contribution of each sieve fraction as a percentage of the total dry weight. Similarly, seasonal dietary variation between size classes was graphically determined by comparing the dry weight contribution of the different prey types as percentages of the total dry weight. Concordance (Kendall's W, Sokal and Rohlf 1981) of the ranks of the dominant prey types was calculated for each species and station in order to examine spatial (between station) variability in feeding habits. Vertical forage site preferences (benthic vs. surface only) were inferred from stomach contents. Prey items found in fish stomachs were categorized as either benthic, midwater, or surface prey (prey microhabitat information was taken from Pennak (1978) and Merritt and Cummins (1984)). The dry weight contributions of surface and benthic prey were calculated for each species x size class x month sample combination. The difference between these weights (surface-benthic) was calculated in order to provide an overall measure of
relative importance of each prey type. Preliminary data analysis revealed that: 1) the data were severely unbalanced with respect to species x size x time combinations, and 2) variances were heterogeneous and untransformable. Therefore, nonparametric Mann-Whitney U-tests were used to extract species forage site differences. Only combinations of size classes x months in which all species were present were used in this analysis (this reduced confounding associated with seasonal and ontogenetic differences).

Feeding data were pooled (all dates and stations) to create a matrix of size classes (variables) by prey types for each species. Cluster analyses of these matrices were used to measure similarity of feeding habits between size classes for each species (ontogenetic relationships). Cluster analysis has been shown to be a robust (sensu Gauch 1985) multivariate procedure for descriptive studies of fish feeding habits (Livingston 1982, 1984, Livingston and Stoner 1984). In this study, clusters of size classes were interpreted as representing distinct ontogenetic dietary progressions, or 'trophic units' (Livingston 1982, 1984). These were fishes that consumed the same kinds of prey in similar proportions. Similarity of feeding habits between pairs of size classes was assessed using the \( \rho \) similarity measure (Matusita 1955, cited in van Belle and Ahmad 1974). This measure is the square root of the product of the proportions of each prey type in each of the two size classes, summed across all prey types (e.g., \( \Sigma (p_xi p_yi) \)). Meeter and Livingston (1978) have discussed the usage and relative merits of this clustering method. The bias properties of the \( \rho \) similarity measure have not been thoroughly investigated (van Belle and Ahmad 1974). An additional clustering algorithm, Czeckanowski's Distance (also known as Bray-Curtis or Schoener's Index; Bloom 1981), was used in order to assess the 'biological meaningfulness' of the results generated by the \( \rho \) measure. If two computationally distinct clustering strategies yield equivalent results, then the patterns are more likely to be real rather than mathematical artifacts (see discussions in Boesch 1977 and Gauch 1985). The flexible grouping strategy (Lance and Williams 1967, discussed in Sneath and Sokal 1973 and Boesch 1977), with \( \beta = -0.25 \), was used for grouping clusters.
Computer analyses were carried out on the Florida State University CYBER 850 computer system, using BMDP8V, SPECS (developed by G. Woodsum, CARRMA) and MATRIX (developed by G. Woodsum and L. Wolfe, CARRMA) statistical programs. Graphics, word processing, and additional data analyses were carried out on a Macintosh® computer, using Microsoft Word 3.01®, Statview®, and Cricket Graph® software.

Results

The Main Channel Fish Community

A total of 51 species was collected from the three main channel stations (Table 1). Station 70 had slightly higher cumulative species richness (47) than Station 68 (39) and Station 61 (40). Cyprinidae, Centrarchidae, and Catastomidae were the most numerically abundant families at all three stations (Figure 2). An analysis of long-term (6 years; courtesy FGFWFC) collection data for the fifteen numerically dominant species (Table 2) indicated high concordance of species ranks (Kendall’s W=86.6%, p<.01), and also suggested that electrofishing was a consistent sampling method. *Hybopsis winchelli, Notropis longirostris, Notropis texanus, and Notropis venustus* were the only cyprinids collected regularly from the main channel. Overall, *Notropis venustus* was the most abundant, followed by *Notropis texanus, Hybopsis winchelli,* and *Notropis longirostris,* respectively (Figure 3). Seasonal patterns of abundance (Figure 4) indicate that *Notropis venustus* (16-122 mm SL) was abundant throughout the year; *Notropis texanus* (21-70 mm SL) was most abundant August through September; and *Hybopsis winchelli* (21-60 mm SL) had low numbers throughout the year. Only 31 *Notropis longirostris* (41-60 mm SL) were collected during the sampling period. Recruitment was not assessed. However, reproduction probably occurred between March and October for all four species (Bresnick and Heins 1977, Heins and Bresnick 1984, Heins and Clemmer 1975, Heins and Davis 1986, Heins and Dorsett 1987, Swift et al. 1977, pers. obs.). Qualitative field observations made during collecting trips indicated that *Notropis longirostris* was most commonly collected from shoals
and sandbars located away from the banks. *Notropis texanus* and *Hybopsis winchelli* were most frequently collected from deeper, somewhat slower, near-shore snag habitats. Abundances of *Hybopsis winchelli* and *Notropis texanus* were highly correlated with one another (r=.624, p<.001; n=36), suggesting that these two species were responding to similar environmental factors. *Notropis venustus* was captured in all habitats sampled, but most frequently away from the shore in swifter waters.

**Cyprinid Feeding Habits**

The stomach contents of 1371 *Notropis venustus*, 1042 *Notropis texanus*, 154 *Hybopsis winchelli*, and 5 *Notropis longirostris* were examined. Most stomachs contained food (*Notropis venustus*: 94%; *Notropis texanus*: 95%; *Hybopsis winchelli*: 89%; *Notropis longirostris*: 100%), and no seasonal trends in gut fullness were noted.

The diets exhibited much intraspecific variability and interspecific overlap (Table 3). However, seven broad prey categories (sand grains [probably digested incidentally], detritus, microalgae, ephemeropteran nymphs, dipteran adults, and fire ants (*Solenopsis* spp.) accounted for more than 92% of the total dry weight consumed by the main channel cyprinids. *Notropis texanus* had the most diverse diet and *Notropis longirostris* the least, although this probably reflects differences in sample sizes. *Notropis venustus* ate primarily terrestrial insects (*Solenopsis* spp. and adult dipterans), microalgae, and detritus. Adult coleopterans (elmids and gyrinids), ephemeropteran nymphs, lepidopteran larvae (pyralids and noctuids), and sand grains were of secondary importance. *Notropis texanus* fed mostly on detritus and microalgae; along with *Solenopsis* spp., sand grains, adult dipterans, and ephemeropteran nymphs. *Hybopsis winchelli* fed primarily on sand grains, chironomid larvae, microalgae, microcrustacea (copepods, ostracods, and cladocerans), *Solenopsis* spp., and ephemeropteran nymphs. *Notropis longirostris* consumed chironomid larvae, sand grains, microalgae, ephemeropteran nymphs, and the exotic bivalve *Corbicula*. Prey size tended to increase with increasing fish size in *Notropis venustus* and *Notropis texanus* (Figure 5). Larger prey items (3-40 mm) included:
ephemeropteran and odonate nymphs, lepidopteran larvae, coleopteran adults and larvae (mostly elmids), isopods, decapods (mostly *Palaemonetes paludosus*), oligochaetes, and an ~40 mm TL *Anolis* lizard (from a 95 mm *Notropis venustus*).

Although similarity between size classes was high, cluster analysis revealed three natural (ontogenetic) groupings of *Notropis venustus* size classes (Figure 6). NOTVEN I (21-50 mm SL) ate mostly microalgae, *Solenopsis* spp., and adult dipterans. NOTVEN II (51-90 mm SL) diets were dominated by *Solenopsis* spp. and detritus, with microalgae and adult dipterans being of lesser importance. Larger prey items (especially ephemeropteran nymphs and coleopteran adults) and *Solenopsis* spp. dominated the diet of NOTVEN III (91-120 mm SL). Three trophic units were also determined for *Notropis texanus* (Figure 6): Smaller individuals (21-30 mm SL) ate primarily *Solenopsis* spp., microalgae, sand grains, and chironomid larvae; intermediate-sized (31-60 mm SL) individuals consumed mostly microalgae and detritus; and the largest individuals (61-70 mm SL) were primarily detritivorous. Cluster analysis did not reveal distinct ontogenetic shifts in feeding habits for *Hybopsis winchelli* (Figure 6) and was not performed on *Notropis longirostris* (only one size class of *Notropis longirostris* was collected and the available sizes of *Hybopsis winchelli* did not cover a very wide range). A second cluster analysis (Figure 7), using the 'trophic units' generated above as variables, indicated considerable interspecific overlap in feeding habits and delineated two major feeding groups. The first group consisted of the trophic groupings HYBWIN I, NOTTEX I, NOTTEX II, NOTVEN I, and NOTVEN II. These fishes ate *Solenopsis* spp., microalgae, and detritus in varying proportions along with chironomid larvae and sand grains. The second feeding group, comprised of NOTTTEX III and NOTVEN III, also ate large amounts of *Solenopsis* spp., microalgae, and detritus; however, large aquatic insects (coleopterans, lepidopterans, ephemeropterans) comprised 33% of their total diet. Seasonal variation within and between the different trophic groupings was quite high for *Hybopsis winchelli*, *Notropis texanus*, and *Notropis venustus*. HYBWIN I ate aquatic insects (mostly chironomid larvae and ephemeropteran nymphs) and sand grains throughout the year (Figure 8). Terrestrial insects contributed significantly to the diet from July through February.
NOTTEX I ate large amounts of chironomid larvae in August; switched to Solenopsis spp. and microalgae October through January; and the few fishes examined from February had fed heavily on small Palaemonetes paludosus (Figure 9). NOTTEX II fed on Solenopsis spp. year-round; microalgae June through February; detritus July through January; and aquatic insects in May (coleopterans), January (ephemeropteran nymphs), and February (trichopteran larvae, coleopterans, and ephemeropteran nymphs) (Figure 10). NOTTEX III ate mostly aquatic insects in April (ephemeropteran nymphs), September (hemipterans), and February (ephemeropteran nymphs and chironomid larvae); detritus in May, November, and February; and microalgae in December (Figure 11). NOTVEN I consumed Solenopsis spp. year-round; ephemeropteran nymphs and dipteran pupae year-round (especially January); and microalgae and detritus August through February (Figure 12). NOTVEN II also ate Solenopsis spp. year round; adult dipterans in May, September, and October; detritus in low levels March through October and larger amounts November through February; microalgae August through January; and aquatic insects (ephemeropteran nymphs, coleopterans, and lepidopteran larvae) throughout the year (Figure 13). NOTVEN III ate ephemeropteran nymphs in March through May and July; odonate (gomphid) nymphs in June and July; lepidopteran larvae in July; microalgae in August and December; Solenopsis sp. in August; and detritus in April, September, November and, December (Figure 14). In general, each group of fishes (species and size classes) appeared to be tracking resources seasonally; they were using similar resources, but at different times and in different amounts.

Spatial (between station) variability of feeding habits was not strongly apparent for Notropis venustus (W=76%; p<.025) and Notropis texanus (W=80%; p<.025) based on a concordance analysis (Kendall's W) of the relative abundances of the top prey items (comprising ≥ 95% of the total dry weight). Solenopsis spp. was the dominant prey item of Notropis venustus at all three stations, with the relative importance of microalgae, detritus, and adult dipterans varying between stations. Notropis texanus ate primarily microalgae at Station 61, and
detritus at Station 68 and Station 70. *Solenopsis* spp. contributed significantly to the diet of *Notropis texanus* at all three stations sampled.

Vertical water column specialization was indicated by an analysis of prey types categorized into benthic or surface prey categories (figure 15). *Notropis venustus* appeared to be feeding mostly at the water's surface because of the large amounts of terrestrial insects found in their stomachs. *Notropis texanus* was a benthic detritivore, but also fed at the water's surface on terrestrial insects. *Notropis longirostris* and *Hybopsis winchelli* were benthic specialists, consuming large amounts of chironomid larvae and filamentous algae. Statistical analyses of the data were hampered by an unbalanced data matrix and severe problems with lack of homogeneity of variances. However, Mann-Whitney U-tests indicated that 41-50 mm SL *Notropis venustus* consumed significantly more surface prey than did *Hybopsis winchelli* ($Z = -3.54$, $p<.001$). *Notropis texanus* and *Hybopsis winchelli* did not differ in this size range ($Z=-1.56$, $p>.10$), as they both ate mostly benthic prey. *Notropis venustus* ate significantly more surface prey than did *Notropis texanus* ($Z=-4.731$, $p<.001$) in the 31-60 mm SL size range.

**Discussion**

**Community Structure**

The Choctawhatchee River main channel fish community has been described previously by Mettee (1970) and Bass et al. (1980). The speciose families Cyprinidae, Centrarchidae, Percidae, and Catastomidae dominate the system, as is typical of other larger Coastal Plain drainages such as the Escambia, Perdido, and Apalachicola (Swift et al. 1986). Species composition appeared to be temporally persistent. Although the structurally similar main channel sites had similar patterns of species composition, comparisons between the main channel sites and the physically distinct tributaries reveal significant differences in the composition of phytoplankton, macroinvertebrate, and fish assemblages (Bass et al. 1980, Livingston et al. 1988).
Patterns of association found in this study (also Bailey et al. 1954, Douglas 1974, Heins and Clemmer 1975, Swift 1970) among the four numerically abundant main channel cyprinids seem to suggest that these species are responding to the same environmental factors, especially discharge (Baker and Ross 1981, Felley and Hill 1983, Felley and Felley 1987, Ross et al. 1987, Livingston et al. 1988). In the Choctawhatchee River, *Notropis texanus* abundance is lowest during peak discharge (Livingston et al. 1988), suggesting a lateral movement of this species onto the inundated floodplain. *Notropis texanus* is the most frequently collected species in the Ochlockonee River floodplain (H. Leitman [USGS] pers. comm.). Seasonal flooding has been shown to influence stream fish community structure (Coon 1982, Finger and Stewart 1987, Matthews 1986, Minckley and Meffe 1987, Ross and Baker 1983, Ross et al. 1985, Schlosser 1985). Ross and Baker (1983) found that abundance of *Notropis texanus* was highly correlated with the extent and duration of the previous year's spring flooding. Additionally, Boschung (1987) documented a 99% increase in *Notropis texanus* abundance and a 71% decrease in *Notropis venustus* abundance following the impoundment of the Upper Tombigbee River (which created extensive backwater habitat).

**Habitat, Morphology, and Forage Site Use**

The Choctawhatchee River cyprinids vary in their vertical and lateral distributions within the main channel, and these patterns of differential resource utilization may reflect morphological specializations (Alexander 1967, Felley 1984, Gatz 1979, Keast and Webb 1966, Mendelson 1975, Werner and Hall 1976, 1977). *Notropis longirostris* and *Hybopsis winchelli* are both adapted for the benthic environment. Hubbs and Walker (1942) noted that the streamlined body, arched nape, large pectoral fins, protruding snout, and inferior mouth are "morphological features [that] adapt *Notropis longirostris* to swimming about and feeding over the open bottom, in current." *Hybopsis winchelli* has well developed maxillary barbels, a slightly extended snout, and an inferior mouth for benthic foraging (Davis and Miller 1967, Reno 1969). These two species appear to be ecologically separated within the river along a lateral
gradient: *Notropis longirostris*, with its larger fins and arched nape, lives in the faster currents associated with the shoal habitats; *Hybopsis winchelli*, lacking such features, is found predominantly in the slower, deeper areas along the erosional shore (pers. obs.). *Notropis venustus*, the largest of the Choctawhatchee cyprinids (Carlander 1969, Livingston et al. 1988), is heavy bodied with a pointed snout and arched nape (Gibbs 1957), allowing it to inhabit the upper parts of the swifter river sections. Heins and Clemmer (1975) found that *Notropis venustus* and *Notropis longirostris* were strongly associated with each other in midchannel environments in a Mississippi system. *Notropis texanus*, on the other hand, is fairly broad relative to its length, has a blunt nose, and a cephalic canal system more similar to that of lentic fishes (Douglas 1974, Swift 1970), explaining its common occurrence in the lower half of the slower, deeper habitats. Swift (1970), Swift et al. (1977), Baker and Ross (1981), and Ross et al. (1987) showed that when collected together, *Notropis texanus* was usually found lower in the water column than *Notropis venustus*. Differential utilization of the water column has been reported for many fish assemblages (Baltz and Moyle 1984, Ebeling and Laur 1986, Gorman and Karr 1978, Keast 1978, Moyle and Senanayake 1984, Schultz and Northcote 1972, Werner and Hall 1976, 1977, Werner et al. 1977, Zaret and Rand 1971); and appears to be fairly common among the North American Cyprinidae (especially *Notropis*) (Baker and Ross 1981, Felley 1984, Gorman 1988a, 1988b, Hoover 1981, Mendelson 1975, Moyle 1973, Ross et al. 1987, Starrett 1950).

Analysis of feeding habits indicated that the Choctawhatchee River cyprinids were feeding in different parts of the water column. *Notropis venustus* consumed mostly terrestrial insects, suggesting a surface-oriented feeding behavior. *Notropis texanus* ate mostly detritus and microalgae from the bottom and midwater. *Notropis longirostris* and *Hybopsis winchelli* consumed chironomid larvae, sand grains, microalgae and other benthic prey. Previous studies of *Notropis venustus* (Hale 1963, Hambrick and Hibbs 1977, Mathur 1972), *Notropis texanus* (Becker 1983, Felley and Felley 1987, Pfliegler 1975), *Notropis longirostris* (Hubbs and Walker 1942, Heins and Clemmer 1975) and the genus *Hybopsis* (Davis and Miller 1967) have had
demonstrated similar patterns. Experimental evidence for differential forage site use is presented in Chapter 2.

**Ontogenetic, Seasonal, and Spatial Variability**

Feeding habits (and associated microhabitat usage) appear to vary with age (and size) in many animal assemblages (see Werner and Gilliam 1984 for review). Livingston (1982, 1984, 1988) and Stoner and Livingston (1984) have shown the importance of assessing ontogenetic variation in feeding habits and cautioned about the "inadequacy of species-level designations" in studies of community trophic processes. Both *Notropis venustus* and *Notropis texanus* exhibited patterns of ontogenetic variation in feeding habits. *Notropis texanus* shifted to larger quantities of detritus with increasing size, and *Notropis venustus* ate proportionately more aquatic insects with increasing size. A general increase in prey size was also noted, suggesting larger fishes were generally able to consume larger prey than smaller fishes. Divergence in dietary overlap between size classes may have an adaptive role in minimizing intraspecific competition in size-structured populations (Keast 1978, Werner and Gilliam 1984).

Seasonal variability of feeding habits was generally high. This has been demonstrated previously in various small stream assemblages (Angermeier 1982, 1985, Starrett 1950, Whitaker 1977). Angermeier (1982) suggested that the behavioral plasticity (i.e., opportunistic feeding habits) exhibited by cyprinids contributes to their success in lotic systems. Certain allochthonous prey types (detritus and terrestrial insects) were utilized by the main channel cyprinids in temporally variable proportions. Detritus, a readily available resource in large, alluvial rivers, was heavily exploited, especially by *Notropis texanus*. Although lacking specific cellulose digesting enzymes, cyprinids possess well developed pharyngeal teeth which enable them to physically extract most of the nutrients, especially protein (Pandian 1987). Hyatt (1979), Goulding (1980), Angermeier and Karr (1983), and Lowe-McConnell (1987) have demonstrated the importance of detritus in riverine trophic ecology. Becker (1983) and Felley and Felley (1987) found large amounts of detritus in the stomachs of *Notropis texanus* year-round, but noted
seasonal increases. Terrestrial insects (adult dipterans and (especially) Solenopsis spp.) also contributed significantly to the diets of the main channel channel cyprinids (particularly Notropis venustus). Fire ants do not appear to affect fishes after ingestion (Ferguson 1962), and are available year-round, especially following storms (pers. obs.). Terrestrial insects are commonly found in the stomachs of cyprinids (Angermeier 1982, 1985, Felley and Felley 1987, Mendelson 1975, Starrett 1950, Surat et al. 1982, Whitaker 1977). Mathur (1972) and Hale (1963) found large amounts of terrestrial insects in the stomachs of Notropis venustus; and Hambrick and Hibbs (1977) found that the diet of Notropis venustus in a Louisiana system was comprised primarily of the termite Reticulotermes flavipes.

Conclusions

The Choctawhatchee River main channel cyprinids exhibited marked variation in feeding habits. This variation had seasonal, spatial, ontogenetic, and interspecific components. The dietary variation found in this study is comparable to that found for cyprinids of smaller streams. Patterns of dietary variation associated with growth were observed for Notropis texanus and Notropis venustus. Dietary analysis indicated that prey selection by these fishes may be a function of forage site (microhabitat) specialization.
CHAPTER 2

DIFFERENTIAL FORAGE-SITE USAGE
BY CYPRINIDS OF THE CHOCTAWHATCHEE
RIVER (FLORIDA)

Introduction

Fish dietary studies frequently reveal patterns of prey selection that appear to reflect forage-site (microhabitat) specialization rather than actual prey-type preferences. Sale (1979) and Ross (1986), in reviews of resource partitioning within fish assemblages, suggested that coupling of trophic and spatial resources may be a generalized phenomenon in fish communities. Resolution of the relationships between spatial and trophic resource use can help in determining what mechanisms (abiotic factors, competition, predation) are responsible for community structure.

Patterns of differential resource by fishes of the speciose genus Notropis have been particularly well documented. These fishes, the most abundant members of the ichthyofauna in Coastal Plain streams and rivers (Smith-Vaniz 1968, Douglas 1974, Swift et al. 1988), usually form multispecies assemblages. Independent studies of notropid feeding habits (Starrett 1950, Mathur 1972, Whitaker 1977, Hoover 1981, etc.) and microhabitat preferences (Baker and Ross 1981, Felley and Hill 1983, Ross et al. 1987, etc.) have indicated that these fishes may be habitat specialists rather than trophic specialists. Studies which have incorporated analyses of both feeding and microhabitat preferences further indicated that these two types of resource use are complexly interrelated (Moyle 1973, Mendelson 1975, Werner et al. 1977, Felley 1984, etc.). Mendelson (1975, p. 227) considered two alternative foraging strategies that might be responsible for the patterns of prey selection he found in an assemblage of Wisconsin notropids:
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 indiscriminantly on whatever prey of a suitable size are available.

Based on observed patterns of species microhabitat usage, prey selection, and prey availability, Mendelson concluded that the latter mechanism was operating in the assemblage he studied.

Experimental studies of forage-site specialization within other groups of fishes provide evidence supporting this hypothesis (Schultz and Northcote 1972, Werner and Hall 1977, Werner 1984, etc.). For example, Schultz and Northcote (1972) noted that spatial specialization was responsible for the dietary divergence between sympatric populations of cutthroat trout and Dolly Varden. They experimentally demonstrated that Dolly Varden were more efficient benthic feeders and cutthroat trout more efficient surface feeders. Werner and Hall (1977) and Werner (1984) have also experimentally demonstrated forage-site specialization within an assemblage of lake centrarchids. Experimental evidence for forage-site specialization is lacking for stream fishes of the genus *Notropis*, the largest group of North American freshwater fishes (over 100 described species; Robins et al. 1980).

The diets of several Choctawhatchee River main channel cyprinid species appear to reflect patterns of prey selection based on differential forage-site use (Chapter 1). In this chapter, I discuss a set of laboratory experiments examining differential forage-site use by the blacktail (*Notropis venustus*) and weed (*Notropis texanus*) shiners, the two most abundant cyprinid species in the Choctawhatchee River main channel. These experiments compared the foraging rates and foraging efficiencies (successful captures/total captures attempted) of these fishes as they fed at artificial benthic and surface forage sites. Based on patterns observed in Chapter 1, I tested the hypotheses that 1) *Notropis venustus* would be the superior surface forager and 2) *Notropis texanus* the superior benthic forager. In addition, preferences for
particular prey types were separated from preferences for particular forage sites (e.g., surface vs. benthic) by holding prey type constant. Laboratory results are related to dietary patterns found in the field.

**Materials and Methods**

**Fish Collection and Maintenance**

*Notropis venustus* and *Notropis texanus* were seined from the Choctawhatchee River main channel and allowed to acclimate in laboratory aquaria for five days. Experimental aquaria were 59.5 cm long, 39.5 cm high, and 30.5 cm deep (~72 L; see Figure 16). Aquaria had undergravel filters covered with ~3 cm of sieved river sand (particle sizes 0.5 to 1.0 mm in diameter) and were filled with well water to a depth of 33 cm above the substrate. The backs and sides of the aquaria were painted black and the fronts tinted in order to minimize external disturbances and facilitate behavioral observations. Twenty-watt flourescent lights were suspended 20 cm above the water's surface and maintained on a 10 hour photoperiod. Preliminary observations indicated that the light intensity affected fish foraging behavior (fishes sat motionless on the bottom of the aquaria); therefore, each bulb was covered with a layer of plain white paper. After adjusting light intensity, fishes moved and foraged actively. Jones (1955), Cerri (1983), and Endler (1987) have demonstrated decreased foraging activity by fishes exposed to bright lighting. Mean water temperature during the experimental period was 18.3 °C (SD=1.2, n=12). Fishes were fed flake food and beef liver *ad libitum* during the acclimation period.

**Experimental Procedure**

Twelve similarly-sized (41-60 mm SL) individuals were randomly assigned to each of four single-species aquaria (two tanks per species). The number of fish per aquaria was based on preliminary laboratory observations, which had indicated that neither species formed actively feeding schools until twelve or more fish were present. Additionally, field studies have indicated
that notropids are group foragers (Mendelson 1975, Pfliegler 1975, Eddy and Underhill 1978, Pers. Obs.). Since the foraging behavior of an individual within an aquarium may have been affected by group dynamics, each aquarium was considered an experimental unit. Preliminary behavioral observations were made of the fishes in order to determine vertical water column preferences. I observed each tank and recorded the water column position (bottom ~0-11 cm, middle ~11-22 cm, or top ~23-33 cm) of each of the 12 individual fish contained therein. Grid marks on the front of each aquarium delineated the three water column levels and facilitated depth measurements. Measurements were made on the day prior to the first foraging experiments (one day after the fishes had been placed into experimental single-species aquaria) between 1100 and 1400. Observations were made randomly at each tank until I had obtained 25 separate counts for each tank (=300 water column position data points for each tank).

Experiments consisted of lowering artificial foraging platforms into the experimental aquaria and allowing fishes to feed for 15 minutes. For surface experiments, an artificial platform was suspended horizontally just below the water's surface in each aquarium so that fishes were exposed to prey from above. For benthic experiments, an artificial platform was placed on the bottom of each aquarium so that the fishes were exposed to prey from below. Forage platforms consisted of 7.62 cm x 7.62 cm x 0.64 cm clear plexiglass squares. Pieces of beef liver (~2 mm x 2 mm x 2 mm; mean wet weight =3.1 mg, SD=0.5, n=21) were pressed into 25 equidistantly spaced holes that had been drilled into each forage platform. Beef liver, a prey type novel to both species, was used in order to separate forage-site specialization (e.g., surface vs. benthic) from prey-type preferences (e.g., benthic dipteran larvae vs. surface-oriented dipteran adults). This approach has been used with favorable results in previous studies of fish (Pazkowski 1983, 1985, 1986) and bird (Wiedenfeld 1988) foraging behavior.

Fishes were allowed to feed for 15 minutes and then forage sites were removed. Foraging rate (the number of prey eaten by 12 individuals in 15 minutes) and foraging efficiency (the number of successful strikes divided by the number of strikes attempted) were recorded as response variables. The surface and benthic trials were both applied to each aquarium each day
and the experiments were repeated for six days (16-22 December 1988). The experiments were
repeated in order to assess the affects of experience (i.e., learning) on foraging behavior. Order
of presentation of surface and benthic trials was determined randomly each day for each
aquarium. The first trials were carried out between 0900 and 1100 and the second trials between
1500 and 1700. Fishes were fed beef liver and flake food ad libitum each day following the
second trials. Both the surface and benthic experiments were two-factor (species x day of trial)
repeated measures designs. For each experiment, species was an among aquarium source of
variation, and day of trial was a within-aquarium source of variation for which repeated
measures were obtained. Natural logarithm transformations of forage rate and arcsine
transformations of foraging efficiency were used in order to reduce the observed heterogeneity of
variances and non-normality of the data.

Results

Patterns of differential water column use by Notropis venustus and Notropis texanus in
the experimental aquaria (Figure 17) were similar to those observed in previous field studies of
1987). Notropis venustus spent more time in the upper third of the experimental aquaria than
Notropis texanus (p<.05, t-test), and Notropis texanus spent more time in the lower third of the
water column than did Notropis venustus (p<.01, t-test). These fishes did not differ in the
amount of time spent in the middle portions of the experimental aquaria (p>.10, t-test). Gorman
(1988a, 1988b) found that notropids maintained in static aquaria had similar relative vertical
preferences as fishes observed in natural streams.

Notropis venustus and Notropis texanus both approached the surface forage platforms at
approximately 45 ° angles. However, Notropis texanus approached the platform more
cautiously, darting to the surface to bite at the platform, and then immediately returning to the
lower two-thirds of the aquaria. Notropis venustus usually approached the surface platforms
more slowly and remained near the platform while handling prey. Individual Notropis venustus
were observed removing two prey items during a single foraging bout. These differences in feeding behavior may account for the observed differences in foraging rate and foraging efficiency. *Notropis venustus* consumed significantly more surface prey than *Notropis texanus* (Figure 18; Table 4). *Notropis venustus* was also a more efficient surface forager than *Notropis texanus* (Figure 19; Table 5), successfully obtaining prey in 93% of all attempts (as opposed to 61% for *Notropis texanus*). Experience (day of trial) did not influence foraging rate or foraging efficiency for either *Notropis venustus* or *Notropis texanus* (Tables 4 and 5).

There were no apparent differences in the foraging behaviors of *Notropis texanus* and *Notropis venustus* at the benthic platforms. Both species slowly approached the platforms at approximately 45° angles and remained close to the platform while handling prey. Individuals of neither species were observed removing more than one prey item during a forage bout. *Notropis texanus* ate considerably more benthic prey than did *Notropis venustus* (Figure 18; Table 6). However, *Notropis texanus* was only slightly more efficient than *Notropis texanus* (p=.1323; Figure 19; Table 7), successfully obtaining prey in 93% of all attempts (as opposed to 85% for *Notropis venustus*). As in the surface experiments, experience (day of trial) did not affect the foraging rate or foraging efficiency of *Notropis texanus* or *Notropis venustus* (Tables 6 and 7).

The patterns of differential forage-site use predicted from dietary analyses (Chapter 1) were similar to those found in this laboratory study. *Notropis venustus*, which consumed mostly surface-oriented prey (e.g., terrestrial insects), was a more active and efficient surface forager than *Notropis texanus*. Conversely, *Notropis texanus*, which consumed mostly benthic prey (e.g., detritus and ephemeropteran nymphs), was a better benthic forager than *Notropis venustus*. These results support the hypothesis that *Notropis texanus* and *Notropis venustus* are forage-site specialists in the Choctawhatchee River main channel.

**Discussion**

Vertical microhabitat segregation within fish communities has been well documented (Werner et al. 1977, Moyle and Senanayake 1984, Moyle and Vondracek 1985, Ross 1986, etc.).
In this study I have shown *Notropis venustus* and *Notropis texanus* occupy different water column positions in experimental aquaria. *Notropis venustus* tended to use the upper two thirds of the water column, whereas *Notropis texanus* tended to use the lower two thirds of the water column. Gorman (1988a, 1988b) found that notropids maintained in static aquaria had similar relative vertical preferences as fishes observed *in situ*. Also, previous descriptive studies have suggested similar patterns of vertical separation for *Notropis venustus* and *Notropis texanus* found in small streams (Swift 1970, Douglas 1974, Swift et al. 1977, Baker and Ross 1981, Felley 1984, Ross and Baker 1984, Ross et al. 1987). Overall, these results support the hypothesis that *Notropis venustus* and *Notropis texanus* are vertically separated within the main channel of the Choctawhatchee River.

Patterns of vertical microhabitat use appear to be strongly coupled with foraging abilities. *Notropis venustus*, the more surface-oriented fish, had a higher forage rate at the surface site than did the benthic *Notropis texanus*. Conversely, *Notropis texanus* consumed more benthic prey than *Notropis venustus*. These findings agree well with results of dietary analyses of *Notropis venustus* and *Notropis texanus*. *Notropis venustus*, the surface oriented species, consumes primarily formicids, adult dipterans, isopterans, and other terrestrial insects (Chapter 1; Hale 1963, Hambrick and Hibbs 1977, Mathur 1972, Felley and Felley 1987). *Notropis texanus* consumes mostly benthic and midwater prey, including detritus, microalgae, and ephemeropteran nymphs (Chapter 1; Becker 1983, Felley and Felley 1987).

Morphology may explain these differences in habitat and foraging patterns (Keast and Webb 1966, Alexander 1967, Gatz 1979, Felley 1984). *Notropis venustus* is heavy bodied with a pointed snout and arched nape (Gibbs 1957), supposedly giving it a foraging advantage in the upper, swifter portions of the water column (Douglas 1974, Felley 1984). *Notropis texanus* is fairly broad relative to its length, has a blunt nose, and a cephalic line system more similar to lentic fishes, all features which should enhance benthic foraging ability (Swift 1970, Douglas 1974, Felley 1984). However, both *Notropis venustus* and *Notropis texanus* are morphologically generalized relative to other Choctawhatchee River main channel cyprinids. For example, the
longnose shiner (*Notropis longirostris*) and the clear chub (*Hybopsis winchelli*) are both relatively specialized for benthic foraging (e.g., inferior mouths). Keast and Webb (1966) have suggested that generalized (i.e., not ventrally or dorsally oriented) mouths increase foraging flexibility in fishes. The relative morphological generality of *Notropis venustus* and *Notropis texanus* probably accounts for the ability of these fishes to use both benthic and surface forage sites. Although *Notropis venustus* and *Notropis texanus* differed significantly in forage rates across forage sites, foraging efficiency did not differ as much, probably also reflecting forage-site flexibility.

Another factor possibly affecting vertical microhabitat use and foraging behavior of these fishes is predation; notropids comprise significant portions of the diets of esocid, lepisosteid, and centrarchid predators (Pfliegler 1978). Cerri and Fraser (1983), Power (1984), and Power et al. (1985) have demonstrated shifts in behavior and microhabitat usage by fishes in response to predation risk. The differences in (antipredator?) behavior exhibited by *Notropis venustus* and *Notropis texanus* while foraging at the surface site may reflect differences in predation risk. Analyses of the stomach contents of 73 main channel Choctawhatchee River piscivores indicated that *Notropis texanus* was the only cyprinid eaten (% dry weight of predator's diet: *Micropterus* spp., 17%; *Esox* spp., 17%; *Lepisosteus* spp., 44%; Livingston et al. 1988). Color patterns may account for the different rates of predation (level of risk) on *Notropis venustus* and *Notropis texanus* (Endler 1986, 1987). *Notropis texanus* has a dark lateral band characteristic of many members of the genus, whereas *Notropis venustus* is a more pallid species, with only a remnant of a lateral band. In the turbid waters that these fishes inhabit, a darkly colored fish may be more apparent to visually foraging predators.

Because a novel prey type was used in these experiments, differences in foraging rate and efficiency between *Notropis venustus* and *Notropis texanus* reflect differences in forage-site specialization (benthic vs. surface) as opposed to prey-type preferences (benthic prey vs. surface prey). These results support the hypothesis that notropids are morphologically adapted for feeding in particular microhabitats, therein selecting whatever prey are available. Previous
descriptive feeding studies of notropids have indicated similar patterns of prey selection based on forage-site preferences (Chapter 1; Starrett 1950, Moyle 1973, Mendelson 1975, Hoover 1981, Surat et al. 1982, etc.). Forage-site specialization may be a foraging strategy common to the genus *Notropis*. 
References Cited


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TABLE 2. Rank abundance of the 15 numerically dominant fishes collected from the main channel Choctawhatchee River (Stations 61, 65, and 70 pooled). Fall collections were made annually (1979, 1983-1987). Collection methods outlined in Bass et al. (1980). Data courtesy G. Bass, FGFWFC.

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TABLE 3. Feeding habits of the main channel Choctawhatchee River cyprinids. Values represent percentage contribution dry weight per prey type for each species. The WCP column indicates the most typical water column position in which a prey item would have been eaten: B = benthic, M = midwater, and S = surface.

<table>
<thead>
<tr>
<th>PREY TYPE</th>
<th>WCP</th>
<th>winchelli</th>
<th>longirostris</th>
<th>texanus</th>
<th>venustus</th>
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<tr>
<td>Sand grains</td>
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<td>1.7</td>
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<tr>
<td>Detritus</td>
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<td>28.9</td>
<td>11.8</td>
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<td>26.5</td>
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<tr>
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