FOOD COMPETITION BETWEEN
TROUT AND DACE IN
THE NORTH PINE RIVER,
MANITOBA.

A THESIS
Presented to
The Faculty of Graduate Studies and Research
University of Manitoba.

In Partial Fulfillment
of the Requirements for the Degree
Master of Science.

by
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May, 1966.

ACKNOWLEDGEMENTS

I wish to thank Dr. H.E. Welch, Chairman of the Department of Zoology, for his guidance and instruction as my thesis supervisor. Thanks are also extended to Dr. F.J. Ward, Department of Zoology, for his constructive criticism of the thesis.

I am indebted to the late Dr. D.R. Franklin, who suggested this interesting study, and to Dr. E.T. Garside for field assistance and guidance on this project.

This study could not have become a reality without the help of the Manitoba Fisheries Branch which supplied the necessary equipment, manpower, financial assistance and time in which to write this report. Mr. B. Kooyman and Dr. K.H. Doan, of the Fisheries Branch, have been a constant source of encouragement in the trying moments of my field work.

Limitations of space prohibit the naming of all those who contributed to my study. These include Conservation Officers, Fisheries Branch Technical Staff, and Graduate Students of the Department of Zoology. A special thanks is extended to Mrs. Catherine Worden for typing this thesis.

APPROVAL SHEET

ABSTRACT

Interspecific competition for food between eastern brook trout (Salvelinus fontinalis, Mitchill) and two species of dace (Rhinichthys cataractae, Valenciennes) and (Rhinichthys atratulus, Hermann) was investigated in North Pine River, Manitoba. Yearling and larger brook trout did not compete for food with the dace as their diets differed; however, fingerling brook trout and dace competed because their diets were similar. Fingerling trout, in a section of the stream containing a greater number of dace, grew slower than those fingerling trout that were in the non-competitive section of the stream.

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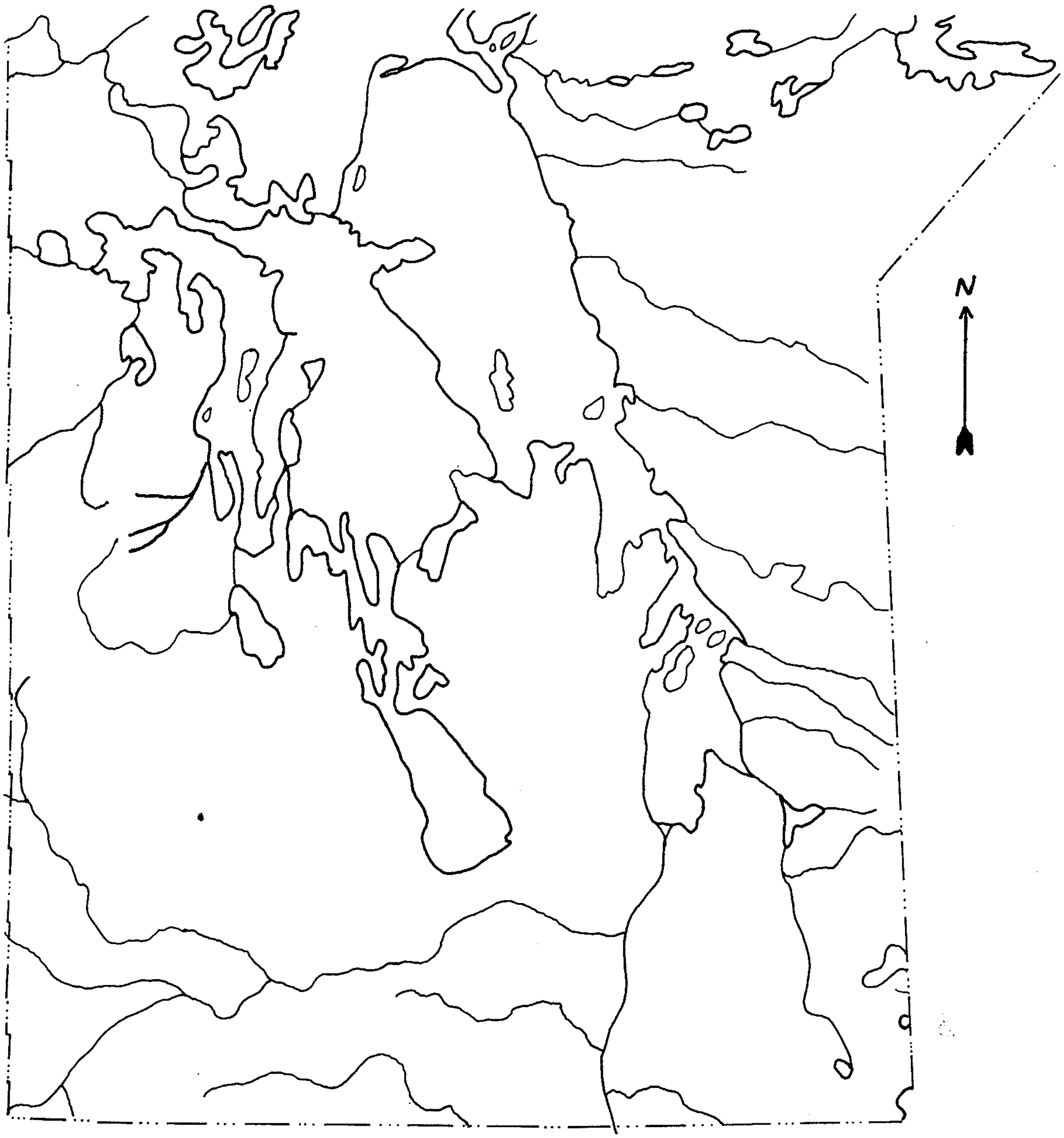
INTRODUCTION

In the summer of 1960 Franklin (MS, 1960) surveyed four streams that flow from the Duck and Porcupine Mountains, Manitoba, and eventually empty into Lake Winnipegosis. He suggested that it would be interesting to ascertain whether food competition existed between the trout and dace in these streams which had previously been stocked with eastern brook trout and rainbow trout.

This study was designed to determine if food competition exists between eastern brook trout (Salvelinus fontinalis, Mitchill) and two species of dace (Rhinichthys atratulus, Hermann and Rhinichthys cataractae, Valenciennes). The hypothesis examined in this study was that if significant interspecific competition for food existed between trout and dace, then it should be reflected in a reduced rate of growth of the trout. To test this hypothesis, a relatively uniform stretch of the North Pine River was selected and divided into four sections. The growth rates of fish in two control sections, one containing only brook trout fry and the other containing only yearling trout, were compared to the growth rates of fish in two other sections, one containing brook trout fry and dace, and the other containing yearling brook trout and dace.

The author started this study in the summer of 1961. North Pine River was selected because its flow of water was relatively uniform throughout the season in contrast to that of other streams in the area. Dace and trout were also numerous in this stream.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LITERATURE REVIEW

Competition

Andrewartha and Birch (1954) defined competition as occurring when a "valuable or necessary resource is sought together by a number of animals (of the same kind or of different kinds) when that resource is in short supply, or if the resource is not in short supply, competition occurs when the animals seeking that resource nevertheless harm one another in the process". Andrewartha and Birch (ibid) rejected competition as embracing predation.

Nicholson (1933) concluded that "any factor having the necessary property for the control of populations must be some form of competition". It is strange that he reached this conclusion, as in a preceding sentence he stated that, "Clearly no variation in the density of a population of animals can modify the intensity of the sun, or the severity of frost, or any other climatic factor ---". It is true that animal populations do not influence climate in nature but it is also true that climatic factors influence animal populations. One cannot regard climatic influences, which fit into Nicholson's definition of competition, as competition; therefore, Nicholson's definition of competition is not accepted in this study.

Gause (1934) demonstrated, both mathematically and experimentally, that when two species compete for the same food in a limited environment, the growth rates of both will be reduced, and in most cases one species will eventually eliminate the other. From his work, Gause concluded that two species cannot co-exist in the same locality if they have identical ecological requirements. This is now known as the Gause's or the competitive exclusion principle.

Gause and Witt (1935) stated that if severe competition exists between two species for food and other resources of the environment, i.e., they occupy the same ecological niche, one species would be expected to replace the other species. Mayr (1963) defined an ecological niche as the "constellation of environmental factors into which a species (or their taxon) fits: the outward projection of the needs of an organism, its specific way of utilizing its environment". Riley (1953) maintained that the niche concept has been used so varyingly, that it often means anything, and usually an undetermined something. Yet he stated that "it has become a truism that no two species can occupy the same niche".

However, in most natural situations the competitive exclusion principle does not operate as pointed out by Elton (1946). He stated, "We do not at present know what maintains the state of equilibrium between the different genera actually found in natural communities analyzed, but must postulate that there is some ecological condition that buffers or cuts down the effectiveness of competition ---". Perhaps, this can be explained to a certain extent, as Mayr (1963) did, in that, "Competition favours the entry into new niches and more generally, adaptive radiation. Thus competition is an element in speciation and is an important cause of evolutionary divergence".

Mayr (1963) defined competition as existing when "two species seek simultaneously an essential resource of the environment that is in limited supply. Two species are in competition when they have a controlling factor in common". The first part of this definition of competition is not complete, for it does not allow for intraspecific competition, i.e., competition among members of the same species. Mayr (ibid) was more interested in the interactions between species than interaction between members of the same species. The second sentence of his definition has the same weakness as was considered in Nicholson's (1933) definition of competition which could by definition include climatic factors as competition factors.

Allee, et al. (1949) stated that "in general, competition occurs when there is a common demand on a limited supply. Competition furnishes a special phase both of co-operation and of disoperation". Most authorities on competition stress the inclusion of organisms and "disoperation" in their definition of competition as witnessed by the preceding definitions of competition. Allee, et al. (ibid) omitted organisms and included co-operation in their interpretation of competition. Thus they were able to demonstrate an example of "competition" where spermatozoa of sea urchins were crowded into a limited space, i.e., competition for space, and remained viable longer and hence there was co-operative "competition" as far as the longevity of the spermatozoa was concerned. This example, as far as the author is concerned, demonstrates the weakness in the competition concept of Allee, et al. Spermatozoa are not organisms and the "competition" for space was not determined by the behaviour of the spermatozoa.

Allee, et al. (1949) contributed to the understanding of competition by stating that predator-prey relationships or parasitism are not included in their concept of competition as was included by Larkin (1956). However, Larkin's general definition of competition is useful and is as follows: "Competition is the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply".

Although the above definitions of competition vary somewhat from each other, they fit the type of interaction discussed in this paper with respect to the eastern brook trout and dace as observed at Pine River, Manitoba. The author's selection of what constitutes competition is best described by Crombie's (1947) definition. He stated "competition is a demand at the same time by more than one organism for the same resources of the environment in excess of immediate supply". Crombie's (ibid) definition contains the three essential elements of competition. Firstly, that more than one organism is involved, and secondly that the simultaneous behavior of these organisms is creating the competition, and thirdly that the item competed for is available to a lesser extent than is required or desired by the organisms in question.

Competition Among Fishes

The following studies on competition among fishes will serve as a source from which certain conclusions are drawn. The conclusions will be summarized at the end of this topic. Lagler, et al. (1962) stated that the most common competitions among fishes are for spawning sites, food, space and shelter.

Larkin (1956) stated that "fishes have a wide tolerance of habitat type, a flexibility of feeding habits, and in general share many resources of their environment with several other species of fish". He maintained that as a result of this, food chains have more breadth and less height of pyramidal numbers than one would expect. "Fresh water fish overcome unfavourable periods of competition to a large extent due to their flexible growth rates and high productive potential," (Larkin, 1956). "In these circumstances it is difficult to separate the role of interspecific competition from other phenomena as a factor of population control," (Larkin, *ibid*).

Nikolsky (1963) claimed that young fishes which have not yet started to eat the same foods as their adults are usually more stenophagic and their diets are more similar to that of other species within a single complex.

Northcote (1954) demonstrated that two species of sculpins living in similar habitats had similar diets, but he did not demonstrate conclusively that competition existed because the qualifying factor (whether the demand of the two species upon the food resources was in excess of the supply) was undetermined.

Fedoruk (1965) found that bass, *Micropterus dolomieui* Lacépède and walleye, *Stizostedion vitreum vitreum* (Mitchill) did not compete for food in Falcon Lake, Manitoba. He established that though they ate a number of common food items, the intensity pattern of feeding demonstrated that each fish had peculiar preferences, and that bass and walleye frequently inhabited different local habitats.

Larkin and Smith (1953) studied the interaction between redside shiners, *Richardsonius balteatus* (Richardson) and Kamloops trout, *Salmo gairdneri* (Richardson). They found three types of interactions; namely, predation by shiners on trout fry, competition for food between the two species and predation by trout on shiners.

Hunt and Carbine (1950) studied the food of young pike, *Esox lucius* Linnaeus in ditches associated with Houghton Lake, Michigan. They noted that as the pike increased in size, the diet shifted from crustaceans to insects to vertebrates. Brook stickleback, golden shiner, blacknose minnow, spottail shiner and mimic shiner competed with pike up to 40 millimeters in length for crustaceans. Yellow perch, brook stickleback, mudminnow, Iowa darter, creek chub and eight other species competed with pike 21 to 50 mm. in length for insects. Little competition from other fish species was observed when pike were of the size (26 to 152 mm.) to consume vertebrates. Yellow perch, mudminnows and creek chubs consumed small amounts of vertebrates.

Echo (1954) examined the relationship between yellow perch, Perca flavescens (Mitchill) and cutthroat trout, Salmo clarki (Richardson) in Thompson Lakes, Montana. The food of yellow perch was largely immature aquatic insects and plankton while the diet of cutthroat trout was mainly mature aquatic insects and small perch.

Svardson (1949a) studied the competition between trout and char, Salmo trutta Linnaeus and Salvelinus alpinus (Linnaeus) and found that char survived better than trout. Char averaged a larger size (65.9mm.) than did trout (64.8 mm.). He conducted this particular phase of the experiment in hatchery troughs with fry of both species.

Nilsson (1963) also studied the interaction of Salmo trutta Linnaeus with Salvelinus alpinus (Linnaeus). He found that trout were territorial whereas char wandered. When food was abundant, the two species had similar preferences; when it was sparse, they differed in their feeding habits. Trout continued to feed on larger aquatic organisms while char fed on plankton. Trout were more aggressive than char under experimental conditions. In impoundments the differences in feeding habits were even more pronounced than in lakes. In lakes the trout were located in the inner shallow parts of the littoral zone while the char were in outer deeper areas of the littoral zone.

Ward (1962) investigated the possibility that young sockeye in their lacustrine habitat might compete with sockeye smolts of successive year classes for available food. Sockeye were found to have a quadrennial spawning cycle, i.e., coming back to fresh water to spawn four years after hatching. Ward (ibid) found one year class or cycle was larger than the following cycles or year classes. The hypothesis that the numerous Cycle I (dominant year class) fish would over crop the available food supply and thus reduce the growth of the following cycles was advanced. However, this was not found to be the case. Actually, smolts belonging to Cycles II, III and IV populations were, on the average, larger than those belonging to Cycle I populations. This indicates that competition between Cycle I juveniles was greater than between juveniles of Cycles II, III and IV. Measurements of the abundance of zooplankton did not indicate that less food was available to Cycles II, III and IV than to Cycle I populations.

Laakso (1950) stated that, from his work on the Yellowstone and Gallatin rivers in Montana, whitefish and trout competed strongly for aquatic food organisms. The number of trout sampled was few and they were both brown and rainbow trout. Laakso sampled the benthos to compare the availability of food organisms and those observed in fish stomachs.

Allen (1951) suggested that an eel, Anguilla dieffenbachii, which occurs throughout the length of the Horokiwi Stream in New Zealand, is probably a significant competitor for food with the brown trout. This eel may also be a trout predator. Other fishes which are likely to compete with the brown trout in the Horokiwi Stream (Allen, ibid) are the inanga, Galaxias atternatus, the smelt, Reptropinna osmeroides, and two species of Gobiomorphus. These, however, were not thought to be as significant as the eel and are more or less confined to the lower portion of the Horokiwi Stream.

Miller (1958) studied competition between hatchery reared trout and wild trout. His experiment at Gorge Creek, Alberta, had two control sections containing only hatchery trout, and one section containing a mixture of wild trout and hatchery trout. Miller concluded that survival of hatchery trout is poor in lakes and streams where resident trout populations already exist. In streams containing resident trout, hatchery reared trout die after release. In the early stages of this competition they are continuously exercising and exhaust some metabolite and die either of acidosis or starvation.

Conclusions that can be drawn from the above literature with reference to competition among fish are:

1. Fish may compete for food, space, spawning sites and shelter.
2. Some fish have a wide tolerance of habitat type and flexible feeding habits that can overcome unfavourable periods of competition as stated by Larkin (1956) and as shown by Nilsson (1963).
3. The food habits of fish change as the fish become larger and older. This was stated by Nikolsky (1963) and demonstrated by Hunt and Carbine (1950) and Allen (1951).
4. Young fish are more stenophagic than their adults and have similar diets to other species within a single complex.
5. The observation that two or more fishes feed on a number of common food items does not necessarily mean that they are competing for food. This statement is supported by the investigations of Northcote (1954) and Fedoruk (1965).

6. Two species of fish may compete for food but since they share a common habitat other reactions may take place. These other reactions can be beneficial to one or the other species at a particular phase of life history. This was demonstrated by Larkin and Smith (1953) and suggested by Allen (1951).

7. One of the first steps to be taken in a food competition study, is to determine if the fish are feeding on similar food organisms. The fish involved in Echo's study (1954) did not compete for food.

8. To determine whether food competition is significant, a study must be designed to measure the effects of food competition either in terms of growth, as Ward (1962) did, or survival, as Svardson (1949a) and Miller (1958) did. However, survival may be influenced by other factors than food competition.

9. In a situation where one species of fish, through competition, dominates another species, the dominated species may change its ecological requirements to offset the strain placed on it by the original competition. This phenomenon was demonstrated by Nilsson (1963).

10. A stronger case for food competition is developed if the availability of food organisms is studied in conjunction with the food found in fish stomachs. This was done by Ward (1962) and Laakso (1950).

Methods of Estimating Importance of Food Items

A review of the literature reveals that four methods are commonly used to establish the importance of various food organisms. These are the numerical, frequency of occurrence, volumetric, and gravimetric methods.

The numerical method consists of counting the number of each type of organism per stomach. The results are expressed by totalling the number of organisms found in all fish stomachs for that particular type of fish.

The frequency of occurrence method consists of recording the number of stomachs containing a particular food item. The results are expressed either in the number or percentage of stomachs containing a particular organism.

The volumetric method is the measurement of the volume of a fluid displaced by various food organisms and then relating this to the total food volume per stomach.

TABLE I

Tabulation of various methods of estimating importance of food items

Methods	Frequency of Occurrence	Volumetric	Gravimetric
Numerical			Allen, 1951
Frequency of Occurrence	Fedoruk, 1965 Echo, 1954 Hunt & Carbine, 1950 Ide, 1942	Northcote, 1954 Benson, 1953 White, 1930 Clemens, 1928	LeBrasseur, 1966
Volumetric		Gee & Northcote, 1963 Ward, 1962 Laakso, 1950 Kuehn, 1949 Moore *et al.*, 1934 Ricker, 1930	

The gravimetric method is the weighing of individual food items and comparing these to the total weight of the stomach contents. Usually the stomach contents are dried so as to avoid the weighing of water.

All the above methods of estimating the importance of types of food items have disadvantages. The importance of smaller organisms are magnified in both the numerical and frequency of occurrence methods. Both the volumetric and gravimetric methods can be misleading when a single bulky or weighty specimen, perhaps of rare occurrence, assumes an unwarranted position of dominance over smaller but more common items. The best method is possibly a combination of either the numerical or frequency of occurrence method combined with the volumetric or gravimetric method, time permitting.

Allen (1951) preferred the numerical and gravimetric methods. He stated that the frequency of occurrence method is adequate but is a less informative method. Allen (ibid) did not state why the frequency of occurrence method is less informative. The author chose the frequency of occurrence method, as this method seems to give a more realistic picture when considering the diet of a population as a whole. This opinion was expressed by Benson (1953) in his work on the brook trout of Pigeon River, Michigan. He suggested that "as mayflies and caddisflies occurred in a larger percentage of the stomachs than did crayfish, they possibly benefited more fish than did crayfish". LeBrasseur (1966) used both frequency of occurrence and gravimetric methods to determine the importance of food organisms in four species of Pacific salmon and steelhead trout.

METHODS

General Methods

Data were gathered from two sources. The first source was a series of field observations that were made during the summers of 1960, 1961 and 1962. The second source was a controlled field experiment that was carried out in 1964. Various techniques utilized in both the observational and experimental studies are discussed below, but the design and detail of the experimental studies will be discussed under its own heading.

Description of The Stream

The work on the North Pine River was conducted in Township 33, Ranges 23 and 24, W.P.M. The stream arises from a number of lakes and springs in the Duck Mountains and flows eastward and empties into Lake Winnipegosis. The stream crosses Provincial Highway Number 10 approximately one mile north of the town of Pine River.

The experimental section of the stream lies in a steep valley. The stream's immediate shoreline supports alder, willow, black and white poplar, and a few black and white spruce. Further back from the stream and up the slopes, the dominant trees are spruce with occasional jack pine and young stands of balsam fir growing in localized areas where previous log-cutting operations were undertaken. The average width of the stream is 20 feet. The bottom is stony with varying sizes of stones and boulders. Some boulders were quite large and created pools on their downstream sides in otherwise fast running water. A number of log-jams resulted from the larger boulders catching trees that have floated downstream.

Benthic Sampling

Franklin (MS. 1960) collected benthic organisms from Pine River with a one square foot Surber Sampler. These samples were preserved in a 70% ethyl alcohol solution and later analyzed by the author. Benthic samples were again collected by the same method in the summers of 1961 and 1964. Five benthic samples were taken with a Surber Sampler from each of the four experimental sections, in the summer of 1964, before rotenone was applied to this experimental area. After the rotenone was administered five similar benthic samples were collected from each experimental section at two week intervals until the end of the study in September. The numbers of benthic samples collected from Pine River in the summers of 1960, 1961 and 1964 were 209, 52 and 120 respectively, for a total of 381 samples. The bottom samples were cleaned of debris and the organisms classified to orders in most cases and counted in the laboratory.

Methods of Collecting, Measuring and Stomach Analyzing of Fishes

Mature brook trout were caught by angling, and fingerling brook trout caught by electrofishing in the summer of 1961. Longnose and black-nose dace were collected by means of a seine in the summer of 1962. Both fry and yearling brook trout were obtained from the Whiteshell Trout Hatchery in the summer of 1964 for the controlled experiment. Longnose and blacknose dace were collected by electrofishing and used in the experiment. At the end of this experiment, in mid September, all fish were collected by electrofishing and/or rotenone and measured to the nearest tenth of an inch from the tip of the snout to the fork in the tail.