A LIFE HISTORY STUDY OF MINNESOTA'S GREAT NORTHERNER: THE IOWA DARTER

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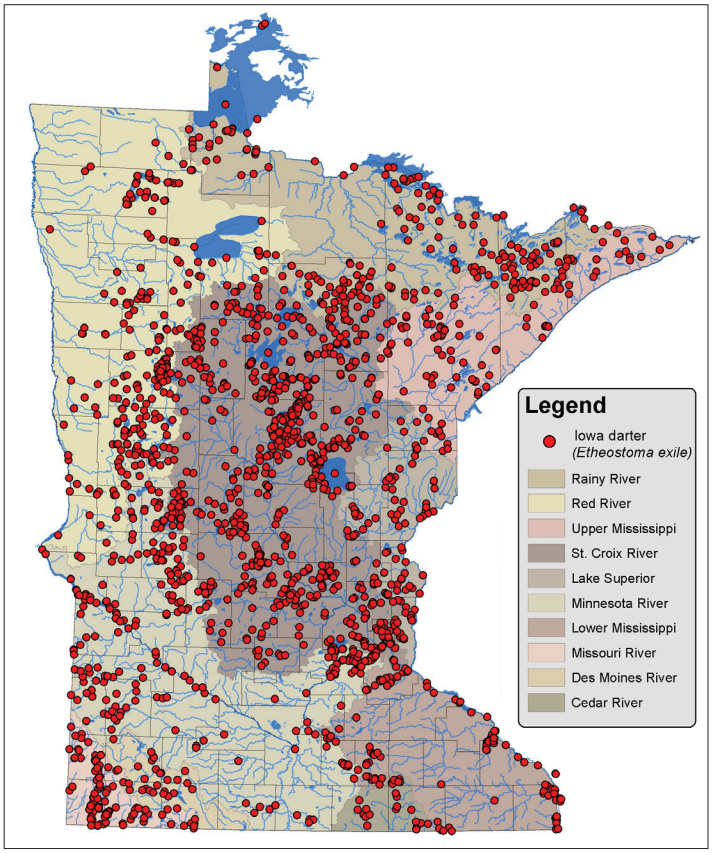

Figure 1. Distribution of the Iowa Darter in Minnesota, based on 2,887 records from 1883–2013. (Map by Nick Proulx, Minnesota DNR).

INTRODUCTION

Ray Katula (1996) coined the name "Great Northerner" to refer to the Iowa Darter (*Etheostoma exile*). This poetic appellation is apt because the Great Northerner ranges further north than any of the other 200+ species of darters, within 40 miles of 60° north latitude! That is not its only distinction. It is the most widespread darter species in Canada and among the seven most widespread darter species in the United States. The Great Northerner also is highly variable in terms of its body shape and color. In Minnesota alone, males looking for mates might wear any one of at least three distinctly different colored suits (see page 11). Even its collection of genes is odd enough to make it hard to say who its closest relatives are. Finally, it is one of eight darter species known to inhabit lakes as well as streams. So, it is a bit surprising that only two populations have been the subjects of detailed life history studies, one in Nebraska (Evans 1974) and one in Wyoming (Copes 1976, published in our very own *American Currents*). Various bits of information on about 17 additional populations scattered from Colorado to Ontario appear in a variety of published and unpublished works.

In Minnesota, the Iowa Darter is one of our most common and widespread fish species. It occurs in every major basin of the state, although it occurs less frequently in areas of intensive row-cropping (Figure 1). We became interested in this species back in the 1980s while studying the larval fishes of Lake Itasca, the official but incorrect headwaters of the mighty Mississippi River. In the lake and the upper reaches of the Mississippi River, colorful males, swollen females, and young of many sizes seemed to swim straight into our nets every time we put them in the water. These colorful bottom-dwelling little cousins of the better-known Yellow Perch and Walleye were begging to be studied.

METHODS

Working out of University of Minnesota's Itasca Biological Station, we collected Iowa Darters from July through November in 1984, May through October in 1985, and April through May in 1986 in the North Arm of Lake Itasca and in the upper reaches of the Mississippi River within the boundaries of Itasca State Park (Clearwater County, Minnesota). In

the lake, we sampled across three depths (0–3 ft, 3–5 ft, 5–8 ft) at three sites approximately 1–2 miles from its outlet to the Mississippi River. In the river, we sampled a large pool, a small pool, two short riffles, and two cobble runs within a 1300-ft reach. The upstream limit of the reach was 1.5 miles downstream from the lake outlet.

In the river, we used small mesh (1/16–1/8 in) bag seines with heavily weighted lead lines, and 3-ft wide (1/16-in mesh) kick nets designed by Jim Erickson (Erickson, 1980). We also used wide-mouth quart canning jar traps designed by Tom Coon (Coon, 1982) to more precisely examine Iowa Darters' movements within the stream habitats. In the lake, we sampled the shallow depth with bag seines and the two deeper depths with a variety of gear that included Tucker trawls, conical ichthyoplankton nets, purse seines, and small otter trawls. Each type of gear, except for the otter trawl, was capable of collecting late larval and juvenile darters as well as adults. On each sampling date, we qualitatively scored darter abundance at each lake depth and within each stream subhabitat (pool, run, riffle) as common (present in every haul), uncommon (present sporadically in hauls), or absent. We scored vegetation in each area as sparse (<1 stem/1ft^2), moderate (1–2 stems/ft^2), or dense (>2 stems/ft^2) by visual estimation.

We kept all specimens we captured and fixed them in 10% neutralized formalin in the field. Prior to taking laboratory measurements, we rinsed darters for 24 hours in running water and blotted them dry with paper towels. We measured standard length (SL) and total length (TL) to the nearest 0.1 mm (about 4 thousandths of an inch). We also measured total body mass (TBM) to the nearest 0.01 g (about 4 ten-thousandths of an ounce), and adjusted body mass (ABM, the mass with all internal organs except gills and kidneys removed) to the nearest 0.1 mg (less than the mass of a speck of pepper). To determine sex, we examined gonads directly, using a microscope when gonads were small. We categorized the developmental state of each female's ovaries using a scheme similar to the one developed by Dave Heins (Heins et al., 1992).

We aged each darter using the scale method, validating annular marks through sequential examination of scales from specimens collected toward the end of one growing season and the beginning of the next. We considered darters caught in June to be 12, 24, or 36 months old, depending on their number of annular marks. To calculate individual growth histories, we used the standard scale-body length method (Lagler, 1956). We also calculated a mean length-at-capture for age-1, age-2, and age-3 specimens collected during the non-growing season (September to May).

To discover food habits, we identified and counted the individual items from the stomachs of up to 10 darters per date and habitat. We counted head capsules as individual food items whenever insects or amphipods were fragmented.

RESULTS AND DISCUSSION

Habitat and seasonal movements

In the Mississippi River, Iowa Darters spent the winter months in deep pools. In early spring (late April-early May), age-1 adults and older fish moved into pool margins to spawn. New-growth aquatic vegetation throughout the area at this time was sparse to absent, but old submerged stems and rhizomes, as well as dead plant debris (detritus), were present around the margin of pools and along parts of the run margins. By late May, breeding adults became very common in the margins of pools and cobble runs where aquatic vegetation, including Canadian Waterweed (*Elodea canadensis*), Wild Rice (*Zizania aquatic*), and various species of sedges (*Carex*), and bulrushes (*Scirpus*), was

Collecting in the littoral zone of Lake Itasca.

Using an Erickson net to collect in the Mississippi River headwaters.

Iowa Darters: female (top left) and males, showing various colorations. (Photos by Konrad Schmidt)

sparse to moderate. Adults continued to disperse downstream along the weedy margins of cobble runs into June but never moved into riffles. They moved from margins to the channels of runs only later in July after rocky substrates were covered with filamentous algae (*Cladophora*) and pondweeds (*Potamogeton*). Throughout the spawning and growing seasons, adults were almost exclusively associated with aquatic vegetation in cobble, sand, and large-particle debris areas, and they avoided areas of soft sediment and small-particle debris. They were active during the day but not at night during this time. In the fall, adults moved back into pools and were completely absent from cobble runs and even pool margins by November.

We captured just two larvae and no age-0 juveniles in the river, even from the margins of runs and within shallow pools. Perhaps they drift or swim into deep pools. All we can say is that age-0 Iowa Darters remain segregated from adults in the river during that first growing season. We presume they join them in the deep pools in fall (or spend their entire first year there), since they are present with older adults there in the spring.

In Lake Itasca, Iowa Darters showed an analogous seasonal movement pattern and affinity for aquatic vegetation. Adults utilized the shallow littoral zone of the lake (the area with rooted aquatic plants) in the spring (April–May) for spawning. They were common there from ice-out to late May over sand, pebble, and cobble substrate covered with large-particle debris. New-growth vegetation at this time was absent, but old-growth vertical and horizontal stems were sparse to moderate. Adult Iowa Darters were present in deeper areas in the spring but were uncommon there. As the spawning season ended (late May–early June), Iowa Darters left the shallow littoral area for the intermediate depth zone (3–5 ft). They were most common in areas of dense muskgrass (*Chara*) and in areas of dense mixed aquatic species (dominated by Wild Rice, bulrush, and Yellow Pond-lily (*Nuphar variegata*). They remained common in this depth zone throughout the growing season and into October, but also dispersed into the deepest littoral depth zone as summer progressed. They did not disperse beyond the littoral zone during the summer; we do not know if they did so over the winter. Iowa Darters have been taken or observed in summer and fall in considerably deeper water in other lakes (Moyle, 1969 and our own observations). These other

lakes had very limited littoral zones. It may be that in Lake Itasca the extensive littoral area—40% of the surface area according to Halpern (1990)—makes it unnecessary for the darters to seek food and avoid predation by moving to deep waters.

During the summer, age-0 Iowa Darters were uncommon in the shallow area, especially during dark hours. They were common in the intermediate depth area, and absent from the deeper waters. This quasi-segregation of age-0 fish and adults was especially strong at all three lake sites in June. Neither age-0 fish nor adults frequented shallow littoral areas of sand and gravel that lacked either muskgrass or emergent vegetation, nor did they associate with sedge mats. They did occur over marl and *gyttja* (soft silt heavily enriched with organic matter), where deposits were 1–2½ inches deep and densely vegetated, but they avoided areas of deeper soft sediment.

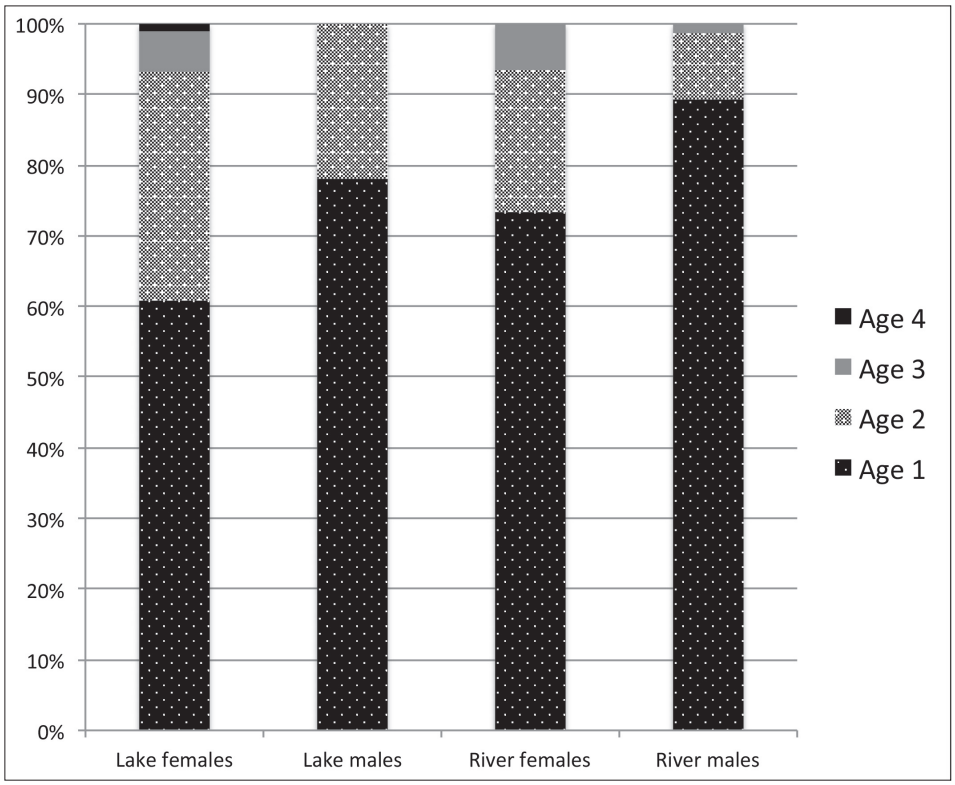

Figure 2. Age composition of Iowa Darters from Lake Itasca and the Mississippi River, based on darters collected July 1984–May 1986.

Across its range, the Iowa Darter inhabits glacial lakes, bog ponds, sluggish streams, and backwaters of larger rivers, where it lives in association with submerged vegetation, including attached algae (Eddy and Underhill, 1974; Becker, 1983; Page, 1983). Results of this study also show a strong association with vegetation in both environments, as well as strong spatial segregation between age-0 fish and adults in the river and a lesser segregation in the lake. Our limited 24-hour observations agree with those of Emery (1973), who suggested Iowa Darters are active mainly during daylight hours.

Age composition and longevity

We aged 275 Lake Itasca and 521 Mississippi River darters. We eliminated young-of-the-year (age 0, 1–4 months old) from our age composition analysis because they were never collected in the river and undoubtedly were underrepresented in the lake. That left us with 151 lake darters. As with many other darter species, most Iowa Darters did not live beyond a second growing season (= age 1), regardless of whether they lived in the lake or in the river (Figure 2). Also, females were more likely than males to reach age 2 or age 3, again regardless of where they lived. Although it looks like darters from the lake lived longer on average than those from the river, statistical analyses did not back up that conclusion. So, maybe they did, maybe they didn't. For sure, it was exceedingly rare for any Iowa Darter to live to a 4th growing seasons (= age 3). Just one darter out of 796 made it to age 4, a lake female who lived 47 months.

Growth

Like many short-lived fish species, Iowa Darters grew very rapidly during their first year (Table 1). On average they reached about 72% of their maximum length by the end of their first growing season. In both lake and river, females grew faster and reached longer average lengths in their first year of life than males did. However, in both environments, males grew faster than females in their second growing season, closing the gap in size differences (analyses in Hatch and Johnson, 1997). Because so few males reached age 3, it is hard to discover sex-influenced size differences in older fish. Another way to view such differences is to ignore age and compare the longest individuals captured. In the lake, the longest female was 62.0 mm TL (a little short of 2½ inches), and the longest male was 57.1 mm TL (2¼ inches). The 10 longest females averaged 60.2 mm (about 21/3 inches), while the 10 longest males averaged 52.9 mm (just a little over 2 inches). In the river, the longest female and male were essentially of equal length: 64.5 mm for the female and 64.1 mm for the male (a titch over 2½ inches for each). The 10 longest females averaged 61.8 mm, while the 10 longest males only reached an average of 58.5 mm (but that's just 13 hundredths of an inch less). Overall, it seems reasonable to conclude that females typically reach slightly greater

lengths-at-age than males do, although it is possible for a given male to attain the same or nearly the same ultimate length as a given female. Differences in mean lengths probably result from a combination of the faster early growth rate and greater average longevity of females. In Carter Lake, Nebraska, females reached longer lengths in their first year than males and then maintained that length difference into the second year (Evans, 1974). Others have stated that females are larger than males, but they did not give specific values or reasons for the differences (Winn, 1958, Copes, 1976, Page, 1983).

We also found that most of the time first-year females and males grew faster and attained longer lengths in Lake Itasca than they did in the Mississippi River (again, analyses in Hatch and Johnson, 1997). Some cohorts (fish that hatch in the same year) of the river population caught up with cohorts of the lake population during their second season of growth, while other cohorts did not. We do not know for sure what causes these growth differences between habitats, but we have argued that they most likely are tied to different growth conditions in the two habitats rather than to differences in size-selective predation or to sampling artifacts (Hatch and Johnson, 1997).

One of the things that made it hard to know for sure if growth really was different between sexes and habitats was the amount of overlap in lengths at successive ages. One-year olds captured during the non-growing season (sexes and habitats combined) ranged from 32.2 to 51.4 mm TL, two-year olds ranged from 44.5 to 62.0 mm TL, and three-year olds ranged from 52.6 to 64.5 mm TL. The range of overlap was greater in the river population than it was in the lake population. This kind of overlap is expected and common in short-lived species with prolonged spawning seasons (Lutterbie, 1976; Burr and Page, 1979; Hatch, 1982; Johnson and Hatch, 1991). However, Copes (1976) reported no overlap at all among ages of Iowa Darters from Sand Creek, Wyoming, and Evans (1974) reported overlap only among females from Carter Lake, Nebraska.

We found similar kinds of overlaps and differences between sexes and habitats when we looked at total body mass (TBM). After calculating the quantitative relationships between weight (technically mass) and length, we were able to determine that within both sexes darters from the river were "plumper" (heavier per unit of length) than darters from the lake. So, while lake darters often grew faster lengthwise than those in the river, they actually did not put on as much weight relative to their length. Overall, we would have to say that growth conditions were better in the river than in the lake, even though the differences they caused were small. If we combine sexes and habitats, here's what we get for typical sizes of Iowa Darters at the end of each of their growing seasons. Age 1: 36–45 mm TL (about 1½ –1¾ in), 0.4–0.6 g TBM (about 0.01–0.02 oz); Age 2: 51–56 mm TL (about 2–2¼ in), 1.0–1.3 g TBM (about 0.04–0.05 oz); Age 3: 57–61 mm TL (about 2¼–2½ in); 1.3–1.6 g TBM (about 0.05–0.06 oz).

Reproductive biology

Based on field observations and laboratory examination of gonads, both males and females were capable of producing mature gametes in their first spring after hatching (age 1), but smaller darters became ripe (exuded functional sperm and eggs) later in the breeding season than larger darters. Our smallest mature male was 37.2 mm TL and the smallest mature female was 35.1 mm TL (both just a little under 1½ in.). In both habitats, Iowa Darters spawned mainly in April and May, but a few spawned as late as early July in the lake. In the lake, males and females were already ripe by the time ice had melted along the shore (ice was still present 10 m from the shoreline). Bottom water temperatures at this time were 4.0–4.5°C (39–40°F). All of this suggests that spawning in the lake either begins under the ice or shortly after ice-out, and at the lowest temperature recorded for any darter species, including previously reported temperatures for this one (Jaffa, 1917; Evans, 1974; Hubbs, 1985). Spawning in the river began at the same time and temperature as in the lake, but the river ice was completely gone. Spawning continued in the river but at reduced rates as water temperatures began to exceed 18°C (64°F). No spawning took place once temperatures reached 23°C (73°F). In the lake, ripe females moved deeper in the littoral zone as water temperatures approached 20°C (68°F). Temperature is one important environmental cue that determines spawning duration, especially spawning cessation, and was likely responsible for the difference in spawning duration between the river and lake (Marsh, 1980; Hubbs, 1985). Based on many observations by others, spawning duration for the Iowa Darter is clearly not related to whether the environment is a lake or a stream (Jaffa, 1917; Winn, 1958; Evans, 1974; Copes, 1976).

In the river, Iowa Darters spawned in the shallow margins (3–12 in deep) of a large pool with a sandy bottom. Their eggs were attached to waterlogged tree bark, twigs, and plant roots. In the lake, older darters typically arrived on the spawning "grounds" before younger darters. They most often spawned in shallow littoral water (usually less than 20 in deep), attaching their eggs to old bulrush stalks, the horizontal stems of water lily, and other plant debris distributed over gravel, cobble, and sand bottoms. Similar spawning habitats and periods have been reported for Iowa Darter populations from other geographic regions. Winn (1958) documented pre-spawning migrations from lakes into inlet streams in Michigan. We did not study this movement in Lake Itasca, but we have found ripe Iowa Darters in the

small stream flowing from Elk Lake into Lake Itasca.

Throughout the spawning season, females from both habitats contained ovaries with groups of eggs at different stages of development. This condition indicates that the Iowa Darter is what we call a multiple-clutch or batch spawner. Rather than ripen and spawn all of its eggs at once, an Iowa Darter ripens and spawns a portion of its eggs (a "clutch"), stops spawning for some days while it ripens another clutch, and then spawns that clutch, and repeats the process. How many clutches it produces and spawns likely is determined by the environmental conditions that control the duration of the spawning period and the nutritive condition of the fish. We determined the clutch size for 14 females from the lake and 16 females from the river. These fish represented females 10–35 months old and 37.2–62.0 mm long. For all 30 females, clutch size ranged from 60 to 374 eggs and was strongly linked to size of the darter, far more so than to age. The relationship to size was stronger in the lake than in the river, and lake females put more effort per size into producing eggs. However, clutch size was higher in the river (284.5 eggs) than in the lake (257.2 eggs), although the difference was not statistically significant. We have no measurements of the number of clutches spawned per female per season. Our clutch sizes compare very closely by length and age to the 63–360 range (mean = 230.2) of Nebraska fish studied by Evans (1974). He is the only other investigator to report clutch size. Others report the total number of eggs containing any amount of yolk in pre-spawning females: 550–2048 (N = 10) in Iowa Darters from Michigan and 312-970 (N unspecified) in darters from Wisconsin (Winn, 1958; Lutterbie, 1976). The Nebraska darters contained 1062–3500 total eggs.

Food habits

The diets of darters from both the lake and the river were comprised almost exclusively of small crustaceans and immature aquatic insects (Tables 2 and 3). Midge larvae (Chironomidae) were the most consistently consumed insect in both habitats, and were the only numerically important insect for lake darters. At times, blackfly larvae (Simuliidae) and small minnow mayfly immatures (Baetidae), both of which are more abundant in flowing water, were just as important or more important than midges in the river diet. Netspinner caddisfly larvae contributed substantially to the river diet on occasion, especially considering they were consistently the largest food item consumed. In the lake, various crustaceans were seasonally as important as midges. In late spring and summer, it was common scuds (*Hyalella azteca*) and various species of water fleas (Cladocera), while in the fall it was copepods (Copepoda) and seed shrimps (Ostracoda). Because of its larger relative size, the common scud probably is more important than its numerical percentage suggests. The scud was also an important part of the spring and fall diet in the river.

Generally the differences in diets between lake and river populations likely reflect food availability differences. The littoral zone of Lake Itasca has a diverse and abundant assemblage of microcrustaceans (water fleas, copepods, and seed shrimps), while the river supports only a modest number of copepods. In contrast, the river is rich with small minnow mayflies, black flies, and netspinner caddisfies, all of which are absent or scarce in Lake Itasca. Midges and common scuds are abundant in both habitats. Overall, the seasonal diets of both populations seem to reflect the opportunistic feeding behavior characteristic of most darter species (Page, 1983). The diets of other populations of Iowa Darters have included all of the food items reported here, as well as dragonflies, stoneflies, aquatic beetles, aquatic worms, snails, and fish eggs.

Most darter species that have been studied are primarily daytime feeders. However, Iowa Darters in Long Lake, Minnesota, fed around the clock, selecting similar food items from hour to hour (Moyle, 1969). We did not determine if feeding occurs at night in either habitat, but lack of nighttime movement in the river (see *Habitat and seasonal movements*) suggests that nocturnal foraging in this habitat is minimal.

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Table 1. Growth in total length (mm) of Iowa Darters in Lake Itasca, the Mississippi River headwaters, July 1984–May 1986. To help interpret: 1½ in. = 38.1 mm, 2 in. = 50.8 mm, 2½ in. = 63.5 mm.

No. annuli	N	Age 1		Age 2		Age 3	
		mean	2SE	mean	2SE	mean	2SE
Lake females							
1	34	45.7	1.3	-	-	-	-
2	10	43.4	2.3	55.6	1.5	-	-
3	2	43.5	11.0	52.7	6.0	57.3	2.9
Empirical		42.1	1.0	54.6	1.3	60.7	1.5
Empirical N			48		25		4
Overall mean		43.8	1.6	54.8	1.0	57.4	1.1
Increment		43.8		11.0		2.6	
Lake males							
1	16	44.1	2.8	-	-	-	-
Empirical		40.8	0.8	52.2	2.0	-	-
Empirical N			49		9		
Overall mean		41.6		52.2			
Increment		41.6		10.6			
River females							
1	127	40.7	0.8	-	-	-	-
2	24	43.4	1.5	55.0	1.7	-	-
Empirical		37.4	0.9	53.7	0.9	59.2	1.4
Empirical N			76		65		16
Overall mean		39.9	0.6	54.2	0.8	59.2	1.4
Increment		39.9		14.2		5.1	
River males							
1	133	39.1	0.7	-	-	-	-
2	9	39.0	2.5	50.8	3.2	-	-
Empirical		36.4	0.6	52.8	1.0	57.1	4.0
Empirical N			116		53		5
Overall mean		37.9	0.5	54.2	0.9	57.1	4.0
Increment		37.9		16.3		2.8	

Table 2. Mean percentage of food items per stomach by number in Iowa Darters collected from Lake Itasca in 1985 and 1986 (N = 10 for each date).

	1985				1986		
Food item	Jun 19	Jul 25	Aug 06	Oct 20	Apr 11	Apr 25	May 24
Crustaceans							
Common scuds	56.1	6.4	5.5	0.8	15.2	7.5	7.3
Water fleas		14.4	18.1	6.1			58.8
Copepods		0.6		44.6	27.3	6.6	
Seed shrimps		1.5	4.9	28.1	3.8	0.3	
Insects							
Midges	26.3	74.8	64.8	20.2	53.0	85.0	30.3
Biting midges	1.8	0.9	4.4			0.3	3.6
Black flies	7.0					0.3	
Small minnow mayflies				0.3	0.8		
Squaregill mayflies	8.8	0.6					
Other food		0.6	2.2				
Total number of items	57	326	182	377	132	319	165
Number of empty stomachs	0	0	1	0	0	0	0

Table 3. Mean percentage of food items per stomach by number in Iowa Darters collected from the Mississippi River in 1985 and 1986 (N = 10 for each date).

	1985					1986		
Food item	May 03	May 26	Jul 11	Aug 08	Oct 19	Apr 12	Apr 27	May 24
Crustaceans								
Common scuds	16.2	17.9			20.9	8.1	21.4	4.1
Copepods	23.0	12.5						
Insects								
Midges	30.4	10.7	16.6	15.5	39.5	62.1	28.6	36.7
Biting midges		7.1						
Black flies	0.7	44.6	24.3	8.1	11.6	21.0	3.6	2.0
Small minnow mayflies	26.4	3.6	58.6	72.3	2.3		7.1	40.8
Other mayflies					7.0	0.8		
Netspinner caddisflies	3.4	1.8	0.6	4.1	18.6	7.3	39.3	16.3
Other food		1.8				0.8		
Total number of items	148	56	169	148	43	124	28	49
Number of empty stomachs	0	0	0	0	0	0	0	0