Environmental Biology of Fishes **51**: 297–308, 1998.

Creation and maintenance of habitat downstream from a weir for the greenside darter, *Etheostoma blennioides* – a rare fish in Canada

Christopher M. Bunt,[1,3] Steven J. Cooke[2] & R. Scott McKinley[1,4]
[1] *Biotelemetry Research, Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada*
[2] *Department of Environment and Resource Studies, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada*
[3] *Senior author*
[4] *to whom all correspondence should be addressed (e-mail: smckinle@sciborg.uwaterloo.ca)*

Received 13.2.1997 Accepted 11.8.1997

Key words: Percidae, microhabitat use, migratory behaviour, fecundity, resource partitioning, fishways, warmwater fish passage, impoundments

Synopsis

The biology, microhabitat use and migratory behaviour of the greenside darter, *Etheostoma blennioides*, was studied at the Mannheim Weir on the Grand River, Ontario during the summer of 1995 and 1996. Officially listed as vulnerable in Canada, greenside darters reached maturity at age 1 and lived up to 4 years. They were found in riffle habitats that consisted of cobble and loose boulders, with large mats of *Cladophora*. This type of unembedded substrate is uncommon in the Grand River watershed. However, local abundance of greenside darters immediately downstream from the Mannheim Weir was likely due to high water velocities from weir discharge, freshets and ice scour which help maintain unembedded riffle areas. Trap data indicated that greenside darters temporally partition this habitat with the stonecat, *Noturus flavus*. Other darter species were not commonly found in areas with greenside darters, whose depth selection and habitat choices were influenced by predators and morphology. Denil fishways at the Mannheim Weir rarely passed greenside darters due to prohibitively high water velocities and exclusion by larger fish.

Introduction

Greenside darters, *Etheostoma blennioides*, were thought to be restricted to five river systems and one lake in Canada prior to 1996 (Dalton 1991). The initial appearance and subsequent localized population explosion of the greenside darter in the Grand River was first recorded in 1995 (Bunt unpublished data). This range extension contrasts the findings of Dalton (1991) who suggested that the Canadian range appeared to be declining, likely as a result of habitat degradation. Following Dalton's recommendations in 1991, the Committee On the Status of Endangered Wildlife in Canada (COSEWIC) recognized the greenside darter as a vulnerable species due primarily to its restricted range and overall rarity.

Spawning areas of the greenside darter are restricted to filamentous algae-covered boulders and rubble (Fahy 1954, Winn 1958 a, b) and destruction of these habitat types cause a decline in greenside darter populations (Dalton 1991). Impoundments on the Grand River may create areas that are unsuitable as greenside darter habitat. However, river barriers may also help to create and maintain areas immediately downstream with characteristic shallow depths and coarse substrate which is free of silt, as suggested by Ligon et al. (1995). The nutrient-rich water of the Grand River may also encourage the lush growth of *Cladophora* on cobble and boulders, which may be important habitat for the greenside darter.

The literature contains one report of greenside darter behaviour and ecology in Canada. Englert & Seghers (1983) examined the habitat segregation among stream darters, including the greenside darter, in the Thames River watershed of southwestern Ontario. They reported that greenside darters were generally found over rubble in shallow water. However, there have been no investigations into the demographics of a greenside darter population in Canada. Reports of upstream dispersion through fishways of small benthic fish, such as darters, are similarly rare.

We present biological and behavioural observations from a large population of greenside darters below an impoundment. Microhabitat preferences and distribution of the greenside darter are discussed as well as factors which contribute to the maintenance of greenside darter populations immediately downstream from a weir. Finally, we examine variables affecting fishway use by greenside darters and implications of fish passage restrictions to the conservation and dispersion of greenside darters in the Grand River.

Methods

The Grand River is a large tributary of Lake Erie in southwestern Ontario. The Grand River watershed covers an area of 6734 km^2 and extends 297 km from Dundalk in the north to Port Maitland in the south.

The topography of the Grand River watershed in the vicinity of the study site can be characterized by rolling and undulating hills and valleys. Medium to coarse textured surface soils are laid over a variety of tills, sands and gravel deposits. The mean annual precipitation in the watershed varied between 813 mm and 965 mm and mean discharges (1989–1995) were 33.19 m^3 s^{-1} (John Bartlett personal communication). Agriculture and increasing urban development have had major effects on the watershed. In the late 1980's, it was deemed necessary to impound the river, which has subsequently impacted the fish community. Water velocities, water temperature, dissolved oxygen, turbidity, river connectivity and geomorphological processes have all been altered because of river impoundment.

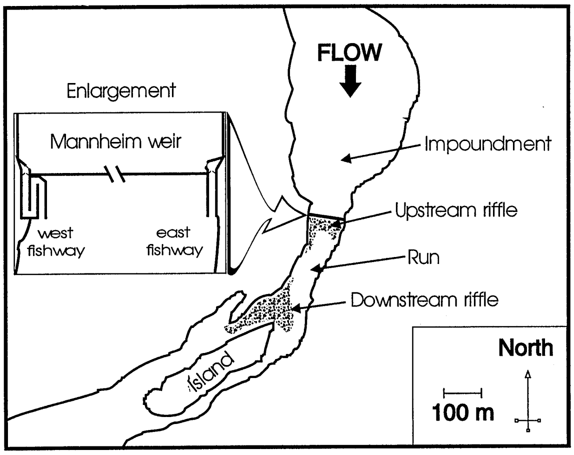

Figure 1. The Mannheim weir on the Grand River, near Kitchener, Ontario. The enlargement shows the west and east Denil fishways and areas near the weir where greenside darters were commonly observed.

The study site (Figure 1) was located on the main stem of the Grand River, near the south end of Kitchener. The site extended 800 m upstream and downstream from the Mannheim Weir (43° 25′ N, 80° 25′ W), which was constructed in 1990 to provide a pool for the extraction of regional drinking water. Upstream from the weir, the habitat was primarily lentic. The channel was relatively void of cover and structure with silty substrate; and, approximately 800 m upstream from the weir, assumed riverine characteristics and began to meander. Immediately downstream from the weir, cobble and boulders covered in *Cladophora* formed riffle areas; much of the substrate found here was large broken rock deposited during construction of the weir. Fifty metres downstream, the riffle terminated into a large and deeper run with finer substrates and scattered boulders. Three hundred metres downstream, the river began to assume the riffle-run-pool sequence and included back-eddy areas. The next impassable barrier was located 17 km downstream, at the Parkhill Dam in Cambridge, which did not have a fishway or fish-bypass channel.

The Mannheim Weir extends 90 m across the river and was equipped with two different Denil fishways at either bank of the river (Figure 1). The west side of the 2 m-high weir was constructed with a 27 m-long reinforced concrete channel which doubled back on itself twice. Two resting pools were provided between the three inclined channels; each was 7.5 m long, with a gradient of 10%. Each channel was fitted with metal baffles designed to dissipate energy through the downward flow of water within the fishway. In contrast, the east bank of the river accommodated a much simpler fishway composed of one 12 m-reinforced channel with a 20% gradient. The width of all channels was 0.6 m.

Habitat identification and fish collection

We divided the study site into impoundment, upstream riffle, run and downstream riffle areas where fish were collected and observed (Figure 1). A backpack electrofisher (Smith-Root Mark VII) was used monthly between June and October 1996 to obtain distributional data for over 400 greenside darters. Crews spot-electrofished, moving upstream in a systematic fashion, while observations were made on the habitat types used by greenside darters. Although some authors (e.g., Gatz et al. 1987) have suggested that electrofishing may bias habitat descriptions because of displacement of individuals from their natural positions during capture, we felt this was not a valid concern with greenside darters. The darters held tight to the cover and when the electrofisher was activated, it was clear which types of microhabitats greenside darters were using. This is supported by research which suggests that electrofishing appears to be an effective method for habitat characterization in shallow, fast-flowing water with large diameter substrates (Heggenes et al. 1990), such as the riffle zone below the Mannheim Weir. Seine nets (15 m long, 5 mm mesh) were also used in the downstream run and backwater areas between June and August 1996. Seining was ineffective over large cobble substrates and in deep impounded areas upstream from the weir.

After capture, greenside darters were measured (TL, mm), weighed (± 0.001 g) and sexed based on colouration and urogenital pore differences. Random samples were dissected to confirm that sexual determinations were accurate. Scales were removed from a subsample of individuals (n = 69), using the method of Lachner et al. (1950), and subsequently cleaned and aged on a projection screen. A minimum of five scale samples from each age-class (except age IV+) for both sexes were examined to verify age classifications. Ovaries from gravid females were removed and weighed on a digital balance (± 0.001 g). Eggs were refrigerated and later enumerated using the gravimetric method. Additional darters were preserved in 95% ethanol for stomach analysis and stomach contents were analyzed using the numerical occurrence method as described by Blake (1977). Diet composition was determined in order to illustrate predominant food types from within each sample. Frequency of occurrence of each food type was calculated to determine the most commonly consumed food type among individuals.

Direct underwater observations by divers (e.g., Keenleyside 1962, Northcote & Wilkie 1963) were made immediately upstream and downstream from the weir, and to a distance of 400 m downstream, between June and August of 1996. Snorkellers moved slowly upstream by holding onto rocks (Keenleyside 1962) and made qualitative notes where greenside darters were located. Cobble and boulders were carefully lifted to ensure no greenside darters were missed (Chipps et al. 1994). Microhabitat preferences of over 200 greenside darters were observed using this method in 1996.

Additional behavioural information was collected by observing fish from the fishways, which were used as overhead vantage points. Fish were observed at the fishway entrances and in the surrounding areas. Qualitative information with respect to position of greenside darters, orientation relative to the water current, proximity to heterospecific fish, proximity to conspecifics and swimming behaviour were documented. Nighttime observations were also made using focused halogen-beam handlights.

Habitat characterization

Habitat variables were collected from the upstream riffle, run and downstream riffle in random 1 m^2 quadrats from areas where greenside darters were generally observed by snorkeling and electrofishing. Depths were measured using a calibrated rod. A Sigma Portable Velocity Meter (PVM) was used to measure water velocity (cm s^{-1}) at the focal point (Fausch & White 1981, Cunjak & Power 1986). Because greenside darters are benthic, all velocities were recorded at the bottom. Substrate was classified according to a modified Wentworth scale, similar to that of Cummins (1962), where boulders were > 256 mm, cobble 64–256 mm, pebble 16–64 mm, gravel 2–16 mm, sand 0.0625–2 mm and silt < 0.0625 mm. Embeddedness was scored using the methods developed by Crouse et al. (1981), where substrate was classified as completely embedded, 3/4 embedded, 1/2 embedded, 1/4 embedded, and unembedded. Embeddedness was considered to be important because greenside darters tend to seek refuge in the interstices beneath and between cobble and boulders. Within the same 1 m^2 quadrat where depth and velocity were measured, the amount of *Cladophora* present was recorded as a percentage of substrate covered, while the presence of other aquatic macrophytes was also noted. We compared the upstream and downstream riffle sections, and the upstream riffle section and the run, using t-tests for independent means ($\alpha = 0.05$) with pooled variances.

Fishway entrance trapping

Wire basket minnow traps were set 2 m downstream from the entrance of both fishways (May–July 1996). Minnow traps were checked twice daily (early morning and late afternoon) and all fish were enumerated. Microhabitat characteristics within 10 m^2 of the east and west fishway entrances were examined for differences as described above. Ten random points were selected within the 10 m^2 areas near the entrances to obtain representative habitat measurements. Microhabitat differences at the fishway entrances were analyzed using a t-test for independent means ($\alpha = 0.05$) with pooled variances.

Fishway use

Fishway traps were checked and cleared at least daily in 1995 (April–July) and 1996 (May–July). Dipnets were used to remove fish from fishway traps and on some occasions, attempts were also made to capture fish in resting pools. Greenside darters caught in the fishway traps were measured and released upstream. Hydraulic conditions within the fishways during upstream spring migrations were also recorded.

Table 1. Habitat variables collected from 1 m^2 quadrats downstream from the Mannheim Weir.

Variable	Upstream riffle (n = 45)	Run (n = 26)	Downstream riffle (n = 15)	West fishway entrance (n = 10)	East fishway entrance(n = 10)
Approximate area (m^2)	3,000	24,000	3,000	10	10
Mean depth (cm) ± SE	25.27 ± 1.78	57.27 ± 4.60	19.93 ± 2.61	26.10 ± 4.19	38.20 ± 3.05
Mean bottom velocity (cm s^{-1}) ± SE	15.8 ± 2.2	13.1 ± 1.8	20.1 ± 2.5	7.1 ± 1.0	14.2 ± 1.8
Mean *Cladophora* cover (%) + SE	59.88 ± 4.39	15.39 ± 2.29	59.67 ± 6.82	55.00 ± 8.33	23.50 ± 7.23
Primary substrate	Boulder	Cobble	Cobble	Boulder	Boulder
Secondary substrates	Cobble, Sand	Pebble, Gravel	Pebble, Gravel	Cobble, Sand	
Embeddedness value	1/4 Embedded - Unembedded	3/4 Embedded – Embedded	1/2 Embedded – Embedded	1/4 Embedded – 1/2 Embedded	1/4 Embedded – Unembedded

Table 2. Stomach contents of greenside darters collected during the summer of 1996 (n = 25). Other stomach contents included aquatic hemipterans and terrestrial insects.

Order	Diet composition (%)	Frequency of occurrence
Ephemeroptera	67.6	0.56
Trichoptera	27.0	0.68
Diptera	4.1	0.28
Ostracoda	1.0	0.12
Other	0.3	0.04

Results

Distribution and habitat use

No greenside darters were captured or observed immediately upstream from the weir where no riffle areas were located. The mid-channel depth was > 2 m, with shallow areas along the banks. The substrate was composed of silt which supported such macrophytes as *Potamogeton pectinatus*, *Elodea canadensis* and *Myriophyllum* spp. Species observed or collected in the impoundment included smallmouth bass, *Micropterus dolomieu*, brown bullhead, *Amieurus nebulosus,* golden redhorse, *Moxostoma erythrurum*, greater redhorse, *Moxostoma valenciennesi*, white sucker, *Catostomus commersoni*, common carp, *Cyprinus carpio*, central mudminnow, *Umbra limi*, common shiner, *Luxilus cornutus*, Johnny darter, *Etheostoma nigrum*, least darter, *Etheostoma microperca* and Iowa darter, *Etheostoma exile*. All adult cyprinid species were rare within 800 m upstream from the weir.

Snorkeling observations and electrofishing downstream from the weir resulted in the location of greenside darters primarily on unembedded large cobble and boulder substrates covered with *Cladophora*. Most greenside darters were located immediately downstream from the weir across the entire width of the upstream riffle. Other fish species commonly observed or collected in this riffle were stonecats, *Notorus flavus*, smallmouth bass, white sucker, northern hog sucker, *Hypentelium nigricans*, rock bass, *Ambloplites rupestris*, pumpkinseed, *Lepomis gibbosus*, largemouth bass, *Micropterus salmoides*, black crappie, *Pomoxis nigromaculatus*, common carp, and many other species of cyprinids. Greenside darters were oriented obliquely to the flow at the base of the weir, and along concrete areas where *Cladophora* was present. Where the upstream riffle terminated into a deeper run, the substrate became much finer (e.g., cobble, pebble, and gravel with scattered boulders) and was largely embedded (Table 1). The run was significantly deeper ($p < 0.05$) and had significantly less *Cladophora* cover than the upstream riffle, where greenside darters were common ($p < 0.05$). The bottom velocity did not differ significantly between the upstream riffle and the run ($p = 0.40$). No greenside darters were observed in the run section except along the shoreline where larger cobble substrates with *Cladophora* and shallower depths were present. Centrarchid predators and stonecats were all found within the run.

Further downstream (> 200 m), shoreline areas had reduced water velocity and finer substrates (e.g., silt, sand and pebble) where no greenside darters were observed. Several silty backwater areas were seined and electrofished, and no greenside darters were collected. In the most downstream sec-

Table 3. Fecundity summary for greenside darters collected during the spring of 1996. No age 3 females were found during this time, although 3-year-old partially spawned females were collected early in the summer.

	Age 1 (n = 5)	Age 2 (n = 6)
Mean number of eggs (± SE)	335.2 ± 44.39	418.8 ± 81.02
Range in fecundity	181–447	231–750
Mean ovary weight (g) (± SE)	0.0674 ± 0.0067	0.1308 ± 0.0161
Mean egg weight (g) (± SE)	0.000216 ± 0.000029	0.000355 ± 0.000056
Range in total length (mm)	52–60	62–69

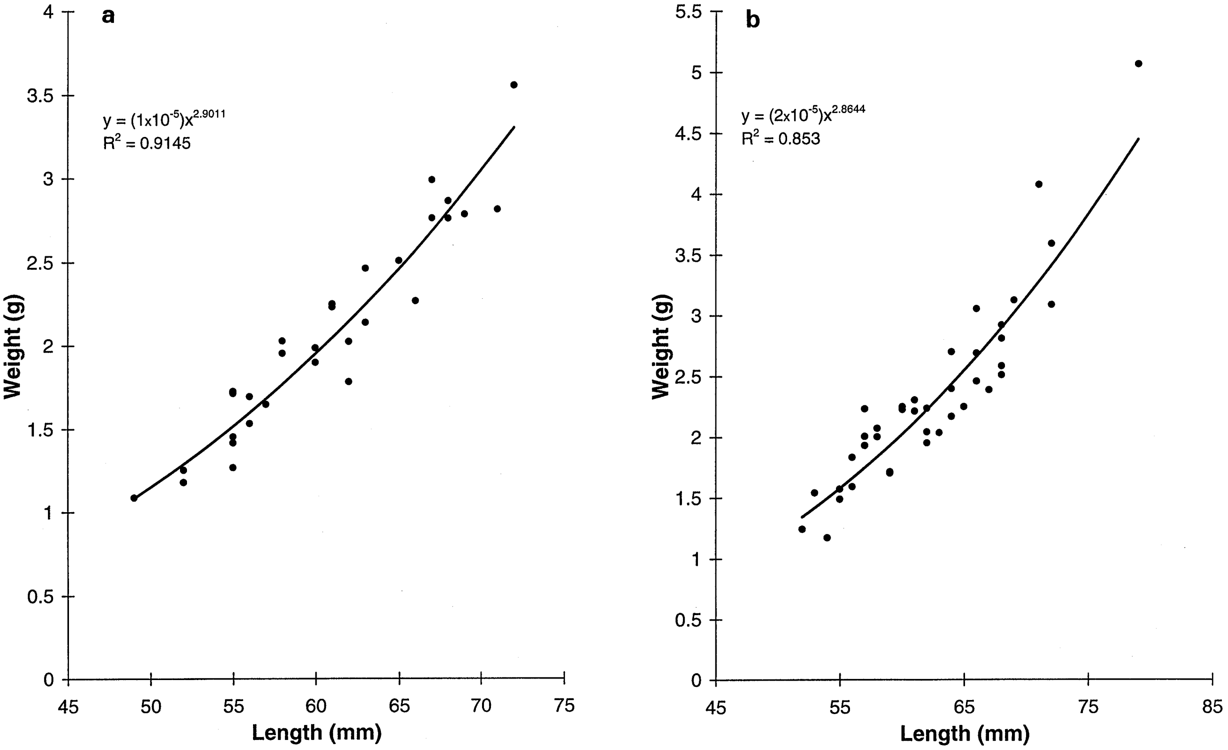

Figure 2. Length-weight regressions for female (a) and male (b) greenside darters from the Grand River. The relationships are defined as weight (g) = $(1 \times 10^{-5}) \times$ total length $(\text{mm})^{2.9011}$ and weight (g) = $(2 \times 10^{-5}) \times$ total length $(\text{mm})^{2.8644}$ for females ($n = 30$, $p < 0.0001$, $r^2 = 0.91$) and males ($n = 39$, $p < 0.0001$, $r^2 = 0.85$), respectively.

tion of the study site, another riffle area was present which also extended across the entire river, but greenside darters were rarely found in this area. However, least darters and Iowa darters, as well as many cyprinids and catostomids used this riffle. The downstream riffle was not significantly different from the upstream riffle (Table 1) in terms of bottom velocities ($p = 0.32$), depth ($p = 0.15$) or *Cladophora* cover ($p = 0.98$), but had finer substrates (e.g., small cobble, pebbles and gravel) which were more embedded. The riffles differed mainly in embeddedness, substrate type and proximity to the weir.

Seining was ineffective near the weir where high water velocities and large cobble substrate were present. However, we successfully seined in shallow areas with finer substrates, where Iowa darters, least darters and Johnny darters were captured; but no greenside darters were found. Snorkeling observations in these downstream areas also resulted in no greenside darter sightings.

Diet analysis

Ephemeropteran and trichopteran larvae were the most important summer food items for greenside darters in the Grand River (Table 2). The majority of individuals preyed upon trichopteran larvae (hydropsychids being the most common of these larvae), followed by ephemeropteran larvae, dipterans, ostracods and hemipterans. Ephemeropterans, predominantly baetids, were the most abundant food item. Dipterans included chironomids and simuliids.

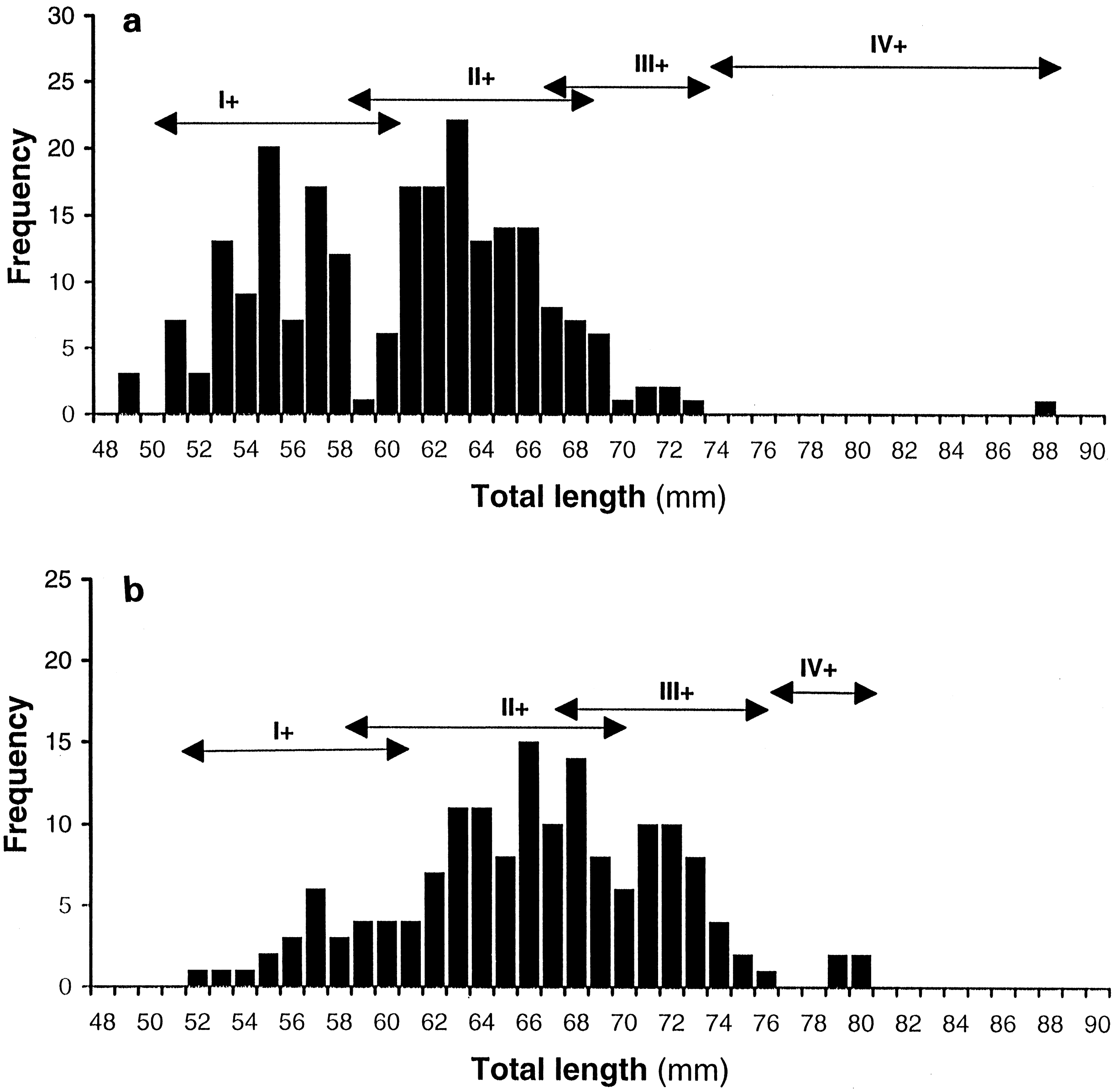

Figure 3. Length-frequency distribution of female (a, n = 223) and male (b, n = 158) greenside darters collected below the Mannheim Weir during June and July 1996.

Fecundity

We found eggs only in age 1+ and age 2+ females (Table 3). Prior to and during spawning, we did not collect any females larger than 69 mm, or older than age 2. Age 2 females contained more eggs than age 1 females, although the range in fecundity overlapped for the two age classes.

Length-weight relationships

The best-fit length-weight regression is described as weight (g) = $(1 \times 10^{-5}) \times$ length $(\text{mm})^{2.9011}$ ($n = 30$, $p < 0.0001$, $r^2 = 0.91$) and weight (g) = $(2 \times 10^{-5}) \times$ length $(\text{mm})^{2.8644}$ ($n = 39$, $p < 0.0001$, $r^2 = 0.85$) for females and males, respectively (Figure 2). The mean length for males was 66.2 mm ± 0.445 (n =

158), while the mean length for females was 60.5 mm ± 0.3 (n = 223). Length-frequency distributions of greenside darters captured in early July were plotted for females and males (Figure 3), and the ratio of males to females was 1:1.4.

Fishway entrance habitat

The region near the west fishway entrance had significantly lower water velocities with more diverse and more embedded substrates compared to the region near the east fishway entrance ($p < 0.001$, Table 1). There were also small patches of sand near large *Cladophora*-covered cobble and boulders near the west fishway entrance. The east fishway entrance had higher velocities ($p < 0.05$), large unembedded boulders, and was free from finer substrates. The mean depth of the west fishway entrance was significantly shallower than that of the east fishway entrance ($p < 0.05$), and *Cladophora* was significantly less abundant on the east side than on the west side ($p < 0.05$).

Fishway entrance trapping

Significantly more ($p < 0.001$) greenside darters were captured in the minnow traps at the west fishway entrance (n = 342) compared to the number of greenside darters collected from traps near the east fishway entrance (n = 28). Blackside darters *Percina maculata*, were caught in both traps on rare occasions, while stonecats were found regularly in both traps when first emptied in the morning. All species were more abundant in the west trap, and greenside darters were the most common species captured during the afternoon trapping periods.

Fishway exit traps

On 13 June 1995, approximately 300 greenside darters were captured in the west fishway exit trap (range 56–79 mm TL), but in 1996, very few greenside darters (< 10) were captured in this area due to high flow conditions. However, greenside darters were captured inside both resting pools of the west fishway between May and mid-July 1996. Within the resting pools, greenside darters were consistently observed against the walls and floor of the fishway in groups of several individuals. These greenside darters were oriented head first, obliquely to the flow, with pectoral and pelvic fins splayed and angled towards the substrate.

Discussion

Creation and maintenance of microhabitats which support large numbers of greenside darters has occurred downstream from a weir. These unique riffle habitats are maintained by pulsed river discharges associated with precipitation, upstream reservoir regulation and freshets. Scouring and perturbation by ice also maintains the unembedded nature of the substrate in these types of riffles. Greenside darters were found only in fast-moving riffle areas immediately downstream from the Mannheim Weir. Riffle habitats consistently appear to be the most important habitat type for greenside darters (Lachner et al. 1950, Englert & Seghers 1983). Kuehne & Barbour (1983) reported that greenside darters were relegated to the margins and heads of riffles. In the present study, we found a similar pattern, although greenside darters were present in reduced abundance in the tails of riffles. Several authors have suggested that substrate composition is a major determinant of the distribution and habitat preferences of benthic organisms such as greenside darters (Page 1983, Hlohowskyj & Wissing 1986). Other commonly studied factors include depth and bottom velocity (Englert & Seghers 1983, Greenberg 1991, Chipps et al. 1994, Stauffer et al. 1996), and macrophytic associations (Englert & Seghers 1983, McCormick & Aspinwall 1983, Greenberg 1991).

Compared to other darter species, greenside darters consistently demonstrate a preference for large substrates (Englert & Seghers 1983, Hlohowskyj & Wissing 1986) which the present study indicates is important; boulders and cobble were the most commonly selected type. Greenberg (1991) found *E. blennioides* to be associated with rapid currents and the aquatic macrophyte, *Podostemon* spp. In the

Grand River, the most common cover types used by greenside darters were cobble and boulders covered with thick mats of filamentous green algae as reported by Greenberg (1991). Hynes (1970) demonstrated that thick growths of *Cladophora* were generally restricted to larger substrates which served as stable attachment sites for the algae. Hlohowskyj & Wissing (1986) suggested that since greenside darters prefer larger substrates, this may have indicated selection for large cobble and boulders which secondarily support attached forms of epilithic algae.

In riffles, greenside darter distributions were strongly influenced by the embeddedness and size of the substrate, and the degree to which it was covered with *Cladophora* – all of which affected the complexity of the area and its value as suitable habitat. Greenside darters require complex habitats with large interstitial spaces which provide cover, as indicated by snorkeling and electrofishing observations. Although the upstream and downstream riffles did not differ significantly with respect to water depth, bottom water velocity or *Cladophora* cover, embeddedness was significantly different. This may have accounted for the abundance of greenside darters in the upstream riffle, and the species' absence from the downstream riffle. The downstream riffle was much more embedded than the upstream riffle and contained finer substrates, providing very little cover between or under large cobble. Such optimal riffles for greenside darters are relatively rare in a large river such as the Grand River. Only in areas of high gradient or immediately downstream from obstructions would substrates be comprised of unembedded boulders and cobble with large mats of *Cladophora*.

Some authors (e.g., Paine et al. 1982, Wynes & Wissing 1982, Stauffer et al. 1996) have examined resource partitioning between darter species; however, few examples exist between darters and non-darter species. The only abundant benthic fish species commonly found in riffles below the Mannheim Weir was the stonecat. However, stonecats were rarely observed in the spillway (where greenside darters were often seen) because they prefer to use riffles with large loose stones (Scott & Crossman 1974, Becker 1983). Unembedded substrates likely provide stonecats, as well as greenside darters, with interstitial cover. During daytime electrofishing collections, stonecats were drawn out from between large cobble and boulders. Minnow traps located at the fishway entrances contained mostly stonecats when first emptied every morning, and afterwards, quickly filled with greenside darters. Stonecats are active during the night, and feed on immature aquatic insects, molluscs, small fish and plant material (Scott & Crossman 1974). Small greenside darters were part of the gut contents of several stonecats we examined. We suggest that greenside darters and stonecats selected similar habitats, but coexisted through temporal habitat and food partitioning. Paine et al. (1982) suggested that food partitioning may be as important as habitat partitioning, although separation of the two is difficult.

During our examinations, we determined that females reached sexual maturity at age 1. The mean number of eggs produced per female increased with age. Fecundity data presented here are lower than previously reported values. Winn (1958a) reported fecundity for age 1 greenside darters (n = 3, mean egg count = 466, range 404–510) and age 2 greenside darters (n = 3, mean egg count = 784, range 773–799). The lower fecundity values observed in the Grand River (Table 3) may have resulted from the longer and colder winters of southern Ontario which limit the energy required to produce large numbers of eggs.

Length-frequency distributions for males and females showed evidence of age class patterns (Figure 3) supported by scales which had clear annuli. Males and females were divided into 4 overlapping age classes, which showed the overlap to be more pronounced for males. It was difficult to make comparisons with previous studies of southern populations due to problems such as different measurement techniques (e.g., standard length vs. total length). Males in the Grand River grew faster than females as previously reported for other populations by Lachner et al. (1950) and Fahy (1954), despite the fact that the largest individual we examined was female. Greenside darters collected in fall electrofishing sessions had grown significantly over the four month summer: age 3 fish which were between 70 and 77 mm in May had attained lengths up to 96 mm by late August.

Greenside darters in the Grand River fed primarily upon ephemeropteran larvae at various stages of development. Hydropsychid trichopteran larvae, often associated with large cobble substrates downstream from impounded areas, were also a common food item. Various benthic dipterans including chironomid and simuliid larvae are important to smaller fish; however, abundance of larvae exhibits extreme seasonal variation. In the greenside darter populations we studied, there was an absence of zooplankton species in the diet except for the occasional ostracod. Turner (1921) examined the stomach contents of greenside darters in the Ohio waters of Lake Erie and in some Ohio streams. Juveniles in Lake Erie fed primarily on chironomid larvae, cladocerans and copepods, while other age classes fed almost exclusively on chironomid larvae. In streams, chironomid larvae were an important food source; however, the diet also included ephemeropteran, and to a lesser degree, trichopteran larvae. Studies by Fahy (1954) demonstrated that in New York tributaries of Lake Ontario, simuliid, chironomid and trichopteran larvae were primarily consumed. Wynes & Wissing (1982) reported there was no indication that greenside darters fed on drift organisms. They showed chironomid pupae and larvae accounted for most food items in the annual diet, with hydropsychid larvae also being an important item. Differences in diet composition among these studies likely reflect regional and temporal differences in prey availability.

Previous studies provided evidence that greenside darters exhibited clear upstream migration behaviour associated with reproduction, as supported by observations at the Mannheim Weir. In the Grand River, greenside darters were observed downstream from the weir throughout the spring, summer and early autumn. Winn (1958a) also observed upstream migration to an impassable barrier: during the non-reproductive season, some adult males were present in riffles below the barrier, but in early spring, a significant increase in the abundance of large males was reported.

Significantly more greenside darters were captured in minnow traps downstream at the west fishway entrance compared to the number of greenside darters collected from traps near the east fishway entrance. Greenside darters were observed maintaining positions on sand substrate, among boulders in very shallow water, near the entrance to the west fishway. The depths near the west fishway entrance were shallower than those at the east side, helping to reduce predation risk by large piscivores. Water velocities at the west fishway entrance were also significantly lower than those recorded at the east fishway. However, none of the velocities recorded at the east fishway should have affected the ability of greenside darters to maintain position among the boulders and cobble. There were lesser amounts of *Cladophora* near the east fishway which may have reduced cover availability. Greenside darters were observed to hold positions in *Cladophora* which covered the outside of the east fishway wall, but rarely occupied the areas which would have facilitated attraction to the fishway entrance.

Subtle microhabitat differences may have affected the ability of greenside darters to locate and successfully approach a fishway entrance. It is likely that failed attempts to traverse habitat types not within the optimal range of, for instance, depth and appropriate cover, restricted access to the east fishway entrance. Considerations of the differences in entrance microhabitats may be important, especially when designing natural fish bypass channels and fishways built to pass benthic species.

Only after a precise set of requirements was satisfied, was it then possible for greenside darters to ascend the west fishway while avoiding predation, as supported by videographic evidence collected from within the west fishway and at both fishway entrances (Bunt unpublished data). For example, during the day of 13 June 1995, following a period when debris was not cleared from upstream trash racks and fishway water levels were too low for large predators, greenside darters were captured in the fishway exit trap. On this date, no other fish species that may have excluded greenside darters were found in the trap. If escape from the fishway exit was not blocked by debris, greenside darters would have had to traverse > 800 m of impounded lentic habitat before reaching any riffle-like areas. Predation risk and lack of adequate foraging habitat would have limited their success. If the fishways were being properly maintained for larger fish species, suitably low water velocities would not occur to allow successful passage of greenside darters. Greenside darters are able to maintain feeding positions in high velocity flows in the weir spillway, but successful use of the fishways was rare. Therefore, the Mannheim fishways do not contribute to the upstream range extension and dispersion of the greenside darter.

High densities of greenside darters downstream from the weir were a direct result of large amounts of *Cladophora*-covered, unembedded cobble substrate which was maintained by hydraulic disturbance and ice scour from the weir. The ability of the greenside darter to maintain feeding positions in high water velocities permitted use of this unique habitat. Other darter species remained in backwater areas, pools, runs and riffles which contained finer, embedded substrates and fewer predators.

Acknowledgements

We thank Gabrielle Held for field assistance, the Municipality of Waterloo for use of laboratory facilities, Art Timmerman (Ontario Ministry of Natural Resources) for use of the electrofishing equipment, and John Bartlett (Grand River Conservation Authority) for river discharge data. Previous versions of this manuscript were improved by comments received from Geoff Power, Lin Wong and two anonymous reviewers. We also thank the Natural Sciences and Research Council of Canada for postgraduate scholarships to C.M.B. and S.J.C. and grant support to R.S.M.

References cited

Becker, G.C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison. 1052 pp.

Blake, B.F. 1977. Food and feeding of the mormyrid fishes of Lake Kainji, Nigeria, with special reference to seasonal variation and interspecific differences. J. Fish Biol. 11: 315–328.

Chipps, S.R., W.B. Perry & S.A. Perry. 1994. Patterns of microhabitat use among four species of darters in three Appalachian streams. Amer. Midl. Nat. 131: 175–180.

Crouse, M.R., C.A. Callahan, K.W. Malueg & S.E. Dominguez. 1981. Effects of fine sediments on growth of juvenile coho salmon in laboratory streams. Trans. Amer. Fish. Soc. 110: 281–286.

Cummins, K.W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. Amer. Midl. Nat. 67: 477–504.

Cunjak, R.A. & G. Power. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. 43: 1970–1981.

Dalton, K.W. 1991. Status of the greenside darter, *Etheostoma blennioides*, in Canada. Can. Field- Nat. 105: 173–178.

Englert, J. & B.H. Seghers. 1983. Habitat segregation by stream darters (Pisces: Percidae) in the Thames River watershed of southwestern Ontario. Can. Field-Nat. 97: 177–180.

Fahy, W.E. 1954. The life history of the northern greenside darter, *Etheostoma blennioides* blennioides Rafineque. J. Elisha Mitchell Sci. Soc. 70: 139–205.

Fausch, K.D. & R.J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Can. J. Fish. Aquat. Sci. 38: 1220–1227.

Gatz, A.J., Jr., M.J. Sale & J.M. Loar. 1987. Habitat shifts in rainbow trout: competitive influences of brown trout. Oecologia 74: 7–19.

Greenberg, L.A. 1991. Habitat use and feeding behaviour of thirteen species of benthic stream fishes. Env. Biol. Fish. 31: 389–401.

Heggenes, J., A. Brabrand & S.J. Saltveit. 1990. Comparison of three methods for studies of stream habitat use by young brown trout and Atlantic salmon. Trans. Amer. Fish. Soc. 119: 101–111.

Hlohowskyj, I. & T.E. Wissing. 1986. Substrate selection by fantail (*Etheostoma flabellare*), greenside (*E. blennioides*), and rainbow (*E. caeruleum*) darters. Ohio J. Sci. 86: 124–129.

Hynes, H.B.N. 1970. The ecology of running waters. University of Toronto Press, Toronto. 555 pp.

Keenleyside, M.H.A. 1962. Skin-diving observations of Atlantic salmon and brook trout in the Miramichi River, New Brunswick. J. Fish. Res. Board Can. 19: 625–634.

Kuehne, R.A. & R.W. Barbour. 1983. The American darters. University Press of Kentucky, Lexington. 177 pp.

Lachner, E.A., E.F. Westlake & P.S. Handwerk. 1950. Studies on the biology of some percid fishes from western Pennsylvania. Amer. Midl. Nat. 43: 92–111.

Ligon, F.K., W.E. Dietrich & W.J. Trush. 1995. Downstream ecological effects of dams. BioScience 45: 183–192.

McCormick, F.H. & N. Aspinwall. 1983. Habitat selection in three species of darters. Env. Biol. Fish. 8: 279–282.

Northcote, T.G. & D.W. Wilkie. 1963. Underwater census of stream fish populations. Trans. Amer. Fish. Soc. 92: 146–151.

Page, L.M. 1983. Handbook of darters. T.F.H. Publications, Neptune City. 271 pp.

Paine, M.D., J.J. Dodson & G. Power. 1981. Habitat and food resource partitioning among four species of darters (Percidae: Etheostoma) in a southern Ontario stream. Can. J. Zool. 60: 1635–1641.

Scott, W.B. & E.J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184. 966 pp.

Stauffer, J.R., J.M. Boltz, K.A. Kellogg & E.S. van Snik. 1996. Microhabitat partitioning in a diverse assemblage of darters in the Allegheny River system. Env. Biol. Fish. 46: 37–44.

Turner, C.L. 1921. Food of the common Ohio darters. Ohio J. Sci. 22: 41–62.

Winn, H.E. 1958a. Comparative reproductive behaviour and ecology of fourteen species of darters (Pisces-Percidae). Ecol. Monogr. 28: 155–191.

Winn, H.E. 1958b. Observations on the reproductive habits of darters (Pisces-Percidae). Amer. Midl. Nat. 59: 190–212.

Wynes, D.L. & T.E. Wissing. 1982. Resource sharing among darters in an Ohio stream. Amer. Midl. Nat. 107: 294–304.