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.

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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.

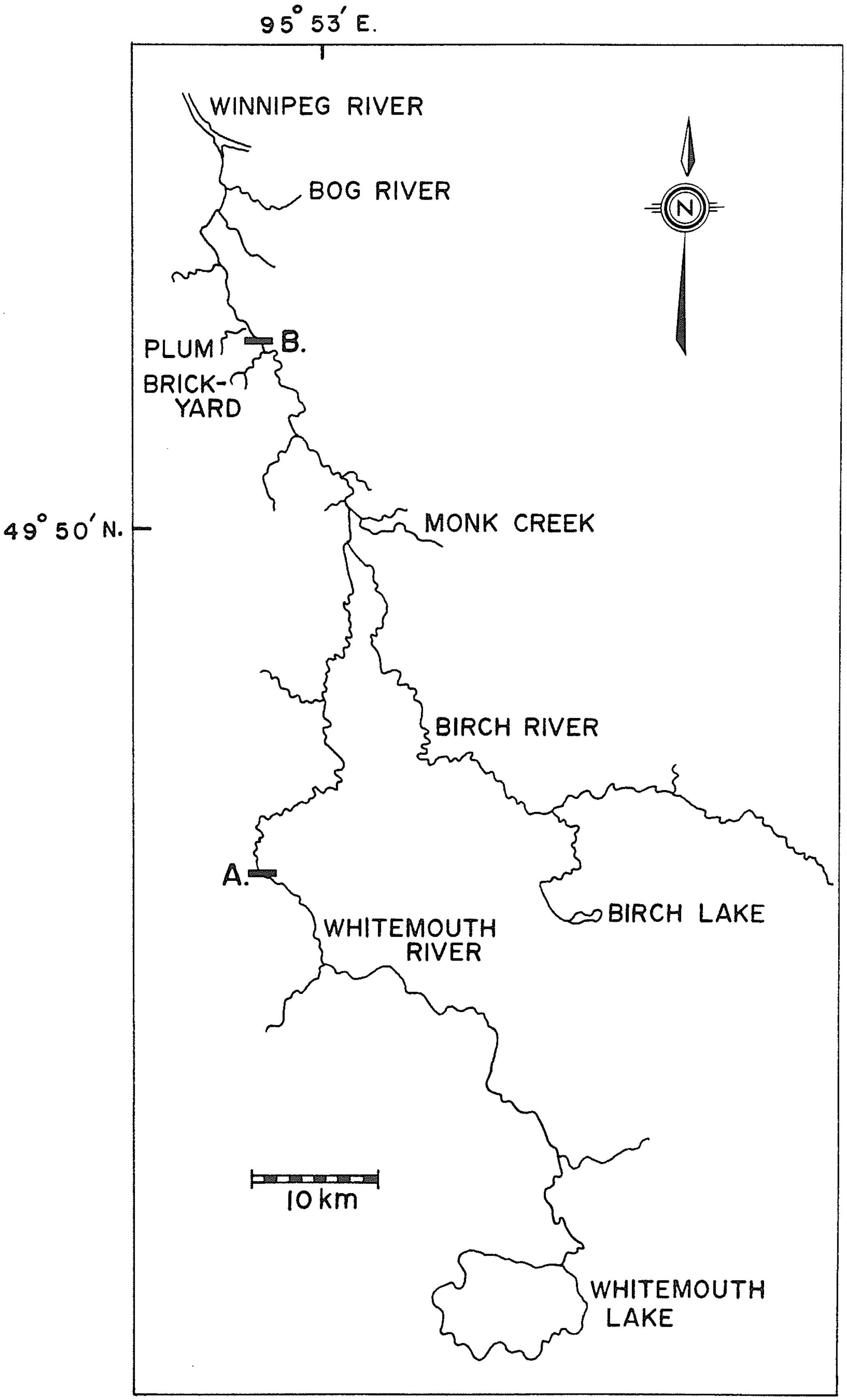

95° 53' E.
WINNIPEG RIVER
BOG RIVER
PLUM
B.
BRICK-
YARD
49° 50' N.
MONK CREEK
N
BIRCH RIVER
A.
WHITEMOUTH
RIVER
BIRCH LAKE
10 km
WHITEMOUTH
LAKE

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^+.

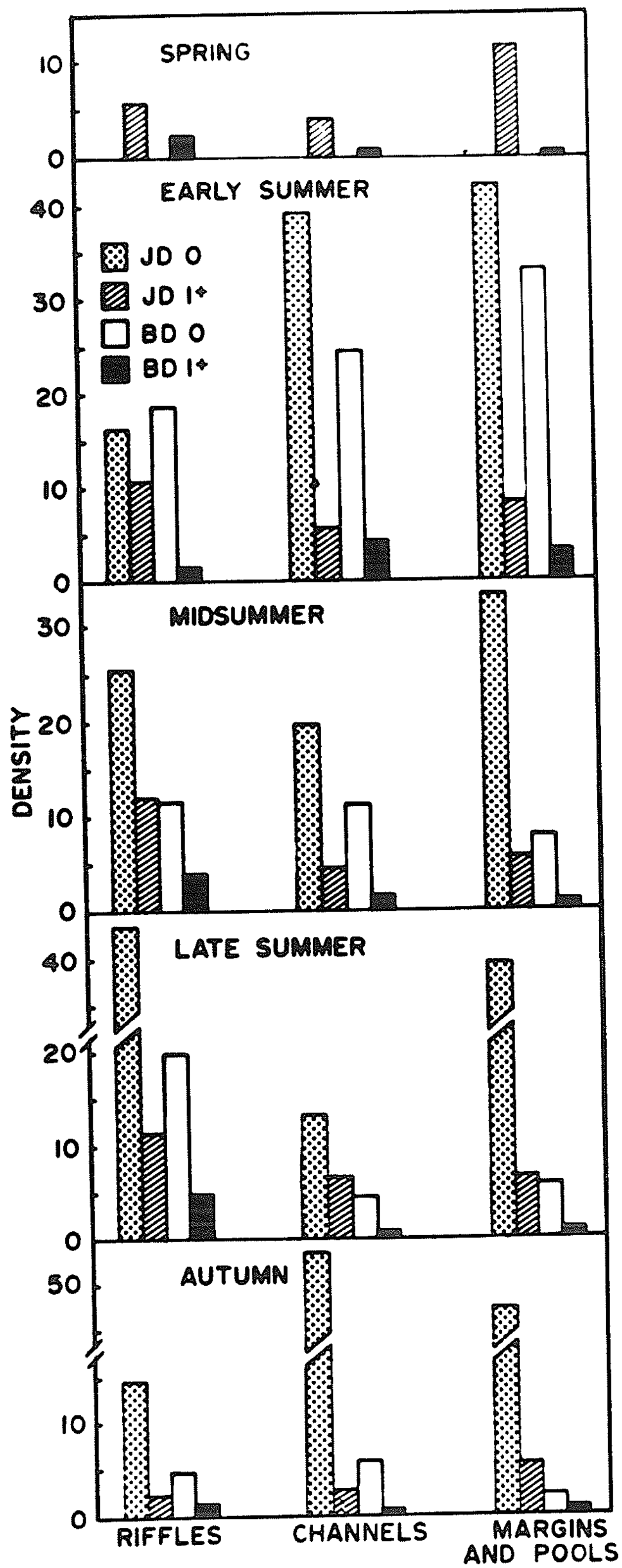

SPRING
EARLY SUMMER
JD 0
JD 1+
BD 0
BD 1+
MIDSUMMER
LATE SUMMER
AUTUMN
DENSITY
0
10
20
30
40
50
RIFFLES
CHANNELS
MARGINS AND POOLS

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^+.

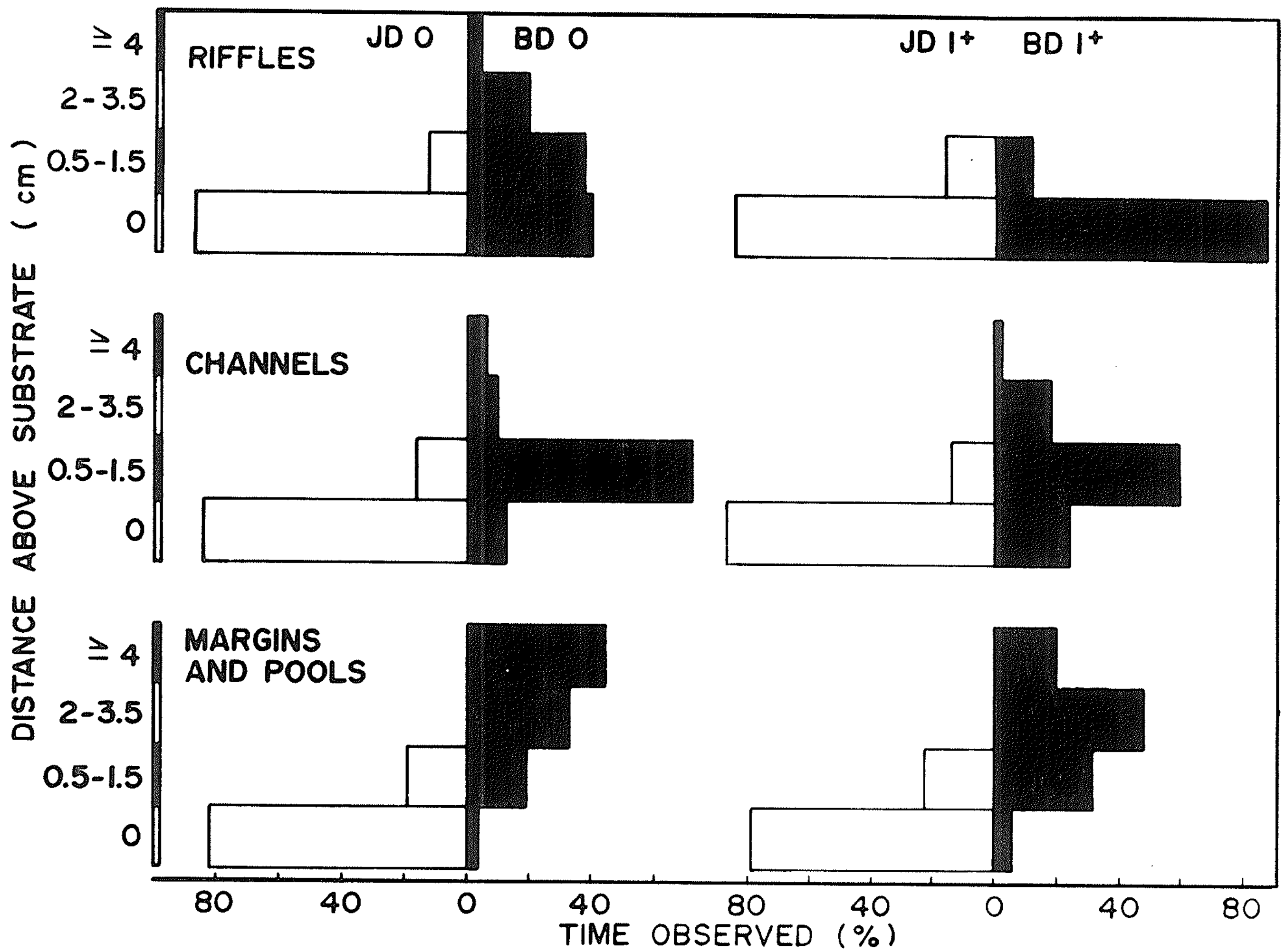

DISTANCE ABOVE SUBSTRATE (cm)
RIFFLES
CHANNELS
MARGINS AND POOLS
JD 0
BD 0
JD 1+
BD 1+
≥ 4
2-3.5
0.5-1.5
0
80
40
0
40
80
TIME OBSERVED (%)

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$\cdot$ min^{-1}), length (cm), and distance travelled (cm $\cdot$ 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.

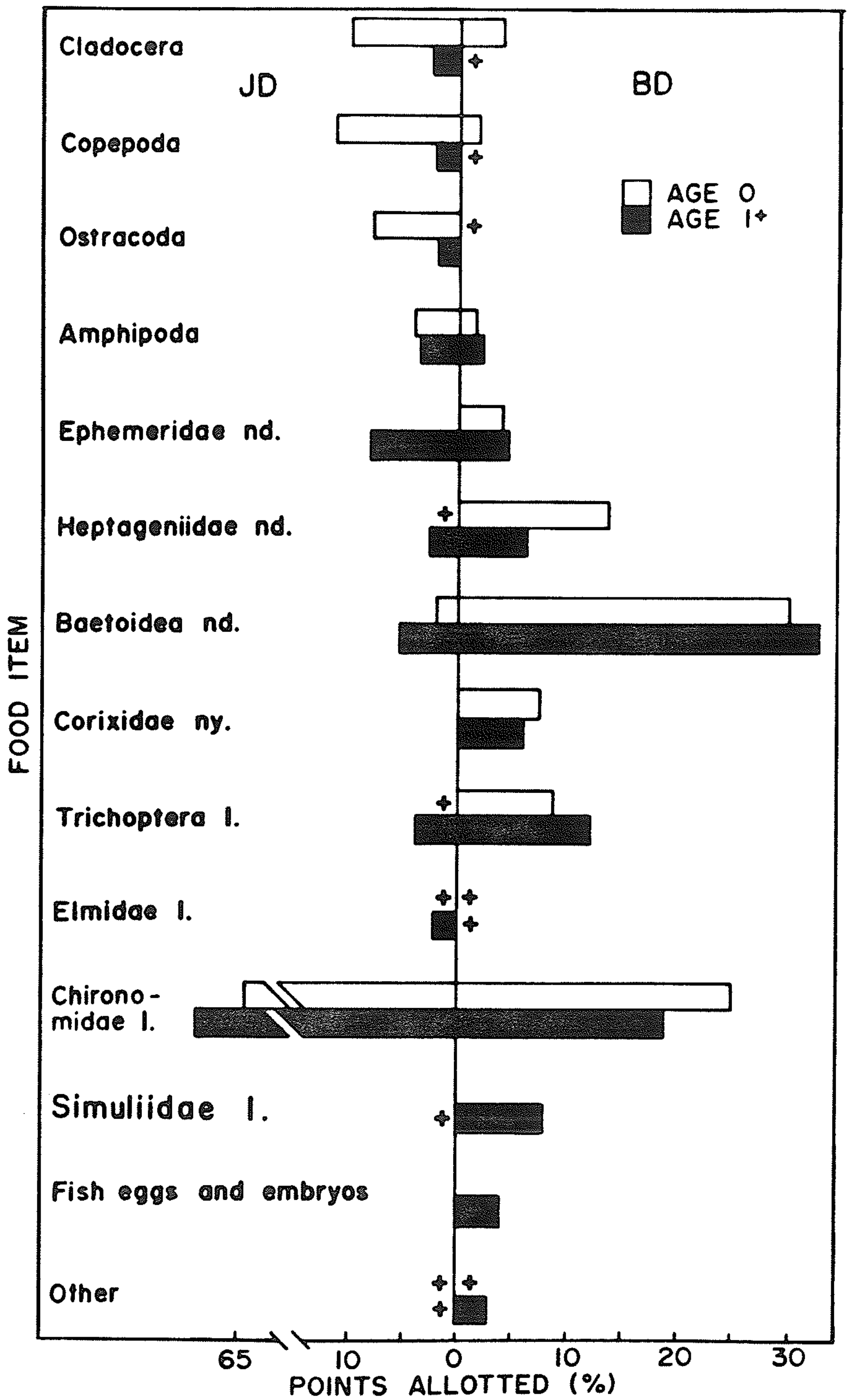
In general, johnny darters changed direction by approximately 30° between successive darts as often as they darted straight ahead (Appendix 3), whereas blackside darters moved straight ahead more often. Results of chi-square tests on the effects of environment occupied and age group are presented in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


Cladocera
JD
BD
Copepoda
AGE 0
AGE 1+
Ostracoda
Amphipoda
Ephemeridae nd.
Heptageniidae nd.
Baetoidea nd.
Corixidae ny.
Trichoptera l.
Elmidae l.
Chirono-
midae l.
Simuliidae l.
Fish eggs and embryos
Other
FOOD ITEM
65
10
0
10
20
30
POINTS ALLOTTED (%)

(spring), and Amphipoda (autumn). Both age groups of blackside darters usually ate very similar proportions of each food item except that age 0 consumed zooplankton in all seasons, especially early summer.

Overlap in diet, $\hat{C}_{\lambda}$, between different age groups of the same species was always greater than 0.70, but between fishes of different species of the same age group it was much lower, usually between 0.13 and 0.43 (Table 8). An exception to the latter occurred in midsummer when diets of age 0 fishes of the two species overlapped by 0.86. Values for diversity in diet were similar between age groups of the same species but were twice as high for blackside darters as for johnny darters (Table 9).

Feeding Behaviour - Johnny darters make feeding darts more frequently than blackside darters in all environments (Fig. 5A). Similarly, age 0 johnny darter feeding dart frequency is everywhere greater than age 1^{+}. Age 0 blackside darters make more feeding darts than age 1^{+} in channels, but not in other environments. For all groups feeding dart frequency is approximately equal in riffles and margins and pools. In channels, frequency is three to four times greater for all groups except age 1^{+} blackside darters, for which it is approximately ½ the rate observed elsewhere (Fig. 5A).

Both riffles and channels were important feeding areas for age 0 fish of both species (Fig 5B). Riffles alone were

Table 8. Overlap in diet. $\hat{C}_\lambda$ values can vary from 0 to 1, indicating completely different to completely overlapping diets, respectively.

Groups compared	Spring	Early summer	Midsummer	Late summer	Autumn
JD 0 *vs*. JD 1^+	-	0.93	0.73	0.91	0.96
JD 0 *vs*. BD 0	-	0.35	0.87	0.40	0.13
JD 1^+ *vs*. BD 1^+	0.43	0.40	0.35	0.26	0.22
BD 0 vs. BD 1^+	-	0.95	0.84	0.70	0.79

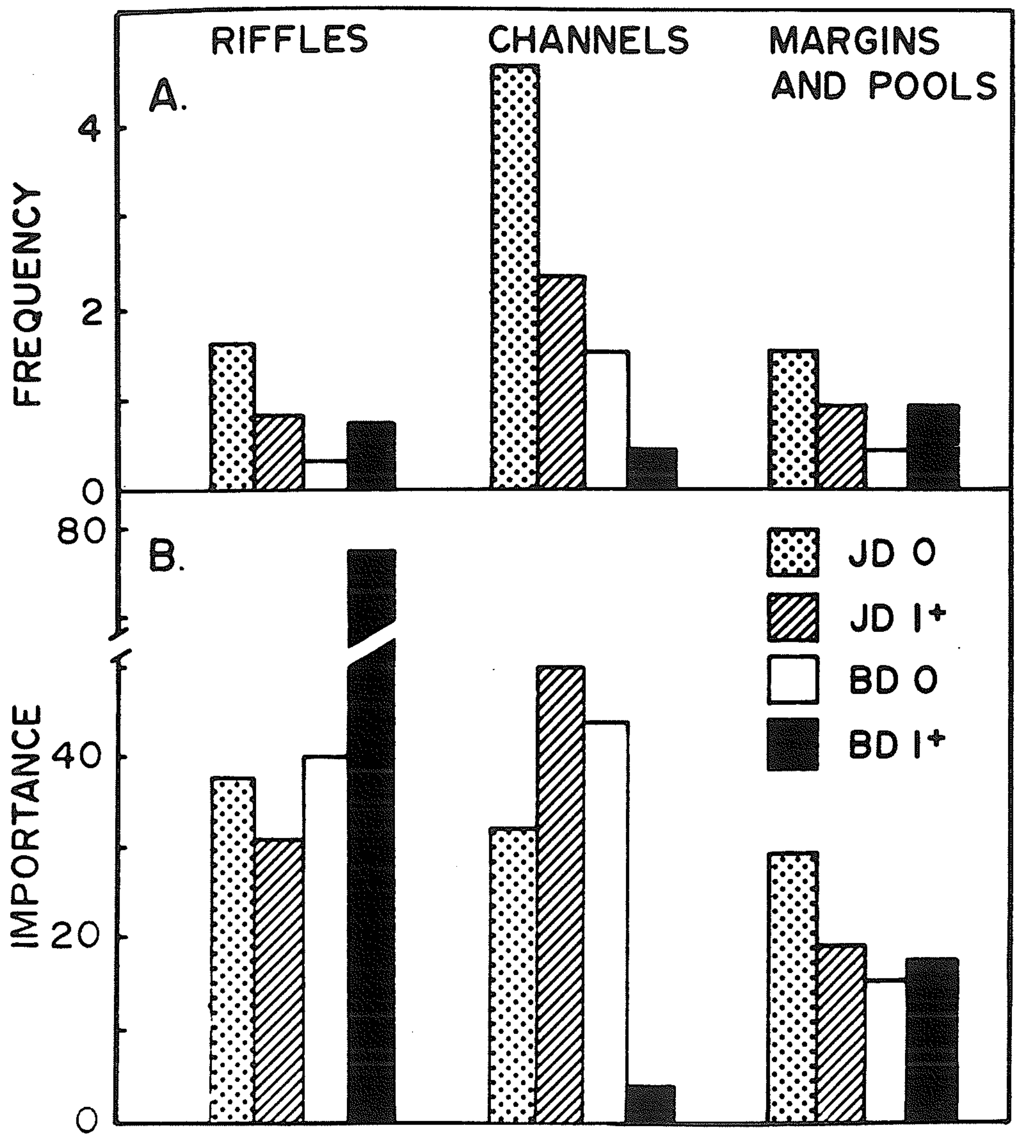
NOTE: JD, johnny darter; BD blackside darter; 0, age 0; 1^+, age 1^+.

Table 9. Diversity in diet from Apr. to Nov., 1977. Higher values indicate greater diversity.

Species	Age Group	$\frac{1}{\Sigma p_i^2}$
Johnny darter	0	2.27
	1+	2.08
Blackside darter	0	5.26
	1+	5.56

Figure 5. A. Feeding dart frequency (number·min^{-1}) in various environments. B. Index of importance of different environments for feeding. Index is the product of feeding dart frequency and relative density within each environment, and expressed on a scale of 1 to 100.

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


RIFFLES
CHANNELS
MARGINS AND POOLS
A.
FREQUENCY
0
2
4
B.
IMPORTANCE
0
20
40
80
JD 0
JD 1+
BD 0
BD 1+

important to age 1^+ blackside darters, whereas all environments were important for feeding to age 1^+ johnny darters. Margins and pools were relatively unimportant for most darters (Fig. 5B).

Mean length of feeding dart was approximately the same between age groups of the same species, but was notably longer for blackside then for johnny darters (Table 10). Length of feeding dart was more variable for blackside darters (Table 10). For johnny darters it was more variable for age 1^+ than age 0 fish, but the reverse situation was observed for blackside darters. Lewontin's (1966) test for comparing variability indicated that differences in variability of feeding dart length existed between all groups except age 1^+ fish of the two species (Table 10).

Based on discriminant analysis of 5 components of feeding behaviour, the two species were correctly differentiated 85.0% of the time. Prediction of group membership was more successful for johnny darters (92.2%) than for blackside darters (77.8%). The components most important as discriminants were pitch, exposure of bite site to current, site of bite, and height above the substrate (Appendix 5). Correlation and covariance values (Appendices 6 and 7) were highest between the latter two variables, and low for all other combinations of variables. For blackside darters pitch was nearly horizontal, and bites were taken from lesser exposed locations, most often from objects or the water about 1 cm above the substrate (Table 11). Johnny darter bites were directed downward onto more exposed locations atop the substrate (Table 11).

Table 10. Length and variability of feeding darts. Lewontin's formula was used to calculate F values for length variability.

Species and age group	Number of bites observed	Mean length (cm)	Coefficient of variation	F value and comparison group:		
				JD 1^+	BD 0	BD 1^+
JD 0	80	0.3	.018	0.55[a]	0.16[a]	0.49[a]
JD 1^+	40	0.5	.032	-	0.30	0.89
BD 0	24	1.5	.108	-	-	2.97[a]
BD 1^+	21	1.2	.037	-	-	-

[a] variability is significantly different, $\alpha = .05$.

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

Table 11. Mean values and standard deviations of discriminant variables of feeding behaviour analysis. Variable values were coded as follows: site of bite - 0 substrate, 1 object above substrate or water; height - 0, 1/2, 1 or 2 cm; exposure - 0 unexposed, 1 partially exposed, 2 completely exposed; pitch - 0 below horizontal body axis, 1 even with horizontal body axis, 2 above horizontal body axis; yaw - 0 directly forward (± 15°), 1 deflected 30° (± 15°) sideward, 2 deflected 60° (± 15°) sideward.

Variable	Species	Mean	Standard deviation
Site of bite	JD	0.08	0.31
	BD	0.90	0.65
Height above substrate	JD	0.07	0.31
	BD	0.91	0.74
Exposure to current	JD	1.94	0.27
	BD	1.44	0.67
Pitch	JD	0.03	0.18
	BD	0.80	0.69
Yaw	JD	0.64	0.55
	BD	0.52	0.52

NOTE: JD, johnny darter; BD, blackside darter.

Higher standard deviations for all components indicated blackside behaviour was more variable (Table 11).

The downward trajectory of 78% of johnny darter feeding darts was directed $\geq 7.5^{\circ}$ below the anterior tip of the premaxilla, compared to only 23% for blackside darters (Table 12). The bite target of the latter species was most frequently (36%) situated within a 15° arc above and below the tip of the premaxilla (Table 11). The degree of sideward deflection of feeding darts was similar for the two species (Table 13).

Time of Activity and Feeding

Both species of darters were active and fed only during daylight hours (Appendix 8).

Morphology

Swimbladder - Swimbladder volume, and hence buoyancy of blackside darters caught in margins and pools, was greater than those from riffles (Table 14). Both age groups were nearly neutrally buoyant in still water, but the swimbladder provided less than 10% of the lift required to attain neutral buoyancy in fish from fast water (Table 14).

Mouth, Head and Gill Raker Morphology - Proportionate dimensions, counts, and shape of several features of the mouth, head, and gill rakers differed significantly between the two

Table 12. Vertical angular component of feeding dart trajectory. Angle above horizontal denoted by +, and below by −.

Species	< -7.5°	-7.5° to +7.5°	+8.0° to +22.5°	+23.0° to +37.5°	> +37.5°
JD (%)	78	15	4	3	0
BD (%)	23	36	26	12	3

NOTE: JD, johnny darter; BD, blackside darter.

Table 13. Sideward deflection of feeding darts (%).

Species	Feeding darts deflected between:					
	0°-15°	16°-30°	31°-45°	46°-60°	61°-75°	76°-90°
JD	25	47	17	0	9	2
BD	31	40	6	15	5	3

NOTE: JD, johnny darter; BD, blackside darter

Table 14. Buoyancy ($mL \cdot g^{-1}$) of blackside darters captured in different environments. ($1.0\ mL \cdot g^{-1}$ = neutral buoyancy.) Number of fish measured is given in parentheses.

Age group	Statistic	Riffles	Margins and pools
0	Mean	.032 (14)	.997 (9)
	S.D.	.047	.129
1+	Mean	.076 (12)	.866 (7)
	S.D.	.081	.179

NOTE: S.D., standard deviation

species (Table 15). The mouth of johnny darters was relatively smaller, positioned ventrally and directed downward when opened (Fig. 6A). The premaxilla was protrusile. Blackside darter mouths were larger, positioned terminally and directed anteriorly when opened. The premaxilla was not protrusile.

The blunt johnny darter head had a steeply sloping forehead, whereas the more acutely pointed blackside darter head had a gradually sloping forehead. Relative dimensions of the head and snout differed little between species except that snout depth was shallower in blackside darters. Johnny darters' eyes were smaller and set more dorsally and closer together than blackside darters'.

Gill raker number and shape differed markedly, with johnny darters possessing fewer (mean 9.0), short, heavy rakers, and blacksides having more numerous (mean 16.3) elongate rakers (Fig. 6B).

Discussion

Although considerable ecological overlap was found between the two species, there were differences in resource dimensions used and appurtenant behaviour and morphology which could account for their coexistence. In these three potential avenues of ecological segregation, johnny darters tended to be comparatively specialized and blackside darters comparatively generalized.

Table 15. Structure of mouth, head and gill rakers. Mean measurement with standard deviation in parenthesis.

Feature	Johnny darter	Blackside darter
Mouth structure		
*mouth diam x 100 / standard l.	6.7 (0.3)	7.7 (0.4)
*mouth position x 100	72.6 (3.7)	62.7 (4.5)
*protrusibility of premaxilla	23.9% (8.6)	2.3% (2.1)
*angular orientation of open mouth	−37° (4.0)	−5.3° (3.4)
Head structure		
head l. x 100 / standard l.	25.5 (1.0)	25.5 (1.7)
* head d. x 100 / head l.	55.2 (2.3)	52.1 (2.1)
* head w. x 100 / head l.	54.2 (4.4)	49.5 (3.8)
snout l. x 100 / head l.	19.3 (1.2)	19.4 (1.7)
* snout d. / snout l.	1.9 (0.1)	1.6 (0.2)
snout w. / snout l.	1.6 (0.1)	1.6 (0.2)
*interorbital w. x 100 / head w.	21.5 (2.3)	31.1 (4.3)
*eye l. x 100 / head l.	27.8 (1.8)	30.0 (2.1)
eye position x 100	53.5 (6.5)	40.1 (7.5)
Gill rakers[a]		
*number on entire first arch	9.0 (0.9)	16.3 (1.2)

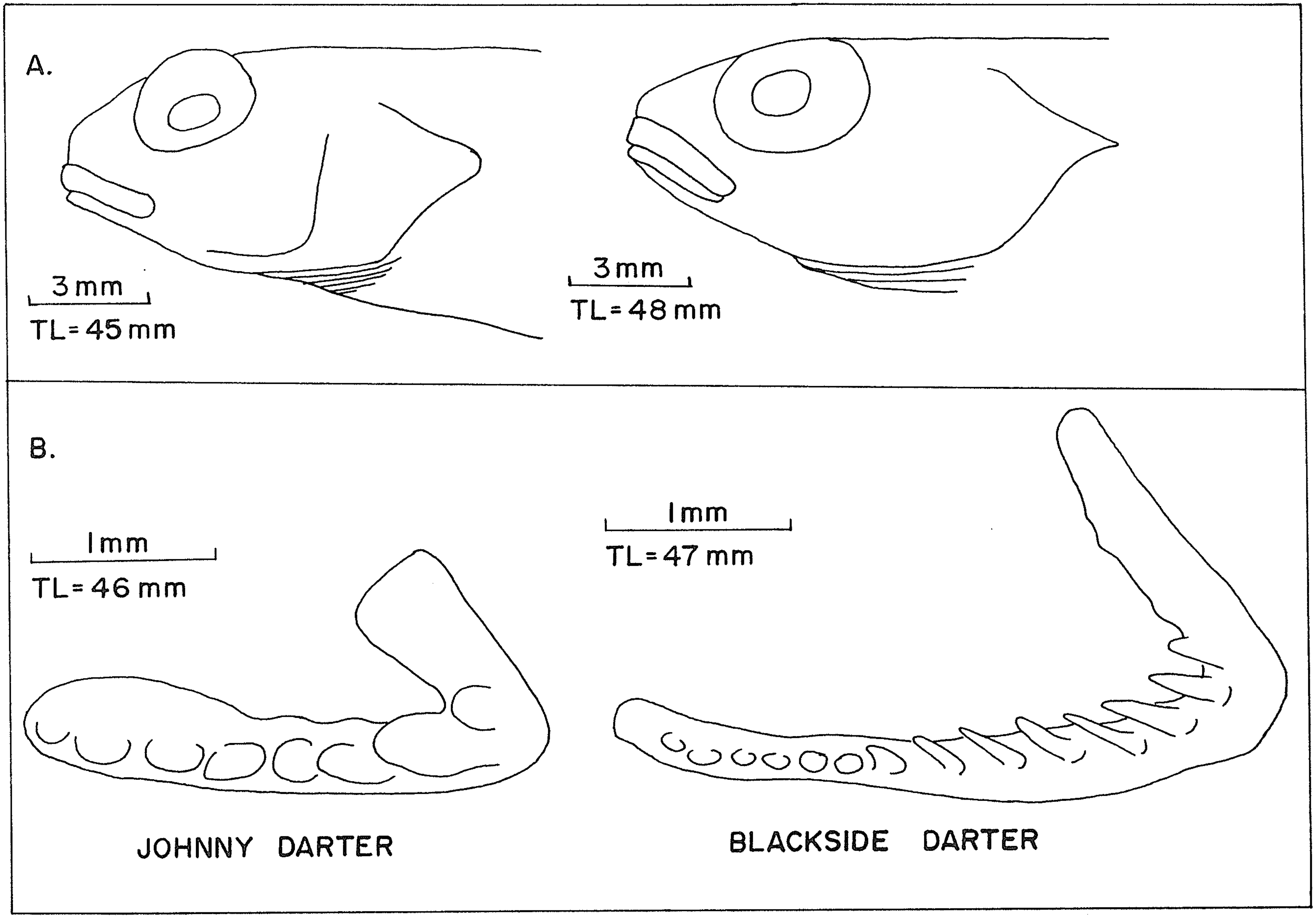
* significantly different, =.05

[a] Dr. G.E.E. Moodie - unpublished data.

NOTE: d., depth; l. length; w., width; - denotes below horizontal.

Figure 6. Morphology of johnny and blackside darters. A. Head structure. B. Gill raker structure.

NOTE: TL, total length.


A.
3 mm
TL = 45 mm
3 mm
TL = 48 mm
B.
1 mm
TL = 46 mm
1 mm
TL = 47 mm
JOHNNY DARTER
BLACKSIDE DARTER

Partitioning of Habitat and the Significance of Swimming Behaviour and Buoyancy

Distribution along the length of the river was very similar for the two species. However, blackside darters ranged slightly farther into more extreme environments (from boulder and slabrock rapids to silty tributaries). Overlap in environments occupied was generally very high. Wide tolerances for water velocity and substrate type for these species have also been found by others (Karr 1963; Page 1972; Scott and Crossman 1973; Speare 1960; Trautman 1957; Winn 1958). Lesser overlap in spring may be attributable to differences in site of reproduction. Johnny darter eggs are deposited on the underside of rocks in water with little or no current (Winn 1958). In contrast, I have observed blackside darters defending spawning territories in riffles flowing $>25\ cm \cdot s^{-1}$, and Petravicz (1938) and Winn (1958) reported this behaviour from "moderate current" and "raceways", respectively.

Patterns of vertical distribution were dissimilar for the two species. Johnny darters were specialized for a benthic mode of life in all environments, whereas blackside darters were more pelagic, particularly in slow moving water. The tendency toward vertical segregation is exaggerated in the larval stage, with johnny darters sitting on the bottom (Balesic 1971; Fish 1932) and blackside darters swimming near the surface (Petravicz 1938).

The swimming behaviour of the two species was not identical. Johnny darters typically sat on the bottom, and moved in short, relatively uniform dashes. They tended to change direction of orientation of successive darts more frequently, which may have increased the field of surveillance. Blackside darters were more active, explored a larger area, and exhibited a greater repertoire of swimming and probing movements.

Because structural modifications can be correlated with various aspects of ecology and behaviour, differences therein may be used to predict and delimit ecological niche, as Keast and Webb (1966) have done in Lake Opinicon, Ontario.

Johnny darters are without a swimbladder, but it is present in blackside darters, and the volume can be regulated to compensate for differences in water velocity. Relative inflation of the swimbladder is the morphological basis for differences in vertical distribution (Gee 1967, 1972; Gee and Northcote 1963). Lack of a swimbladder restricts johnny darters to the bottom and confers more stereotyped behaviour. Blackside darter behaviour is more plastic since regulation of swimbladder volume facilitates use of the vertical dimension of the environment.

A variable but negative buoyancy allows a fish to hold position in a variety of water velocities (the faster the velocity the lower the buoyancy) (Gee 1977). A near neutral buoyancy allows for ease of movement in still water both in horizontal and vertical planes. The latter holds true only over short vertical distances, usually $<$1m, as typically found in streams.

Partitioning of Food-type and the Significance of Feeding Behaviour and Relevant Morphology

The diet of both species was primarily immature aquatic insects, which agrees with the findings of others (e.g. Balesic 1971; Flemer and Woolcott 1966; Forbes 1880; Karr 1963; Pearse 1918; Turner 1921). Throughout the ice-free period johnny darter prey was almost exclusively chironomid larvae and small crustaceans. Chironomidae are usually benthic sprawlers and burrowers (Coffman 1978), and the Crustacea are found near the bottom in slower moving water (Hynes 1970). Blackside darter diet included the same items as that of johnny darter, but prey organisms were taxonomically and behaviourally more diverse. Ephemeroptera nymphs often conceal themselves beneath and between stones by day (Bishop 1969). Those present in the stomachs were mostly clinging and swimming, with some burrowing, forms (Edmunds 1978). Corixidae are swimmers and climbers (Polhemus 1978). Trichoptera larvae were mostly Hydropsychidae, which spin nets and cling to rocks in fast water (Wiggins 1977). Simuliidae larvae also hold fast to the substrate in fast water (Grenier 1949), and Amphipoda are benthic crawlers and swimmers (Hynes 1954). Furthermore, Chironomidae, Ephemeroptera, Simuliidae and Amphipoda commonly enter the drift (Waters 1972). Seasonal changes in important taxa in the diet of blackside darters may reflect opportunistic feeding on items whose life history cycle causes seasonal change in availability.

Overlap in food consumed between comparable age groups of the two species normally ranged from 0.13 to 0.43 but might have been even lower if level of prey identification had been more refined, or if size of food organism had been analyzed. The only high value for interspecific overlap (0.86 between age 0 fishes in midsummer) arose from the common consumption of chironomid larvae, a ubiquitous and often exceedingly abundant food source. Other workers have found increased trophic overlap to correspond with increased food abundance (Keast 1965, 1970; Nilsson 1965; Ross 1977; Werner and Hall 1976; Zaret and Rand 1971).

Both species similarly exploit different environments for feeding, but their feeding behaviour differs markedly. Johnny darters specialize in pecking downward at items on the substrate. Blackside darters tend to feed in a microhabitat slightly above that of the johnny darter. The horizontal pitch, higher site and height of bite and more pelagic swimming behaviour enable them to prey upon organisms relatively inaccessible to johnny darters (e. g. Corixidae). Trautman (1957) even observed blackside darters rising to the surface for insects. Feeding at different levels in the water column is not an uncommon segregation mechanism in otherwise similar coexisting fishes (Keast 1970).

The greater variability of feeding dart length and all components quantified for discriminant analysis reflects the more varied repertoire of feeding movements used by blackside darters in capturing behaviourally diversified prey.

Morphology of the mouth and gill rakers is adapted to feeding ecology. Johnny darters' structure predisposes them to engulf smaller items from the substrate, whereas the more generalized blackside darter morphology enables them to seize more types of prey from more varied microhabitats sometimes quite distant from the bottom.

The higher position of johnny darter eyes and their latero-medial movement may enhance specialization for ventrally directed visual acuity (as described by Curd's [1966] examination of retinal structure) by making acute line of sight more perpendicular. Blackside darters' field of greatest visual acuity is less specialized, with eye position and movement permitting more lateral and anterior vision. Darters are known to be sight feeders (Curd 1966; Roberts and Winn 1962), thus position of eyes and retinal specializations can be correlated with feeding habits (Ahlbert 1969; Tamura 1957).

Johnny darters had fewer, shorter, stouter gill rakers than blackside darters. Kliewer (1970) studying whitefish, and

Larson (1976) studying sticklebacks, have found similar differences in gill raker structure between benthic- and pelagic-feeding forms.

Partitioning of Time

No evidence for resource partitioning by time of day was found, although Keast and Welsh (1968) reported differences in feeding times between species. Schoener (1974) indicated that temporal partitioning is rarely as important as space or food. Because time cannot be depleted like space or food, nor does it exhibit the variability prerequisite for specialization, Ricklefs (1973) considers partitioning of time an unlikely mechanism of ecological differentiation.

However, age 0 fishes may to some degree have temporally partitioned the environment occupied and food in early spring. Young blackside darters were found earlier in margins and pools, and appeared to move sooner into channels and riffles than johnny darters. They were also longer, grew faster (Karr 1963), and had relatively larger mouths than johnny darters, enabling them to handle larger prey items. Gibbons and Gee (1972) found evidence of temporal partitioning of stream margin habitat by differential time of hatching of longnose and blacknose dace. Svärdson (1949) presented examples of closely related species of coregonids whose differential growth rate was fundamental to their ecological segregation.

Thus, in terms of the habitat resource dimension, neither distribution along the length of the river, nor environments occupied differed markedly between the two species, but the precise vertical distribution did. This difference was related to relative height in the water column at which fishes swam, and thus to the swimbladder, and was magnified in slower water velocities. In terms of the food resource dimension, benthic immature insects and small crustaceans were eaten by both species, but different prey taxa appeared in different proportions in the diets. Johnny darters specialized on chironomid larvae, and the behaviour and structures involved in perceiving (retinae), capturing and manipulating food (mouth and gill rakers) were correspondingly specialized to obtain food efficiently. Blackside darter diet was more diverse, their feeding behaviour more variable, and food detection and manipulation structures were more generalized. Time of day was not important in subdividing habitat and food resources available to the two species, but differences in time of hatching, in conjunction with size and growth rate, may have served to segregate age 0 fishes to some degree. Hence, a variety of mechanisms permit johnny and blackside darters to exploit resources slightly differently and obviate intense ecological overlap.

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Appendix 1. Length frequency of darters collected in various seasons.

Length (mm)	Species	Spring	Early summer	Mid-summer	Late summer	Autumn
$<$25.0	JD	3	1181	-	-	-
	BD	1	-	-	-	0
25.0-29.9	JD	47	34	1535[a]	581[a]	105[a]
	BD	0	773[a]	-	-	0
30.0-34.9	JD	154	6	80	806	257
	BD	3	71	-	30[b]	1
35.0-39.9	JD	88	60	58	268	107
	BD	5	5	590[c]	112	14
40.0-44.9	JD	36	134	174	90	41
	BD	29	1	35	193	28
45.0-49.9	JD	12	55	129	157	28
	BD	17	11	11	38	12
50.0-54.9	JD	7	13	55	81	18
	BD	9	23	38	12	4
55.0-59.9	JD	4	2	7	17	6
	BD	4	48	39	22	2
60.0-64.9	JD	0	0	1	5	1
	BD	9	17	28	18	3
65.0-69.9	JD	0	0	0	0	0
	BD	1	9	13	6	7
$\geq$70.0	JD	0	0	0	0	0
	BD	1	3	6	3	1

[a] includes fish $<$25.0 mm

[b] includes fish $<$25.0 mm and 25.0 to 29.9 mm

[c] includes fish 25.0 mm to 34.9 mm

NOTE: JD, johnny darter; BD, blackside darter.

Appendix 2. Fishes (other than johnny and blackside darters) in various zones of the Whitemouth River system. Number of sites sampled is given in parenthesis, and number of sites of capture is tabulated.

Species	Family	Head-waters (3)	Mid-course (18)	Lower course (3)	Birch River (12)	Tributaries (4)
Ichthyomyzon fossor	Petromyzontidae	-	5	-	1	1
Umbra limi	Umbridae	1	-	-	-	-
Esox lucius	Esocidae	1	6	1	-	-
Nocomis biguttatus	Cyprinidae	1	13	1	2	-
Notropis cornutus	Cyprinidae	1	17	1	2	3
N. rubellus	Cyprinidae	-	15	-	2	-
Pimephales promelas	Cyprinidae	3	11	-	-	-
Rhinichthys cataractae	Cyprinidae	-	14	-	2	2
Catostomus commersoni	Catostomidae	1	11	1	-	2
Moxostoma macrolepidotum	Catostomidae	-	7	1	1	-
Culaea inconstans	Gasterosteidae	2	3	-	1	-
Ambloplites rupestris	Centrarchidae	-	9	-	-	-
Etheostoma exile	Percidae	1	-	-	-	-
E. nigrum	Percidae	-	18	3	2	3
Percina maculata	Percidae	1	18	3	2	4
P. caprodes	Percidae	-	9	2	-	1
Stizostedion vitreum	Percidae	-	3	1	-	-

Appendix 3. Frequency (%) of darts oriented at various angles with respect to preceeding dart. Age groups and environments occupied are combined within each species.

Angle of orientation (±15°)	JD	BD
0°	32.8	38.8
30°	34.3	26.7
60°	15.8	12.1
90°	13.3	17.1
other	3.0	5.2

NOTE: JD, johnny darter; BD, blackside darter.

Appendix 4. Chi-square tests for the effect of three variables, A. environment occupied, B. age group, and C. species and age group on dart orientation frequency. $\chi^2_{(.05,\ 2)} = 5.99$

A. Environments compared	Species	Age group	χ^2
R,C,M/P	JD	0	4.63
		1^+	8.68[a]
	BD	0	28.53[a,b]
		1^+	5.12[a]
R,C	BD	0	10.85[b]
R,M/P	BD	0	18.08[b]
C,M/P	BD	0	16.94[b]

B. Age groups compared	Environment occupied	Species	χ^2
0, 1^+	R	JD	14.27[b]
	C	JD	4.27
	M/P	JD	2.60
0, 1^+	R	BD	8.24
	C	BD	5.91
	M/P	BD	11.83

C. Species and age groups compared	Environment occupied	χ^2
JD 0 vs. BD 1^+	combined	23.40
JD 1^+ vs. BD 1^+	combined	2.48
JD 1^+ vs. BD 1^+	R	5.64
JD 1^+ vs. BD 1^+	C	3.22
JD 1^+ vs. BD 1^+	M/P	3.46
JD 0 vs. BD 0	R	9.45
JD 0 vs. BD 0	C	13.71
JD 0 vs. BD 0	combined, M/P	4.31
JD 1^+ vs. BD 0	combined, R	14.79
JD 1^+ vs. BD 0	combined, C	29.21
JD 1^+ vs. BD 0	combined, M/P	11.19

[a] $\chi^2_{(.05,\ 3)} = 9.49$

[b] Variable does affect dart orientation frequency.

NOTE: R, riffles; C, channels; M/P, margins and pools; JD, johnny darter; BD, blackside darter; 0, age 0; 1^+, age 1 .

Appendix 5. Standardized discrimination function coefficients. The absolute value of each coefficient represents the contribution of its associated variable to the discriminant function.

Variable	Coefficient
Site of bite	-0.28
Height above substrate	-0.29
Exposure to current	0.34
Pitch	-0.38
Yaw	0.13

Appendix 6. Within group correlation matrix for discriminant analysis of feeding behaviour.

	Site of bite	Height above substrate	Exposure to current	Pitch	Yaw
Site	1.00				
Height	0.78	1.00			
Exposure	0.03	0.02	1.00		
Pitch	0.40	0.27	-0.04	1.00	
Yaw	0.04	0.15	-0.10	-0.05	1.00

Appendix 7. Within groups covariance matrix for discriminant analysis of feeding behaviour.

	Site of bite	Height above substrate	Exposure to current	Pitch	Yaw
Site	0.26				
Height	0.23	0.32			
Exposure	0.01	0.01	0.26		
Pitch	0.10	0.08	-0.01	0.25	
Yaw	0.01	0.05	-0.03	-0.01	0.29

Appendix 8. Time of activity and feeding.

Time of day	Minutes of observation		Mean number of darts · min^{-1}		Mean number of feeding darts·min^{-1}	
	JD	BD	JD	BD	JD	BD
1:00[c]	10	1	2.2	0.0	0.0	0.0
4:00[b]	14	11	2.0	2.7	0.1	0.0
5:00[c]	10	1	2.5	0.0	0.2	0.0
6:00[a]	14	14	11.5	32.5	1.6	1.4
8:00[b]	14	14	8.0	21.1	1.6	1.8
9:00[c]	10	1	1.8	23.0	0.2	0.0
10:00[a]	14	14	9.6	23.9	1.2	1.8
12:00[b]	14	14	5.2	30.9	1.6	0.4
14:00[a]	14	14	10.4	29.0	1.1	1.0
16:00[b]	20	20	8.0	24.4	1.1	0.3
17:00[c]	10	10	7.6	13.5	1.8	0.8
18:00[a]	14	14	11.6	40.5	1.6	1.6
20:00[b]	17	10	5.1	10.1	0.4	0.1
21:00[c]	10	1	2.5	2.0	0.0	0.0
22:00[a]	14	11	3.3	2.8	0.1	0.0

[a] July 30 - Aug. 1, 1977

[b] Aug. 22 - 24, 1977

[c] Aug. 21 - 22, 1978

NOTE: JD, johnny darter; BD, blackside darter.