THE UNIVERSITY OF MANITOBA

COEXISTENCE AND RESOURCE PARTITIONING IN TWO SPECIES OF DARTERS (PERCIDAE), *Etheostoma nigrum* AND *Percina maculata*

BY

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Abstract

This study investigated partitioning of resources along the dimensions of space, food and time, by two closely related species of fish, johnny darters *Etheostoma nigrum*, and blackside darters *Percina maculata*, in the Whitemouth River system, Manitoba. Germane behaviour and morphology were also studied.

Both species were abundant in the midcourse, and occupied all environments throughout the ice-free season. Their microhabitats and use of space could be differentiated. Johnny darters were exclusively benthic and relatively inactive, whereas blackside darters were less restricted to the bottom, especially in slower water velocities, and were more active.

Both species consumed benthos, but diversity of prey taxa differed considerably. Johnny darter diet was essentially limited to chironomids and crustaceans. Diet of blackside darters was more diverse and included Simuliidae, Corixidae, Elmidae, and several families of Ephemeroptera and Trichoptera, in addition to chironomids and crustaceans.

Feeding behaviour was more stereotyped in johnny darters in terms of length of dart, site, height and target area of the bite, and body pitch. In all these features, blackside darters were more variable and generalized.

The degree of morphological specialization also differs between species. Johnny darters lack a swimbladder, restricting them to a benthic mode of existence. Adaptations to feed efficiently from the substrate include ventral mouth position, protrusile premaxilla, dorsal retinal acuity and eye position, and relatively fewer, shorter gill rakers. Blackside darters, in contrast, have retained the swimbladder and make use of the vertical dimension of the environment. They feed in more varied microhabitats and are less specialized morphologically with a terminal mouth, non-protrusile premaxilla, lateral and anterior retinal acuity, more lateral eye position, and more numerous, more elongate gill rakers.

TABLE OF CONTENTS

Introduction

Gause's principle (1934) implies that coexisting species partition rather than compete for resources. Species may subdivide resources along the following dimensions, listed in decreasing order of importance: habitat, food-type, and time (Pianka 1969; Ricklefs 1973; Schoener 1974). Behavioural mechanisms may serve to establish partial exclusion between species whose residential and nutritional requirements (i.e. their niches) overlap (Antonelli et al. 1972). Indirect studies of resource partitioning have used morphological differences of structures involved in resource use, as indicators of ecological differences (e.g. Findley 1976; Keast and Webb 1966; Roughgarden 1974; Schoener 1971). Hespenheide (1973) has discussed the extent to which morphology can be used to describe ecology, and Klopfer(1973) the interdependence of morphology and behaviour.

Schoener's (1974) exhaustive review of resource partitioning studies indicates that fishes, especially those in running water, have received comparatively little attention. This study was undertaken to examine the degree of overlap in each of the three resource dimensions, and mechanisms of ecological differentiation, between johnny darters, *Etheostoma nigrum* Rafinesque, and blackside darters, *Percina maculata* (Girard) which coexist in the Whitemouth River, Manitoba. A combined approach investigating each resource dimension, behaviour and morphology was used. Specific objectives were to describe where these fishes were found and their mobility within environments, to analyze diet and feeding behaviour, to investigate temporal differences in activity and feeding, and to compare morphology which may be adapted to differential resource utilization.

Speciation in darters, a tribe of stream-dwelling freshwater fish of eastern North America, has been so extensive that several lineages now occupy the same or very similar habitats (Page 1972). Such overlap prompts inquiry into how resources are partitioned to permit coexistence (e.g. Page and Schemske 1978). Both johnny and blackside darters are widely distributed in streams and rivers and have much more flexible habitat requirements than most other darters (Page 1972; Scott and Crossman 1973). Johnny darters are sometimes found in lakes, and range from northeastern Saskatchewan to southern Quebec, southward to the Gulf of Mexico drainage in Mississippi, and down the Atlantic coast to Florida (Hubbs and Lagler 1964). Blackside darters are not known to occur in lakes, and range only from the southeastern prairie provinces and southern Ontario, down the western slope of the Appalachian mountains to the Gulf coast from Alabama to northeastern Texas (Scott and Crossman 1973). The taxonomy and biology of johnny darters has received considerable attention (see Collette and Bănărescu 1977; Scott and Crossman 1973). Page (1972, 1974, 1976, 1977) and Page and Whitt (1973a, 1973b) have analyzed diversity in the genus Percina but the ecological role of blackside darters (P. maculata) is largely unknown.

Methods

Study Area

The Whitemouth River system drains approximately 4500 km^2 of flat plain in southeastern Manitoba, Canada (Fig. 1). It was divided into 5 zones, as outlined in Table 1. Collections were made in each zone during the ice-free period of 1977 to describe the distribution of darters along the length of the river system, and their abundance within environments.

Fish Collections

A 1.8 x 1.2 m two-man seine with 6 mm square mesh was either hauled in water velocities $<25\ cm \cdot s^{-1}$, or the net was held stationary and the upstream substrate systematically kicked and disturbed driving fishes into the net in velocities $>25\ cm \cdot s^{-1}$. Collections were made through relatively uniform habitat, and were repeated once to ensure thorough sampling. To analyze density of both species of darters within particular environments by age group (young of the year or age 0, and fish which had overwintered one or more times or age 1^+, were determined by length frequency), and by season, collections were concentrated in zones of greatest abundance. The seasons were defined as following: spring - 20 April to 26 May, early summer - 27 May to 29 June, midsummer - 5 to 15 July, late summer - 15 to 23 August, and autumn - 23 Sept. to 6 Nov. Water velocity (measured by timing a floating object), depth, and substrate were described for each collection, and their range in variation categorized into

Figure 1. Whitemouth River system, Manitoba. A. Division between headwaters and midcourse. B. Division between midcourse and lower course.

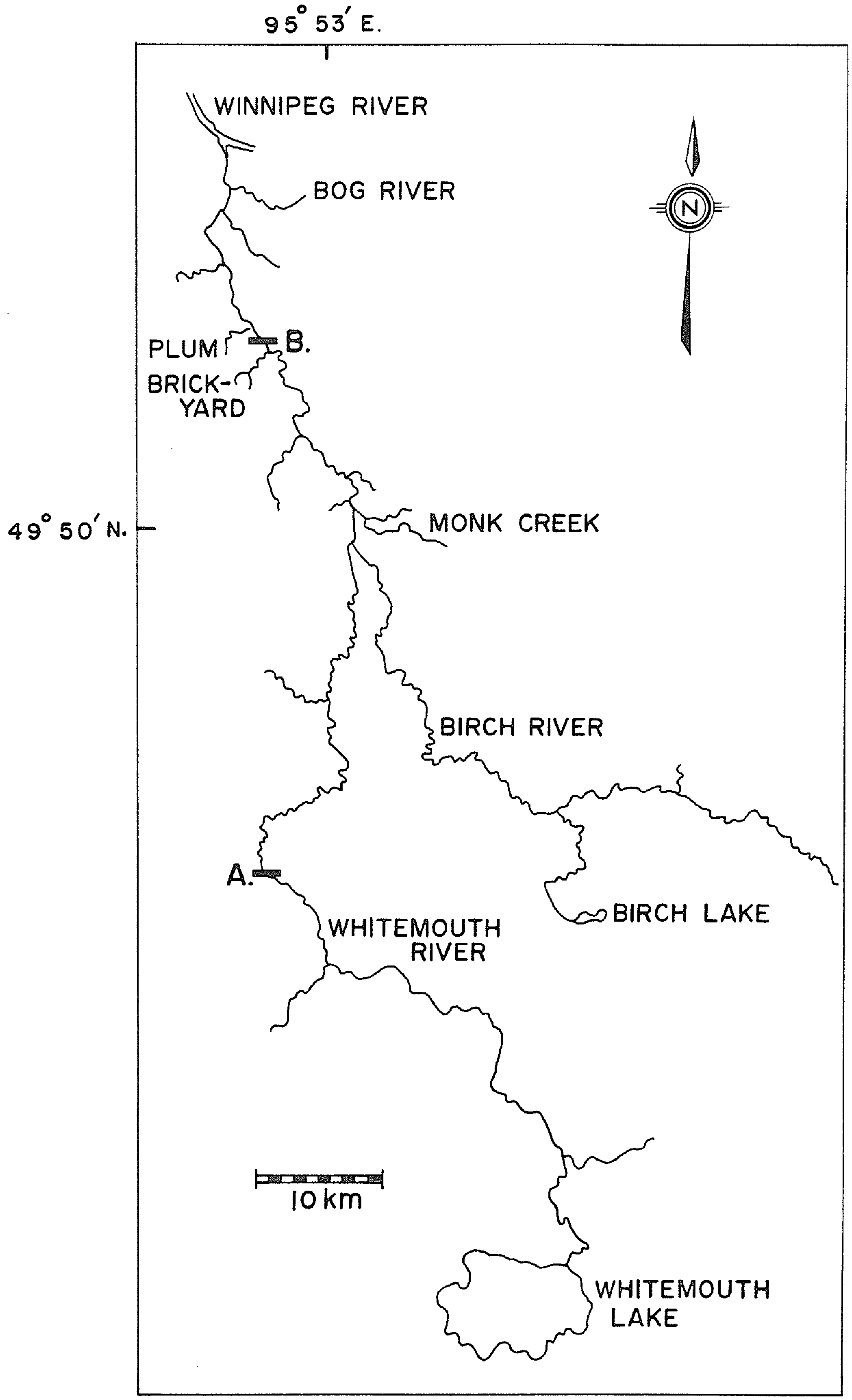

95° 53′ E.
WINNIPEG RIVER
BOG RIVER
PLUM
B.
BRICK-
YARD
49° 50′ N.
MONK CREEK
BIRCH RIVER
A.
WHITEMOUTH
RIVER
BIRCH LAKE
10 km
WHITEMOUTH
LAKE
N

Table 1. Zones of the Whitemouth River system. Diameter of particle size as follows: silt 1/16 mm, sand 1/16 - 2 mm, pebble 2 - 64 mm, cobble 64 - 256 mm.

Zone	Length (km)	Width (m)	Substrate	Characteristics
Headwaters	34	3.5 - 18	silt	meander through marsh, bog and forest
Midcourse	45	18 - 36	sand, pebble, some cobble	winds gently, with numerous shallow riffles
Lower course	16	36 - 76	silt	relatively straight, wide and well-entrenched
Birch R.	lower 19	12 - 16	sand, pebble, some cobble	relatively straight with shallow riffles
Tributaries [a]		3 - 5	silt	meander through crop and pastureland

[a] Monk, Brickyard and Plum Creeks, Bog River

3 environments - riffles, channels, and margins and pools (Table 2).

All fishes collected (excluding individuals >20 cm) were preserved in 10% formalin, and both species of darters were analyzed for length frequency and diet. Approximately 20 fish from each age group were selected in proportion to their relative density in each environment, in each season, and their stomach contents examined. To study diet, a modification of Hynes' (1950) point method was used. Each taxon was identified and its estimated volume weighted according to stomach fullness. Modification consisted of assigning <1 point to minor quantities of small items, rather than disregarding their contribution to the diet. Overlap in diet was calculated using Morisita's (1959) index, $\hat{C}_\lambda$, as modified by Horn (1966). An empirical measure of diversity was calculated using $\frac{1}{\Sigma p_i^2}$ (MacArthur 1972), where p_i is the proportion of the diet contributed by the i^{th} food item taxon.

Observations of Behaviour

To obtain information on microhabitat occupied, time of activity, and swimming and feeding behaviour, darters were observed in the river by using wet suit, faceplate and snorkel. Target area of bite was studied in the laboratory.

Microhabitat Occupied - Microhabitat observations examined whether differences in vertical distribution or in proximity to obstructions to current existed between species or age groups.

Table 2. Characteristics of environments occupied by darters.

Environmental variable	Riffles	Channels	Margins, pools
Surface velocity ($cm \cdot s^{-1}$)	>25	5-25	<5
Principal substrate	cobble, pebble	pebble, sand	sand
Water depth (cm)	15-45	30-60	15-100

To study vertical distribution in each environment, 10 fish of each age group of each species were observed for 1 min apiece. Height in the water column (±0.5 cm) was estimated and recorded every s. Average amount of time spent at each height was calculated and converted to a percentage. Exposure to current was studied in riffles and channels. Ten fish of each age group of each species were spotted non-systematically and their position described as unexposed (behind and between objects, or sitting in a depression), partially exposed (somewhat sheltered by an object, or sitting on a slope), or exposed (swimming or sitting in the open or on a mound).

Time of Activity and Feeding - To see whether darters temporally segregate space or feeding, times of activity and feeding activity were investigated in a channel environment. The number of darts and feeding darts (darts culminating in a bite) made in 1 min by each of 7 fish of each species and age group were counted. These observations were made every 4 h during a 24 h period on three separate occasions. A flashlight, held above the water surface and beamed peripherally to the observation area, was used at night.

Mobility within Environments and Feeding Behaviour - Mobility within environments was studied to examine whether differences in manner of space utilization could be identified. Elements analyzed were frequency, length and orientation (from dorsal aspect) of darts. During 1 min observation periods, these elements were recorded (or estimated) for 10 separate fish of both age groups of both species in each environment. The product of mean frequency and mean dart length was calculated to estimate distance travelled. To examine whether environments occupied, age group, and/or species affected dart orientation frequency, chi-square values were calculated.

Feeding behaviour was investigated to compare methods of procuring food. Elements examined were frequency of feeding darts in different environments, length of feeding darts, attitude (pitch and yaw) of the fish when biting, and features of the bite (site of bite, distance above the substrate, and degree of exposure to current). Methods to determine frequency and length of feeding darts were identical to swimming darts (above). The product of feeding dart frequency and density of individuals was calculated and expressed on a scale of 1 to 100, to provide an index of importance of different environments for feeding. For feeding darts, mean length was calculated and variation in length compared between species and age groups using Lewontin's (1966) ratio,

$$F = \frac{(s^2_{\log})_1}{(s^2_{\log})_2},$$

where s^2 signified variance. In each environment one bite by each of 15 individuals of each species and age group was analyzed for pitch (above, at, or below the horizontal body axis), yaw (directly forward, or deflected 30° or 60° sideward), site of bite (taken from water or substrate), estimated distance above the substrate, and degree of exposure to current (unexposed, partially exposed, or exposed). Discriminant analysis was performed on attitude and features of the bite.

To locate more precisely the target area of bite (given indirectly by field data on pitch and yaw), fish were observed in an aquarium (30 x 15 x 21 cm) in the laboratory. It was illuminated from above and surrounded by opaque screening. Sides, back and bottom were measured off in a 0.5 cm grid to permit localization of each fish (mouth) along 3 co-ordinates. Twenty live adult brine shrimp (*Artemia salina*) were introduced into a glass cylinder (25 x 1 cm diam), graduated at 0.5 cm intervals and secured vertically in the aquarium. Initial position of fish, and position of target shrimp were recorded for a total of 200 bites by 10 adults of each species. (Blackside darters had been held in current prior to observation, and were benthic.) Angular components of the trajectory of the feeding dart were calculated to localize target area of bite.

Morphology

To examine the relationship between morphology and ecology, swimbladder volume was determined to relate buoyancy to water velocity, and mouth, head and gill raker structure were studied in relation to diet and feeding behaviour.

To determine if blackside darters could regulate buoyancy to compensate for variation in water velocity between environments, the swimbladder volume of fish from current ($>$25 cm s^{-1}) and still ($<$5 cm$\cdot s^{-1}$) was measured in the field. (Johnny darters lack a swimbladder.) The procedure of Gee (1970) was used on 7 fish of each age group in midsummer and repeated in autumn.

Mouth structure was studied on 10 freshly killed specimens of each species by measuring diameter, position, premaxilla protrusibility, and angular orientation of the open mouth. Maximum diameter of the rounded mouth was measured (±0.17 mm) by inserting a tapered cylindrical steel probe calibrated in increments of 0.33 mm. All mouth and head measurements (excluding mouth diameter) were made under 6X magnification, and unless herein defined, as described by Hubbs and Lagler (1964). Measurements were proportionated as indicated in Table 15, and Student's t-test was used to investigate differences between species. Mouth position was described by measuring the vertical distance from the antero-ventral tip of the premaxilla to the occiput and divided by head depth. Premaxilla protrusibility measurement technique was outlined by Keast and Webb (1966). Angular orientation of the mouth was described by measuring the angle between an extension of the horizontal margin of the preopercle through the corner of the mouth, and the bisector of the angle of the jaws when the mouth was wide open.

To study head structure, slope of the forehead was described, head length, depth and width, snout length, depth and width, least fleshy interorbital width, and eye length and position were measured. Head length excluded the opercular membrane. Snout depth and width paralleled head depth and width but were taken at the anterior margin of the eye. Eye position was described by measuring suborbital depth to the isthmus and dividing by head depth through the centre of the eye.

To study gill raker structure, rakers of both limbs of the first arch were enumerated and their length compared visually between species. Rakers of 34 johnny darters and 29 blackside darters were examined.

Results

Distribution and abundance

Based on length frequency (Appendix 1), 2 age groups (age 0 and age 1^+) of each species were distinguishable in early, mid and late summer (Table 3). In spring, age 0 fish were not yet present, and in autumn, very few age 1^+ fish were caught. Blackside darters were approximately 10 mm longer than johnny darters of the comparable age group.

Johnny and blackside darters were not found in the headwaters, but were abundant in the midcourse and the Birch River, and present, although not abundant in the lower course and tributaries (Table 4).

Table 3. Size ranges (± 0.05 mm) of age groups.

Season	JD 0	JD 1^+	BD 0	BD 1^+
Spring	-	25 - 59.9	-	30 - 64.9
Early summer	20 - 29.9	30 - 59.9	25 - 39.9	40 - 79.9
Midsummer	20 - 34.9	35 - 64.9	30 - 44.9	45 - 74.9
Late summer	25 - 39.9	40 - 64.9	30 - 49.9	50 - 74.9
Autumn	25 - 44.9	45 - 64.9	30 - 54.9	55 - 74.9

NOTE: JD, johnny darter; BD, blackside darter; 0, age 0; 1^+, age 1^+.

Table 4. Density ($no \cdot m^{2})^{-1}$ of darters along the length of the river.

Zone	Area sampled (m^2)	Johnny darters	Blackside darters
Headwaters	52	0	0
Midcourse	1946	3.0	1.1
Lower course	377	0.6	0.2
Birch River	313	1.6	0.7
Tributaries	138	0.5	0.3

Johnny darters were the more abundant species. Other fishes present in the Whitemouth River system are recorded in Appendix 2.

Density within Environments - In the midcourse, both species were found over a wide range of water velocities, depths and substrates. They were present in each environment during each season (Fig.2). Age 0 group of both species were more abundant than age 1^+ at all times (excluding spring), in all environments.

Some seasonal shifts in density between environments occurred. Age 1^+ johnny darters were more abundant in margins and pools in spring and autumn but in summer were most abundant in riffles. Age 0 johnny darters were more abundant in the slower water of channels and margins and pools when they first appeared in early summer and again in autumn, but were distributed throughout all three environments in mid and late summer. In all seasons except early summer, age 1^+ blackside darters were more abundant in riffles than in either channels or margins and pools. Density of age 0 blackside darters was greatest in channels and margins and pools in early summer, but shifted to channels and riffles at other times.

$\hat{C}_\lambda$ values exceeded 0.82 indicating a high level of overlap between species in environments occupied (Table 5). Exceptions were between age 1^+ of the two species in spring, and between different age groups of different species in autumn.

Figure 2. Density (number of fish·10 $m^{2^{-1}}$) of darters according to environment and season, within the midcourse of the Whitemouth River.

NOTE: JD, johnny darter; BD, blackside darter; 0, age 0; 1^{+}, age 1^{+}.

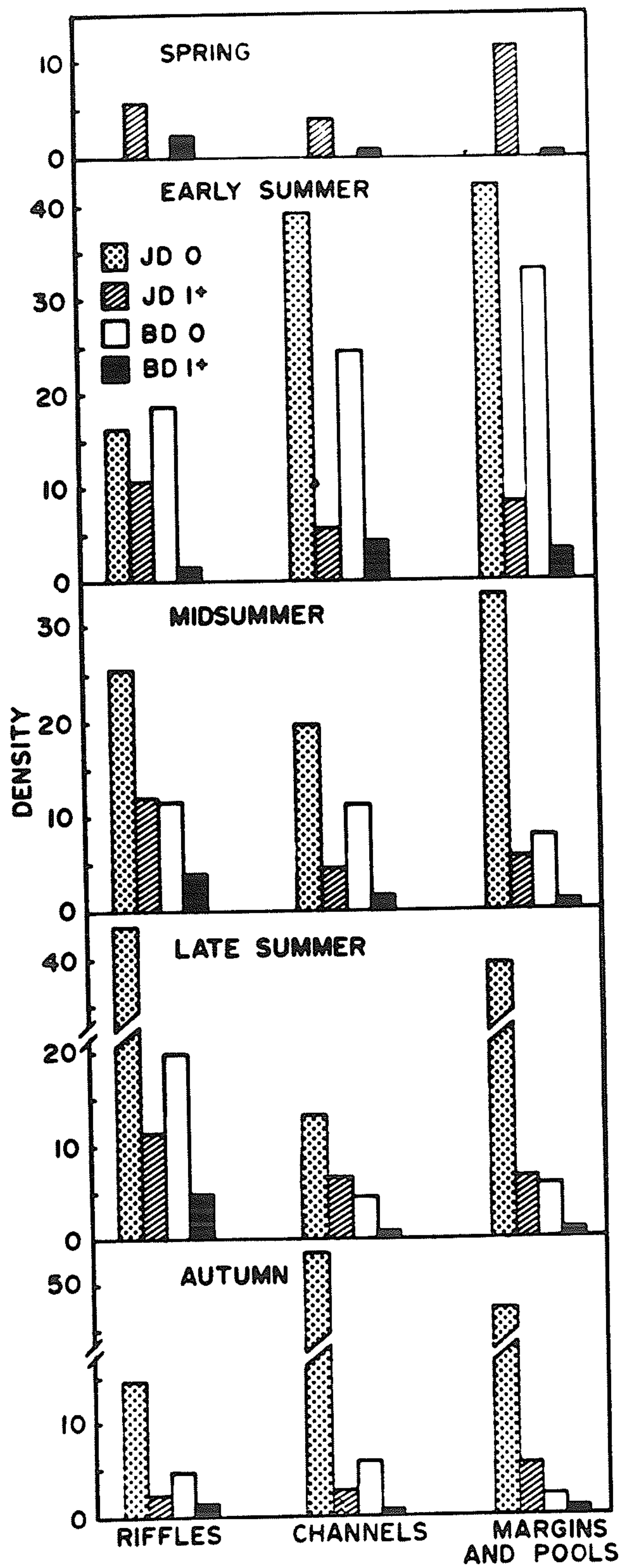

SPRING
EARLY SUMMER
MIDSUMMER
LATE SUMMER
AUTUMN
JD 0
JD 1+
BD 0
BD 1+
DENSITY
0
10
20
30
40
50
RIFFLES
CHANNELS
MARGINS AND POOLS

Table 5. Index of overlap, $\hat{C}_{\lambda}$, in environments occupied in different seasons.

Groups Compared	Spring	Early summer	Mid-summer	Late-summer	Autumn
JD 0 *vs*. JD 1^+	-	.847	.890	.958	.885
JD 0 *vs*. BD 0	-	.982	.937	.915	.831
JD 0 *vs*. BD 1^+	-	.990	.826	.837	.789
JD 1^+ *vs*. BD 0	-	.924	.923	.935	.743
JD 1^+ *vs*. BD 1^+	.525	.828	.987	.848	.935
BD 0 *vs*. BD 1^+	-	.958	.912	.979	.855

NOTE: JD, johnny darter; BD, blackside darter; 0, age 0; 1^+, age 1^+ .

Microhabitat Occupied - Johnny darters were almost exclusively benthic in all environments and were not observed more than 1.5 cm above the substrate (Fig. 3). Blackside darters were more pelagic, depending upon environment occupied and age group. They were most benthic in riffles, and became increasingly pelagic with decreasing water velocity (Fig. 3). In margins and pools, they were observed above 1.5 cm from the substrate for more than 60% of the time. Age 0 blackside darters were more pelagic than age 1^+ in all environments.

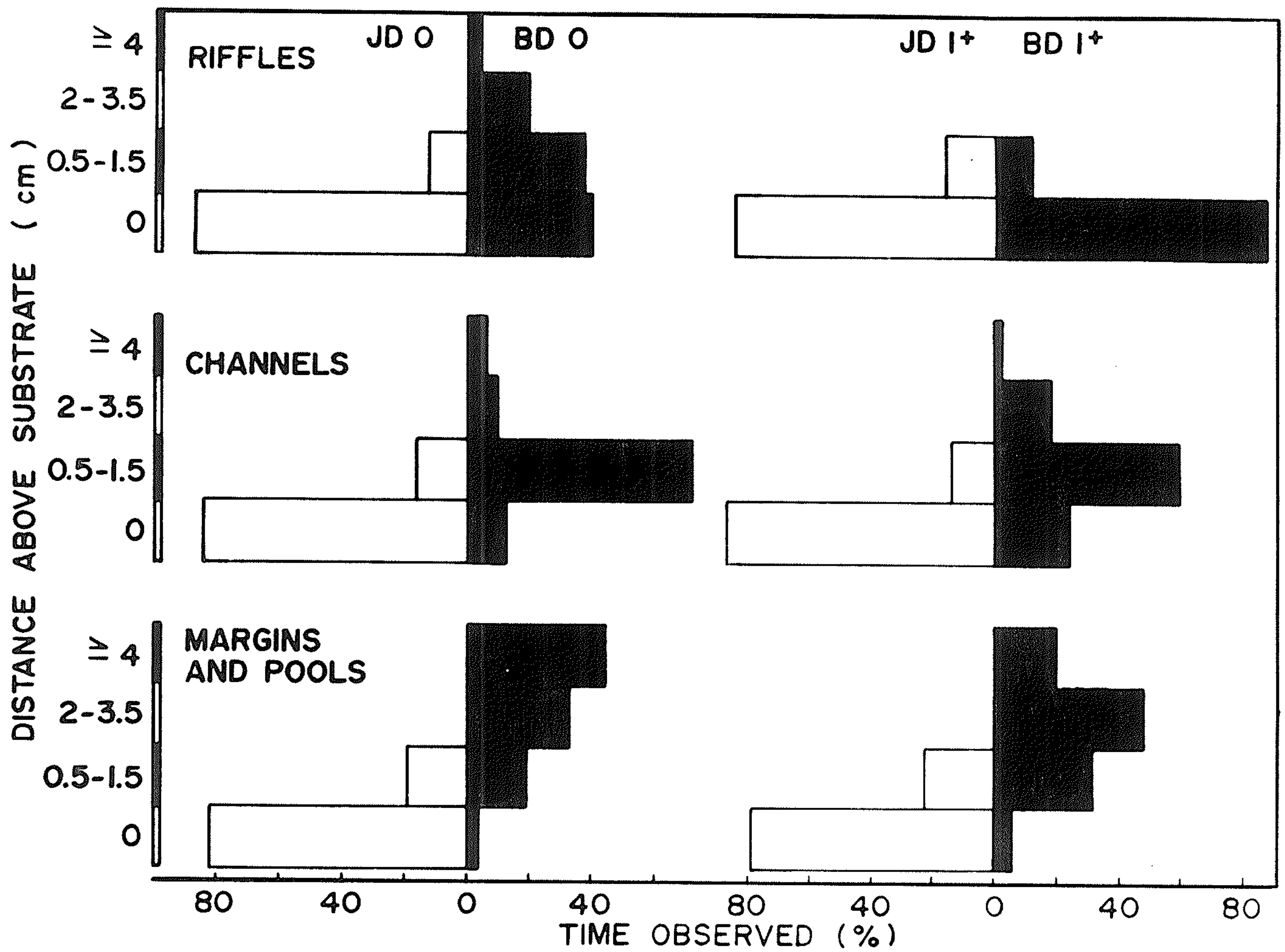
Both age groups of both species were more commonly observed in situations fully exposed to current than in either unexposed or partially exposed (Table 6). Similar proportions of each group were recorded under the same conditions indicating little environmental segregation in terms of degree of exposure to current.

Mobility within Environments - The frequency of darts (10 - 15 $\cdot$ min^{-1}) by johnny darters was similar between environments and age groups (Table 7). Blackside darters were more active than johnny darters (15 - 30 $\cdot$ min^{-1}), and most active in channels (28 - 30 darts $\cdot$ min^{-1}). Age groups of blackside darters were comparably active, except in riffles where age 0 was less so than age 1^+.

In all environments, mean dart length and distance travelled per min of age 1^+ of both species exceeded that of age 0 fish, and

Figure 3. Vertical distribution of darters in different environments.

NOTE: JD, johnny darter; BD, blackside darter; 0, age 0; 1^{+}, age 1^{+}.



RIFFLES
CHANNELS
MARGINS AND POOLS
JD 0
BD 0
JD 1+
BD 1+
≥ 4
2-3.5
0.5-1.5
0
DISTANCE ABOVE SUBSTRATE (cm)
80
40
0
40
80
40
0
40
80
TIME OBSERVED (%)

Table 6. Frequency (%) of fish observed at various degrees of exposure to current.

Exposure	JD 0	JD 1^+	BD 0	BD 1^+
Unexposed	12.5	19.6	25.0	25.0
Partially exposed	39.2	38.2	40.0	35.0
Exposed	48.3	42.2	35.0	40.0

NOTE: JD, johnny darter; BD, blackside darter; 0, age 0; 1^+, age 1^+.

Table 7. Mean dart frequency (number· min^{-1}), length (cm), and distance travelled (cm · min^{-1}) by darters in various environments.

Environment	Species and age group	Mean dart frequency	Mean dart length	Mean distance travelled
Riffles	JD 0	10.1	2.6	26.3
	JD 1^+	13.3	3.0	39.9
	BD 0	15.7	2.9	45.5
	BD 1^+	23.3	3.6	83.8
Channels	JD 0	13.6	1.5	20.4
	JD 1^+	11.5	2.8	32.2
	BD 0	28.0	3.6	100.8
	BD 1^+	29.9	3.0	89.7
Margins and pools	JD 0	14.9	1.3	19.4
	JD 1^+	12.8	2.9	37.1
	BD 0	18.6	2.5	46.5
	BD 1^+	21.7	3.3	71.6

NOTE: JD, johnny darter; BD, blackside darter; 0, age 0; 1^+, age 1^+.

blackside darters exceeded johnny darters of the same age group (Table 7). The only exception occurred in channels where age 0 blackside darters outdistanced age 1^+. Each age group of blackside darter covered approximately twice the distance of the same age group of johnny darter. Environment occupied did not affect distance travelled for any group, except age 0 blackside darters which moved farthest in channels.

In general, johnny darters changed direction by approximately 30° between successive darts as often as they darted straight ahead (Appendix 3), whereas blackside darters moved straight ahead more often. Results of chi-square tests on the effects of environment occupied and age group are presented in Appendix 4.

Diet and Feeding Behaviour

Diet - Chironomid larvae predominated in the diet of johnny darters in all seasons (Fig. 4). Age 0 also regularly consumed small crustaceans (Cladocera, Copepoda and Ostracoda). Age 1^+ ate large quantities of Ephemeridae naiads (mayflies) in midsummer, and Amphipoda in autumn. Blackside darters also normally consumed some chironomid larvae, and age 0 ate small crustaceans but these items constituted a smaller proportion of the total diet (Fig. 4). Their food was more variable in number of taxa taken and in seasonally important taxa. It included Ephemeroptera (Ephemeridae, Heptageniidae and Baetoidea), Corixidae, Trichoptera, Simuliidae

Figure 4. Diet of darters from Apr. to Nov., 1977. Baetoidea includes Siphlonuridae, Baetidae, Baetiscidae (rare), and Leptophlebiidae.

NOTE: l, larvae; nd, naiads; ny, nymphs; JD, johnny darter; BD, blackside darter; +, less than 1%.