Dietary Specialization by the Speckled Darter, *Etheostoma stigmaeum*, on Chironomid Larvae in a Mississippi Stream

John B. Alford[a] and David C. Beckett

Department of Biological Sciences, University of Southern Mississippi
Hattiesburg, Mississippi 39406-0001 USA

E-mail: jba81@msstate.edu

ABSTRACT

We determined the foraging mode of the speckled darter (*Etheostoma stigmaeum*) in a small blackwater stream in Mississippi at two levels of prey classification and identified speckled darter prey that were selected or were not selected. Chironomids dominated speckled darter diets (relative abundance 33.0-92.3%, seasonally), and they also dominated the resource base (relative abundance 46.3-74.9%, seasonally). High proportional similarity (PS) and low niche breadth (NB) values suggested that the speckled darter fed opportunistically on a small range of available prey, (PS>0.58 and NB<0.27, seasonally). When chironomids were identified to genus/species, PS and NB values were low (PS<0.37 and NB<0.23, seasonally), suggesting the darter fed selectively on a small number of invertebrate taxa. At this finer level of classification, the speckled darter fed like a classic specialist, selecting only one to three taxa seasonally. The speckled darter selected the chironomids *Polypedlium convictum* gr., *Stelechomyia perpulchra*, *Xylotopus par*, *Nilotanypus* sp., *Psetrocladius elatus*, and *Psetrocladius* sp. (Manly's α>0.111).

INTRODUCTION

Darters are small freshwater fishes that feed on benthic invertebrates (Forbes 1880, Scalet 1972, Mathur 1973). Numerically dominant prey types generally include chironomids, trichopterans, ephemeropterans, simuliids, and microcrustaceans (Schenk and Whiteside 1974, Paine et al. 1982). However, the diet of the speckled darter, *Etheostoma stigmaeum*, is poorly understood. Only one study has reported the food habits of the speckled darter, but it lacked detailed information. O'Neil (1980) reported that, in Alabama, chironomids numerically dominated the speckled darter diet, while ephemeropterans, trichopterans, and microcrustaceans were also present.

The speckled darter belongs to the subgenus *Doration* and ranges from eastern Oklahoma, southeastern Kansas, and western Louisiana to western Virginia, northwest Georgia, and western Florida and is present in Gulf drainages from the Sabine River in Louisiana to the Pensacola Bay Drainage (Page 1983). The preferred habitat of the speckled darter is clear, deep (to 1 m) pools, often below riffles in streams with moderately swift current. Pools inhabited usually have sand or a mix of sand/gravel substrates (Cordes and Page 1980, Ross 2001).

The purpose of this study was to describe the seasonal dietary habits of the speckled darter from a southern Mississippi stream. Our objectives were: 1) to describe the non-chironomid and chironomid prey consumed by the speckled darter in a small blackwater stream in Mississippi, 2) to determine the foraging mode of the speckled darter by relating numerical diet composition to prey availability and 3) to identify the prey taxa that were seasonally selected by the speckled darter. Because it is a gape-limited suction feeder, constrained to particular stream habitats (Page 1983, Ross 2001), we predicted that the speckled darter in Beaverdam Creek would feed opportunistically on a relatively small range of available prey taxa, regardless of taxonomic scale. That is,

[a] Present address: Mississippi State University, Department of Wildlife and Fisheries, Box 9690, Mississippi State, MS 39762, USA.

the relative abundances of prey taxa from the speckled darter diet would reflect the relative abundances of the most abundantly available prey taxa within the darter's resource base.

METHODS AND MATERIALS

Speckled darters were collected seasonally (fall 1999, summer 2000, winter 2001, and spring 2001) from a second-order stretch of Beaverdam Creek near Brooklyn, Mississippi in Forrest County. Beaverdam Creek is a low-gradient, first to fourth-order tributary of Black Creek, which is part of the Pascagoula River drainage. We used 3.0 x 3.2 m nylon seines with 33 mm mesh to collect darters from typical darter microhabitats (Page 1983, Ross 2001) defined by very shallow riffles of water containing submerged snags as well as gravel and sand substrates. Because of the extreme density of woody debris in the stream, the primary method of collection was a kick-set with some upstream seine hauls over gravel and leaf litter microhabitats.

Three riffle sites in Beaverdam Creek were sampled for darters until three consecutive seining efforts yielded zero darters. Riffle sites were located in a second-order portion of the stream and were separated from each other by a series of runs and pools at distances of approximately 75 meters. Each riffle site was a highly heterogeneous habitat with a sandy bottom; snags covered most of the stream channel. The cover (visual observation) of snags in the riffles was approximately 50-60%, while sand microhabitats were distributed patchily, making up about 20-30% of the substrates. Gravel runs comprised about 10% of the substrate at each site. Leaf litter covered approximately 10% of the riffle sites and was located just downstream or upstream of riffles along turns. All fish were killed in sodium bicarbonate to prevent regurgitation. They were then fixed in 10% formalin at the site and later preserved in 70% ethanol.

Darter digestive tracts were dissected from the esophagus to the cloaca, and all prey items were removed. One head capsule counted as one individual prey item, while other insect parts that separated from bodies such as wings, legs, eyes, caudal filaments, or thoracic segments were not counted as individual prey items.

To compare darter diet composition with prey availability, invertebrates were collected from substrates in summer 2000, winter 2001 and spring 2001. Invertebrates were removed from four substrate-types (snags, leaf litter, gravel, and sand) to determine the relative abundances of all benthic invertebrate groups that comprised the resource base. Three samples of each substrate-type were collected while holding a 63 μm mesh sieve directly downstream from the collection point to catch drifting invertebrates that may have become dislodged from the substrates during the sampling process (Soluk 1985). Only substrates at the most downstream portion of riffle sites were sampled in order to minimize induced invertebrate drift that might influence darter prey selection. Submerged snags (woody debris) were collected directly from the stream bottom. Leaf litter was sampled by grabbing leaves submerged along turns in the stream channel. The gravel samples were grabbed by hand, and only the gravel lying on the surface of the streambed was sampled.

The substrate samples containing invertebrates were fixed and preserved in 70% ethanol at the field site. Sand samples were taken back to the laboratory for elutriation—a process that prevents excessive sorting. Because the invertebrates in sand samples were hard to distinguish, they were stained with Rose Bengal. Snag, leaf litter, and gravel samples were processed by gently removing invertebrates from the substrates using a toothbrush. This invertebrate removal process was conducted directly over a sieve, and invertebrates were then washed into clean sample jars.

Chironomids were identified using Epler (1995) and Wiederholm (1983). Other aquatic insect groups were identified using Wiggins (1977), Berner and Pescador (1988), Epler (1996), Merritt and Cummins (1996), and Pluchino et al. (1999).

The relative abundances of benthic invertebrate prey taxa from darter diets (r_i) were calculated as the sum of all individuals of an invertebrate taxon divided by the sum of all prey items from the darter diets. Similarly, the relative abundances of invertebrate taxa from the resource base (q_i) were determined. The q_i values were then weighted to reflect the percent cover of each substrate-type from the stream channel. Levins' niche breadth index (NB) was used to determine if darters fed on a relatively large or small array of prey taxa (Levins 1969). The index is a normalized modification of Simpson's dominance index (Rachlin et al. 1989). Values of NB range from approximately zero (specialist) to one (opportunist).

Using NB alone to determine diet selectivity is a major weakness because it does not reflect the relative abundance of available prey in the resource base. Therefore, in conjunction with NB, we used proportional similarity (PS) (Feinsinger et al. 1981, Rachlin et al. 1989) to determine the foraging mode of the speckled darter at two taxonomic scales: chironomids identified to family and chironomids identified to genus/species. Proportional similarity measures the probability that the relative abundance of taxa from darter diets had the same relative abundance as in the resource base. Values of PS range from zero to exactly one. Values close to zero would mean that the speckled darter fed selectively (i.e., specialized) on invertebrate prey. Values approaching one would mean that the speckled darter fed opportunistically, because they consumed invertebrate taxa in similar proportion to their availability in the resource base. To evaluate the precision of the diet similarity indices, standard errors for PS and NB estimates were calculated using the jackknife method (Smith 1985).

Proportional similarity and niche breadth describe general foraging patterns, but they do not identify specific prey taxa that are selected or not selected. Consequently, Manly's alpha (Chesson 1978, Manly et al. 1993) was used to compare the relative abundance of each prey taxon from darter diets to the relative abundance of the same taxon in the resource base; therefore this index identified prey taxa that were selected or not selected. Values less than 1/m indicate that a prey taxon is consumed disproportionately less than its relative abundance in the resource base (i.e., not selected). Values at or near 1/m indicate that a prey taxon is consumed in direct proportion to its availability (i.e., not selected), and values greater than 1/m indicate a prey taxon was consumed disproportionately more than its relative abundance in the resource base (i.e., selected). The value m is the number of available prey taxa in the resource base.

RESULTS AND DISCUSSION

Diet Composition

Throughout the study, we collected 45 speckled darters (TL 31.0-44.0 mm) and identified 360 invertebrates from their digestive systems. From summer 2000 to spring 2001, we collected and identified 2,158 invertebrates from the resource base. With the exception of winter 2001, chironomid larvae dominated speckled darter diets in Beaverdam Creek (Fig. 1). In the fall, summer, and spring collections, chironomids numerically comprised 82.3%, 85.1%, and 92.3%, respectively, of all invertebrate prey taxa. Microcrustaceans, primarily the cladoceran *Bosmina* sp., comprised a higher relative abundance (37.5%) to darter diets in the winter, probably because speckled darters were frequently collected in pools at the downstream end of riffles during the winter sampling period. These slower current velocities in these pools allowed zooplankton to inhabit them. Other invertebrate taxa consumed by darters in every season included larval ceratopogonids and microcrustaceans. The larval beetle *Stenelmis* sp. was consumed in all seasons except winter 2001. Early instar stonefly larvae (Perlidae) were consumed in the fall, while trichopteran larvae (mostly Philopotamidae) and naidid worms were consumed only in winter.

Chironomids comprised the largest proportion of invertebrate taxa from the resource base seasonally, 46.3% in summer 2000, 73.4% in winter 2001, and 74.9% in spring 2001. Other seasonally abundant invertebrate groups included the beetle *Stenelmis* sp. (5.9-20.6%), the philopotamid caddisfly *Chimarra* sp. (2.1-8.5%) oligochaetes (5.7-7.6%), and ceratopogonids (1.0-4.7%). Invertebrates that were seasonally available, but incidental (<2% relative abundance), included the mayflies *Stenonema* sp., *Isonychia* sp., and *Baetisca* sp., perlid stoneflies, the beetle *Ancyronyx* sp., gomphid odonates, hydrachnid water mites, and the isopod *Asellus* sp.

When the chironomid prey were resolved to genus/species, 35 chironomid taxa were identified from speckled darter diets throughout the entire study period (17 taxa in fall 1999, 20 in summer 2000, 9 in winter 2001, and 21in spring 2001). In fall 1999, the most common chironomid prey included *Rheosmittia* sp., *Corynoneura* sp., and *Thienemanniella* sp., and these comprised 67.8% of all chironomid prey taxa, numerically. In summer 2000, *Cladotanytarsus* sp. and *Stempellina* sp. dominated darter

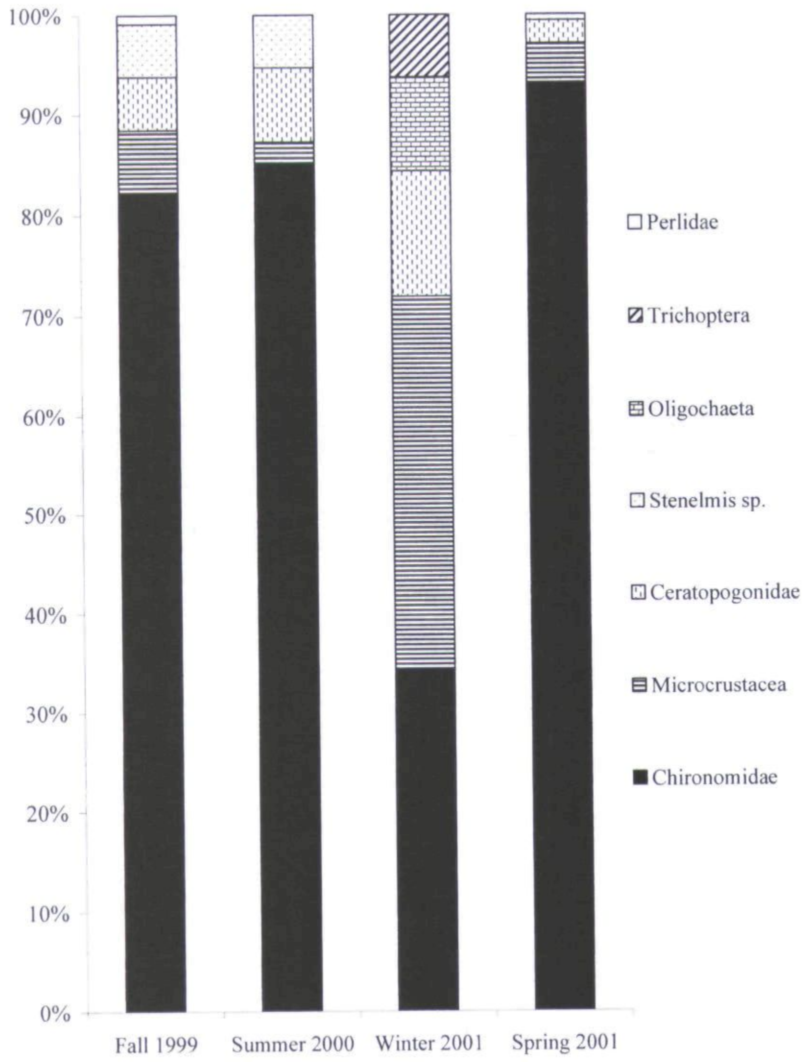

Figure 1. Percent relative abundances of invertebrate prey taxa by season in the diet of the speckled darter in Beaverdam Creek, Mississippi.

diets, totaling 40.5% of all chironomid prey. In winter 2001, *Tanytarsus* sp. made up 30.0%, and in spring 2001, *Ablabesmyia mallochi*, *Orthocladius* sp., and *Psetrocladius* sp., contributed 74.5% of the chironomid prey. These seasonal shifts may reflect the short generation times of chironomids and their consequential emergences as adults. Thus, the relative abundance of chironomids from the resource base may have changed due to different phenologies among the chironomid taxa (Beckett 1992).

Speckled darters consumed primarily mobile or conspicuous chironomid taxa. For example, *Corynoneura* sp., *Thienemanniella* sp. and *Orthocladius* sp. are sprawling grazers that scrape diatoms and periphyton from the surfaces of substrates; *Cladotanytarsus* sp. and *Tanytarsus* sp. are tube-dwelling deposit feeders that periodically emerge from their silken tubes to feed on detritus that has collected near the tube's opening; and *Ablabesmyia mallochi* is a relatively large, sprawling predator that forages on other chironomids and oligochaetes (Wiederholm 1983).

Dietary Specialization

When chironomids were identified only to family (Fig. 2), it appeared that the

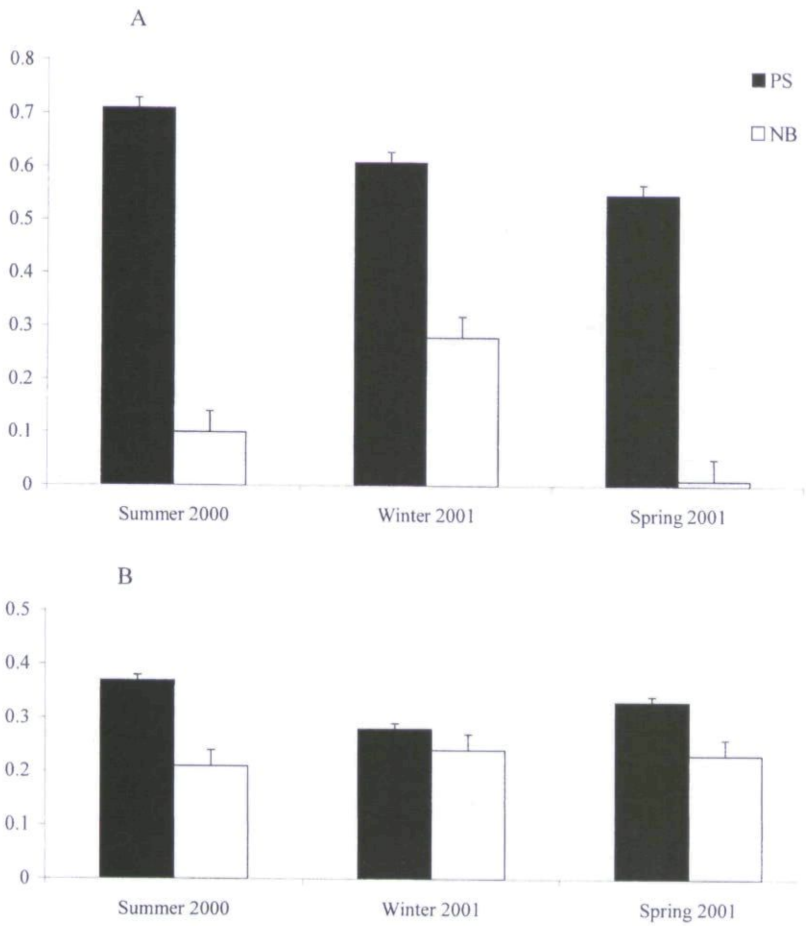

Figure 2. Proportional similarity (PS) and niche breadth (NB) values for speckled darter diets in Beaverdam Creek, Mississippi when chironomids were identified to family (A), and when chironomids were identified to genus/species level (B). Standard errors are indicated.

speckled darter fed opportunistically on a relatively small range of available prey taxa (i.e., seven out of approximately 22 available taxa from summer 2000 to spring 2001). At this level of classification, PS values were relatively high (greater than or near 0.60 across seasons; standard errors <0.02) and NB values were low (less than 0.28 across seasons; standard errors <0.05). Speckled darters had low NB values in summer 2000 and spring 2001 because they fed disproportionately more on ceratopogonids and chironomids (Manly's α >0.232; Table 1). In winter 2001, the family Chironomidae was not selected (Table 1). The Manly's alpha for microcrustacean prey was large (0.935), but these microcrustaceans (primarily the cladoceran *Bosmina* sp.) were not epibenthic taxa. Consequently, they were not collected from substrates, so the Manly's alpha value for Microcrustacea was inflated.

When we analyzed the data with chironomids identified to the genus/species level, both PS and NB values were closer to zero for all seasons (Fig. 2). Therefore, speckled darters from Beaverdam Creek fed more like classic specialists when chironomids were resolved past the family level. The speckled darter apparently selected just one to three taxa (Manly's α >0.111 for each season), and they were all chironomids (Table 1). Comparatively large chironomids, such as the wood-mining (*Stelechomyia perpulchra* and *Xylotopus par*) and predatory larvae (*Nilotanyous* sp.), and mobile sprawlers and climbers (*Psetrocladius* sp. and *Polypedilum scalaenum* gr., respectively) were selected. These species were likely more susceptible to predation than other taxa which burrow into substrates or seek shelter in tubes or sediment. For example, speckled darters consumed *Rheosmittia* sp. in small proportions (<7% relative abundance per season), but

Table 1. Relative abundances and Manly's alpha values describing selective predation by speckled darters on invertebrate taxa when chironomids were identified at different levels of taxonomic resolution. Percent relative abundances are from darter diets (r_i) and the resource base (q_i). Genera and species are chironomids. The value m is the number of available taxa in the resource base.

Season	Primary prey	r_i	q_i	Manly's α
	Taxonomic resolution: family			
Summer 2000 (m=13)	Chironomidae	85.1	46.2	0.499
	Ceratopogonidae	7.4	4.7	0.431
Spring 2001 (m=14)	Chironomidae	92.8	74.9	0.232
	Ceratopogonidae	2.3	0.6	0.750
	Taxonomic resolution: genus/species			
Summer 2000 (m=55)	*Polypedilum convictum* gr.	6.7	0.2	0.339
	Stelechomyia perpulchra	15.6	1.4	0.111
Winter 2001 (m=51)	*Xylotopus par*	3.1	0.2	0.120
Spring 2001 (m=60)	*Nilotanypus* sp.	5.5	0	0.409
	Psetrocladius elatus	16.6	0.5	0.175
	Psetrocladius sp.	10.3	1.1	0.256

this chironomid is a comparatively small, obligate sand-dweller that is often the most abundant invertebrate in these substrates (Soluk 1985). Consequently, many of these individuals may have escaped predation by speckled darters. Other invertebrates such as *Stenelmis* sp., Trichoptera, and oligochaetes (Table 2), were seasonally available (>5.0% relative abundance) but were not selected (Manly's α<0.05 for each season),

Although an overwhelming proportion of studies showed that darters appear to feed opportunistically (33 out of 36 publications; see Alford 2005 for literature review), a few researchers have found evidence of selective predation by darters. Strange (1991) used PS and NB indices and found that the johnny darter (*Etheostoma nigrum*) fed selectively by consuming disproportionately more chironomid larvae relative to its availability. In his study, ephemeropterans comprised the most numerically dominant invertebrate group in the resource base, whereas chironomids comprised a considerably lower proportion of available prey. Phillips and Kilambi (1996) found that the orangethroat darter (*Etheostoma spectabile*), exhibited active selection for chironomids when compared to its availability in the environment. Schlosser and Toth (1984) showed selective predation by the fantail darter (*Etheostoma flabellare)* and the rainbow darter (*Ehteostoma caeruleum*) on particular chironomid taxa. They found that the chironomid *Orthocladius* sp. comprised 60-80% of the gut contents of the fantail darter and rainbow darter regardless of seasonal prey availability.

Sympatric darters are known to segregate spatially among microhabitats within stream reaches (Matthews et al. 1982, Martin 1984), and they partition food resources (Paine et al. 1982, Hlohowskyj and White 1983). The speckled darter in Beaverdam

Table 2. Available prey taxa that were relatively abundant in the resource base at Beaverdam Creek, Mississippi. Percent relative abundances are from darter diets (r_i) and the resource base (q_i). The value m is the number of available taxa in the resource base. An asterisk represents a chironomid genus/species.

Season	Invertebrate prey taxon	r_i	q_i	Manly's α
Summer 2000 (m=55)	Trichoptera	0	8.5	0
	Parametriocnemus sp. *	1.1	4.5	0.003
	Rheocricotopus robacki *	6.7	3.5	0.023
Winter 2001 (m=51)	Chironomidae	34.4	73.4	0.03
	Stenelmis sp.	0	6.8	0
	Cladotanytarsus sp. *	0	12.0	0
	Tanytarsus sp. *	9.4	5.7	0.013
Spring 2001 (m=60)	*Stenelmis* sp.	0.5	5.9	0
	Oligochaeta	0	5.7	0
	Corynoneura sp. *	0	6.6	0
	Polypedilum scalaenum gr. *	3.4	7.7	0.005
	Tanytarsus sp. *	5.5	8.1	0.008
	Thienemannimyia gr. *	0	9.0	0

Creek occurs sympatrically with three other darter species (Alford 2005). Beaverdam Creek is a very heterogeneous stream with several microhabitats (i.e., substrates) and appears to contain a large variety of prey items. Because they inhabited particular portions of riffles (i.e., sand patches), it is not surprising that the speckled darter would specialize on one to three invertebrate taxa out of 51-60 seasonally available taxa. Specialists flourish in habitats with plentiful resources and relatively stable environments (MacArthur and Connell 1966, King 1971, Pianka 1983). Environmental disturbances are detrimental to specialists, while generalists tend to persist following a perturbation (Pianka 1983). The sample sites where speckled darters were collected are located within a very heavily forested area with very minimal human impacts. These favorable conditions allow the speckled darter to specialize and thrive in Beaverdam Creek.

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