THE UNIVERSITY OF MANITOBA

COMPARATIVE ECOLOGY OF TWO SYMPATRIC SPECIES OF DACE, *RHINICHTHYS CATARACTAE* AND *RHINICHTHYS ATRATULUS*, IN THE MINK RIVER, MANITOBA

by

JOHN R. H. GIBBONS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

MASTER OF SCIENCE

Department of Zoology

WINNIPEG, MANITOBA

October, 1971

ABSTRACT

The Great Lakes longnose dace (Rhinichthys cataractae cataractae) and the western blacknose dace (Rhinichthys atratulus meleagris) occur sympatrically in the middle portion of the Mink River, Manitoba. Their abundance is associated with high gradient (7 m./km.), which results in rapid water velocities and gravel or rock substrates, and with plant detritus, which supports the insect fauna used as food.

Fry of both species were found in July, but longnose hatch earlier and grow faster than blacknose dace. For a short period both species are found together in shallow, silted margins of the stream, of little or no current. Longnose move out into fast water in July and August when they are between 25 and 30 mm in length, while the majority of blacknose remain in the margins for up to one year, until they reach a fork length of about 45 mm. Thereafter, blacknose are found mainly in channels (15-45 cm/sec) and longnose in riffles (> 45 cm/sec). Blacknose males are territorial over pea-sized gravel, longnose males over small rocks in riffles. There is a marked habitat difference between the sexes of both species during spawning, females entering territories only when completely ripe. In the late fall, blacknose adults and juveniles were found only in beaver

ponds, while longnose were found under large flat stones in riffles.

The diet of the two species is strikingly similar. Longnose and blacknose in their first twelve months fed almost exclusively on the families Baetidae, Tendipedidae and Hydropsychidae, but their proportions differed. Hydropsychidae was always the major food item by weight for older longnose. Older blacknose were similar, but they switched to Tipulidae and Ephemeridae in May and October. Surber samples of benthic fauna were taken in a riffle and a channel. Baetidae and Tendipedidae were highly foraged by both species.

Despite their similar diet, the degree of spatial and temporal isolation between the two species is thought sufficient to allow for their coexistence.

ACKNOWLEDGEMENTS

I thank my colleague, Bob Moshenko, for his help and advice on techniques of the field study. The assistance of L. Deckter and K. Machniak is gratefully acknowledged. Above all, I thank my supervisor, Dr. J. H. Gee, for his guidance and encouragement throughout the project.

The research was supported through grants from the National Research Council of Canada and the Fisheries Research Board of Canada.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF PLATES

LIST OF FIGURES

INTRODUCTION

The Great Lakes longnose dace, *Rhinichthys cataractae cataractae* (Valenciennes) and the western blacknose dace *Rhinichthys atratulus meleagris* Agassiz are two small cyprinid fishes whose overlapping distributions result in their sympatric occurrence in many water systems.

The geographic distribution of the Great Lakes longnose dace is still uncertain since full distinction from other subspecies has yet to be clarified. Hubbs and Lagler (1958) report it as occurring in the drainage basin and around all the shores of the Great Lakes, in the St. Lawrence R. as far as Montreal, and in river systems in parts of Wisconsin, Michigan and Indiana.

The western blacknose dace is also found throughout the entire Great Lakes drainage basin, except around the east end of Lake Ontario. Elsewhere it is distributed from northeastern Nebraska, Iowa, North Dakota, the drainage of Lake Winnipegosis and the Lake of the Woods region to the northern part of the Ohio river system (Hubbs and Lagler 1958). Unlike the longnose dace, the western blacknose is uncommon in lakes, being reported most abundant in small, cool tributaries. Both *R. c. cataractae* and *R. a. meleagris* occur in the Mink R., Manitoba (Bartnik, 1970).

The purpose of the present study was to investigate sympatric populations of Rhinichthys in the Mink R. with respect to the principle of Gause. Often termed 'the principle of competitive exclusion, it states, in essence, that no two species can coexist in the same locality if they have identical ecological requirements. Lagler et al (1962) stated that the most common competitions among fishes are for spawning sites, food, space and shelter.

The sympatric occurrence of closely related species, often of the same genus, is a problem that has been widely investigated in a variety of taxonomic groups (eg., Miller on gophers, 1964; Beauchamp and Ullyott on triclads, 1932; Kohn on prosobranchs, 1959). In nearly all cases differences in resources utilized, such as food, or environment occupied, were found. In some cases two species were found together using the same resources, which were temporarily superabundant.

It has also been shown that ecological differences been two species are often magnified by interaction due to competition, sometimes coupled with predation (eg., Larkin and Smith, 1953; Johannes and Larkin, 1961; on the interaction between redside shiners and Kamloops trout). This phenomenon was termed interactive segregation by Brian (1956) and has been reviewed in fishes by Nilsson (1966) and by Miller (1967) for other taxonomic groups. It is believed typical of newly evolved faunas, whose 'preferences' exhibit considerable plasticity and can change in the presence or absence of interacting species.

There are a number of publications which include aspects of the ecology of one or both species of *Rhinichthys*. In some cases the subspecies was not mentioned, but the majority here concentrate on the Great Lakes longnose and the western blacknose. Kuehn (1949), Reed (1959) and Becker (1962) found aquatic Diptera and Ephemeroptera the major food items of longnose dace. Gerald (1966) found baetid mayfly nymphs the main diet of longnose, while Schlick (M.S., 1966) indicated that sympatric populations of the two species ate very similar foods, with Trichoptera and Ephemeroptera the most numerous items. Moore *et al*. (1934) noted that blacknose dace fed mainly on Diptera larvae and pupae (Tendipedidae and Tipulidae), Ephemeroptera and Trichoptera.

Only limited information on the environments occupied is given in the above papers. Becker (1962) generally found *R. c. cataractae* to frequent fast, shallow water with gravel or rubble bottoms, while *R. a. meleagris* was usually found between fast and slow water, or in eddies behind rocks. Bartnik (1970), who worked on isolating mechanisms between the two species measured densities of mature fishes during the spring reproductive period in currents above and below 45 cm/sec. He found that the majority of adult blacknose were in water below 45 cm/sec while the majority of adult longnose were in water above this velocity. However, considerable overlap existed.

The present study provides information on: the distribution and abundance of the two species in the Mink R.; their densities in different environments throughout the life cycle; and on food present and food consumed.

PLATE 1. Longnose dace male in spawning colour.

PLATE 2. Blacknose dace male in spawning colour.

MATERIALS AND METHODS

A. Study Area

The Mink R. originates in the Duck Mountains, southwestern Manitoba, and flows eastwards for 47 km to Dauphin L. It arises in part from a number of springs. The upper reaches are sluggish and twisting, with substrates mainly of sand and silt. After a distance of some 7 km, the gradient becomes steeper and the stream cuts more deeply into the surrounding valley. Riffles and fast channels begin to appear, while the substrate now contains increasing amounts of gravel and rock. These conditions persist for some 15 km until the stream ends abruptly in a Phragmites-covered marsh that extends 2 km eastward before any visible outlet appears. The lower section, which leads from marsh to lake, is 23 km in length. For the most part it is a straightened man-made ditch with a dyke on either side to prevent flooding of surrounding farmland in spring.

B. Distribution of Dace in the Mink R. and Abundance in Particular Environments

From May to October 1970, dace were collected from all possible places in the Mink R. From these collections limits of distribution of both species along its length could be defined. Furthermore, abundance of dace in different environments, within parts of the stream occupied, could be determined.

PLATE 3. Upper zone of Mink River.

PLATE 4. Lower zone of Mink River.

Prior to making a collection in any environment, except a riffle, the area to be sampled (5-25 m^2) was enclosed using barrier nets (5 meshes/cm). Care was taken to create as little disturbance as possible and to seal off the enclosure quickly. Then fishes were taken using a two-man seine (5 meshes/cm). Seining continued until no fishes were taken on three successive hauls. In riffles, fishes were taken by kicking the substrate as vigorously as possible and driving fishes into a seine net held downstream. This procedure was repeated as quickly as possible and continued till no fish were taken on successive kicks.

The numbers of dace collected from each area so sampled were recorded. Some were immediately preserved for later examination of stomach contents, while others were anaesthetised in M.S. 222 (ethyl m-aminobenzoate methane sulphonate 1.3 gm/l), measured to the nearest mm (fork length), sexed and then released. Other species were counted and released (see Appendix).

Several environmental variables were measured for each area sampled. These included; water and air temperatures, area sampled, maxima and minima of water depth and surface velocity (by timing a floating object over 3 m), and a description of the substrate. For the latter, four categories of particle size were used; mud and sand (up to 0.2 cm), gravel (0.2-5.0 cm), small rocks (5.0-15.0 cm), and large rocks (>15.0 cm). The percentage that each category contributed to the bottom was estimated. Each area sampled was kept as homogenous as possible with respect to the above variables. Other details noted were; amount and kinds of aquatic and overhanging vegetation, number of seine hauls made, water turbidity, weather, and the immediate position of the area sampled in relation to the stream as a whole.

From the outset it was apparent the two species were found in particular environments within the stream as were different age classes within each species. Although a stream tends towards a heterogenous continuum, seven basic environments were arbitrarily defined, primarily on the variables of water velocity, depth and substrate composition. Their descriptions are summarised in Table I. The densities of young-of-the-year, juvenile and adult fish of each species (from frequency/length) were determined for every environment.

C. Food Present, Food Consumed and Feeding Behaviour

Collections of dace for digestive tract analysis were made at least once per month. They were preserved in 10% formalin within ten minutes of capture and later transferred to 40% isopropyl alcohol. Prior to dissection, fishes were dried lightly on paper towelling, weighed (± 0.0025 g) and measured to the nearest mm fork length. Each species was divided into two groups; fish in their first twelve months and fish thirteen months or older (from

TABLE 1. Description of basic environments within the Mink River.

Environment	Pool edge, margins	Pools, Slow channels	Medium channels	Shallow, fast channels	Gravel riffles	Small rock riffles	Large rock riffles
Number	1	2	3	4	5	6	7
Velocity cm/sec	0-15	0-15	15-30	25-45	45-100	45-100	45-120
Substrate Composition	90%+ Silt& Sand	Sand (30%+) Gravel (10%+) Rock (20%+)	Sand (10%+) Gravel (40%+) Rocks (10%+)	Sand (5%+) Gravel (30%+) Rocks (20%+)	75%+ Gravel	75%+ Small Rocks	75%+ Large Rocks
Depth Range (cm)	7-25	35-130	30-50	10-35	7-25	7-35	10-35
Remarks	Often found adjacent to swift waters such as riffles	Covers a wide range of environments including beaver ponds.	A common environment.	Approaches a riffle, but water not so turbulent. Prevalent in spring.	Usually fairly homogeneous in substrate type.	Common between pools or channels. Often contains components of environments 5 + 7.	Uncommon, with scattered distribution.

PLATE 5. Pool edge and margins.

PLATE 6. Slow channel.

PLATE 7. Medium channel.

PLATE 8. Fast channel.

PLATE 9. Gravel riffle.

PLATE 10. Small rock riffle.

PLATE 11. Large rock riffle.

PLATE 12. Barrier enclosure.

frequency/length). At least fifteen fish in each group were examined for every month from May to October. The entire digestive tract, from stomach to anus, was removed and opened under shallow water in a Petri dish. Food items were identified, where possible, to family and counted. After completion of dissection of a particular group from a particular month, the total weight of each family as a food item was measured (± 0.001 g).

The presence of food items in the stream bed was examined using a Surber sampler, from June to October 1970. A small rock riffle and a medium channel were studied. Ten samples, each of 1 $ft.^2$ (0.093 m^2), were taken from each of the two environments per month. Organisms were separated from substrate and preserved in 40% isopropyl alcohol. After later identification to family and counting, they were dried lightly on filter paper for one minute and weighed (± 0.001 g).

Samples of drift organisms were taken over twenty four hours using a Surber sampler. Water velocity and depth of immersion of the sampler were measured. From these results the volume of water passing through could be calculated. Examination of material collected followed the same proceedure as used in benthic sampling.

Observations of feeding behaviour were made using a face-plate and snorkel. Dace were observed in June, August and September 1970 in a variety of environments at different points along the stream (see Appendix).

RESULTS

A. Distribution and Abundance of Dace in Major Ecological Zones along the Length of the Mink River

The environment of a stream changes over its length. Information was collected to describe such changes and to determine if any relationship exists between the presence of dace and particular environmental variables. The Mink R. was divided into upper, middle and lower zones (Fig. 1) on the basis of several ecological characters and the densities of dace within each zone were estimated.

(i) Ecological Zones of the Mink River

Several distinct physical and biological differences were found between upper, middle and lower zones, and where possible, quantified (Table 2). Stream gradient and the amount of overhanging vegetation were considered the most important primary variables affecting the distribution and abundance of fishes.

The average gradient in the middle zone was approximately twice that of other parts of the stream and this feature profoundly affects water velocity and substrate composition. In the upper zone the sluggish flow was accompanied by a bottom composed largely of sand and silt. Occasional shallow channels of moderate flow were encountered, while riffles were very scarce. The middle zone contained

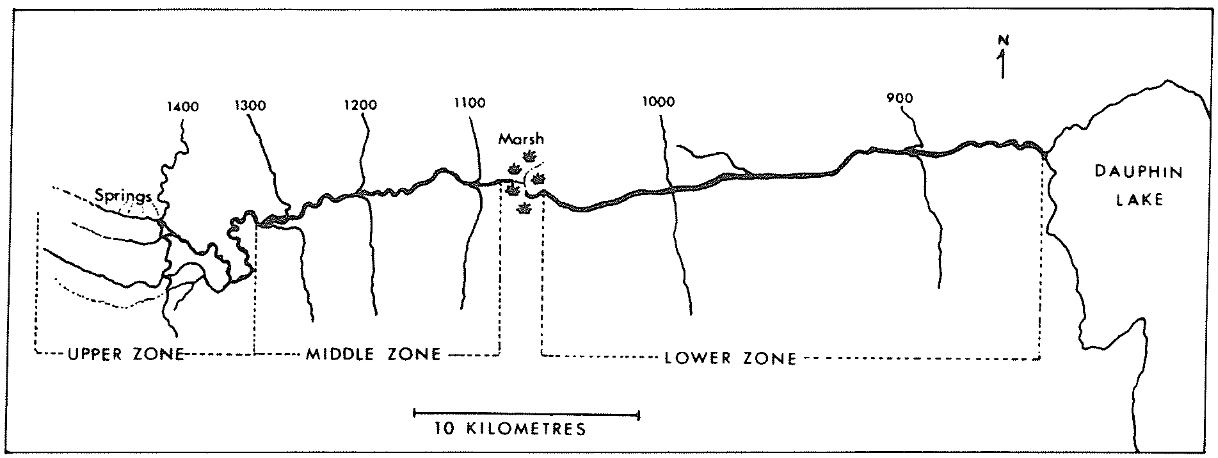

N
1400
1300
1200
1100
1000
900
Marsh
Springs
DAUPHIN
LAKE
UPPER ZONE
MIDDLE ZONE
LOWER ZONE
10 KILOMETRES

TABLE 2. Comparison of environmental factors in the three zones of the Mink River.

Factors	Upper	Middle	Lower
1. Average Gradient to nearest metre	4m/km	7m/km	3m/km
2. Water velocity	sluggish 90% < 25 cm/sec	most rapid frequent riffles	sluggish occasional riffles
3. Substrate composition	over 90% silt and sand	all types from silt to rocks	over 90% gravel and rock
4. Maximum summer water temperature	19° C	26° C	29° C
5. Aquatic vegetation	mainly angio-sperms rooted near the margins	mosses and green algae on rocks	angiosperms rooted between rocks
6. Overhanging vegetation	high over 70%	high over 70%	low less than 10%
7. Amphipoda	*Gammarus*	none	*Hyallela*
8. Aquatic insects and Wt. ratio in drift - July	Limited benthic much free swimming	much benthic few free swimming	limited benthic much free swimming
	-	100% benthic	6.2% benthic 93.8% F.S.
9. Plant drift July mg/m^3	much 187.2	much 298.5	little 0.9

numerous riffles and channels of rock or gravel substrate, though a considerable proportion of slow water, in the form of silted pools, margins and beaver ponds, was maintained. The lower zone, which contained long stretches of slow water, separated by isolated riffles, had substrates composed entirely of rocks and gravel, while silt and sand were absent. Reasons for this phenomenon are given below.

The upper zone is fed by a number of springs whose waters were never found to exceed 5° C throughout the summer of 1970. As a consequence, water temperatures of this zone were always relatively cool, not exceeding 19° C. Both upper and middle zones were heavily shaded by overhanging vegetation though higher water temperatures were recorded in the latter. In contrast, the lower zone was highly exposed, due to dyking and a lack of overhanging vegetation, so that water and air temperatures were usually similar.

Differences in aquatic and overhanging vegetation are noted in Table 2. For upper and middle zones the margins and immediate shoreline supported *Carex*, *Typha*, *Scirpus*, *Salix* and occasional stands of Phragmites. Further back were *Cornus*, poplar, alder and spruce. The leaves of these terrestrial plants, particularly *Salix*, formed a major part of the drifting detritus and striking differences were found between the three zones (Table 2).

The lack of drifting detritus in the lower zone, together with the sandy soil found there, limited silt to a minimum, and rendered a porous stream bed so that much of the flow, particularly in summer, was beneath the substrate. For the same reasons, waters of the lower zone were always of high transparency even in spring or after a storm, a contrast to other parts of the stream. Drought was experienced there in August and September, when no visible flow was evident, though there were occasional isolated pools.

Invertebrates from the three zones were recorded. Apart from Amphipoda, most of the differences were in degree. The upper and lower sections supported numerous free swimming insects such as Corixidae, Dytiscidae and Odonata, while benthic Hydropsychidae, Tipulidae and Tendipedidae were prominent in the middle zone.

High densities of fish species other than Rhinichthys were taken in both the upper and middle zones at all times of the year. In contrast, fishes were exceedingly scarce in the lower zone apart from the temporary presence of spawners from the lake.

(ii) Distribution and Abundance of Dace in the Three Ecological Zones

Sympatric populations of Rhinichthys c. cataractae and Rhinichthys atratulus meleagris were most abundant in the middle zone (Table 3). From the low numbers of fry taken in other zones it is probable that many dace found there are emigrants from the middle zone.

TABLE 3. Densities of dace in the seven basic environments within each of the three ecological zones of the Mink River for all collections, May - October, 1970.

Zone	Environment	Area sampled m^2	Species: Numbers of Longnose Captured F	J	A	Numbers/m^2	Numbers of Blacknose Captured F	J	A	Numbers/m^2
Upper	1	36	0	0	0	0	3	1	1	0.14
	2	72	0	0	1	0.01	0	2	7	0.13
	3	46	0	0	1	0.02	0	3	9	0.26
	4	not encountered								
	5	not encountered								
	6	10	0	1	4	0.50	0	0	0	0
	7	not encountered								
Middle	1	167	33	2	0	0.21	342	187	0	3.17
	2	397	4	3	3	0.03	28	120	124	0.69
	3	235	10	18	14	0.18	29	210	212	1.07
	4	475	122	56	110	0.61	222	308	335	1.82
	5	214	382	86	45	2.40	59	89	14	0.76
	6	296	54	134	212	1.35	12	51	116	0.61
	7	238	57	129	311	2.09	24	50	78	0.64

Zone	Environment	Area sampled m^2	Species: Numbers of Longnose Captured				Numbers of Blacknose Captured			
			F	J	A	Numbers/m^2	F	J	A	Numbers/m^2
Lower	1	not encountered								
	2	99	0	0	0	0	0	0	0	0
	3	269	0	0	0	0	2	3	10	0.06
	4	112	0	0	0	0	0	1	6	0.06
	5	84	7	14	2	0.27	0	0	0	0
	6	230	3	31	46	0.35	0	0	1	<0.01
	7	not encountered								

F - fry

J - juvenile

A - adult

The lower zone was devoid of dace for most of its length. However, a limited number of both species was taken immediately below the marsh in July. None were taken there in August, September, or October. Small numbers of longnose dace were taken at an isolated riffle 3 km from Dauphin Lake from May to September. Forty-five longnose were taken 7 km from the mouth of the stream, on a rocky wave-washed shore of the lake itself, an environment resembling a riffle.

The upper zone was not sampled very extensively, but longnose and blacknose dace were rare.

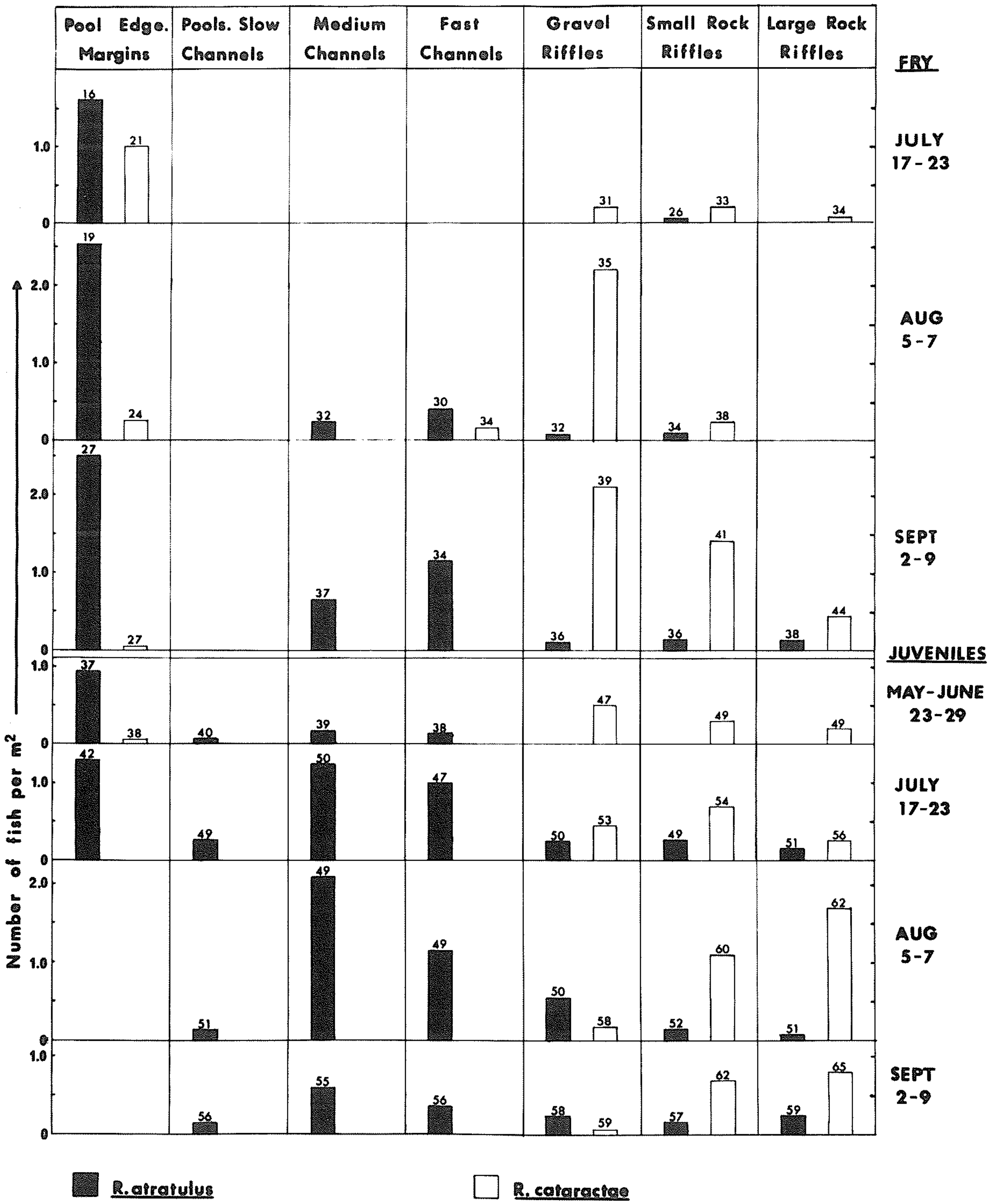
B. Distribution of Dace in Different Environments

The purpose of this section is to examine the distribution of the two species in different environments in the middle zone of the Mink R., and to determine if there is any spatial and/or temporal isolation during their life cycle. Differences in distribution of the sexes are also investigated. It is assumed that both species were caught in each environment with the same degree of efficiency.

(i) Distribution of Fry

In July, fry of both species were abundant around pool edges and in margins of the stream (Fig. 2). Longnose fry were larger than blacknose fry, a consequence of earlier spawning in the former species (Bartnik, 1970). Size ranges were 17-28 mm for longnose and 11-21 mm for blacknose. Lower densities of longnose fry were encountered in gravel and small rock riffles. These were larger fry than those taken in margins (Fig. 2), and ranged from 25-35 mm in fork length.

In August and September high concentrations of blacknose fry were maintained in margins of the stream. But considerable numbers of larger individuals, exceeding 25 mm in length were found in other environments, especially in medium and fast channels. In the same period nearly all the longnose fry disappeared from margins, moving into gravel and small rock riffles (Fig. 2). This transition took place, almost without exception, when the fish were



Pool Edge. Margins
Pools. Slow Channels
Medium Channels
Fast Channels
Gravel Riffles
Small Rock Riffles
Large Rock Riffles
FRY
JULY 17 - 23
AUG 5 - 7
SEPT 2 - 9
JUVENILES
MAY - JUNE 23 - 29
JULY 17-23
AUG 5-7
SEPT 2-9
Number of fish per m²
R. atratulus
R. cataractae

between 25 and 30 mm in length. In October qualitative sampling revealed that longnose were mainly in riffles, while blacknose were in channels, pools and beaver ponds.

(ii) Distribution of Juveniles

Distribution of juvenile dace in May and June was similar to that of fry in August and September (Fig. 2), though densities were lower in all environments owing to the increased flow in spring. The greatest concentrations of longnose juveniles were again in gravel riffles, while blacknose remained in high density in the shallow, silted margins of the stream.

From July to September, as they increased in size, longnose juveniles showed gradual changes in environment occupied, leaving gravel riffles for small rock riffles. Finally, in August and September, greatest concentrations were found in large rock riffles. Major changes in the environment of blacknose juveniles were meanwhile occurring. In July, approximately one year after hatching, large numbers of individuals reached a length of 45 mm (Fig. 2). Nearly all blacknose above this size had left the margins, mainly for medium and fast channels. By August 1970, when all juveniles exceeded 45 mm, this transition was complete (Fig. 2). Results for blacknose in September were basically similar to those obtained in August except that densities were somewhat lower in most environments. In October long stretches of the stream were seined in search of dace without success. Blacknose juveniles were found only in beaver ponds, from which they were taken with considerable difficulty. All longnose juveniles were caught under flat stones in large rock riffles.

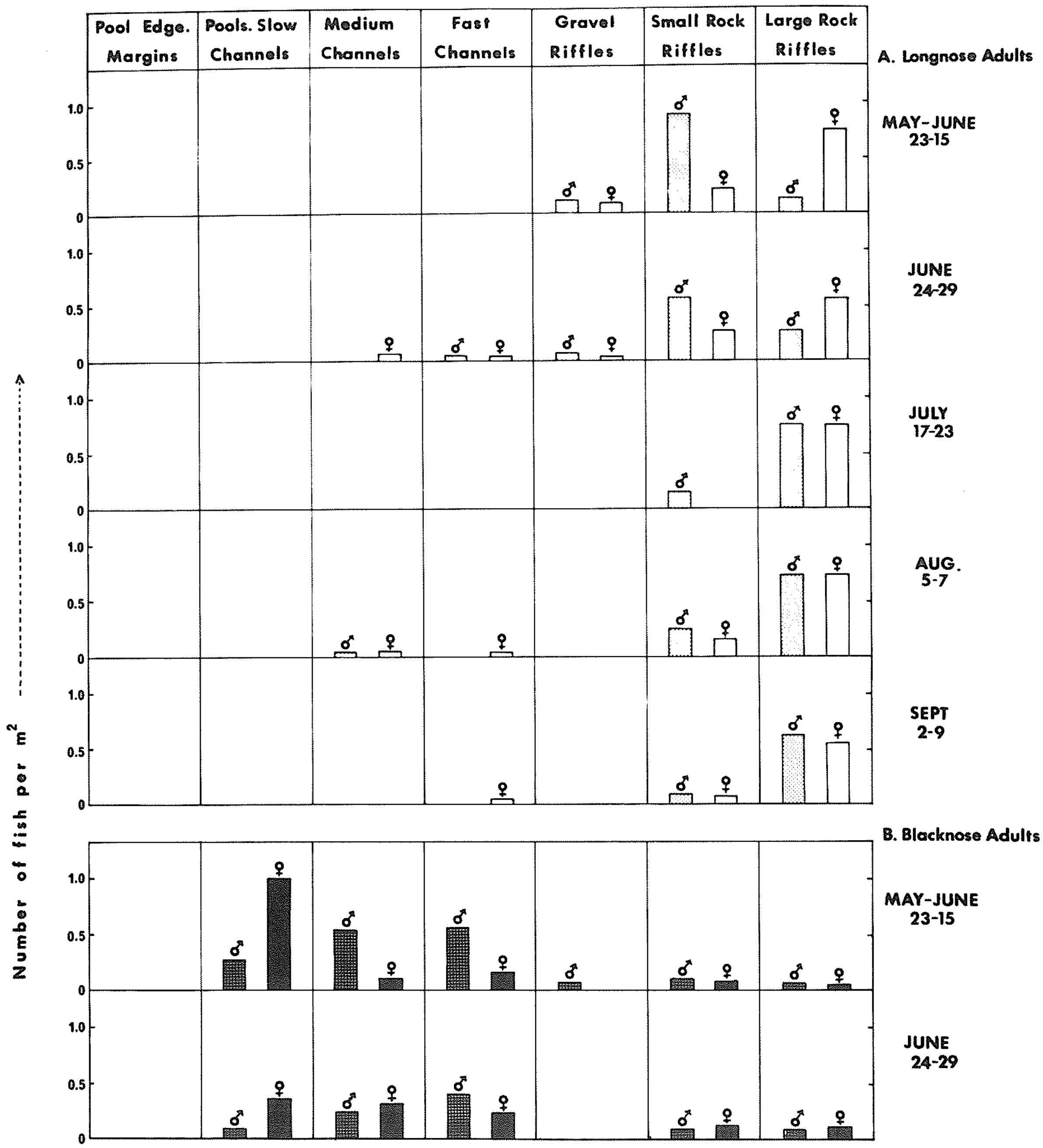
From frequency/length data longnose are adult by the following spring, almost two years after hatching. However, the majority of blacknose do not spawn until their third year (see appendix).

In their second year as juveniles blacknose were found mainly in medium and fast channels in July, August and September, a situation very similar to that of first year juveniles that have left the margins. During spawning in May and June, second year juveniles were commonly found in medium and slow channels.

(iii) Distribution of Adults

Adult dace are fish that spawned in May and June 1970. From frequency/length longnose were either second, third or fourth year individuals while the great majority of blacknose were in their third year.

In collections from May 23rd to June 15th longnose males were found in high density in small rock riffles, the place of spawning of this species (Bartnik, 1970). Lower densities of longnose males were found in gravel and large rock riffles (Fig. 3A). Females were taken, for the most part, in the latter environment. Smaller concentrations of mostly gravid females were taken in small rock riffles. In



Pool Edge. Margins
Pools. Slow Channels
Medium Channels
Fast Channels
Gravel Riffles
Small Rock Riffles
Large Rock Riffles
A. Longnose Adults
MAY-JUNE 23-15
JUNE 24-29
JULY 17-23
AUG. 5-7
SEPT 2-9
B. Blacknose Adults
MAY-JUNE 23-15
JUNE 24-29
Number of fish per m2
1.0
0.5
0

late June these differences in distribution of the sexes, though still significant, were much reduced. Few gravid females remained, and several large adults were taken in atypical environments, such as medium channels. These fish seemed near death, and most had fungal diseases and/or abrasions. Thereafter, from July to September, the majority of male and female longnose were found in high concentration in large rock riffles with no significant difference in sexual distribution. Much lower densities of adults were found elsewhere, for example in fast channels and small rock riffles. In October, adult longnose were taken only under flat stones in large rock riffles, with considerable difficulty.

Blacknose spawn in medium and fast channels (Bartnik, 1970). Results of sampling in May and early June 1970 gave high densities of males in these environments (Fig. 3B). Females, along with juveniles (>45 mm) were found mainly in slow channels. Females taken in medium and fast channels were often gravid, or actually spawning. Several adults were taken in large and small rock riffles so that some overlap with longnose exists. By late June (Fig. 3B) environmental differences between males and females were greatly reduced.

In late June and mid-July, a large proportion of the adult blacknose taken were extremely thin and emaciated in appearance. Furthermore, their numbers were greatly reduced in the latter month. It was therefore concluded the majority had died after spawning. Unfortunately the situation was complicated because larger second year black-nose juveniles had grown rapidly and closely resembled adults during this time. Spawners and non-spawners were therefore indistinguishable.

C. Food Present and Food Consumed

The purpose of this section is to investigate the food habits of different age classes of the two species, and to provide information on food availability and feeding behaviour. Collections of dace from the middle zone of the river were examined from May to October 1970.

(i) Food Present

Surber samples of invertebrate fauna were taken from a small rock riffle and a medium channel, typical environments of adult and juvenile longnose and blacknose dace, respectively, from June to October 1970.

In the riffle (Table 4), Hydropsychidae were the most numerous organism, and accounted for over 60% of the weight at every collection period. Of secondary importance by weight were Limnephilidae (June only) and Tipulidae (July to October). Baetidae and Tendipedidae were never very abundant, but are shown for subsequent comparison with food consumed. Other families (Table 4) which on more than one occasion accounted for over 1% of weight included Perlidae, Elmidae, Helicopsychidae and Tabanidae. The total number of organisms increased throughout the study period; while the total weight, after dropping slightly in July, increased from August to October.

The medium channel was a less productive environment than the small rock riffle, and consistent faunal differences were found between them (Table 4). Those families making

TABLE 4. Results of Surber sampling in a small rock riffle and a medium channel.

Date / Family	Area sampled 10 sq. ft. (0.93 sq. m.) Wt. in gms. 24-28 June No.	Wt.	%Wt.	17-23 July No.	Wt.	%Wt.	31 Aug.-1 Sept. No.	Wt.	%Wt.	5-7 October No.	Wt.	%Wt.
Small Rock Riffle												
Baetidae	12	0.03	0.7	62	0.15	4.5	24	0.05	0.6	42	0.06	0.3
Hydropsychidae	215	3.26	77.2	258	2.14	64.1	811	5.79	67.2	1272	12.53	70.8
Tendipedidae	15	0.04	0.9	56	0.20	6.0	72	0.15	1.7	12	0.01	0.1
Limnephilidae	4	0.48	11.3	0	0	0	8	0.08	0.9	30	0.33	1.7
Tipulidae	2	0.03	0.7	5	0.28	8.4	33	1.70	19.7	88	2.65	15.0
Others	28	0.38	9.1	112	0.57	17.0	198	0.85	9.9	237	2.12	12.0
Total	276	4.22	99.9	493	3.34	100	1146	8.62	100	1681	17.70	99.9
Medium Channel												
Baetidae	5	0.01	0.5	37	0.09	5.2	21	0.05	2.0	15	0.03	0.8
Hydropsychidae	39	0.28	13.6	76	0.52	30.1	187	0.86	34.1	140	1.17	29.5
Tendipedidae	42	0.07	3.4	191	0.39	22.5	362	0.57	22.6	46	0.06	1.5
Limnephilidae	11	1.51	73.0	5	0.56	32.4	2	0.02	0.8	1	0.03	0.8
Tipulidae	1	<0.01	0	1	0.01	0.6	4	0.11	4.4	17	1.29	32.5
Ephemeridae	0	0	0	0	0	0	2	0.17	6.7	3	0.31	7.8
Others	18	0.16	7.7	71	0.16	9.2	150	0.74	29.4	173	1.08	27.2
Total	116	2.07	100	381	1.73	100	744	2.52	100	395	3.97	100.1

the greatest contribution to biomass in this environment were, in order of importance: (a) June--Limnephilidae and Hydropsychidae, (b) July--Limnephilidae, Hydropsychidae and Tendipedidae, (c) August to September--Hydropsychidae and Tendipedidae, (d) October--Tipulidae and Hydropsychidae. Tendipedidae and Hydropsychidae were the most numerous families in all months from June to October. Ephemeridae were encountered only in the medium channel from the end of August to October. Other families (Table 4) which on more than one occasion contributed over 1% of the weight were Perlidae, Elmidae, Heptageniidae and Helicopsychidae.

Drift samples were also taken from June to October 1970. Plant debris was always the major constituent and accounted for over 90% of the weight at every collection (Table 5). Relatively few insects were taken and families were similar to those from bottom samples, with the addition of Corixidae, Gyrinidae, Sialidae and some terrestrial insects. However, far higher proportions, by weight, of Baetidae were encountered at all times in comparison with benthic samples, as were Limnephilidae in June and July.

(ii) Food Consumed

Two groups from each species were used in digestive tract analysis. These were; fish in their first twelve months of life, and fish over twelve months of age, i.e., adults and larger juveniles.

The food consumed by longnose and blacknose in their

TABLE 5. Results of drift sampling the middle zone.

Average numbers and weight (mg.) of drift organisms per 100 m^3 of water taken over 24 hours.												
Date	26 June 1970			22 July 1970			31 Aug. 1970			6 Oct. 1970		
Flora												
Total weight	23,551.8			29,854.6			116,145.2			51,001.8		
Major Constituents	Salix, algae, moss			Salix leaves			Salix & Taraxum			Leaves & seeds		
Fauna-benthic	No.	Wt.	%Wt.	No.	Wt.	%Wt.	No.	Wt.	%Wt.	No.	Wt.	%Wt.
Baetidae	2.8	17.2	7.5	2.5	14.1	19.0	1.8	12.7	10.0	4.2	20.5	6.3
Hydropsychidae	1.4	16.7	7.3	1.8	16.6	22.4	7.4	65.5	52.1	3.9	38.8	11.9
Tendipedidae	0.4	0.9	0.4	0	0	0	1.0	1.7	1.4	0.7	1.4	0.4
Limnephilidae	1.4	187.9	81.9	0.4	38.5	52.0	0	0	0	0	0	0
Tipulidae	0	0	0	0	0	0	0.4	23.5	18.7	3.5	213.4	65.6
Others	0.5	6.7	2.9	0.3	4.9	6.6	1.9	22.3	17.7	4.7	51.2	15.7
Total-benthic	6.5	229.4	100	5.0	74.1	100	12.5	125.7	100	17.0	325.3	99.9
Corixidae	0	0	0	0	0	0	6.1	77.8	18.0	39.5	523.7	100.0
Gyrinidae	0	0	0	00	0	0	21.3	346.2	80.1	0	0	0
Sialidae (adult)	0	0	0	43.2	290.3	98.4	0	0	0	0	0	0
Diptera (terrest.)	1.3	6.5	100.0	0.9	4.7	1.6	1.7	8.1	1.9	0	0	0
Total-nonbenthic	1.3	6.5	100.0	44.1	295.0	100.0	29.1	432.1	100.0	39.5	523.7	100.0
Total fauna	7.8	235.9	100	49.1	369.1	100	41.6	557.8	100	56.5	849.0	100

first twelve months was similar in quality with Tendipedidae, Hydropsychidae and Baetidae making the greatest contribution of any family by weight (Fig. 4). But the quantity of each item consumed varied throughout the year and differed between species.

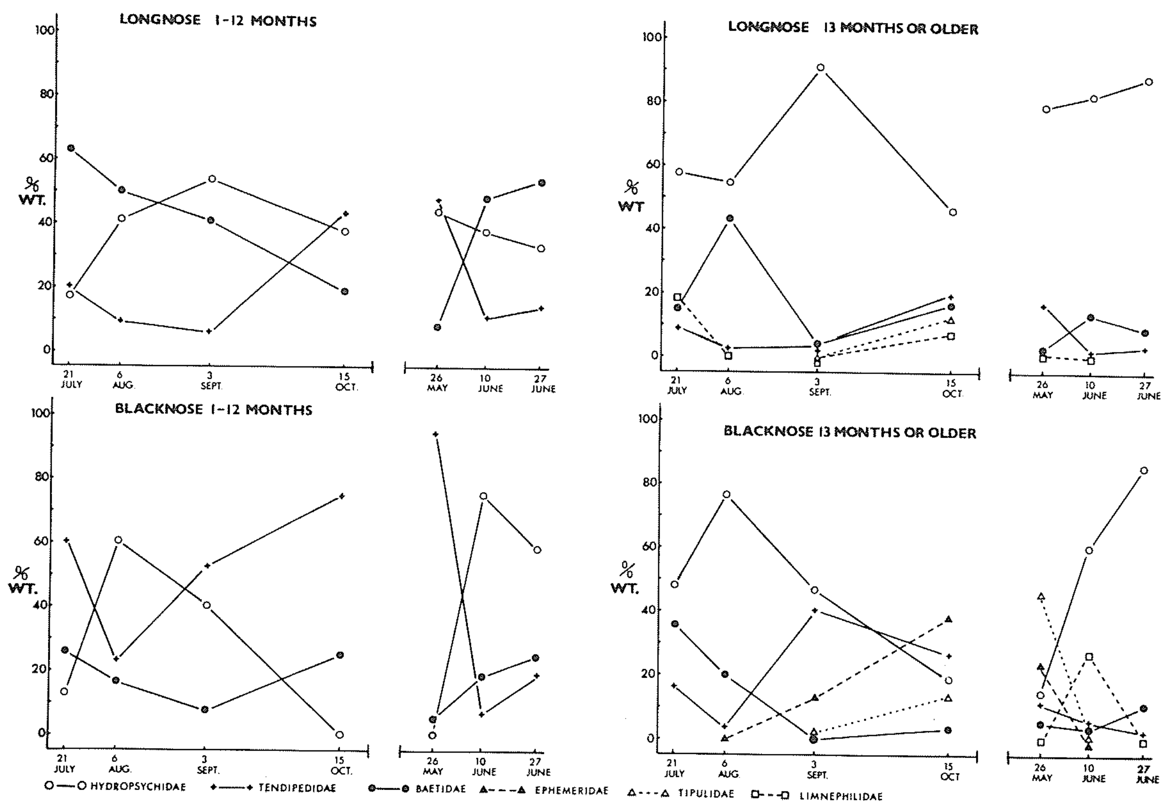
Adult and juvenile longnose and blacknose dace over twelve months of age also consumed similar items of food, consisting of Tendipedidae, Hydropsychidae, Baetidae, Limnephilidae and Tipulidae. Ephemeridae, eaten by blacknose dace were the only exception (Fig. 4). In both species Hydropsychidae accounted for over 50% of the weight of the diet from early June to September with Baetidae of secondary importance in late July and early August. But in May and October longnose dace continued to eat Hydropsychidae as the major item, while blacknose dace consumed mainly Ephemeridae and Tipulidae.

(iii) Forage Ratios

The forage ratio of a particular insect family was obtained by dividing the numerical percentage in the digestive tract by its numerical percentage in the benthic sample. This is one way of comparing the food present as bottom organisms with the food eaten by the fish (Usinger, 1956).

Forage ratios were calculated for the two age classes of each species of dace using the numerical percentage of food items present in benthic samples and in digestive

FIGURE 4. A seasonal comparison of the weight contributions of the more frequent insect families found in the digestive tract contents of both species of *Rhinichthys*.



LONGNOSE 1-12 MONTHS
LONGNOSE 13 MONTHS OR OLDER
BLACKNOSE 1-12 MONTHS
BLACKNOSE 13 MONTHS OR OLDER
% WT.
21 JULY
6 AUG.
3 SEPT.
15 OCT.
26 MAY
10 JUNE
27 JUNE
HYDROPSYCHIDAE
TENDIPEDIDAE
BAETIDAE
EPHEMERIDAE
TIPULIDAE
LIMNEPHILIDAE

tracts collected on the following dates:

Date of benthic sample	24-28 June	17-23 July	31 Aug-1 Sept.
Date of collection of fish for digestive tract analysis	27 June	21 July	3 Sept.

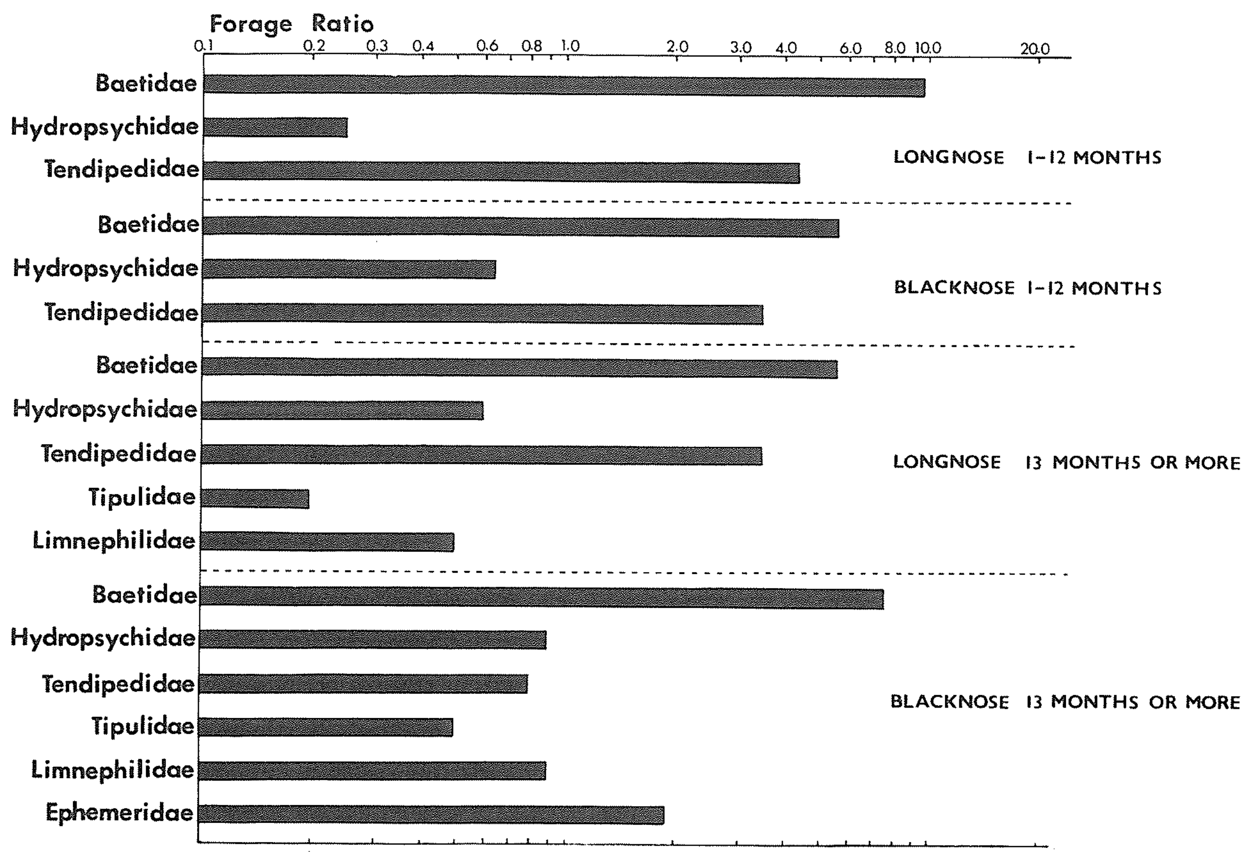
Forage ratios for blacknose dace were calculated using items collected in benthic samples from a medium channel, while samples from a small rock riffle were used to calculate forage ratios for longnose dace.

In the first year fish of both species Baetidae and Tendipedidae had high forage ratios (Fig. 5), especially in longnose. Hydropsychidae had low values, but considerable differences existed between the species. This family had 0.25 in longnose and 0.6 in blacknose. In fish over twelve months of age Baetidae again had very high values but Tendipedidae were less important in blacknose when they dropped to 0.8. Hydropsychidae, on the other hand, showed considerable increases in both species.

In first year fish of both species Limnephilidae, Tipulidae and Ephemeridae all had forage ratios of zero (not shown). In larger fishes Tipulidae and Limnephilidae were below one in both species, though each of these families had higher values in blacknose. Finally, Ephemeridae had a value of 1.9 in blacknose, but this family was not encountered in the riffle.

The high forage ratios found for Baetidae and

FIGURE 5. Forage Ratios for insect families in different age groups of longnose and blacknose dace.



Forage Ratio
0.1
0.2
0.3
0.4
0.6
0.8
1.0
2.0
3.0
4.0
6.0
8.0
10.0
20.0
Baetidae
Hydropsychidae
Tendipedidae
LONGNOSE 1-12 MONTHS
Baetidae
Hydropsychidae
Tendipedidae
BLACKNOSE 1-12 MONTHS
Baetidae
Hydropsychidae
Tendipedidae
Tipulidae
Limnephilidae
LONGNOSE 13 MONTHS OR MORE
Baetidae
Hydropsychidae
Tendipedidae
Tipulidae
Limnephilidae
Ephemeridae
BLACKNOSE 13 MONTHS OR MORE

Tendipedidae indicate that these families were either the most preferable or most available food groups. Results of drift sampling indicate the latter in the case of Baetidae. Other organisms, which are not shown in Fig. 4, and represented as "others" in Tables 4 and 5, all have very low forage ratios, and since they are unimportant as food items they are omitted in Fig. 5.

(iv) Coefficients of Similarity of Food

For comparison of the diet of different size groups within or between species, a coefficient of similarity can be calculated. (Whittaker and Fairbanks, 1958). The coefficient is derived from the formula: Cps. = 100 - 0.5 $\Sigma(a_i - b_i) = \Sigma\min(a_i, b_i \ldots)$, where a_i is the percentage of category i in the diet of species a, and b_i is the percentage of category i in the diet of species b. Calculation was based on the percentage weight contribution of each insect family and applied to the diet of (i) fish of the two species in their first twelve months,(ii) fish of the two species thirteen months or over, (iii) fish of the same species from the two age groups mentioned above.

Table 6 shows these coefficients of similarity. Values form 0-33% indicate a dissimilar diet, while 33-66% indicates moderate similarity and values above 66% a very high similarity.

The diet of longnose and blacknose in their first year is consistently moderately similar. For fish of the

TABLE 6. Coefficients of percentage similarity of diet.

Date	Type of Comparison: Interspecific		Intraspecific	
	BN_1 v LN_1	BN_2 v LN_2	BN_1 v BN_2	LN_1 v LN_2
21st July	59	72	55	41
6th August	67	77	74	87
3rd Sept.	53	50	81	61
15th October	63	42	30	73
Winter				
26th May	53	31	17	63
10th June	63	68	69	53
27th June	71	97	72	44

BN_1 - blacknose 0 - 12 months

BN_2 - blacknose 13 months or more

LN_1 - longnose 0 - 12 months

LN_2 - longnose 13 months or more

two species over twelve months of age the diet is highly similar in June, July and early August. However in September, October and May the diet was dissimilar or moderately similar.

A similar phenomenon is seen when comparing the diet of the two size groups of blacknose dace. Their diet was usually moderately or highly similar except in October and May.

The diet of the two size groups of longnose dace was similar throughout the year especially in early August and mid-October.

DISCUSSION

Coexistence of sympatric populations of longnose and blacknose dace is made possible by temporal isolation of fry and by spatial isolation between older individuals into different environments throughout the life cycle. Water velocity, depth and substrate are important. However, the diet of the two species is strikingly similar during most of the growing season. Dace were most abundant in the middle zone of the Mink River.

A. Distribution and Abundance of Dace Along the Length of the Mink River

The average gradient and the amount of drifting detritus influence a wide variety of other physical and biological factors. These were considered the most important primary variables in indirectly determining the distribution and abundance of dace.

Gradient is of major importance in determining the range of water velocities and the type of substrate. It is in areas of steep gradient that riffles or channels with rock or gravel bottoms are encountered and these provide a suitable environment for both species. Longnose dace have been widely reported in the literature as being confined to riffle areas in cool streams of high gradient. Becker (1962) found longnose in turbulent water over gravel and rubble substrates in streams of high gradient. He took few specimens from the Plover River, which has a milder gradient. Gee and Northcote (1963) noted that longnose were most abundant in riffle areas of the Fraser River. Kuehn (1949), Reed (1959), Bartnik (1970) and others all emphasize the prevalence of longnose in riffles, which are, by their nature, characteristic of moderate or steep stream gradient.

The importance of stream gradient has also been emphasized for blacknose dace. Burton and Odum (1945), working on a tributary of Craig Creek, found a stretch of moderate gradient approximately 6m/km, then a long stretch of low gradient followed by steep gradient of 16m/km. Blacknose dace were absent from the slow section, but present in the stretches of higher gradient. However, in another creek of exceptionally steep gradient (63m/km) black-nose were uncommon or absent. The first case is similar to that found in the Mink River, where the middle zone had an average gradient (Table 2) of 7m/km and supported high densities of both species of dace. In other zones, which had a lower gradient dace were uncommon or absent. Starret (1950) found that western blacknose dace appear limited in distribution to upper stretches of small creeks. Such limitation to small streams, usually not more than ten feet wide, and of steeper gradient than is found in sluggish prairie streams, has been generally found for the species. Paloumpis (1958) did not find blacknose dace in streams of low gradient during three years of collecting, while studying the responses of minnows to flood and drought.

The importance of plant debris, such as fallen leaves, to stream fauna has been demonstrated by Egglishaw (1964). He has shown that the micro-distribution of most of the fauna is correlated with the amount of organic detritus, and that insects seek it out and concentrate on it. Minshall (1967), Ulfstrand (1968) and others have emphasised that allochthonous plant material is the most important primary source of energy for stream fauna, and is made available to higher trophic levels, such as fishes, through the activities of detritus feeding insects. The productive capacity in the valley and the amount of over-hanging vegetation is therefore more important than primary production in the stream itself, which may, due to shading, be very low, and yet apparently support a dense fauna (Hynes, 1970). The upper and middle zones of the Mink River contained large amounts of drifting detritus and supported dense faunas of fishes, though the two species of Rhinichthys were uncommon in the upper section for reasons of gradient mentioned above. Very little plant detritus was taken in drift samples from the lower section and the density of all fish species was exceedingly low. Little overhanging vegetation was present in this zone, and furthermore the marsh acts as a filter for organic material from upstream. Emergent waters from this marsh, which also acts as a powerful geographic barrier, were of high transparency.

Therefore, a steep gradient and abundant plant detritus render the appropriate substrates and insect fauna which favour the presence of both species of Rhinichthys.

B. Environments Occupied by Rhinichthys sp. During their Life Cycle

For most of their life cycle longnose and blacknose dace exhibit a marked degree of spatial segregation into different environments, and though fry of both species may be found together for short periods in shallow pools or margins of little or no current, considerable temporal isolation exists.

Prior to discussing their distribution in different environments something must be mentioned about age and growth in each species. For the western blacknose dace Hubbs and Cooper (1936) state that "Most blacknose dace do not reach maturity until the third summer of life; probably very few spawn in their second summer." Frequency length data from the present study are in complete agreement with these findings. For longnose dace Reed (1959), working in Pennsylvania, found adult fish in their second, third, fourth and fifth years. The sex ratio was equal in the second and third years, but more females than males were found in their fourth summer, and all fifth year fish were females. Similar results were obtained in the present study, but no fifth year fish were encountered. However, Reed was working in a more southern latitude and far larger, and perhaps older, specimens of longnose were taken.

In laboratory experiments simulating field conditions Bartnik (1970) found the first longnose spawning act 18 days prior to the first blacknose spawning. Collections from the field revealed peaks of gonad weight/body weight an average of two weeks earlier for longnose. Assuming a similar rate of egg development for both species, longnose therefore emerge from the substrate earlier and are present in the margins before blacknose fry. Sampling in mid-July and early August revealed that longnose fry grow extremely rapidly and by the latter month the majority had moved out into gravel riffles. Longnose and blacknose fry are therefore together for only a short time. Longnose were between 25 and 30 mm when they left the margins for fast water (>45cm/sec). Gee (personal communication) has found that about this size (18-27 mm) this species can make its maximum buoyancy adjustment, from near neutral to high degree of negative buoyancy. Jones (1957), Nelson (1961) and Gee (1968) have all noted the advantages of negative buoyancy in fast water, which is attained by reducing swimbladder volume. On the other hand, blacknose between 25 and 30 mm remained mostly in still shallow water (eg., pool edges and margins). Fish of a similar size--18-29 mm are incapable of making a significant buoyancy adjustment and remain at near neutral buoyancy (Gee personal communication). The majority of blacknose remained in the shallow margins until they were

45 mm fork length, a period of almost twelve months. A smaller proportion were found in moderate current (20-45cm/sec) between lengths of 25 and 45 mm. Gee (personal communication) has found that at a mean length of 32 mm blacknose are capable of adjusting buoyancy from neutral to negative by decreasing swimbladder volume. The ability to adjust increases with size in this species. The fact that blacknose fry live in shallow waters appears adaptive in combatting predation. The major piscivorous fish in the Mink River was the creek chub, Semolitus atromaculatus, and this species was commonly taken in slow, deep channels.

The separation of adult longnose and blacknose into riffle and channel environments seems fairly clear cut. There is limited overlap. Each species seems best adapted to swim and feed in its own environment. Bartnik (1970) has found that this spatial segregation extends to nesting sites. The redds of longnose dace were in small rock riffles, while those of blacknose were mainly in gravel in velocities of 22.5 to 45 cm/sec (= medium and fast channels).

Results from the late fall, when ice cover was already present in places, indicate that blacknose move into beaver ponds for the winter, while longnose remain in large rock riffles sheltered under flat stones.

The study of environments demonstrates a remarkable amount of segregation between the species and this may be the most important factor in their coexistence.

C. Diet of the Two Species

In contrast to their spatial distribution, diet of the two species was, at times, strikingly similar. Larkin (1956) has noted that freshwater fishes are generally not highly specialised feeders and when occuring together may eat the same kinds of food but in different proportions. This situation did occur through part of the study period, but in certain months, eg., June, July and August for larger longnose and blacknose the proportion that each insect family contributed by weight was also similar. Divergences in their diet in September, October and May, were almost certainly the result of blacknose having moved into slower, deeper waters, such as those of beaver ponds, during these months. Ephemeridae, which burrow in sand and mud, are abundant in this environment, whereas Hydropsychidae are scarce. This is reflected in the change in diet of larger blacknose which switched from Hydropsychidae to Ephemeridae and Tipulidae during these months. Longnose remained in riffles and Hydropsychidae was maintained as the most important food family.

For fish in their first twelve months both species fed almost exclusively on Baetidae, Hydropsychidae and Tendipedidae, but their proportions differed. Longnose fed mainly on the first two families while blacknose ate more Tendipedidae. The small rock riffle generally contained more Baetidae and Hydropsychidae and less Tendipedidae than the medium channel, so that differences in diet appear to be the result of faunal differences between the environments occupied by the two species. Dace in this size group did not eat Limnephilididae, Tipulidae and Ephemeridae. Nymphs or larvae from these families were probably too large for small fish to eat.

It is apparent that longnose and blacknose exhibit considerable plasticity in their diet. For example Gerald (1966) found that for adult longnose Baetidae were the most important food item by volume, while Hydropsychidae were of minor importance. In the present study Hydropsychidae were always the most important item by weight. However, results of benthic sampling were also different in the two studies. Hydropsychidae made up a far smaller proportion of the weight in Gerald's study compared with mine. Yet, despite these differences, similar forage ratios were derived for a number of insect families. For example, in both studies Baetidae had the highest forage ratios while Hydropsychidae were always below unity.

D. Coexistence and Conclusions

The occurrence of sympatric species that have similar diets but live in different environments is unusual in fresh water fishes. Differences in diet are usually comparable with, or greater than, the degree of spatial segregation. For example, Gee and Northcote (1962) found that _Rhinichthys cataractae_ occupied riffles and fed on aquatic insects while yearling and older _Rhinichthys falcatus_ remained in slow water and fed heavily on terrestrial insects when present. Balesic (M.S. 1971) working on four species of darter (_Percina_ and _Etheostoma_ sp.) found that in the majority of cases they were in different environments. However, when they were in the same environments they tended to feed on different foods. Other studies eg., between different species of _Coregonus_ (Lindstrom and Nilsson, 1962) and between trout and char (Svardson, 1949) show similar phenomena. The food available to _Rhinichthys cataractae_ and _Rhinichthys atratulus_ may be in short supply for both species, but owing to spatial segregation, coexistence becomes possible since different portions of the same food crop are utilized. It has been noted that some spatial overlap occurs between the species, but even here the two species may still consume different portions of the food supply since longnose feed mainly between and under rocks and stones, while blacknose concentrate on upper and down-stream surfaces (see appendix).

The above situation has been demonstrated by Heatwole and Davis (1965) in three species of ichneumon wasp (_Megarhyssa_ sp.) all of which parasitize the wood boring larva of the pigeon tremex, _Tremex collumba_, and have a very similar ecology. These larvae are found at varying depths in the wood, and since a female Megarhyssa must insert the full length of her ovipositor to successfully parasitize a larva, it follows that only a certain percentage are available to the wasp. Since the three species have significantly different ovipositor lengths with respect to their means and standard deviations, it is evident that they do not compete for the same larvae, but parasitize different segments of the total host population.

Interactive segregation, the process by which ecological differences between species are magnified by interaction, may be a factor in the divergence of *Rhinichthys cataractae* and *Rhinichthys atratulus* into different environments. However, this cannot be clearly demonstrated without also studying the species when they are allopatric. Since *R. cataractae* has a much greater geographic range this remains a possibility.

If interactive segregation occurs between sympatric species then there are two possible outcomes, depending on the relationship of fundamental niches (Miller, 1967).

(a) In the case of overlapping niches: species A and B have fundamental niches which show partial overlap. In this case one or both species withdraw from part of the fundamental niche so that overlap no longer occurs.

(b) In the case of the included niche: the fundamental niche of species A lies entirely within that of species B. In this case it is axiomatic that species A be the superior competitor, otherwise extinction would result.

Species B survives outside the zone of overlap.

Phenotypic plasticity of buoyancy (Gee, personal communication) allows longnose dace to occupy the complete range of water velocities available in the Mink River whereas blacknose are much more restricted and seem never able to attain the reduced buoyancy required to occupy fast riffles. A situation similar to (b) above may therefore occur with blacknose displacing longnose from slower velocities. Longnose were found, on occasion, in still waters remote from a riffle, in the upper zone of the stream (Bob Moshenko, personal communication).

Thus *R. cataractae* and *R. atratulus* coexist because to a great extent they live in different environments. Both species require a moderate to steep stream gradient and an abundance of benthic insects, which appear to feed primarily on plant detritus such as fallen leaves. In all studies to date longnose are found mainly in riffles, while blacknose are found in channels of moderate velocity. Both species feed mainly on benthic insects and their diet is quite similar. Considerable plasticity is exhibited in their food habits, but results of this and one other study indicate that an underlying preference for certain food items exists.

LITERATURE CITED

LITERATURE CITED

Balesic, H. 1971. Comparative ecology of four species of darter (Etheostominae) in Lake Dauphin and its tributary, the Valley River. M. Sc. Thesis, University of Manitoba. 77 p.

Bartnik, V. G. 1970. Reproductive isolation between two sympatric dace, Rhinichthys atratulus and Rhinichthys cataractae, in Manitoba. J. Fish. Res. Bd. Canada 27:2125-2141.

Beauchamp, R. S. A., and P. Ullyott. 1932. Competitive relationships between certain species of fresh water triclads. J. Ecol. 20:200-208.

Becker, G. C. 1962. Intraspecific variation in Rhinichthys c. cataractae (Valenciennes) and Rhinichthys atratulus meleagris Agassiz and anatomical and ecological studies of Rhinichthys c. cataractae. Ph.D. Thesis, University of Wisconsin. 279 p.

Brian, M. V. 1956. Segregation of the ant genus Myrmica. J. Anim. Ecol. 25:319-337.

Burton, G. W., and E. P. Odum. 1945. The distribution of stream fish in the vicinity of Mountain Lake, Virginia. Ecology 26(2):182-194.

Egglishaw, H. J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. J. Anim. Ecol. 33:463-476.

Gee, J. H. 1968. Adjustment of buoyancy by longnose dace (Rhinichthys cataractae) in relation to water velocity. J. Fish. Res. Bd. Canada. 25:1485-1496.

________, and T. G. Northcote. 1963. Comparative ecology of two sympatric species of dace (Rhinichthys) in the Fraser River system, British Columbia. J. Fish. Res. Bd. Canada 20(1):105-118.

Gerald, J. W. 1966. Food habits of the longnose dace, Rhinichthys cataractae. Copeia 1966(3):478-485.

Heatwole, H., and D. M. Davis. 1965. Ecology of three sympatric species of parasitic insects of the genus Megarhyssa (Hymenoptera: Ichneumonidae) Ecology 46:140-150.

Hubbs, C. L., and G. P. Cooper. 1936. Minnows of Michigan. Bull. Cranbrook. Inst. Sci. No. 8:95.

________, and K. F. Lagler. 1958. Fishes of the Great Lakes Region. Ann Arbor. The Univ. of Michigan Press. 213 pp.

Hynes, H. B. N. 1970. The ecology of stream insects. Ann Rev. Entomol. 15:25-42.

Johannes, R. E., and P. A. Larkin. 1961. Competition for food between redside shiners (Richardsonius balteatus) and rainbow trout (Salmo gairdneri) in two British Columbia lakes. J. Fish. Res. Bd. Canada 18:203-220.

Jones, F. R. Harden. 1957. The swimbladder. In Margaret E. Brown (ed.), The Physiology of Fishes. Vol. II. Academic Press, Inc., New York. pp. 305-322.

Kohn, A. J. 1959. The ecology of Conus in Hawaii. Ecol. Mongr. 29:47-90.

Kuehn, J. H. 1949. A study of a population of longnose dace (Rhinichthys c. cataractae). Proc. Minn. Acad. Sci.17:81-87.

Lagler, K. F., J. E. Bardach, and R. R. Miller. 1962. Ichthology. John Wiley and Sons Inc., New York. 545 pp.

Larkin, P. A. 1956. Interspecific competition and population control in freshwater fish. J. Fish. Res. Bd. Canada 13:327-342.

________ and S. B. Smith. 1953. Some effects of the introduction of the redside shiner on the Kamloops trout in Paul Lake, British Columbia. Trans. Amer. Fish. Soc. 83:161-175.

Lindstrom, T. and N.-A. Nilsson. 1962. On the competition between whitefish species. In Le Cren, E. D., and M. W. Holdgate (eds.) The Exploitation of Natural Animal Populations. Blackwell Scientific Publications, Oxford. pp. 326-340.

Miller, R. S. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. Ecology 45:256-272.

________. 1967. Patterns and processes in competition. Advances in Ecol. Res. 4:1-74.

Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology, 48:139-149.

Moore, E., J. R. Greeley, C. W. Greene, H. M. Faigenbaum, F. R. Nevin and H. K. Townes. 1934. A problem in trout stream management. Trans. Amer. Fish. Soc. 64:68-80.

Nelson, E. M. 1961. The comparative morphology of the definitive swim bladder in the Catostomidae. Am. Midland Naturalist, 65(1):101-110.

Nilsson, N.-A. 1966. Interactive segregation between fish species. In Shelby D. Gerking (ed.) The Biological Basis of Freshwater Fish Production. Blackwell Scientific Publications, Oxford. pp. 295-313.

Paloumpis, A. A. 1958. Responses of some minnows to flood and drought conditions in an intermittent stream. Iowa State College Journ. of Sci. 32:547-561.

Reed, R. J. 1959. Age, growth and food of the longnose dace, Rhinichthys cataractae in northwestern Pennsylvania. Copeia 1959:160-162.

Schlick, R. O. 1966. Food competition between trout and dace in the North Pine River, Manitoba. M. Sc. Thesis, University of Manitoba, 43 pp.

Starrett, W. C. 1950. Food relationships of minnows of the Des Moines River, Iowa. Ecology 31(2):216-233.

Svardson, G. 1949. Competition between trout and char (Salmo trutta and Salvelinus alpinus). Rep. Inst. Freshwater Res. Drottingholm 29:108-111.

Ulfstrand, S. 1968. Benthic animal communities in Lapland streams. A field study with particular reference to Ephemeroptera, Plecoptera, Trichoptera and Diptera Simuliidae. Oikos Suppl. 10:129pp.

Usinger, R. L. 1956. Aquatic insects of California. Univ. Calif. Press, Berkeley and Los Angeles. 508pp.

Whittaker, R. H., and C. W. Fairbanks. 1958. A study of plankton copepod communities in the Columbia Basin, southeastern Washington. Ecology 39:46-65.

APPENDICES

APPENDICES

1. Other Species of Fish Taken in the Mink River.

Approximately 20,000 fishes other than Rhinichthys c. cataractae and Rhinichthys atratulus meleagris were taken in the Mink River from May to October 1970. Of these, the pearl dace, Semolitus marginata was the most abundant species from headwaters to marsh. Other species that were numerous in this region were: the common shiner, Notropis cornutus; the creek chub, Semolitus atromaculatus; the brassy minnow, Hybognathus hankinsonii; the white sucker, Catostomus commersoni; the johnny darter, Etheostoma nigrum; and the brook stickleback, Culaea inconstans. Occasional fathead minnow, Pimephales promelas were also taken.

The lower stations supported a very different fish fauna. Of the above mentioned species, only the white sucker and johnny darter were commonly found here, though a limited number of the others mentioned were taken immediately below the marsh in early summer. Instead several new species were encountered, all of which migrate from the lake. Fry of the northern pike, Esox lucius, were taken in late May but adults had by this time disappeared. These pike fry, though growing rapidly, decreased in number throughout the summer and fall. Few were taken in October.

Adult white suckers of 0.5-2.0 kg., much larger than those encountered in populations above the marsh, were taken in May but had disappeared from the stream by the end of June. Sucker fry were found in May and June. Finally adults of three other species of darter *Percina caprodes*, *Etheostoma exile* and *Percina shumardi* were found throughout the lower section until August.

2. Age and Growth in Longnose and Blacknose Dace.

From May to September 1970, 1,932 longnose and 2,371 blacknose dace were measured for length/frequency information. For many of the months the division into separate year classes was by no means clear. Blacknose were generally the easier species to age, particularly in July, August and September (see Fig. A). In longnose the situation is complicated by a pronounced sexual dimorphism. In order to overcome this problem separate graphs of frequency/length were plotted for males and females, revealing that, within each year class, females tend to be larger. Fig. B is derived from the results of these findings.

Figures A and B show that fry of both species grow extremely rapidly from July to September, so that by the latter month overlap may already occur with the preceeding age class. However, the growth rate appears to be rather low from September to May in both species. Longnose from years II, III and IV were found in spawning condition, but nearly all adult blacknose were year III fish.

FIGURE A. Frequency/length data for blacknose dace showing suspected divisions between year classes.

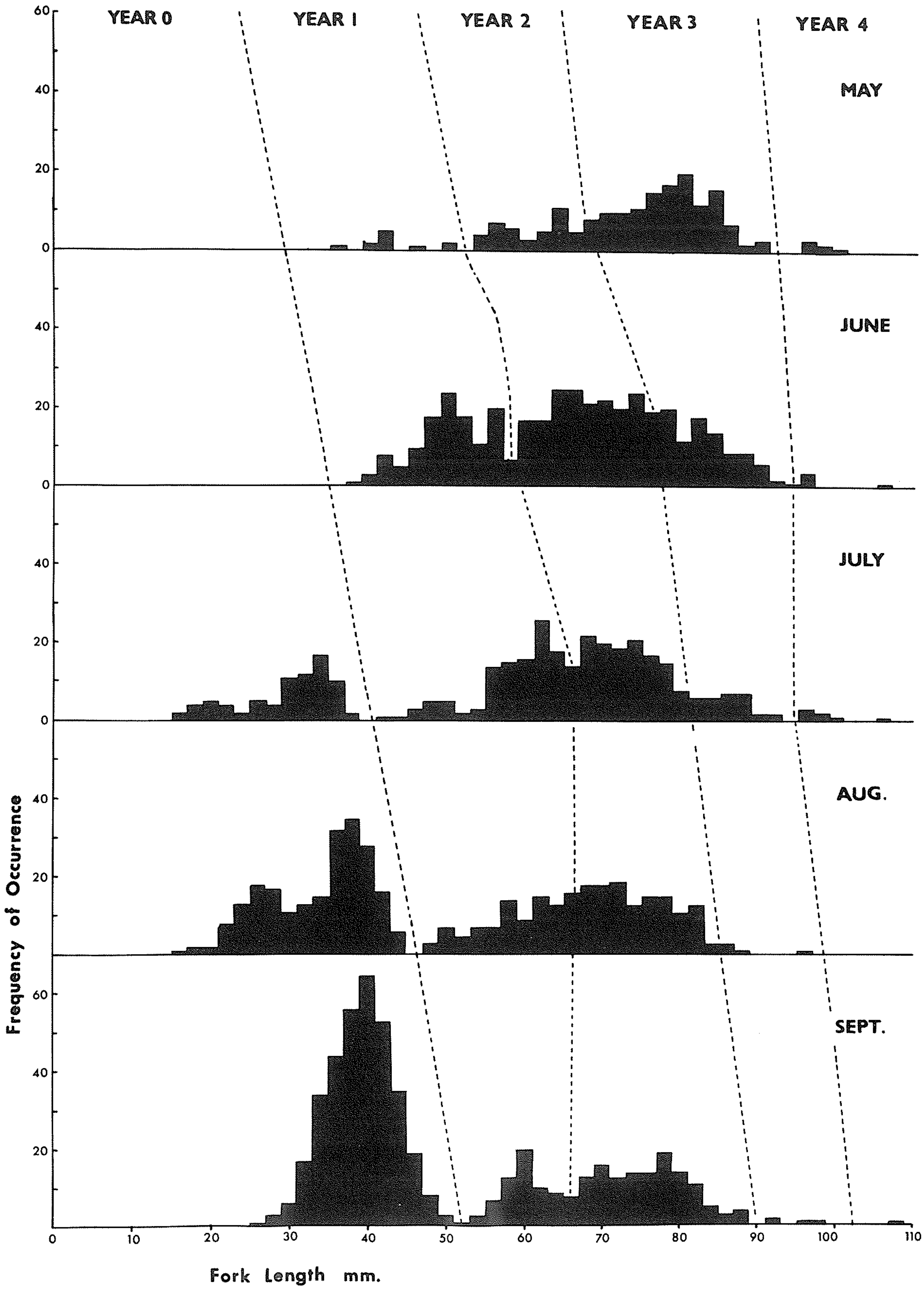
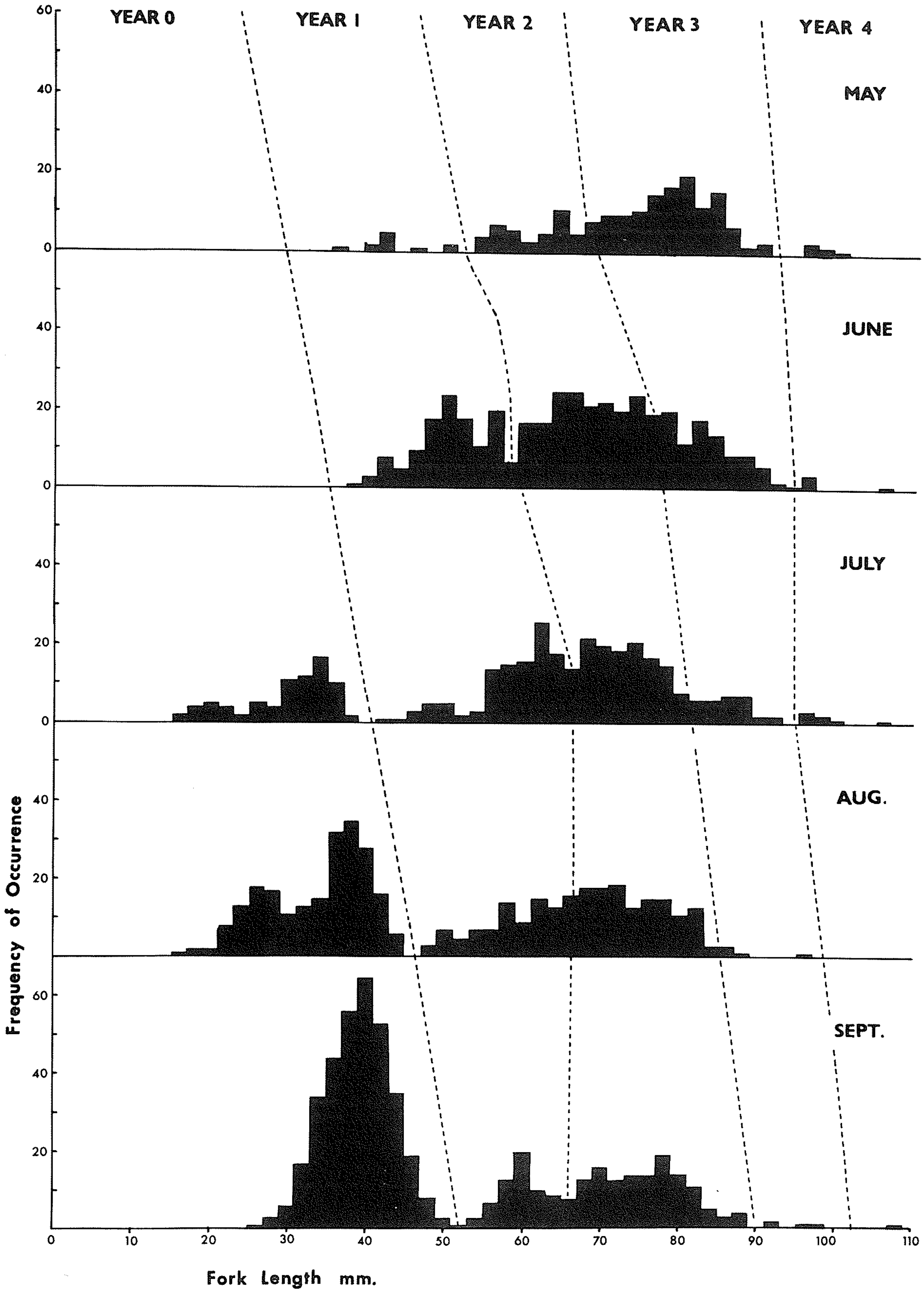

YEAR 0
YEAR 1
YEAR 2
YEAR 3
YEAR 4
MAY
JUNE
JULY
AUG.
SEPT.
Frequency of Occurrence
Fork Length mm.
0
10
20
30
40
50
60
70
80
90
100
110

FIGURE B. Frequency/length data for longnose dace showing approximate divisions of year classes after derivation by other means (see text).



YEAR 0
YEAR 1
YEAR 2
YEAR 3
YEAR 4
MAY
JUNE
JULY
AUG.
SEPT.
Frequency of Occurrence
Fork Length mm.

3. Feeding Behaviour

Dace were observed in the stream at intervals from June 3 to September 5, 1970. Within each species two size groups could be arbitrarily defined on the basis of differing behaviour patterns, partly the result of environmental differences.

Longnose young-of-the-year, 25-45 mm in length were observed mainly in gravel and small rock riffles. Usually they were not more than 1 cm off the bottom. Groups of three to ten fish were commonly observed obtaining food mainly from the surfaces of, and between, algae encrusted stones and rocks. While feeding the body is tilted downwards, facing into the current at angles between 20° and 45° to the horizontal.

Longnose juveniles and adults 50-100 mm in length form a second group. They were observed mainly in large and small rock riffles. In these environments the swiftest waters are encountered. However, in the vertical layer from the water-substrate interface to approximately 5 cm above, still water or even a backcurrent often exist. It is here that larger longnose spent most of their time. Unlike young-of-the-year, fish in this group spend a high proportion of their time in a stationary position on the bottom, aided by observable negative buoyancy, and by outstretched pectoral and pelvic fins, which help to maintain position, since they are normally placed in crevices or depressions between rocks. This habit increased from less than 30% of the observation time in June, when fish were spawning and territorial, to over 90% in September when water temperatures were below 15° C. These fish swim extremely close to, or actually in contact with the bottom, except when making extremely rapid darting movement. In the latter case, when moving upstream, they may rise to 10 cm above the substrate, and travel a distance of 1 metre.

A hovering motion was also observed, in moderate to swift current. Position is maintained by gentle undulation of the tail, with anterior end of the pectoral fins sloping downward. Food is approached from any direction even in strong currents. In feeding the long snout is inserted into narrow crevices between rocks with short, rapid thrusts at food. Often the snout appears to be used as a wedge and considerable disturbance of stones and small rocks can occur. The body can be held at many angles during feeding, and is often upside down. Longnose adults were also seen feeding on limnephilid caddisfly larvae. The tip of the snout is pushed into the case and the larva, or part of it, is extracted by a series of rapid jerky, movements backwards. Other methods of feeding included snapping at drift while hovering or swimming against the current, and light browsing over the surface of rocks from an almost stationary position on the bottom. It appears that olfactory and tactile senses are important in feeding. From time to time solitary individuals were seen for brief intervals passing through pools.

However, in pools feeding was never observed and longnose appeared to be disturbed in this environment. The fins stirred up clouds of silt on the bottom and the fish would move through into faster water without pause. Most of the larger longnose were either solitary, or in small groups of two to five fish. At times, two fish were seen lying side by side on the bottom.

Blacknose dace from 20-45 mm form the third group. These fish were observed mainly in shallow water of little or no current. Large numbers of these juvenile blacknose were seen in June. In association with them were larger less numerous juvenile creek chub. Definite shoals of ten to fifty fish containing both species were observed moving slowly along the margins. Their food appeared to be suspended matter such as drift and detritus, as well as midge larvae, presumed abundant here. Foraging was observed at all levels from the surface downwards, and at times benthic matter was taken. At this stage of development the mouth is narrow and almost terminal. In channels these fish have problems maintaining themselves against current, but in the sheltered, silted pools they swim with ease in all directions. In August and September blacknose fry were observed in the same environment and their manner of swimming and feeding is very similar to that of the juveniles in June.

Blacknose adults, and juveniles above 45 mm in length are found in a variety of environments, but chiefly in medium and fast channels of shallow to moderate depth. Small groups of 3-10 fish swimming 2-5 cm above the bottom were commonly observed. Feeding takes place mainly on the upper and downstream surfaces of algae encrusted rocks 5-15 cm in diameter. These are usually situated at the boundary between slow deep water and shallow rapids. Blacknose dace were observed darting up to these sites and rasping at attached materials with one to several nibbling bites. During this process the snout is tilted downwards and the fish faces upstream on most occasions. Unlike longnose adults, blacknose dace very rarely rest on the bottom and the angle of the body is seldom more than 50° to the horizontal. The mouth is subterminal and food is approached from downstream or the side. These fish were able to extract whole caddisflies from their cases, but the process was not observed in detail. Some drift feeding was observed on occasion. By turning over submerged rocks one quickly attracts large numbers of blacknose dace, which feed voraciously on the newly exposed food. These fish were seldom observed in swift, turbulent water and then only temporarily. However, at times blacknose were seen in eddies behind very large rocks in riffles. A blacknose adult was observed moving upstream in a large rock riffle in August. Halfway through the fish paused for three minutes, gasping on the bottom, apparently exhausted. It then continued upstream. This was the only occasion upon which a blacknose was observed resting on the bottom.