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# Selective predation by four darter (Percidae) species on larval chironomids (Diptera) from a Mississippi stream

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**Abstract** We determined seasonal foraging modes of four sympatric darter species, *Etheostoma lynceum*, *E. stigmaeum*, *E. swaini* and *Percina nigrofasciata*, from Beaverdam Creek, Mississippi (USA) at two scales of taxonomic resolution: (1) chironomid prey identified to family and (2) chironomid prey identified to genus/species. When chironomids were identified to family, high proportional similarity (PS) and low niche breadth (NB) values suggested the darters fed opportunistically on a relatively small number of available prey taxa. In contrast, when chironomids were identified to genus/species, concordant low PS and NB values suggested the darters fed like classic specialists, selecting a small number of prey taxa relative to prey availability in the resource base. The darters selected just one to four chironomid taxa from 52 available taxa across seasons. Our study shows that the scale of taxonomic resolution used to identify darter prey may influence the characterization of darter foraging modes.

**Keywords** Proportional similarity · Niche breadth · Prey selection · Foraging mode · Chironomidae

## Introduction

Darters are benthic freshwater fishes that consume a wide variety of benthic invertebrate taxa such as ephemeropterans, plecopterans, and trichopterans, as well as simuliids, isopods, ceratopogonids, and hydrachnids (Mathur 1973; Paine et al. 1982; Knight and Ross 1994; Rakocinski 1997). However, chironomid larvae are the most numerically abundant prey taxon consumed by darters (Shenck and Whiteside 1977; Layzer and Reed 1978; Cordes and Page 1980; Matthews et al. 1982). Ephemeropterans and trichopterans are known to contribute volumetrically because of their relatively large size, but chironomids are just as important volumetrically to darter diets (Martin 1984). Additionally, chironomids typically dominate the composition of invertebrates in southeastern coastal plain streams from the US (Benke et al. 1985). Consequently, most studies describing darter food habits find the relative abundances of prey from darter diets generally reflect the relative abundances same taxa from the resource base.

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Most researchers have concluded that darters feed opportunistically on a relatively small number of available prey taxa. For example, Strange (1993) compared the gut contents of 593 fantail darters, *Etheostoma flabellare*, to available prey and showed that this species fed as an opportunist. He found that chironomids were numerically the most important food item in all seasons, and there was no difference in diet among juveniles and adults. Meanwhile, the fantail darters avoided ephemeropterans which comprised a large proportion of the invertebrates from the resource base. Knight and Ross (1994) found that the bayou darter, *Etheostoma rubrum*, fed opportunistically on chironomids by number and weight (39 and 41% relative occurrence), followed by hydrachnids by number (22%), and simuliids by number (20%).

Chironomid head capsules are the only body parts not completely digested by darters, but morphological characteristics of the head capsules conveniently allow taxonomists to identify chironomid larvae to the genus/species level. However, because the preparation and identification process is labor-intensive, chironomid prey from darter diets or their resource base are rarely identified to genus/species. Studies that have identified chironomid prey of darters past family level lacked detailed information about uncommon chironomid taxa, or no information was given about the relative availability of chironomid taxa within the resource base. Because chironomids are extremely diverse (Wiederholm 1983; Epler 1995), occupy several functional feeding and habit guilds (Merritt and Cummins 1996) and dominate darter diets, our study focused on selective predation by darters on chironomid prey.

We compared the numerical relative abundances of prey taxa from the diets of four sympatric darter species to the relative abundances of prey from the darters' resource base. The darter species were the brighteye darter, *Etheostoma lynceum*, the speckled darter, *Etheostoma stigmaeum*, the gulf darter, *Etheostoma swaini*, and the blackbanded darter, *Percina nigrofasciata*. The purpose of this study was to (1) describe the foraging mode of the four darter species from a southern Mississippi stream, (2) compare the foraging mode of the darter species at two scales of prey classification and (3) identify the prey taxa that were selected or not selected based on their relative availability. From previous research on darter food habits, we hypothesized that the four-darter species would feed opportunistically on a relatively small range of available prey taxa when chironomids were identified to family and when chironomids were identified to genus/species. We predicted that the relative abundances of prey from darter diets would be proportional to the relative abundances of the same prey from the darters' resource base, regardless of the scale of taxonomic resolution.

## Materials and methods

### Sampling period and study site

Darters and invertebrates were sampled on three to six occasions during three seasons. The sampling periods occurred during summer 2000 (Jul–Aug), winter 2001 (Jan–Feb), and spring 2001 (Apr–May) from a second-order portion of Beaverdam Creek near Brooklyn, MS (USA) in Forrest County. During the fall of 2000, current velocities and water levels were too high to sample safely, thus no collection was made. Beaverdam Creek is a blackwater coastal plain stream that courses through the Desoto National Forest, and it is part of the Pascagoula River drainage in southeast Mississippi (Slack 1996).

Three interconnected riffle sites were sampled during each season at Beaverdam Creek. Darters were collected at each riffle site until three consecutive seining efforts yielded zero fish. Riffle sites were separated from each other by a series of runs and pools at a distance of approximately 75 m . We used 3.0 m × 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 woody debris as well as gravel and sand substrates. Because woody debris was extremely dense in the stream channel (percent cover 60%), darters were collected by kick-sets downstream from these substrates. Seine hauls were conducted upstream over gravel (percent cover 10%), leaf litter (percent cover 10%) and sand microhabitats (percent cover 20%).

### Invertebrate sampling protocol

Because animals perceive resource availability differently from the researchers, we sampled invertebrates directly from substrates within the darters' resource base (as opposed to using a bottom sampler or kick-net). The resource base consisted of invertebrates collected from the four substrate-types covering the riffle sites (i.e., woody debris, gravel, leaf litter and sand). Immediately prior to darter sampling, three samples of each substrate-type were collected into 750 ml sample jars while holding a sieve (63 μm mesh) directly downstream from the sampling point. Sieves were used to catch drifting invertebrates that may have become dislodged from the substrates during the sampling process. Only substrates at the most downstream portion of riffle sites were sampled to minimize induced invertebrate drift that might influence darter prey selection. The substrate samples containing invertebrates were fixed and preserved at the field site in 70% ethanol. Sand samples were taken back to the laboratory for elutriation—a process that prevents excessive sorting. Woody debris, leaf litter and gravel samples were processed at the lab by gently removing invertebrates from the substrates using a toothbrush. For example, a portion of a snag, a piece of gravel or an individual leaf was brushed under running water onto sieves to separate the attached invertebrates from the substrate material. The invertebrates were washed into clean sample jars using a water bottle. Consequently, the invertebrate removal process minimized sort time and increased sorting precision (i.e., it increased the chances of visually locating and counting an individual invertebrate specimen).

All fishes were sacrificed at the field site in sodium bicarbonate to prevent regurgitation. All prey items were removed from the digestive systems of each fish with forceps and placed in 70% ethanol. 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 recorded as individual prey items. All invertebrates were identified to the lowest practical taxon with an assortment of dichotomous keys (Wiederholm 1983; Epler 1995; Merritt and Cummins 1996). To identify chironomids to genus/species, chironomids were mounted individually on microscope slides containing CMCP mountant and viewed at 400×–1,000×.

### Analysis

Darter foraging modes were determined by comparing the numerical relative abundances of invertebrate taxa in the gut contents of each darter species to the relative abundances of the same invertebrate taxa collected from the resource base (a combination of all invertebrates from all substrate-types). This process was carried out at two scales of invertebrate identification. First, non-chironomid invertebrates were identified to their lowest practical taxon while chironomids were identified only to family. Then, foraging mode was determined at a finer taxonomic scale, when chironomids were identified to genus/species.

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). The equation is as follows:

$$1/\left(s^{*}\sum r_i^2\right),$$

where "s" represents taxa richness or total number of invertebrate taxa found in the diet. Again, "$r_i$" is the relative abundance of taxon $i$ that contributed to the diet of each darter species. Values of NB are from $1/s$ (specialist) to 1.0 (generalist).

Using NB alone to describe foraging mode is a major weakness because it does not reflect the relative abundances of available prey in the resource base. Dickman (1986) argued that proportional similarity and niche breadth should be used together to obtain a broader, more complete dietary assessment. In conjunction with Levins' NB, proportional similarity (PS) (Feinsinger et al. 1981; Rachlin et al. 1989) was used to determine the foraging mode of a darter species at both taxonomic scales.

In our study, proportional similarity measured the probability that the relative abundance of invertebrate taxa from a darter species' diet had the same relative abundance in the resource base. Values of PS ranged from 0 to exactly 1.0. Values close to zero meant that a darter species fed selectively (i.e., specialized) on invertebrate prey. Values approaching 1.0 meant that a darter species fed opportunistically, because the invertebrate taxa were consumed in similar proportion to their availability in the resource base. The equation for PS is as follows:

$$1 - 0.5\sum|r_i - q_i|,$$

where $r_i$ is the relative abundance of prey taxon $i$ that contributed to the species' diet, and $q_i$ is the relative abundance of the same taxon that existed in the resource base. To evaluate the variability of the diet similarity indices, standard errors for PS and NB estimates were calculated using the jackknife method (Smith 1985). The jackknife method is a re-sampling technique that estimates the precision of the diet similarity estimates.

We used the index Manly's α (Chesson 1978; Manly et al. 1993) to identify specific prey taxa that were selected or not selected. Manly's α is the best index for describing resource preferences by populations (Krebs 1989), especially when the relative abundances of resources are known. The equation for Manly's α is as follows:

$$\alpha_i = r_i/q_i\left[1\Big/\sum(r_i/q_i)\right],$$

A taxa richness value ($m$) is the number of prey taxa possible in the resource base. A value less than $1/m$ indicated a prey taxon that was consumed disproportionately less (i.e., not selected) than its relative abundance in the resource base. Values at or near $1/m$ indicated that a prey taxon was consumed in direct proportion to its availability (i.e., not selected), and values greater than $1/m$ indicated a prey taxon was consumed disproportionately more (i.e., selected) than its relative abundance in the resource base.

# Results

All four darter species were collected seasonally from the three-riffle sites within Beaverdam Creek. Occasionally, all four species were collected in one kick-set. Over the entire study period, we examined the diets of 39 *E. lynceum* (TL 23.0–45.0 mm; BWM 100–1,050 mg), 26 *E. stigmaeum* (TL 31.0–44.0 mm; BWM 80–980 m g), 22 *E. swaini* (TL 35.0–48.0 mm; BWM 100–1,090 mg), and 51 *P. nigrofasciata* (TL 36.0–73.0 mm; BWM 450–1900 mg). We identified 2,298 invertebrates from darter diets across seasons (710 in summer, 527 in winter, and 1061 in spring). From the resource base, we identified 2,161 invertebrates across seasons (1003 in summer, 493 in winter, and 665 in spring). Species–sample curves (Fig. 1) revealed that an appropriate number of individual fish from each darter species was collected seasonally to adequately assess diet composition (Brower et al. 1997). Depending on the darter species, a minimum of 5–12 fish were required to account for all possible prey taxa the darters could potentially consume within a particular sampling period.

## Diet composition and prey availability

Chironomids were the most numerically dominant invertebrate taxon consumed each season by each darter species, with the exception of *E. stigmaeum* in winter (Fig. 2). Microcrustaceans (mainly the cladoceran *Bosmina* sp.) were heavily consumed by *E. stigmaeum* in winter (37.5% relative abundance). Chironomid larvae were numerically more important in the diet of *E. lynceum* (75.5–79.5% relative abundance across all seasons), *E. stigmaeum* (summer and spring, 85.1% and 92.8% relative abundance, respectively), and *E. swaini* (75.0–89.9% relative abundance across all seasons) than in the diets of *P. nigrofasciata* (51.9–69.9% relative abundance across seasons). However, blackbanded darter diets were more diverse than other darters, containing more invertebrate taxa. *Percina nigrofasciata* consumed 8–11 taxa seasonally, whereas the *Etheostoma* spp. consumed 4–8 taxa seasonally. Other invertebrates that contributed to darter diets were the mayfly nymphs *Isonychia*

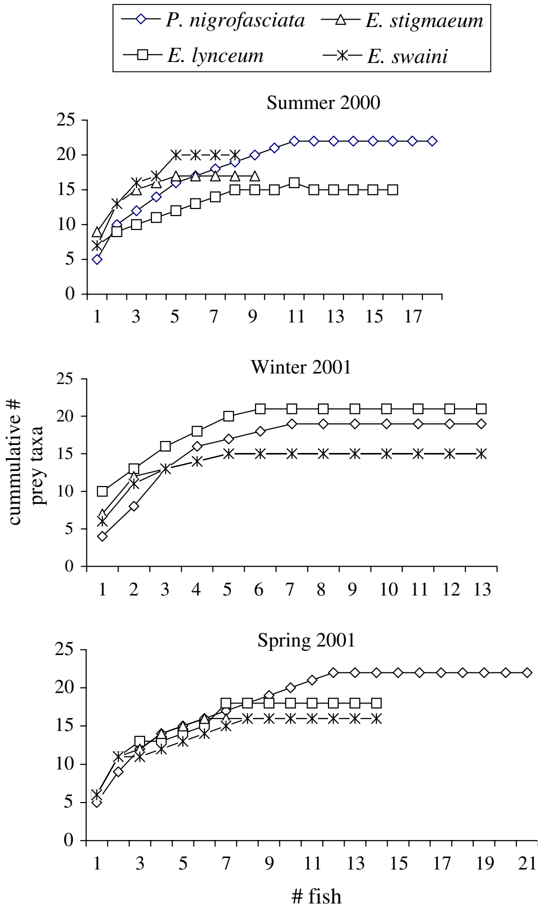


**Fig. 1** Species-sample curves describing the number of fish needed seasonally to assess darter diets from Beaverdam Creek, MS

sp. and *Stenonema* sp., trichopterans (mostly philopotamids, probably *Chimarra* sp.), ceratopogonids (Diptera), odonates (mostly gomphids), *Caecidotea* sp. (Isopoda), and simuliids (mostly *Simulium* sp.) (Fig. 2). However, these prey taxa were much less abundant than chironomids in darter diets across seasons.

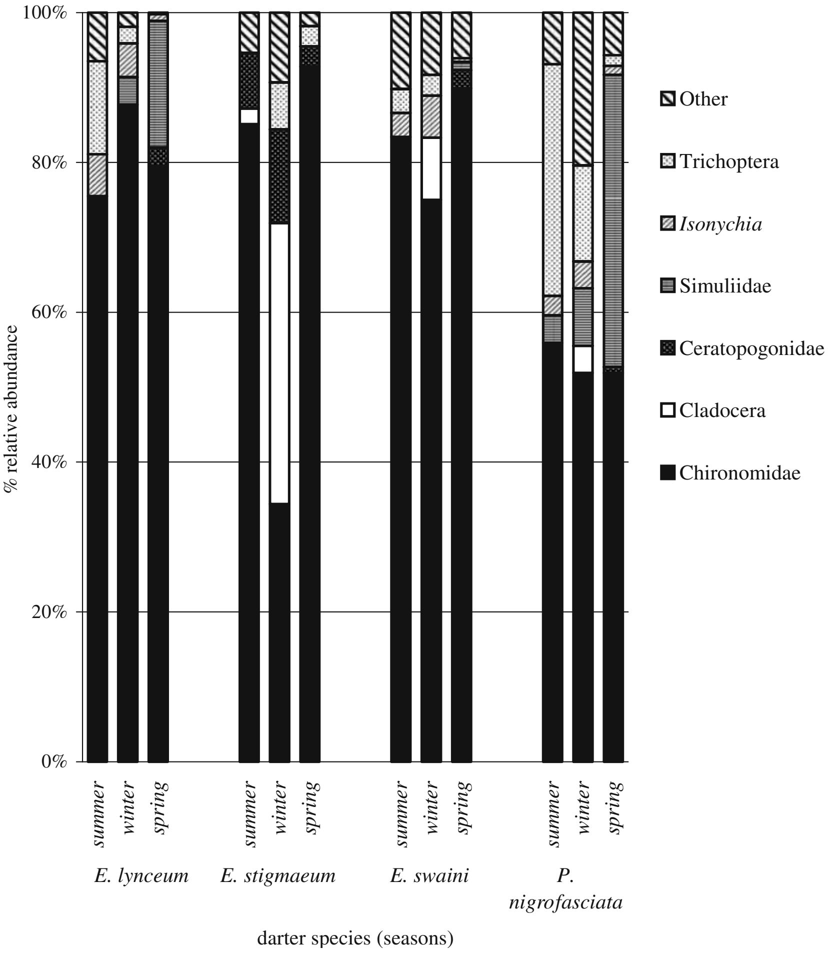
The dominance of chironomid larvae in darter diets was reflected in the resource base (Fig. 3). The relative abundance of chironomid larvae varied from 46.3% in summer, to 73.4% in winter, then to 74.9% in spring. Across seasons, oligochaetes (5.0–7.6%), hydrachnids (0–5.0%), ceratopogonids (3.1–4.7%), the trichopteran *Chimarra* sp. (1.1–8.5%), simuliids (0.6–4.4%), perlid stoneflies (0.6–2.4%), and the mayflies *Isonychia* sp. (0.1–1.9%) and *Stenonema* sp. (0.1–1.9%) were all present in much smaller proportions in the resource base compared to that of the Chironomidae (Fig. 3). *Stenelmis* was the only non-chironomid taxon that made up greater than 8.5% relative abundance during any season. During summer 2000, *Stenelmis* comprised 20.6% of the resource base, but they were much less abundant in winter 2001 (6.8%) and spring 2001 (5.9%).

Compared to other groups, a large number of chironomid taxa were identified from the resource base and darter diets. Within the chironomid family, there were 30–34 genera/species identified from the resource base across seasons. The darter species combined consumed 25–32 chironomid taxa across seasons. Although a relatively large number of chironomid taxa were available to darters in a variety of abundances, darters consumed an average of just 2.3–7.3 chironomid taxa fish$^{-1}$ (Table 1). In addition, darters consumed a substantial number of chironomid individuals per fish across seasons (on average, 6.3–38.0 chironomids fish$^{-1}$ season$^{-1}$) (Table 1). For example, in the spring, the maximum numbers of chironomids identified from one individual fish of a darter species were 34 in *P. nigrofasciata*, 51 in *E. swaini*, 65 in *E. stigmaeum* and 92 in *E. lynceum*.

## Foraging mode

When chironomids were identified to family level, relatively high PS values (0.57–0.78; standard errors <0.02) and low NB values (0.12–0.37; standard errors <0.04) suggested that all darter species fed opportunistically on a relatively small number of available prey taxa across seasons (Fig. 4). Although they fed on some taxa in proportion to their availability, other available taxa were consumed disproportionately less than their relative abundance. For example, *Stenelmis* sp., philpotamid trichopterans, perlid stoneflies, hydrachnids and oligochaetes contributed very little to darter diets compared to their relative abundance in the resource base. At this level of chironomid classification, we failed to falsify our first hypothesis and concluded that darters fed as opportunists on a relatively small number of available prey taxa.

**Fig. 2** Percent relative abundances of invertebrate prey in the diets of four darter species from Beaverdam Creek, Forrest Co., MS. Each bar graph represents the relative abundances of prey from summer 2000, winter 2001, and spring 2001



In contrast, when chironomids were identified to genus/species level, PS and NB values were low for all darter species across seasons with the exception of *P. nigrofasciata* in spring 2001 (Fig. 4). Depending on the darter species, PS varied from 0.27 to 0.43 (standard errors <0.01), while NB values varied from 0.10 to 0.24 (standard errors <0.04) seasonally (Fig. 4). Therefore, at the finer level of prey identification, we falsified our second hypothesis and concluded that darters from Beaverdam Creek fed more like classic specialists than as opportunists. They selected particular taxa because, at this level of chironomid classification, darters fed disproportionately more on a small number of available prey taxa, regardless of the low relative abundances of the taxa in the resource base (see Table 3 for a comparison of relative abundances of selected prey).

## Selected prey taxa

*Etheostoma lynceum* and *P. nigrofasciata* fed opportunistically on chironomids (Table 2) when identified to family ($\alpha_i < 0.05$, seasonally). In contrast, *E. stigmaeum* selected chironomids in summer 2000 and spring 2001 ($\alpha_i = 0.43$ and 0.23, respectively), whereas *E. swaini* selected chironomids only during summer 2000 ($\alpha_i = 0.20$). Darters seasonally selected other invertebrate taxa, like the mayflies *Isonychia* sp. and *Stenonema* sp., simuliids, ceratopogonids, *Caecidotea* sp. (*E. lynceum* only, summer) and odonates (*P. nigrofasciata* only, summer) (Table 2). In winter 2001, *E. stigmaeum* appeared to select Microcrustacea (primarily the cladoceran *Bosmina* sp.; $\alpha_i = 0.94$). However, because they are planktonic, microcrustaceans were not collected from the substrate samples on which epibenthic

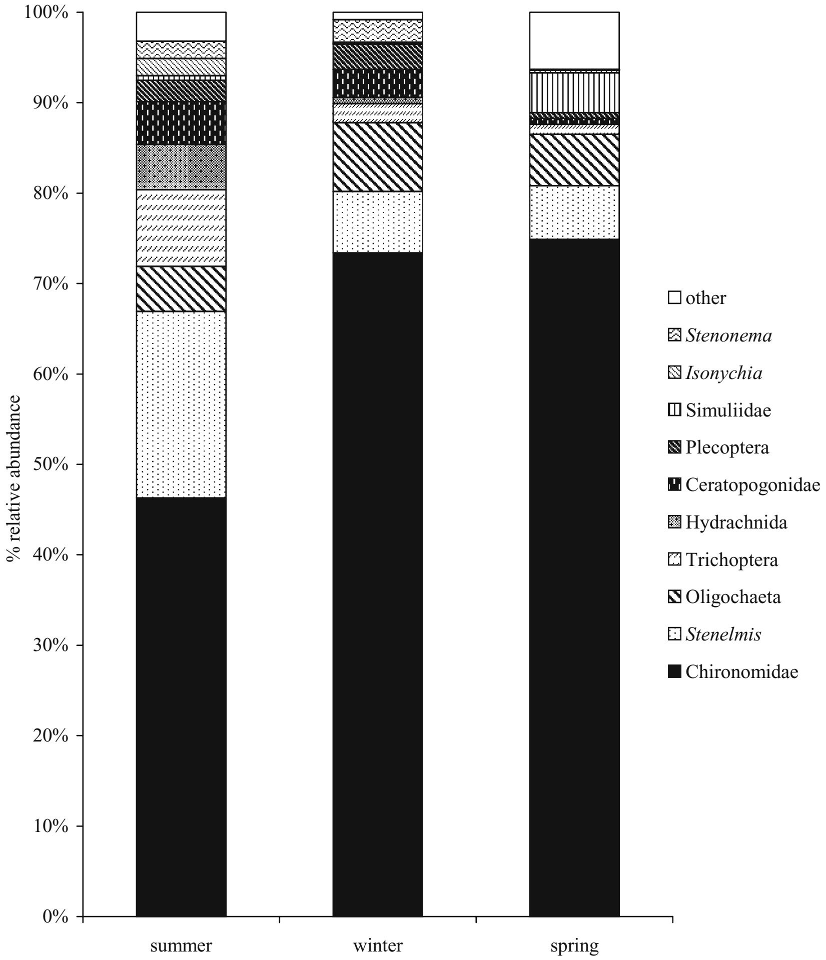


**Fig. 3** Percent relative abundances of invertebrate taxa collected from substrates in Beaverdam Creek, Forrest Co., MS. Each bar graph represents the relative abundances of available invertebrate prey from summer 2000, winter 2001, and spring 2001

**Table 1** Abundances of chironomid taxa and individuals from darter diets and their resource base at Beaverdam Creek, MS from summer 2000, winter 2001, and spring 2001

| Darter species | Summer | Winter | Spring |
|---|---|---|---|
| | Mean ( chironomid taxa eaten fish$^{-1}$ season$^{-1}$ | | |
| *E. lynceum* | 4.3 (0–8) | 7.2 (4-8) | 6.3 (5-9) |
| *E. stigmaeum* | 5.2 (2-7) | 3.3 (0-7) | 4.0 (1-10) |
| *E. swaini* | 6.0 (4-8) | 2.3 (0-5) | 7.3 (6-8) |
| *P. nigrofasciata* | 3.3 (1-8) | 3.1 (0-8) | 4.4 (0-9) |
| | Mean ( of chironomid individuals eaten fish$^{-1}$ season$^{-1}$ | | |
| *E. lynceum* | 18.1(0-35) | 24.4 (6-35) | 38.0 (0-92) |
| *E. stigmaeum* | 8.9 (3-17) | 12.1 (0-42) | 17.3 (1-65) |
| *E. swaini* | 6.3 (1-13) | 8.7 (0-16) | 30.0 (16-51) |
| *P. nigrofasciata* | 9.1 (1-37) | 10.5 (0-42) | 10.3 (0-34) |

Numbers in parentheses represent the minimum-maximum of data points

invertebrates typically occur. Consequently, the Manly's $\alpha$ value for microcrustacea was inflated, so the diet selection estimate for *E. stigmaeum* in winter was biased.

When chironomids were identified to genus/species level, darters selected particular chironomid taxa in addition to other invertebrate taxa. Although 30–34 chironomid taxa were available seasonally in Beaverdam Creek, darters selected just one to four of those taxa (Table 3). In some cases, chironomids were the only prey consumed disproportionately to their availability.

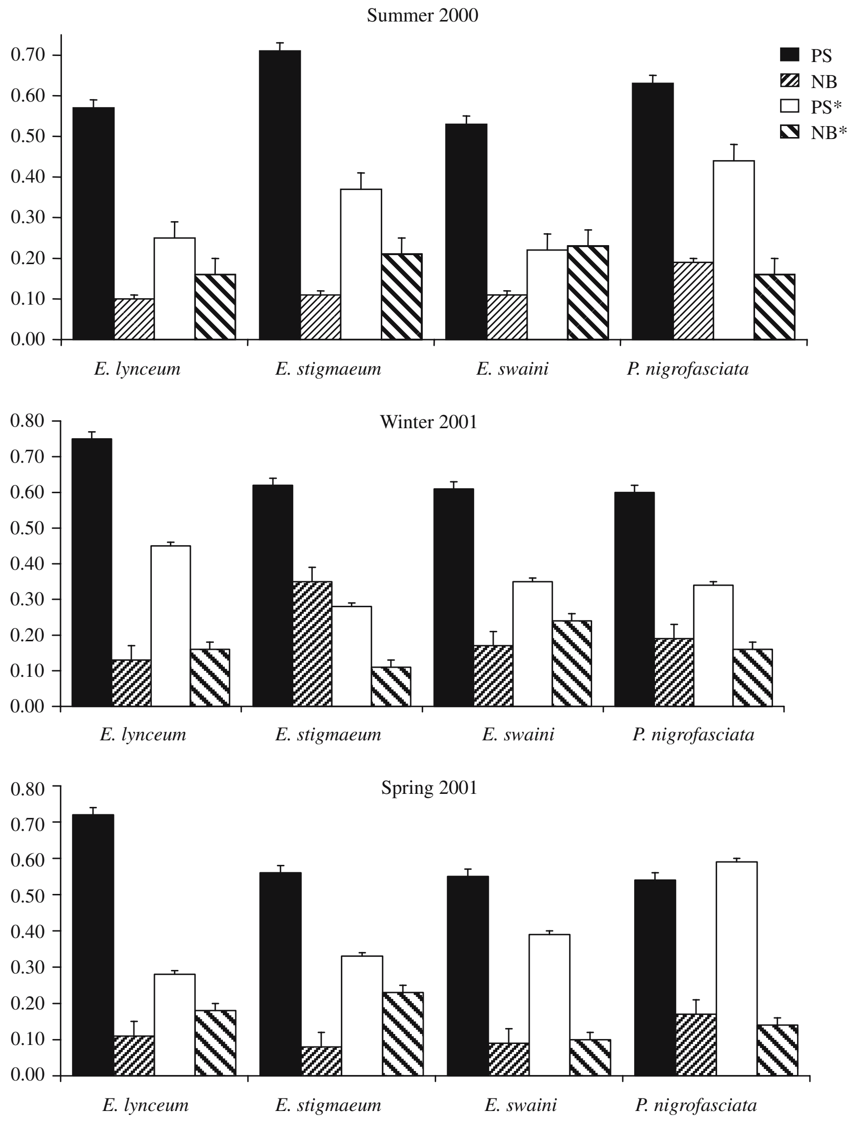


**Fig. 4** Seasonal proportional similarity (PS) and niche breadth (NB) values that describe the foraging mode of darters feeding on invertebrates from Beaverdam Creek, MS. Error bars are the jackknife estimates of standard error for the PS and NB indices. Bars with no asterisk represent the PS and NB values when chironomids were identified to family. Bars with an asterisk represent PS and NB values calculated when chironomids were identified to genus/species

Interestingly, darters did not select some of the most seasonally available chironomid taxa. These taxa were either not consumed by darters, or they contributed very little to darter diets ($r_i < 1.0\%$).

## Discussion

When describing the foraging mode of Beaverdam Creek darters, it is important to consider the taxonomic scale at which their prey is identified. Although darters fed opportunistically on invertebrate prey, when chironomids were identified to family, they fed as specialists when chironomids were identified to genus/species (except for *P. nigrofasciata* in spring 2001). Additionally, of the 53 chironomid taxa available in the resource base throughout the study period, a particular darter individual consumed <11 chironomid taxa.

It is well documented that chironomids are very important to darter diets (Wehnes 1973; Schlosser and Toth 1984; Strange 1997). Meanwhile, darters are typically classified as opportunists feeding on an array of benthic invertebrates (Hlohowskyj and White 1983; Strange 1991; Strange 1993), because relative abundances of prey in the diets usually reflect those prey

**Table 2** Manly's $\alpha$ ($\alpha_i$) describing selective predation by darters on invertebrate prey

| Darter species | Invertebrate prey | $\alpha_i$ | $r_i$ | $q_i$ |
|---|---|---|---|---|
| Summer 2000 ($1/m = 1/19 = 0.053$) | | | | |
| *E. lynceum* | *Isonychia* sp. | 0.15 | 5.6 | 1.9 |
| | *Caecidotea* sp. | 0.61 | 1.2 | < 0.1 |
| *E. stigmaeum* | Ceratopogonidae | 0.50 | 7.4 | 4.7 |
| | Chironomidae | 0.43 | 85.1 | 46.2 |
| *E. swaini* | Chironomidae | 0.20 | 70.3 | 46.2 |
| | *Isonychia* sp. | 0.19 | 3.2 | 1.9 |
| | *Stenonema* sp. | 0.57 | 9.7 | 1.9 |
| *P. nigrofasciata* | Odonata | 0.50 | 1.5 | < 0.1 |
| Winter 2001 ($1/m = 1/15 = 0.067$) | | | | |
| *E. lynceum* | Simuliidae | 0.51 | 3.7 | 0.1 |
| | *Isonychia* sp. | 0.43 | 4.5 | 0.1 |
| *E. stigmaeum* | Microcrustacea | 0.94 | 37.5 | 0 |
| *E. swaini* | *Isonychia* sp. | 0.53 | 5.6 | 0.1 |
| *P. nigrofasciata* | Simuliidae | 0.51 | 0.6 | 0.1 |
| Spring 2001($1/m = 1/22 = 0.045$) | | | | |
| *E. lynceum* | Ceratopogonidae | 0.30 | 2.5 | 0.6 |
| | Simuliidae | 0.31 | 16.9 | 4.4 |
| *E. stigmaeum* | Ceratopogonidae | 0.75 | 2.7 | 0.6 |
| | Chironomidae | 0.23 | 92.8 | 74.9 |
| *E. swaini* | Ceratopogonidae | 0.30 | 2.4 | 0.6 |
| *P. nigrofasciata* | *Isonychia* sp. | 0.30 | 1.9 | 0.3 |
| | Simuliidae | 0.40 | 39.7 | 4.4 |

Chironomids were identified only to family. Percent relative abundances of invertebrates from darter diets ($r_i$) and the resource base ($q_i$) are shown. Manly's $\alpha$ values $> 1/m$ represent selection predation by a darter species on an invertebrate taxon. The abbreviation "gr." represents species groups from Epler (1995)

abundances in the resource base. Similarly, in Beaverdam Creek, chironomid larvae numerically dominated the diets of four sympatric darter species; whereas other available prey types such as larval *Stenelmis* beetles, perlid stoneflies, oligochaetes and hydrachnids were bypassed. Although darters selected other non-chironomid taxa, like *Isonychia* sp., simuliids, and ceratopogonids, they fed opportunistically on the most abundantly available prey (i.e., the Chironomidae), causing PS values to be relatively high (near and above 0.60). Phillips and Kilambi (1996) found that *Etheostoma spectabile* fed exclusively on the family Chironomidae ($r_i = 99\%$) and exhibited active selection for chironomids when comparing their availability in the environment (Ivlev's Electivity Index [IE] = 0.03, where values near 0 represent active selection; values near 1.0 represent opportunists). In contrast, they found that *Percina caprodes* may have fed opportunistically on chironomid prey ($r_i = 47\%$, IE = 0.43). Similarly, in our study, *P. nigrofasciata* fed opportunistically in spring at both levels of prey classification. In addition, *P. nigrofasciata* tended to consume more taxa than the *Etheostoma* spp.

Because we did not observe darters directly in the stream or control for confounding effects such as spatial partitioning among substrate-types by darter species, we cannot conclude that darters actively sought out particular prey. They could have segregated themselves spatially among microhabitats (e.g., substrate-type) and fed opportunistically on available prey within those microhabitats (Ross 1986; Ross et al. 1987). Although the darter species occupied the same riffle sites, selective predation (low NB and low PS values) may indicate either the presence of interspecific competition or lack of competition (Lawlor 1980; Glasser and Price 1988). We do not know if darter food resources were limited in Beaverdam Creek. Thus, any apparent competitive interactions between the darter species may have resulted from historic processes (e.g., past competition) leading to phylogenetic divergence among their foraging modes (Ross 1986).

Selective predation by Beaverdam Creek darters may be influenced by behavioral characteristics of chironomid prey. In our study, darters selected mobile scrapers, (*Parakiefferiella* sp. and *Thienemanniella* sp.), tube-building detritivores (*Dicrotendipes* sp., and *Rheotanytarsus* sp.) or active predators (*Nilotanypus* sp. and

**Table 3** Manly's α ($\alpha_i$) describing selective predation by darters on invertebrate prey

| Darter species | Invertebrate prey | $\alpha_i$ | $r_i$ | $q_i$ |
|---|---|---|---|---|
| Summer 2000 $1/m = 1/55 = 0.018$) | | | | |
| *E. lynceum* | *Caecidotea* sp. | 0.14 | 1.3 | < 0.1 |
| | *Dicrotendipes* sp.* | 0.31 | 8.5 | 0.3 |
| | *Parakiefferiella* sp.* | 0.15 | 6.9 | 0.5 |
| | *Thienemanniella* sp.* | 0.15 | 2.8 | 0.2 |
| *E. stigmaeum* | *Stelechomyia perpulchra* * | 0.11 | 15.6 | 1.4 |
| | *Polypedilum convictum* gr.* | 0.34 | 6.7 | 0.2 |
| *E. swaini* | *Chironomus* sp. * | 0.35 | 6.5 | <0.1 |
| | *Thienemannimyia* gr.* | 0.12 | 6.5 | 0.3 |
| *P. nigrofasciata* | *Demicryptochironomus* sp.* | 0.14 | 1.1 | <0.1 |
| Winter 2001($1/m = 1/51 = 0.02$) | | | | |
| *E. lynceum* | *Isonychia* sp. | 0.30 | 4.5 | 0.2 |
| | Simuliidae | 0.25 | 3.7 | 0.2 |
| | *Polypedilum aviceps* gr. | 0.07 | 7.1 | 1.4 |
| | *Rheotanytarsus* sp.* | 0.14 | 26.4 | 2.6 |
| | *Thienemanniella* sp.* | 0.08 | 11.9 | 2.0 |
| *E. stigmaeum* | Microcrustacea | 0.72 | 37.5 | 0 |
| | *Xylotopus par** | 0.12 | 3.1 | 0.2 |
| *E. swaini* | *Isonychia* sp. | 0.34 | 5.6 | 0.2 |
| | *P. aviceps* gr.* | 0.09 | 11.1 | 1.4 |
| | *Stenochironomus* sp.* | 0.08 | 2.8 | 0.4 |
| *P. nigrofasciata* | *Isonychia* sp. | 0.17 | 3.7 | 0.2 |
| | Simuliidae | 0.35 | 3.7 | 0.2 |
| | *Microtendipes pedellus* gr.* | 0.16 | 10.5 | 0.6 |
| | *Rheotanytarsus* sp.* | 0.08 | 21.1 | 2.6 |
| Spring 2001($1/m = 1/60 = 0.017$) | | | | |
| *E. lynceum* | *Thienemanniella* sp.* | 0.07 | 15.9 | 2.4 |
| | *Thienemanniella xena** | 0.16 | 21.1 | < 0.1 |
| | *Tvetenia* sp.* | 0.50 | 6.7 | 2.4 |
| *E. stigmaeum* | *Nilotanypus* sp.* | 0.41 | 5.5 | 0 |
| | *Psetrocladius* sp.* | 0.18 | 10.3 | 1.1 |
| | *Psetrocladius elatus** | 0.26 | 16.7 | 0.5 |
| *E. swaini* | *Stenonema* sp. | 0.07 | 1.2 | 0.2 |
| | *Polypedilum aviceps* gr.* | 0.09 | 7.2 | 1.4 |
| | *Psetrocladius* sp.* | 0.16 | 5.1 | 0.5 |
| | *Psetrocladius elatus** | 0.24 | 17.5 | 1.1 |
| | *T. xena** | 0.07 | 6.6 | 1.5 |
| *P. nigrofasciata* | Simuliidae | 0.13 | 38.1 | 4.8 |
| | *Isonychia* sp. | 0.10 | 1.8 | 0.3 |
| | *Stenonema* sp. | 0.13 | 1.2 | 0.2 |
| | *Nilotanypus* sp.* | 0.13 | 1.2 | 0.2 |
| | *Psetrocladius* sp.* | 0.11 | 3.0 | 0.5 |

An asterisk represents a chironomid taxon. Percent relative abundances of invertebrates from darter diets ($r_i$) and the resource base ($q_i$) are shown. Manly's α values $>1/\mathrm{m}$ represent selection predation by a darter species on an invertebrate taxon. The abbreviation "gr." represents species groups from Epler (1995)

*Thienemannimyia* gr.). Free-ranging chironomids like *Nilotanypus* sp., *Polypedilum* sp., and *Thienemanniella* sp. might have been more susceptible to predation, and tube-dwellers that spent more time outside of their shelters feeding may have been more susceptible to predation (Hershey and Dodson 1985; Hershey 1987). Sih and Moore (1990) reviewed 42 studies that examined dietary preferences by aquatic predators on zooplankton and aquatic insects, and they found that 37 out of 42 (88%) cases reported prey activity and movement as the primary cause of predator diet compositions. Active selection by predators was observed in only 8 (19%) of the cases.

Prey behavior may affect the selectivity of darters, but prey size may be just as important. *Percina nigrofasciata* and *P. sciera* exhibited size-selective predation on stream invertebrates in Red Creek, Mississippi (Rakocinski 1991). Perhaps Beaverdam Creek darters selected chironomids, simuliids, mayflies, and ceratopogonids because they are the right size for the suction-feeding mechanism employed by these fishes. These prey have soft cylindrical bodies that would minimize handling time by darters. In contrast, *Stenelmis* beetles, which were not selected, have relatively hard exoskeletons that might inhibit darters from consuming them.

## Summary

This study shows the importance of identifying darter prey to genus/species level. Chironomids are a very important dietary component of Beaverdam Creek darters, but only one to four chironomid genera/species were selected on a seasonal basis. When describing the foraging mode of aquatic predators, it is important to consider how the proportion of prey-types (e.g., sizes, taxa, guilds) from the diet relates to the availability of those prey-types in the environment. Many studies regarding the feeding ecology of darters do not report on prey availability. Additionally, limitations in taxonomic expertise may bias the description of darter foraging modes. Darters most certainly do not choose prey based on their taxonomic classification, but identifying prey to genus/species may allow researchers to understand the significance of particular prey taxa to aquatic predator diets.

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