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COMPETITION BETWEEN BROOK AND BROWN TROUT
FOR RESTING POSITIONS IN A STREAM

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COMPETITION BETWEEN BROOK AND BROWN TROUT FOR RESTING POSITIONS IN A STREAM

By

Kurt Daniel Fausch

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ABSTRACT

COMPETITION BETWEEN BROOK AND BROWN TROUT FOR RESTING POSITIONS IN A STREAM

By

Kurt Daniel Fausch

Competition between brook and brown trout was examined using wetsuit diving to view daytime positions held by adult brook trout in 1600 m of a stream before and after the removal of the brown trout. After the brown trout were removed, brook trout over 15 cm chose resting positions more often in shade and with more favorable water velocity characteristics. This microhabitat shift was strongest for brook trout over 20 cm. There was no significant shift in brook trout feeding positions. The observed microhabitat shift indicated interference competition between brook and brown trout for a critical resource, which was resting microhabitat.

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INTRODUCTION

Brook trout (*Salvelinus fontinalis*) are reported to have undergone recent decline in abundance in the eastern United States. Accompanying this have been reductions in growth rate, maximum body size and life span, as well as changes in spatial distribution within streams (Webster, 1976). Brown trout (*Salmo trutta*) may have been responsible for much of the change in brook trout distribution and abundance in running waters where the two species are sympatric.

Although allopatric populations of the two species have been investigated, little study has been devoted to brook and brown trout in sympatry, and the characteristics of their interaction are largely unknown. The objective of this study was to determine whether interspecific competition occurs between brook and brown trout and, if so, to define the mechanism and critical resource of the competition. In this paper, niche and habitat variables are considered "resources."

Besides interspecific competition, other types of interactions, such as predation, may be important in the relationship between brook and brown trout. In addition, environmental and genetic factors affect the distribution and abundance of the two species. After a brief history of the introduction of each species into Michigan waters, previous research concerning environmental and genetic factors, and predation will be discussed. Then, some applications of the theory of interspecific competition to salmonids will be presented before outlining specific objectives of this study.

Historical Perspective

Brook trout were not indigenous to Michigan's lower peninsula. The report of Houghton's survey of Michigan (Hubbard in Smedley, 1938) emphasized that brook trout were found only in the upper peninsula, while the Michigan grayling (*Thymallus tricolor*) occupied most cold water lotic habitats in the lower peninsula. If brook trout inhabited any lower peninsula streams, their invasion from the upper peninsula, or deliberate transport by white settlers are thought to have occurred rather recently. In any case, by 1870, they were well established north of about 45° north latitude (Smedley, 1938; Westerman, 1974).

The first introductions of hatchery-reared brook trout occurred in 1879 in southwestern Michigan streams. The decline of the grayling in the Au Sable River led to the stocking of brook trout there in 1885. Brook trout flourished and showed exceptional growth in many streams, with reports of fish reaching 2 to 4 pounds in less than 5 years (Smedley, 1938). During this period, the Pere Marquette and Au Sable were considered the finest brook trout rivers in the United States. But by 1906, about 3 decades later, catches of large brook trout were no longer reported from Michigan's big rivers (Smedley, 1938). Since then, brook trout have practically disappeared from some streams in lower Michigan and inhabit mostly smaller tributaries and headwater areas.

During the period of expanding brook trout populations and grayling decline, brown trout were also introduced. In 1883, eggs were received from Germany and the fry planted in the Pere Marquette River. Further shipment of eggs resulted in the introduction of brown trout into many Michigan waters including the Au Sable system in 1891 (Westerman, 1974). However, after a few decades considerable doubt arose about the effects of brown trout on native salmonids, and the amount of further stocking fluctuated according to public opinion (Smedley, 1938). Although originally introduced in hopes of occupying those areas left unfavorable for brook trout by agriculture and pollution, brown trout now inhabit most main channel portions and many small tributaries of cold water streams in lower Michigan.

In streams where both species occur, brook trout are most abundant in headwater areas, but brown trout seem to become more abundant in upstream areas each year. These patterns of distribution are not well documented, but exist as personal observations of trout fishermen and aquatic biologists. This evidence, coupled with the comparatively small size and high mortality of brook trout leads these people to further the hypothesis of competition between the two species.

Previous Research

In addition to interspecific competition, there are several other factors that may affect the interaction between brook and brown trout, helping to produce the observed patterns of distribution and abundance. These include physical factors, differential growth and mortality, genetic selection and predation.

Physical Factors of the Environment

Investigations of the response of brook and brown trout to physical environmental factors have most often dealt with the species singly. Care must be exercised in applying inferences from allopatric to sympatric situations because the responses may be altered in sympatry. The distribution of brook and brown trout in streams often resembles longitudinal zonation, first described by Shelford (1911). Subsequent investigators have used a number of climatic and morphometric factors to explain the replacement of species from headwaters to mouth (Burton and Odum, 1945; Huet, 1959; Sheldon, 1968). Among these have been stream temperature, altitude, gradient, water velocity and depth, all of which are interrelated.

The research on brook and brown trout, especially in streams of higher altitude and gradient, shows that temperature is a major factor affecting their distribution. In a study of longitudinal zonation in Virginia mountain streams, Burton and Odum (1945) observed that brook trout were limited downstream by a midsummer maximum temperature of 19°C, although they also acknowledge the effects of altitude and channel gradient on stream fish. Vincent and Miller (1969) studied the effects of the altitude-temperature complex on the distribution of brook and brown trout in a Colorado mountain stream. They observed the familiar pattern of brook trout occupying the headwaters and proposed that brown trout were limited upstream by suitable minimum water temperatures for growth, and brook trout limited downstream by interaction with brown trout. Gard and Flittner (1974) and Lane and Skrzynski (1972) found similar distributions for the 2 species along temperature-altitude gradients and also proposed temperature as a limiting factor to the upstream distribution of brown trout. However, in the Austrian Alps, allopatric brown trout occur in remarkably small, high gradient brooks (R.J. White, unpublished data). This may result from differences in genotype of the brown trout studied.

The temperature requirements of the 2 species are reported to be nearly identical (MacCrimmon and Marshall, 1968; MacCrimmon and Campbell, 1969). However, as Allen (1969a) pointed out, optimal temperatures for the full range of activity and stress for each species are more important. Slight differences in the optimum physiological temperatures for brook and brown trout may affect their interaction at some point along the stream continuum or during a certain period of the year.

Gradient and water velocity are related to altitude and temperature, with streams at high altitudes being characterized by low temperatures, high gradient and high velocity. The research on water velocity preferenda for the 2 species is incomplete and confusing. Studies of brook trout preference were conducted in natural surroundings (Wickham, 1967; Griffith, 1972), whereas brown trout were exposed to a limited range of velocities in artificial channels (Baldes and Vincent, 1969; DeVore, 1975; Bassett, 1978). The results indicate that brook trout prefer lower water velocities than brown trout. From the distribution of the 2 species along altitude gradients, one might expect brook trout to prefer identical or slightly higher water velocity than brown trout. The response of each species to water depth has not been investigated, although brook trout may have some competitive advantage in shallow streams and brown trout in deeper water (R.J. White, personal comm.).

A final pair of related physical factors which may affect the specie's interaction are light and overhead cover. Separate investigations into the activity of the 2 species in relation to light indicate that they are both crepuscular, photonegative and highly cover-oriented (Gibson and Keenleyside, 1966; Chaston, 1968; Gibson and Power, 1975). However, field observations by fishermen and aquatic biologists indicate that the activity of the 2 species is very different in streams. Brown trout larger than 30 cm most often feed after sunset, whereas the largest brook trout that one can find in streams are usually less than 30 cm, and these feed mainly during the day.

Butler and Hawthorne (1968) tested one brown trout (402 mm) and one brook trout (238 mm) separately for cover preference--but in the presence of various smaller trout. The brown trout was slightly more cover-oriented than the brook trout, but this may have been due to its greater length and much greater weight (525 g vs. 175 g). The smaller trout also may have confounded the results. Research concerning the light preferred by brown trout has recently been completed (J. Gruber, in preparation).

Differential Growth and Mortality

In contrast to physical environmental factors, differential growth and mortality may alter the interaction between brook and brown trout with more direct effects on the abundance and size structure of the populations. Although differential growth is affected by natural environmental factors, differential mortality may more often be a result of human activities.

Differential growth implies that a cohort of one species is able to grow faster and gain an advantage over the other species. In naturally sympatric pairs of salmonids, earlier emergence of one species from gravel redds has the same effect, resulting in larger fish throughout the first summer of life. Brook and brown trout probably emerge from redds over extended but about equal periods, but brown trout fry are thought to be larger at emergence than brook trout (R.J. White, personal comm.). If this were the case, brown trout could maintain a consistent size advantage during the first summer of life. However, research concerning the early life history of the 2 species in sympatry is lacking. Differences in growth rate may be caused by differential growth-temperature relationships for brook and brown trout, yet again, no data are available to substantiate this. Instead, it is likely that slower growth and higher mortality of brook trout results primarily from selective angling mortality.

Evidence from exploited sympatric populations indicates that brook trout are much more vulnerable than brown trout to angling (Cooper, 1952, 1953; Marshall and MacCrimmon, 1970). In exploited brook trout populations, this high vulnerability results in very few fish surviving to age III and therefore, a truncated age distribution (Cooper, 1952, 1953; McFadden, 1961; Cooper, Boccardy and Andersen, 1962; Wydoski and Cooper, 1966; McFadden, Alexander and Shetter, 1967; Warner, 1970; Jensen, 1971). Unexploited brook trout populations show survival to age V (Hoover, 1939; Reimers, 1958; Cooper, 1967; Jensen, 1971; O'Conner and Power, 1976) and in some to ages VIII and IX (Doan, 1948; Webster, 1976).

Brown trout, with low vulnerability to angling, typically show little difference in the age structure, age at sexual maturity and growth between exploited and unexploited populations (Beyerle and Cooper, 1960; McFadden and Cooper, 1964; Marshall and MacCrimmon, 1970).

Genetic Selection

Reestablishment of the balance of birth and death rates in exploited brook trout populations takes place by drastic changes in age specific fecundity, with selection for early sexual maturity (Jensen, 1971). In addition, since angling is thought to crop the largest, fastest growing individuals (Cooper, 1952; McFadden, 1961), selection for slow growth has been proposed (Miller, 1957). Because much growth in early maturing fish must be sacrificed to courtship and reproduction, the problems of selection for slow growth and early maturity by angling are probably related.

Predation

Predation is another factor that may alter the interaction between brook and brown trout through changes in the population structures of both species. Recent research has shown that brown trout larger than 30 cm consume far more young brook trout than young brown trout. Estimates by Alexander (1977) of the number of young trout eaten by predatory brown trout indicate that ratios of brook to brown trout consumed were 16:1 and 35:1 in two sections of a Michigan stream under different angling regulations. In the same stream sections, avian predation of both species was substantial (Alexander, 1976). Mortality of brook trout by avian predation was higher than of brown trout both in terms of numbers and percent of the total populations. However, birds generally consumed a larger percentage of age-0 and age-I brook trout and a larger percentage of age-II and age-III brown trout in the respective populations.

Interspecific Competition

The final aspect of the interaction between the 2 species to be considered, and the one chosen for this study is interspecific competition. However, it is first necessary to reiterate the principles of interspecific competition and to consider some applications to studies of salmonids in general, and to brook and brown trout in particular.

Applications of Theory

The early proponents of the theory of interspecific competition stated that no 2 species could stably coexist if their use of resources was too similar. This theory, known as the "competitive exclusion principle," fell into disfavor because of inherent circular reasoning and was rejected as a working hypothesis (Hardin, 1960). However, the more recent concept of the "limiting similarity" between 2 species (MacArthur and Levins, 1967) may be less applicable to the problem of species introductions than the earlier principle of competitive exclusion. This more recent approach considers the degree to which resource use of 2 species can be similar and still allow coexistence. However, the hypothesis of limiting similarity concerns stable communities, and seems of little value in the case of brook and brown trout, as the species do not appear to coexist in a stable manner. I believe that an approach similar to the original competitive exclusion principle is more useful than the hypothesis of limiting similarity when investigating unnatural sympatry produced by introduction of a similar species. The essential questions of this approach are: 1) Are the 2 species too similar in resource use to coexist in sympatry; and 2) If resource use is too similar, can the resultant interspecific competition be demonstrated and described?

To examine this hypothesis, a direct experimental approach may be used (Schoener, 1974) because the species have not evolved genotypic differences in sympatry. In this approach, the system is perturbed away from the present condition by removing or adding individuals of one species and measuring the response by individuals of the other species. To ensure that adequate research is accomplished, Schoener's guidelines for studying interspecific competition and resource partitioning should be followed. In particular, it is important to determine the mechanism of the competition and the resource dimensions critical to the interaction. Because the 2 similar species are not expected to be distributed along resource axes, nor will their populations probably be in equilibrium, little else of the theory of interspecific competition may be useful.

Further insight into the interaction between brook and brown trout may be gained from inspection of the sympatric pairs of salmonids previously studied. With the 14 major species of salmonids present in North America, there are many possible combinations of species representing natural and unnatural sympatry.

Natural Sympatry

Research on naturally sympatric salmonid pairs often reveals some mechanism to minimize competition for a limiting resource. This mechanism entails similar resource use in allopatry and segregation along some resource axis in sympatry. Nilsson (1967) termed this plasticity in fishes interactive segregation, after its use by Brian (1956). Interactive segregation between brown trout and arctic char (*Salvelinus alpinus*) occurs when food becomes limiting in impoundments (Nilsson, 1965). Hartman (1965) found segregation between parr of coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) when suitable living space became limiting in streams. Either brook or brown trout, when naturally sympatric with Atlantic salmon (*Salmo salar*), are able to exclude this species from favorable territories. Thus, in sympatry with either species, Atlantic salmon have developed optimal strategies and segregate into different habitats than in allopatry (Lindroth, 1955; Gibson, 1966). During the first summer of life, segregation between sympatric salmonids often occurs along gradients of water velocity and depth near the margins of streams. This segregation is caused by differential emergence and has been observed between chinook salmon (*O. tshawytscha*) and steelhead trout (Chapman and Bjornn, 1969; Everest and Chapman, 1972).

Unnatural Sympatry

The pairs of salmonids that, through introduction, now exist in unnatural sympatry are less apt to have developed mechanisms to reduce competition. However, natural differences are often sufficient to separate the species along some resource axis. The introduction of brook and brown trout to the western United States produced many unnatural sympatric associations with native salmonids. In Montana, the numerical decrease of native cutthroat trout (Salmo clarki) after the introduction of brook trout led Griffith (1972) to study this unnatural sympatry. He found that a combination of differential emergence by young trout and segregation of adults by microhabitat and water velocity resulted in fairly effective natural separation of the 2 species. He also proposed that vulnerability to angling was the major factor in the decline of the cutthroat trout. Coexistence of rainbow and brown trout, another unnatural sympatry, is also attributed to use of different microhabitat by adults. In a study of the pools in another Montana stream, Lewis (1969) found that rainbow trout used faster water velocities and more open positions than brown trout, thus minimizing competition.

If brook and brown trout were similar enough in resource use, this would preclude the existence of a natural mechanism of segregation. However, the small number of investigations concerning brook and brown trout in sympatry are the results of surveys of fish distribution and abundance and do not define specific characteristics of their interaction. Only one study (Nyman, 1970) has attempted to investigate differences in food and habitat of brook and brown trout, but used angling to collect the 2 species in

Newfoundland streams. The limitations of this method prevented pinpointing microhabitats used by either species, although Nyman qualitatively described the use of marginal habitats by brook trout in sympatry with brown trout. He found no differences in food items for the 2 species in sympatry or allopatry and because diet composition varied with relative abundance of food items throughout the season, concluded that neither species was very selective.

Specific Objectives

In view of the effects of brown trout introduction on brook trout populations, an hypothesis of interspecific competition by direct interaction for a limited resource (termed interference competition, Pianka, 1974) seemed a logical starting point for this study. In addition, space has been shown to be a critical resource for salmonids (Chapman, 1966; Allen, 1969b), and suitable positions or microhabitat for brook and brown trout are probably a limiting resource in most streams. (The terms "position" and "microhabitat" are used interchangeably in this paper.) Therefore, I advanced the hypothesis that brown trout are able to exclude brook trout from optimal positions by direct interference. Removal of brown trout from a stream with approximately equal numbers of each species was thought to be the best method of testing the hypothesis. The expected ecological release of brook trout into more optimal positions would provide evidence for interspecific competition, using the pre-removal brook trout population as a control. The study was planned to coincide with summer base flow discharge, so that the reduction in suitable living space might heighten competition for optimal positions to measurable levels. By removing brown trout during the period of greatest competition for space, it was hoped that comparison between position characteristics of brook trout in sympatry versus those in allopatry would result in a statistically separable difference. Moreover, measuring a variety of brook trout position characteristics might provide evidence for the mechanism of interspecific competition. Techniques of underwater observation and measurement of trout positions similar to those used by Griffith (1972) and Everest and Chapman (1972) were employed. It should be noted that the necessity of direct observation limited this study to daytime positions of trout.

Specific objectives for this study were:

1) To test the hypothesis of interspecific competition between brook and brown trout by removal of brown trout and measurement of possible microhabitat shifts by brook trout.

2) If interspecific competition was established, to determine the mechanism and the critical resource.

STUDY AREA

The Drainage Basin

The East Branch of the Au Sable River emanates from a number of small bog lakes in the north central region of Michigan's lower peninsula. From its source at Barnes Lake, the stream flows predominantly south and west toward the town of Grayling and confluence with the main stream of the Au Sable River (Figure 1). The drainage basin of this fourth order stream is 196.8 km^2 (Bent, 1970). The stream ordering system used here follows the Strahler modification of Horton's (1945) system. In both the headwater bogs and the lower reaches, the watershed is vegetated primarily with hardwoods and brush. In contrast, the vegetation of the area surrounding the mid-reaches of the stream is mainly conifers and brush (Hendrickson, Knutilla and Doonan, 1973). The stream flows 30.5 km and drops 30.5 m from source to mouth, a gradient of 1 m/km.

Stream Channel Characteristics

In the headwaters the gradient is low (0.74 m/km) and the bed materials are mainly silt and sand. Average width is 9.75 m; mean depth, 70 cm. The gradient in the middle and downstream reaches increases to 1.7 m/km. The bed of the middle reach is mostly sand. In the lower reach,

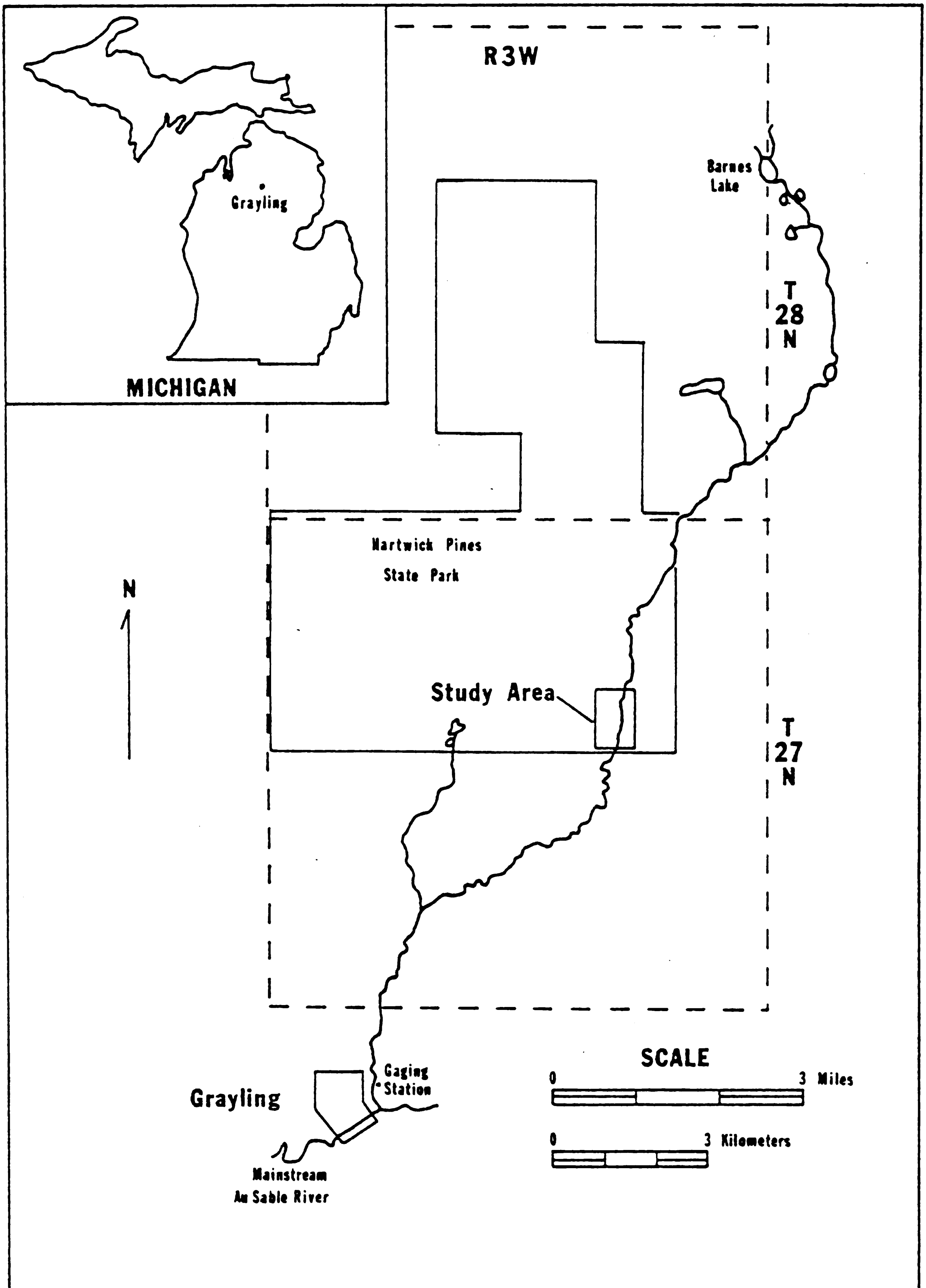


Figure 1. The East Branch of the Au Sable River.

the bed is sand and gravel. The average width decreases to about 7.6 m in both areas and the average depth to 60 cm. Throughout the stream's length the predominance of sand in the bed results in cross-sections that are uniformly wide and shallow with few pools greater than one meter deep.

The East Branch of the Au Sable River, hereafter referred to as the East Branch, shows a very stable flow regime. The ratio of 10% to 90% duration discharge is 1.53 near the study area (Hendrickson, et al., 1973). According to the same investigators, the hardness of the stream water is 170 mg/l $CaCO_3$ and the pH about 8.0. An index of base-flow, groundwater yield, is quite high (.00466 $m^3/sec.km^2$). A stream gauging station is maintained by the U.S. Geological Survey near the mouth of the stream (Figure 1). Records from this facility were used to determine stream discharge during the period of study.

Specific Location

The study area lies in Crawford County, 7.75 km north and 5.5 km east of the town of Grayling, Michigan. The entire study area is within Section 14 of Township 27 North, Range 3 West, and consists of 1800 m measured upstream from the south border of this section (Figure 2). The stream is of third order in the study area, which lies near the middle of the stream's length and about 13 km upstream from the mouth. Two gravel roads cross the study area, one at its downstream end and the other about 1100 m upstream from that

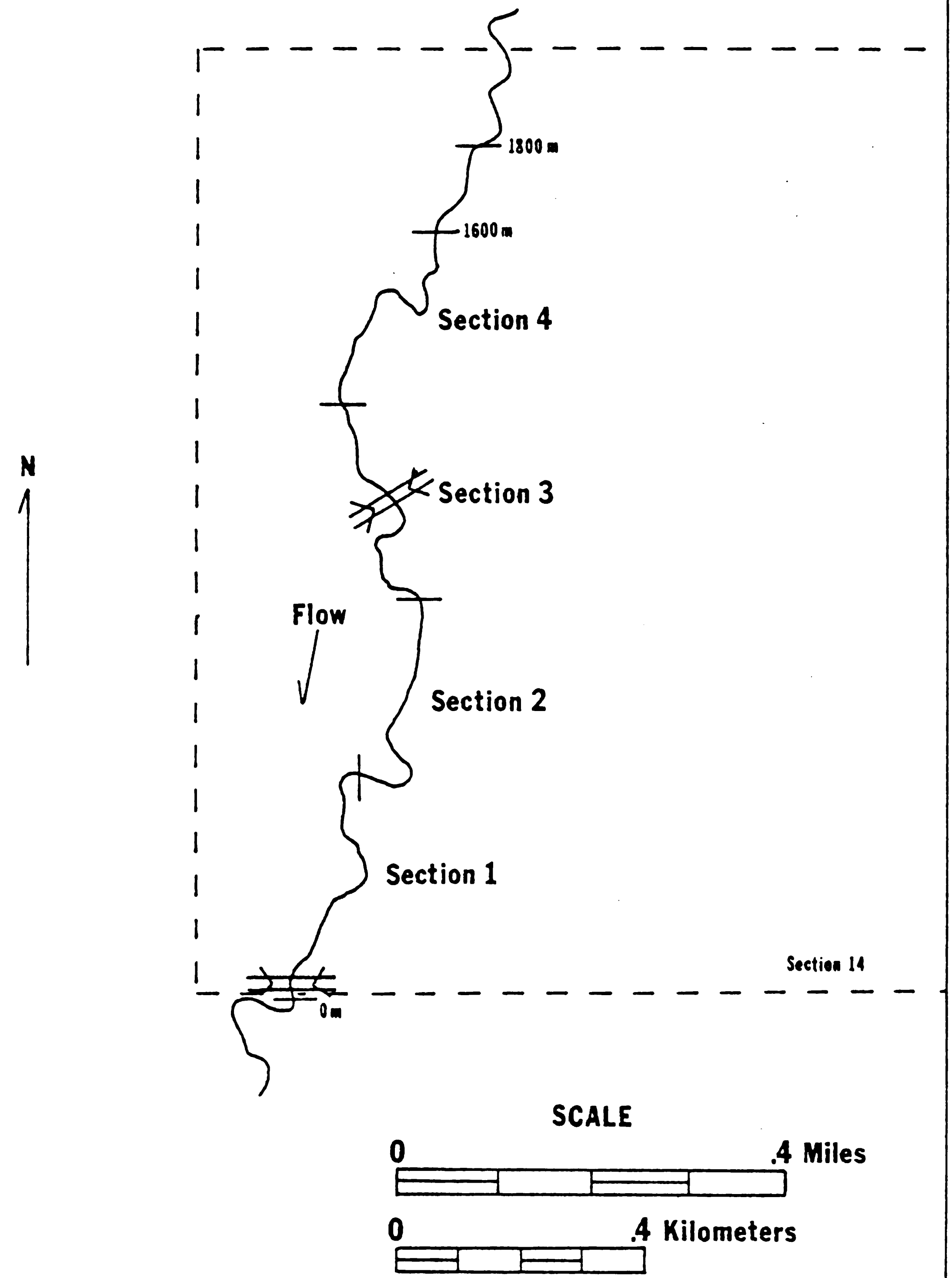


Figure 2. The study area.

point. The roads permit public access to the stream close to Hartwick Pines State Park. The park, an adjoining campground and a state highway are located about 1.5 km northwest of the study area by road.

Biota

Valisneria spp. is the most abundant aquatic macrophyte in the study section. It proliferates along the silted margins of the stream where the water velocity is reduced and the stream generally less than 30 cm deep. The most abundant visible invertegrates are the larvae of *Brachycentrus spp.* (Order Trichoptera) which frequently attach to the *Valisneria* and to many of the larger pieces of streambed gravel.

Resident fishes include brook trout, brown trout, sculpins (Cottidae), darters (Percidae) and minnows (Cyprinidae). Single specimens of bluegill (*Lepomis macrochiris*) and yellow perch (*Perca flavescens*) were also collected during the study.

Man's impact on the biota includes angling and management of the stream for trout. Stocking records (1942-1977) show great variety in the numbers and species of hatchery-reared trout introduced into the stream. Yearling and older brook trout (175-330 mm) were stocked each year from 1942 to 1964 in numbers ranging from 200 to 16,500 and in all areas from Section 2, T27N-R3W, downstream to the mouth. Brown trout were stocked in various places along the lower half of the stream from 1953 to 1955--adults (175-200 mm) in small numbers in 1953 and 1954 (1125 and 700 respectively) and 16,700 yearlings (100-175 mm) in 1955. About 700 adult rainbow trout were released each year in 1949, 1953 and 1955, and 200 adults were released in 1954, all near the mouth of the stream.

Numerous artificial cover devices have been installed throughout the study area. These devices are built of logs and are basically of 2 types: wing deflectors and log crib bank covers. They are believed to have been built in 1962-1963, although some were restorations of devices that were built during the 1930's (G.T. Schnicke, Michiagn DNR, personal comm.). Although many of the cover devices were placed contrary to present knowledge of stream hydraulics and trout behavior, and many of them have deteriorated, they still provide most of the instream cover for trout.

METHODS

The daytime positions of adult brook trout were observed by diving with mask and snorkel before and after the removal of most brown trout from the study area by electrofishing. Thus, brook trout were observed in sympatry before the brown trout were removed and in allopatry after the removal. Observations in sympatry were made during July 21-23 and on August 11, 1977. The gap in sampling was due to rain and fishing pressure. The brown trout were removed by electrofishing on August 12, 13, and 14, 1977. The positions of brook trout in allopatry were observed during August 20-23, 1977. A few adult brown trout positions were also recorded during the period before their removal.

Underwater Observation

Diving usually was done for 3-4 hours each morning and afternoon beginning about 0830 h and 1330 h respectively (EDT). Although direct sunlight did not touch the stream surface until about 0930 h, brook trout were almost always active before this. Because of this, I began diving during this early morning period even though the visibility was not optimal then. Light was reduced to similar low levels by early evening, but I rarely observed trout that late because I usually was too tired.

A 6 cm thick wetsuit equipped with hood, boots, three-window face mask, snorkel and weight belt was worn while diving. In addition, loose black rubber gloves that could be easily removed were worn to keep the hands warm. All of the equipment worn, except the yellow weight belt was black. The instruments used to measure characteristics of brook trout positions included a wooden ruler marked in 5 cm intervals and wire stakes with bright plastic flagging attached, both carried under the weight belt while diving. A plastic meter stick and 3 midget Bentzel speed tubes, used to measure current velocity, were carried by an assistant walking in the stream about 100 m behind me. The midget Bentzel speed tubes were constructed and calibrated from instructions provided by Dr. Fred H. Everest (Everest, 1967). Each of the 3 tubes measured a different range of current velocity: 0-30, 30-60 and 60-115 cm/sec.

Observations began at the downstream border of the study area for each 4-day period. I progressed 200-300 m upstream during each half day, depending on the character of the channel and the number of fish observed. To ensure observation of different fish throughout the 4-day period, diving began upstream from the previous stopping point each morning and afternoon. After brown trout removal, the first 300 m and the last 400 m of the study area were not observed. These zones at the study area margins served as buffers against the effects of brown trout immigration.

While diving, I crawled upstream using only my hands, slowly investigating the main channel and all of the cover in the stream that may have harbored trout. Approaching slowly from downstream allowed me to observe trout in their natural positions and disturbed them very little if done with care. Because cover for adult trout was primarily provided by artificial cover devices, these and natural cover were the areas most thoroughly investigated.

When an adult trout was sighted, I remained motionless for 1-2 minutes to determine whether the fish had been disturbed. If not, I located the focal point of its activity in reference to the stream bed. During this period of motionless observation, I mentally noted the species of fish, the type of position (resting or feeding), the focal point, the distance of the fish's head from the substrate and the size class of the fish. Resting and feeding positions were easily separated on the basis of microhabitat characteristics and behavior of the fish, both of which will be described more fully in the Results section. Trout observed were grouped into three, 5-cm size classes: 15-20 cm, 20-25 cm and 25-30 cm. To distinguish between the various size classes, the length of the fish was noted in reference to the stream bottom. The wooden ruler was then used to verify the fish's size class using the stream bottom references. This procedure was necessary due to the magnification of objects underwater, causing them to appear both 25% larger and 25% closer (Sport Diver Manual, 1975). After a little practice, the size classes of trout were easily judged without this aid. Because the size of trout could only be judged to the nearest centimeter at best, the size classes overlap for easy reference.

After location of the focal point of activity, I placed a metal stake in the stream bed directly below the position of the fish. The information thus far collected was recorded by the assistant, who then brought the rest of the equipment upstream. I reentered the stream and measured the water velocity at the focal point and the maximum water velocity within 60 cm of the focal point using the Bentzel speed tubes. Water depth at the focal point and the distance to nearest overhead cover from this point were also measured. Overhead cover was arbitrarily defined as artificial or natural cover that contacted the stream bank and was capable of fully obscuring the fish from overhead view. This was most often a wing deflector, a natural undercut bank or a mass of overhanging alder roots (*Alnus spp.*).

Classification of positions according to type of illumination was regarded as a minor objective of this study. A submersible light meter initially used was incapable of registering light intensities as great as those usually encountered. Therefore, I resorted to 3 subjective classifications: direct sunlight, indirect light and shade. Positions where sunlight touched the stream bed were recorded as direct sunlight. The category of indirect light included positions illuminated by reflected or diffused sunlight as well as sunlight filtering through trees or bank vegetation.

Positions in the dark recesses beneath instream cover were classed as shade. No overcast days occurred during observation.

Electrofishing Procedure

Prior to electrofishing, the lower 1600 m of the study area was divided into four 400 m sections. The upstream boundary of each section was marked with bright plastic flagging tied conspicuously to streambank vegetation. Mark-and-recapture electrofishing was employed to inventory the brook trout population in the lower 1600 m only. The entire 1800 m study area was electrofished on 3 consecutive days, August 12-14, 1977. The marking and recapture runs for brook trout were made on the first and third days respectively. Brown trout longer than 100 mm captured in the 1800 m on all 3 runs were removed from the stream. However, all results presented are for brown trout from the lower 1600 m only, so that they are comparable to those for brook trout. On the second day of electrofishing only brown trout were netted. This measure provided an extra day for the redistribution of the marked brook trout into the unmarked population.

The electrofishing unit consisted of a small plastic boat carrying a 250-v, 1.75-kw DC generator. The 3-man electrofishing crew proceeded upstream, one man towing the boat and each carrying an anode and hand net. A cathode, made of brass screen fastened to styrofoam, trailed behind the boat. Since artificial and natural cover held most of the trout, these areas were electrofished intensively. The crew surrounded each of these areas and simultaneously began short quick jabs into openings and underneath the cover. This method proved most efficient because of the element of surprise. In addition, the most upstream crew member could effectively drive fish downstream into the fields of the other 2 electrodes. Between areas of large cover, the crew moved upstream abreast, each electrofishing his third of the stream bed and underneath banks. Captured fish were transferred to a tub of water in the boat. When the upstream boundary of a section was reached, a perforated tub liner containing the fish was removed from the boat and placed in the stream. While the electrofishing crew continued upstream, 2 additional men processed the catch.

All trout captured were anesthetized with tricaine methane sulfonate (MS-222), measured to the nearest millimeter, and weighed to the nearest gram. Scale samples were taken from all sizes of trout of both species for age determination. The lower tip of the caudal fin was clipped on the marking run to provide an identifying mark for recaptured brook trout. Separate record sheets were kept for each stream section. After processing, brook trout were transported back downstream and released at the beginning of the section. This facilitated redistribution of the brook trout, owing to olfactory orientation to their previous positions in the stream.

The 167 brown trout longer than 100 mm were retained in a live box after processing and later transported in an aerated tank to an old DNR hatchery raceway at Grayling. The raceway was 3.4 m wide and 61 m long and was supplied with a continuous flow of water from the East Branch of the Au Sable River. Cover was available to fish under aquatic vegetation and floating planks attached to anchored trees. Nine days after the electrofishing, when observations were complete, the remaining 91 brown trout were released at the downstream end of the study area. The drastic loss of trout was attributed to a heron often seen near the raceway because most of the fish that had disappeared were small. Other possible reasons for the loss were predation by mink, vandalism or escape.

Calculation of Population Estimates

A major objective in choosing the study area was to locate equal numbers of brook and brown trout in sympatry. Although the East Branch stream section was selected from DNR fish surveys (G.R. Alexander, Michigan DNR, personal comm.), electrofishing provided a current estimate of the numbers of brook and brown trout of each size class that inhabited each stream section.

Brook Trout

Population estimates for brook trout were calculated from the Schaefer modification of the Petersen method (Regier and Robson, 1967):

$$\hat{P} = \left[\frac{(m+1)(r+u+1)}{(r+1)}\right] - 1$$

$\hat{P}$ = estimated population
m = number of fish marked during first run
r = number of marked fish recaptured during second run
u = number of unmarked fish captured during second run

The efficiency of capture by electrofishing for salmonids increases with length (McFadden, 1961). Therefore, to minimize the bias introduced by this differential efficiency, separate population estimates were calculated for each 50 mm size class for the whole study area. Since the numbers of brook trout in the 200-349 mm range were too small to calculate a valid population estimate, they were combined with 150-199 mm fish to give a total estimate for the 150-349 mm size class. In this study, it was found that the efficiency of recapture (r/r+u) for brook trout size classes 150 mm and larger was a constant 60%, thus justifying this procedure. The total estimate was then reapportioned into 50 mm size classes according to the relative proportions of the sums of m+u. This method of combination and reapportionment reduces error because larger individual units are used, especially of recaptures on which the method is based (Cooper, 1952).

Procedures outlined in Davis (1964) indicated that a binomial distribution was appropriate for estimating the confidence interval of the population estimate for each size class in this specific sample. The graphs of Adams (1951) were used to derive the 95% confidence interval for each population estimate. These confidence limits were then reapportioned among stream sections using the method described for population estimates. Finally, the total 95% confidence limits for each stream section were calculated by summing the upper and lower interval limits for each size class in the section.

Brook trout biomass estimates for the size classes in each stream section were calculated by multiplying size class population estimates times average body weight for the size class. Confidence intervals for the biomass estimates were similarly calculated by multiplying the 95% confidence limits of each population estimate times average body weight for the size class involved. Biomass estimates and interval limits were then summed to give the total biomass estimates and the confidence interval for each stream section. The population density of brook trout in each size class was calculated for both numbers and biomass. Size class totals for the entire 1600 m of stream were divided by 1.6 to find numbers and biomass per kilometer of stream.

<u>Brown Trout</u>

Because brown trout were removed during each electrofishing run, a population estimate based on the mark-recapture method was not applicable. Instead, 2 procedures based on the catch per unit of effort were used to calculate a population estimate. The first of these was an improved Leslie estimate (Ricker, 1975), which consisted of a simple linear regression of catch per electrofishing run (y) against cumulative catch of all previous runs plus half of the catch for the present run (x). The population is estimated from the x-intercept, which corresponds to the cumulative catch if the entire population were captured by electrofishing. The second method was identical to the first except that instead of calculating the regression, the lines were fitted by inspection. These 2 methods were used to estimate separately the population of all brown trout, and the population of fish larger than 150 mm. The latter size group represents brown trout that potentially competed with the observed brook trout for positions. Biomass of brown trout was calculated for the size classes in each section by summing the weights of the individual fish in each size class captured from that stream section. The numbers and biomass of brown trout per kilometer of stream were calculated in the same manner as those for brook trout.

Age Determination

The age structure and growth of each population was determined by inspection of 100 brook trout and 94 brown trout scales. Impressions of scales were made in cellulose acetate using a roller press and examined with a microprojector. Fish of each age were separated into 10 mm size classes for comparison of growth. The lengths of all individuals in each age group were averaged to give the mean length at each age. Since age 0 brook and brown trout were not sampled for scales, the length frequency histogram of fish captured by electrofishing is presented instead for each species. Brown trout of age 0 were easily separated from those of age I by a large gap in the histogram. Brook trout were less easily separated but an upper limit of 109 mm was chosen from the area of the histogram with fewest individuals between the modes of age 0 and I fish.

Statistical Analysis of Brook Trout Positions

The major objective of this study was to test the hypothesis of interspecific competition by measuring the microhabitat shift of brook trout after brown trout were removed. Since individual fish were not identified, evidence for this shift can only be provided by statistical differences between the position characteristics of brook trout in allopatry when compared to those in sympatry. Results of these statistical analyses are necessarily viewed in light of observations made while diving. Because of the behavior observed for brook trout (see Results), positions were analyzed separately for feeding and resting positions, as well as for 2 size classes.

The 5 major dependent (y) variables measured about the position of each individual brook trout were: 1) focal point water velocity, 2) maximum water velocity within 60 cm of the focal point, 3) water depth, 4) distance from the substrate and 5) distance from nearest overhead cover. These dependent variables are correlated since all 5 were measured about each brook trout position. Therefore, instead of considering each variable separately, a multivariate approach was used. In this method of analysis, all variables are considered simultaneously, so that differences between vectors of means and between matrices of variances and covariances are tested. The last variable, distance from nearest overhead cover, is defined as zero for resting fish. Therefore, the remaining 4 variables were used in the analysis and the fifth tested separately for feeding fish.

Brook trout positions were partitioned into 4 "cells" according to the 2 levels of each of the independent variables: population type (sympatry, allopatry) and position type (resting, feeding) (Table 1). It was hoped that a multivariate analysis of variance could be applied to this factorial design, using the large body of position data from 15-20-cm brook trout. However, the requirement of homogeneous variance among cells could not be met, even after 4 transformations and the exclusion of one outlier. Instead of reverting to a univariate analysis of variance for each dependent variable, it was deemed more appropriate to apply a separate multivariate T^2-test to each of the 4 combinations of 2 adjacent "cells" (ie. sympatry, resting vs. sympatry, feeding). Because the multivariate T^2-test is analogous to the univariate t-test, this is the same procedure that would be used to test the main effects in any analysis of variance if the interaction was found to be significant. However, since these 4 separate T^2-tests are not independent, the overall Type I error is increased slightly. With high levels of confidence, this problem is usually not bothersome (J.L. Gill, Department of Dairy Science, M.S.U., personal comm.).

		Population Type	
		Sympatry	Allopatry
Position Type	Resting	n = 16 m = 5	n = 27 m = 3
	Feeding	n = 24 m = 5	n = 19 m = 5

n = number of 15-20-cm brook trout

m = number of 20-25-cm brook trout

Model: Y_1 = Focal point current velocity

Y_2 = Maximum current velocity within 60 cm

Y_3 = Water depth

Y_4 = Distance from substrate

$$\begin{bmatrix} Y_1 \\ Y_2 \\ Y_3 \\ Y_4 \end{bmatrix}_{ijk} = \begin{bmatrix} \mu_1 \\ \mu_2 \\ \mu_3 \\ \mu_4 \end{bmatrix} + \begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \\ \alpha_4 \end{bmatrix}_i + \begin{bmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \\ \beta_4 \end{bmatrix}_j + \begin{bmatrix} \alpha\beta_1 \\ \alpha\beta_2 \\ \alpha\beta_3 \\ \alpha\beta_4 \end{bmatrix}_{ij} + \begin{bmatrix} E_1 \\ E_2 \\ E_3 \\ E_4 \end{bmatrix}_{ijk}$$

Table 1. Initial analysis of variance design.

Although the data for 2 of the T^2-tests met the assumption of homogeneous variance, the other 2 data sets showed heterogeneous variance even after 4 transformations were applied. In these latter cases, the data were randomly paired and the differences between each pair of observations used in a similar manner to the univariate paired t-test.

After the data for 15-20-cm fish were analyzed, I noticed that position characteristics of the small sample of 20-25-cm brook trout were very different in sympatry than in allopatry. In addition, the analysis of positions chosen by smaller trout, and literature on salmonid ecology suggested that a new variable formed from the difference between the maximum water velocity within 60 cm and the focal point water velocity would be more indicative of shifts in brook trout positions after brown trout removal. This variable was termed the "water velocity difference."

Initially, a univariate analysis of variance using the same two-way factorial design was applied to the water velocity difference for 20-25-cm brook trout to determine the overall response. The variance was again heterogeneous among cells, but was corrected by a transformation of $y'=1/y$. To further define the microhabitat shift, 2 multivariate T^2-tests were applied, to test differences between positions in sympatry versus allopatry for feeding and then resting fish. However, only 3 position characteristics were used: water depth and distance from substrate.

A simple t-test was used to determine differences between distance from nearest overhead cover for feeding brook trout in sympatry versus those in allopatry. A chi-square test was employed to test the departure of the ratio of brook to brown trout observed in visible resting positions from the expected ratio calculated from the estimated populations of brook and brown trout. In both of these procedures, the 2 size classes of trout (15-20-cm, 20-25-cm) were tested separately.

A summary of the univariate and multivariate statistical techniques used to determine differences between brook trout positions in sympatry and allopatry is presented in Table 2. All multivariate procedures are described in Kramer (1972).

Table 2. Summary of statistical analyses. Dependent variables are designated by X's.

Comparison (test used)	Homogeneous variance	Water velocity (cm/sec)			Water depth (cm)	Distance (cm)	
		Focal point	Max. at 60 cm	Difference		To bed	From cover
15-20-cm Brook Trout							
Sympatry vs allopatry							
For resting fish (multivariate pooled T^2)	Yes	X	X		X	X	
For feeding fish (multivariate pooled T^2)	Yes	X	X		X	X	
For feeding fish (univariate t)	Yes						X
Resting vs feeding							
When sympatric (multivariate paired T^2)	No	X	X		X	X	
When allopatric (multivariate paired T^2)	No	X	X		X	X	
Brook vs brown trout							
Ratio of visible resting fish (chi-square)							
20-25-cm Brook Trout							
Population and position type* (analysis of var.)	Yes**			X			
Sympatry vs allopatry							
For resting fish (multivariate pooled T^2)	Yes			X	X	X	
For feeding fish (multivariate pooled T^2)	Yes			X	X	X	
For feeding fish (univariate t)	Yes						X
Brook vs brown trout							
Ratio of visible resting fish (chi-square)							

*See Table 1.

**Homogeneous variance after transformation of y'=1/y.

RESULTS

Although the major objective of this study was to investigate the interspecific competition between brook and brown trout, of equal importance is the determination of the mechanism of any such competition. Besides reporting the effects of the population manipulation on the positions of brook trout, other aspects of the ecology and behavior of the 2 species lend valuable insight into the mechanism of competition. Thus, the daytime behavior of the 2 species, their population size, age and growth are presented as well as the effects of brown trout removal on brook trout position choice.

Daytime Behavior of Trout

The daytime behavior of trout was partitioned into fairly distinct microhabitats, although the different sizes and species of trout occupied these microhabitats in different proportions. Microhabitats fell into 3 general categories: feeding, resting and deep cover.

Microhabitat Types

Feeding microhabitat consisted of an indistinct area of stream bottom near the thalweg, defined as the deepest point of the channel cross-section. Characteristics of this area included an unvegetated clean sand and gravel substrate and position beneath a principle line of drift. Within this indistinct area, specific feeding stations were provided by areas of low water velocity behind protuberances of the stream bed. Another type of position that was included as feeding microhabitat occurred in the 3 large pools one meter or more in depth. Here, loose dominance hierarchies were observed in which the largest or dominant fish maintained position at the head of the pool and fed on the largest incoming items of invertebrate drift. The positions in the pool were not distinct, with trout most often occupying turbulent areas of low water velocity near the pool bed.

Resting microhabitat chosen by trout was nearly always beneath some form of overhead cover. Overhead cover was available under the downstream ends of artificial wing deflectors where floods had scoured depressions in the gravel substrate. During low flows, these depressions provided areas of lower water velocity. In addition, the deflector offered complete overhead concealment and the attendant shade.

Deep cover consisted of positions that were well concealed from both overhead and lateral view. For large fish of both species, deep cover was merely a more concealed form of resting microhabitat and the 2 will not be distinguished in further discussion. For smaller trout, deep cover probably provided secure hiding cover from terrestrial and underwater predators. Natural undercut banks and the points at which artificial cover devices (wing deflectors and log cribs) joined the stream bank were areas of deep cover for trout. When viewed underwater from the side, many of the small

natural undercut banks showed an overhang coming within a few centimeters of the stream bed, but these opened into large cavities behind. Trout were well concealed in the cavity behind these overhangs and were not readily visible. Large spacious undercut banks in the 3 large pools also provided excellent deep cover for trout.

Behavior of 15-20-cm Trout

Adult brook trout at 15-20-cm most frequently occupied resting positions during the day, moving to feeding microhabitat in response to emerging insects. When few insects were emerging, these brook trout remained behind one feeding station most of the time, making infrequent forays to the surface. If insect emergence was fairly continuous, the fish were more active and fed from several feeding stations in succession. During periods of heavy insect emergence, some brook trout would swim vigorously in areas of high water velocity nearer the surface to feed on adult insects. Thus, although 15-20-cm brook trout occupied feeding positions in response even to low levels of invertebrate drift, increased emergence of insects stimulated feeding activity.

After insects ceased emerging, brook trout returned to resting microhabitat beneath the downstream ends of log deflectors and in other areas of cover. When fish of this size class were disturbed while feeding, they moved in short dashes upstream, but always swam quickly downstream around me when they reached some limit of 1-2 meters from their original focal point. When disturbed from resting positions, these brook trout usually moved into deep cover positions closer to the bank.

Only five 15-20-cm brown trout were seen during the study. Of these, 3 were observed in pools, occupying dominance hierarchies with brook trout of the same size class. The other 2 brown trout were observed in resting positions. One of the 2 brown trout was lying close beside a brook trout of the same size class beneath a small undercut bank. Interspecific agonistic behavior was never observed between any brook and brown trout.

Behavior of 20-25-cm Trout

Adult brook trout of 20-25-cm were not often observed, but occupied feeding and resting positions. Only one 25-30-cm brook trout was observed. It is included with 20-25-cm brook trout in further analysis and discussion. With the exception of pool hierarchies, these large brook trout moved to feeding positions only when substantial invertebrate drift was available. Although feeding behavior was similar to small brook trout, 20-25-cm brook trout were less active, feeding from one feeding station at all times. In addition, these fish chose feeding positions that afforded some protection from predators in the form of partial overhead cover, water depth or shade. Of the 18 brook trout observed in this size class, 4 were feeding as the dominant fish in a pool dominance hierarchy. Large brook trout were more easily disturbed than those of smaller sizes and quickly retreated to deep cover positions with little provocation. Brown trout larger than 20 cm were sighted on only 2 occasions. Both fish were occupying resting microhabitat and moved to deep cover positions after being disturbed.

Trout less than 15 cm of both species were age 0 and small age I fish. Although this size class was not specifically studied, I noted that they generally occupied positions too small for larger fish. These positions were often in the open portions of the channel, behind some small obstruction or near the edge of _Valisneria_ beds where the water velocity close to the stream bed was somewhat reduced from velocities nearby in the channel. When disturbed, these fish repeatedly swam about 30 cm upstream and settled to the stream bottom.

Although large fish were more easily disturbed than small fish, I believe that all trout used in the analysis occupied undisturbed positions. Because trout larger than 20 cm quickly moved into concealed positions, even when disturbed slightly, those observed were probably undisturbed and in their original positions. However, feeding fish of both species larger than 25 cm probably fled into deep cover positions before I came close enough to see them.

Insect emergence varied diurnally and seasonally during the study. During sympatric observations, _Tricorythodes spp._ mayflies (Order Ephemeroptera) emerged from early morning until about 1100 h (EDT). During observations in allopatry, few _Tricorythodes_ were emerging. Instead, a few small mayflies believed to be _Baetis spp._ and a variety of midges (Order Diptera) usually emerged during the afternoon.

Visibility in the stream decreased markedly from morning to afternoon throughout the study. Visibility was usually 4 m or more when morning observation began and decreased to 2.5 m or less by late afternoon (1630 h EDT). Rainfall has little effect on the streamflow of this sandy drainage basin, and the turbidity produced by evening rains more often was greater during the following morning than afternoon. Thus, turbidity was not responsible for the decrease in visibility, and the causes are not known.

Water temperatures increased throughout each day, but generally decreased as the study progressed. During observations before brown trout removal (July 21-23, August 11), water temperatures were usually 15 C in the morning and 18 C in the afternoon. The morning and afternoon water temperatures were about 11 C and 14 C respectively during observations after the removal (August 20-23).

Stream Discharge

The mean daily discharge for each day of observation is presented in Table 3 (U.S. Geological Survey, Okemos, Michigan). Also presented are: monthly means for July and August, 1977; monthly means and standard deviations for February, July and August, 1959-1973; and 7-day low flows with 1-, 2- and 10-year recurrence intervals for 1959-1973.

The mean monthly discharge for July and August 1977 were lower than the respective monthly means for 1959-1973,

Table 3. Streamflow discharge and low flow characteristics for the East Branch of the Au Sable River, measured at Grayling, Michigan (site shown in Figure 1).

Date	Discharge (m^3/sec)
1977 Observation Periods	
July 21	0.99
July 22	0.93
July 23	0.85
August 11	0.93
August 20	0.93
August 21	0.91
August 22	0.91
August 23	0.88
1977 Monthly Means	
July	0.87
August	0.91
Monthly Means for 1959-1973	
February	1.02 ± 0.23*
July	1.10 ± 0.22
August	1.04 ± 0.22
7-Day Low Flows	
1-year recurrence	1.21
2-year recurrence	0.80
10-year recurrence	0.58

*standard deviations.

but only July differed by slightly more than one standard deviation. This indicates that summer baseflow for 1977 was low, but not significantly lower than normal. The discharge for the period of study varied from 0.85-0.99 m^3/sec. In reference to the recurrence intervals for 7-day low flows, the discharge for the study period and the summer baseflow discharge for 1977 fell between the 1- and 2-year recurrence interval flows. Because February is generally the month of lowest discharge for this stream, the recurrence intervals for low flows are not strictly comparable with summer baseflows. However, this comparison still indicates that the period of observation was during summer baseflow and that baseflow was not significantly lower than normal.

Population Estimates

Trout were observed in the study area in frequencies consistent with their relative abundance. Brook trout smaller than 200 mm were regularly seen, while larger brook trout were less often observed. Brown trout of all sizes were rarely seen for reasons of relative abundance and behavior. These observations were confirmed by the population estimates for each species.

In many respects the East Branch was ideal for electrofishing, with very few large, unwadeable pools and water of high conductivity. This was reflected by a high (60%) efficiency of recapture for brook trout larger than 150 mm and the nearly complete removal of brown trout from the study area.

Brook Trout

Brook trout abundance in each of the 4 stream sections is presented in terms of numbers (Table 4) and biomass (Table 5). The number of 50-149 mm brook trout increased in upstream sections, whereas brook trout larger than 150 mm occurred in about equal numbers among stream sections. Brook trout smaller than 200 mm constituted 99% of the population and contributed 94% of the biomass. Biomass of brook trout followed the same general pattern, with totals for 50-149 mm brook trout increasing in upstream sections. Biomass was about equal among sections for brook trout larger than 150 mm. The 95% confidence intervals for total numbers and biomass in each stream section show that section one held significantly lower numbers and biomass of brook trout. This is consistent with the lower amount of artificial and natural cover available to trout in that section.

Brown Trout

The numbers of brown trout captured in each section on 3 electrofishing runs are presented by size class in Table 6. The biomass of these fish is presented in Table 7. All size classes of brown trout were about evenly distributed among sections with a slight trend of more fish in the upstream sections. Total biomass also increased in upstream sections, with section one again containing much less biomass of brown trout than the other 3 sections. Brown trout numbers and biomass were about evenly distributed among size classes with the largest totals occurring in the 150-199 mm size

Table 4. Brook trout population estimates by 400-m sections.

Total length size class (mm)	Study section 1	2	3	4*	Total (1600m)	95% CI
50-99	46	203	223	422	894	579-1571
100-149	52	88	107	165	412	347-492
150-199	65	77	67	94	303	268-351
200-249	2	6	4	4	16	15-20
250-299					0	-
300-349			1		1	1-1
Total	165	374	402	685	1626	1209-2434
95% CI	132-219	279-558	300-605	499-1058	1209-2434	

*The upstream section.

Table 5. Brook trout biomass (kg) estimates by 400-m sections.

Total length size class (mm)	Study section 1	2	3	4*	Total (1600m)	95% CI
50-99	0.24	1.22	1.34	2.74	5.54	3.59-9.75
100-149	1.08	1.97	2.39	3.65	9.09	7.66-10.86
150-199	3.06	3.46	3.13	4.39	14.04	12.42-16.26
200-249	0.19	0.62	0.41	0.39	1.61	1.52-2.03
250-299					0.00	
300-349			0.27		0.27	0.27-0.27
Total	4.57	7.27	7.54	11.17	30.55	25.46-39.17
95% CI	3.94-5.52	6.11-9.31	6.34-9.65	9.07-14.69	25.46-39.17	

*The upstream section.

Table 6. Number of brown trout captured by 400-m sections.

Total length size class (mm)	Study section 1	2	3	4*	Total (1600m)
50-99	5	13	7	16	41
100-149	2	1	5	4	12
150-199	21	17	20	25	83
200-249	7	5	5	4	21
250-299	5	8	8	4	25
300-349	3	5	3	3	14
350-399	1	3	1	1	6
400-449		1	3		4
450-499					0
500-549				1	1
550-599				1	1
Total	44	53	52	59	208

*The upstream section.

Table 7. Biomass (kg) of brown trout captured by 400-m sections.

Total length size class (mm)	Study section 1	2	3	4*	Total (1600m)
50-99	0.03	0.07	0.03	0.08	0.21
100-149	0.07	0.02	0.14	0.10	0.33
150-199	1.01	0.91	1.12	1.47	4.51
200-249	0.72	0.47	0.50	0.33	2.02
250-299	1.02	1.57	1.51	0.76	4.86
300-349	0.97	1.43	0.93	0.88	4.21
350-399	0.40	1.56	0.67	0.56	3.19
400-449		0.75	2.07		2.82
450-499					0.00
500-549				1.52	1.52
550-599				1.80	1.80
Total	4.22	6.78	6.97	7.50	25.47

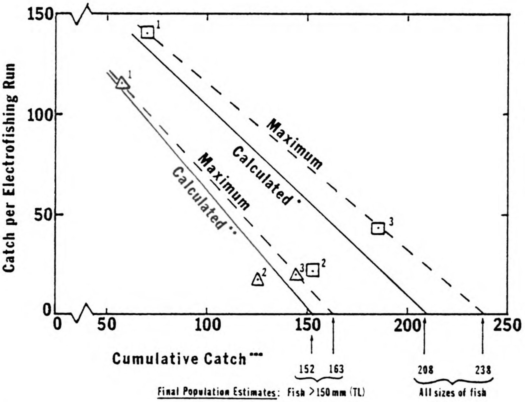
*The upstream section.

class.

Two estimates of the brown trout population were calculated, one for fish larger than 150 mm and one for all brown trout (Figure 3). Difficulty was encountered in calculating the Leslie population estimate because of the low number of brown trout captured during the second day of electrofishing. When equations were fit to the data by linear regression, estimates of 152 and 208 fish respectively were calculated. Both of these estimates were equal to or less than the number of brown trout actually captured for the respective size groups. In order to arrive at maximum estimates of brown trout in the stream, lines were fit to the data points by inspection (Figure 3). This yielded maximum estimates of 163 fish larger than 150 mm and 238 brown trout in total. The brown trout captured represented 95% and 87% of these estimates respectively.

Comparison of Trout Populations

Estimated numbers of brook trout are compared to brown trout captured by 50 mm size classes in Figure 4. Brown trout smaller than 200 mm were much less abundant than brook trout of the same size. Only one brook trout larger than 250 mm was collected, whereas moderate numbers of brown trout of all sizes to 600 mm were captured. The abundance of brook and brown trout was grossly unequal in all size classes except 200-249 mm. In addition, Tables 4 and 6 indicate that all sections except section one held



*Calculated Y=184.84 -1.21x

**Calculated Y=201.75-0.97x

***Cumulative catch plus one-half catch for present run.

Figure 3. Leslie population estimate for brown trout captured by electrofishing. Calculated regression (——) and maximum estimates (- - -) are shown for all brown trout (⊡) and for fish larger than 150 mm (△). Superscript numbers denote run.

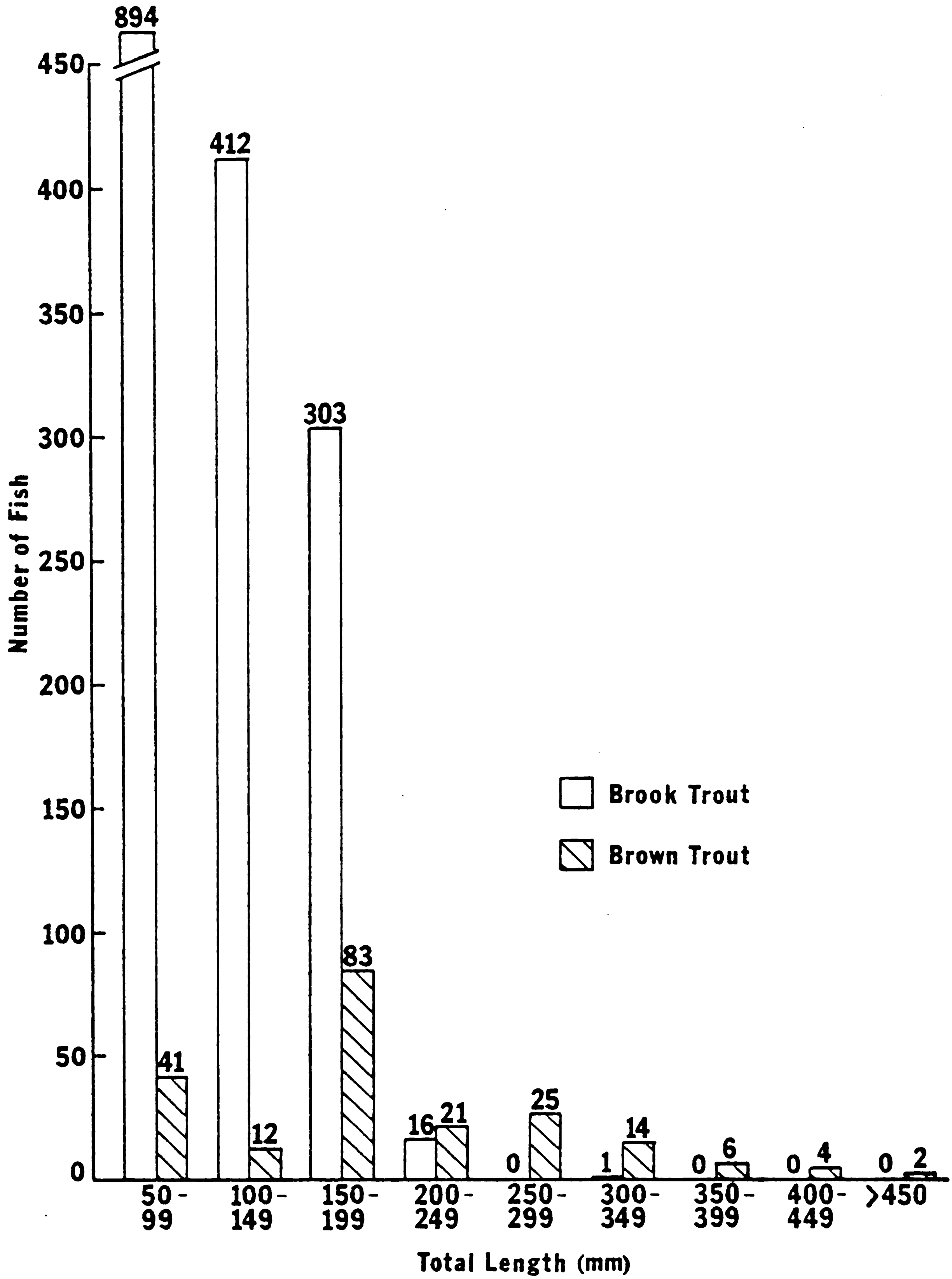


Figure 4. Comparison of brook and brown trout by 50 mm size class.

about equal numbers of 200-249-mm brook and brown trout.

The population densities of brook and brown trout in terms of numbers and biomass per kilometer of stream are presented by 50 mm size class in Table 8. As previously stated, most of the brook trout biomass was contributed by 50-199-mm fish, whereas the biomass of brown trout was more evenly distributed among size classes. The standing crop (kg/km) for East Branch trout is compared to standing crops for other Michigan and Wisconsin streams in Table 9. In comparison to studies where many years of data were collected, the standing crop of East Branch trout fell within the ranges of standing crops determined for all streams except Lawrence Creek and Big Roche-a-Cri Creek, both in Wisconsin.

Age and Growth of Trout Populations

The age composition for the samples of brook and brown trout are presented in Table 10. Scale samples were taken from a disproportionate number of large fish of both species. Therefore, numbers of fish in each age group are not indicative of abundance.

The first 3 age groups of brook trout overlap each other greatly in length. Fish of ages 0 and I probably overlap in length, but this was precluded by the arbitrary division between the 2 groups (see Methods). It is evident from scale samples and from the population estimate that few brook trout survived past their third year of life (age II). Only one brook trout of age III and larger than 300 mm was captured.

Table 8. Population density of brook and brown trout by number and biomass.

Total length size class (mm)	Brook Trout		Brown Trout		Total Trout	
	Number per km	Kg per km	Number per km	Kg per km	Number per km	Kg per km
50-99	559	3.46	26	0.13	585	3.59
100-149	257	5.68	8	0.21	265	5.89
150-199	189	8.77	52	2.82	241	11.59
200-249	10	1.01	13	1.26	23	2.27
250-299			16	3.04	16	3.04
300-349	1	0.17	9	2.63	10	2.80
350-399			4	1.99	4	1.99
400-449			3	1.76	3	1.76
450-499						
500-549			1	0.95	1	0.95
550-599			1	1.12	1	1.12
Total	1016	19.09	133	15.91	1149	35.00

Table 9. August-September standing crops of trout in various Michigan and Wisconsin streams. Ranges are shown where many years of data were collected.

Stream and locality	Length of study section (km)	Number of years of study	Kg per km			Reference
			Brook	Brown	Total	
East Branch Au Sable River, Mich.	1.6	1	19.1	15.9	35.0	This study
Pigeon River, Mich.	2.4	1	11.7	45.4	57.1	Enk, 1977
Pigeon River, Mich.	9.7	17	8.5-25.7	9.0-20.8	19.0-44.0	White, Hansen and Alexander, 1976
Hunt Creek, Mich.	1.7	9	26.7-45.2	--	26.7-45.2	White, Hansen and Alexander, 1976
Salmon Trout River, Mich.	4.5	1	10.0	--	10.0	Enk, 1977
Big Roche-a-Cri Creek, Wis.	10.3	9	6.4-17.5	2.0-4.7	10.9-21.7	White, 1972
Big Roche-a-Cri Creek, Wis. (best section)	3.4	9	12.8-33.3	0.0-2.2	14.7-33.7	White, 1972
Lawrence Creek, Wis.	5.4	11	52.1-83.4	--	52.1-83.4	Hunt, 1974

Table 10. Age composition for samples of brook and brown trout captured by electrofishing in the East Branch of the Au Sable River, August 12-14, 1977. Mean lengths at each age are given below.

Total length	Brook Trout				Brown Trout					
size class (mm)	0	I	II	III	0	I	II	III	IV	V
60-69	6				2					
70-79	38				14					
80-89	87				21					
90-99	85				4					
100-109	32									
110-119		*								
120-129		7				*				
130-139		4				1				
140-149		18				1				
150-159		18				3				
160-169		14	1			5				
170-179		14	2			4				
180-189		7				8				
190-199		2	1			2				
200-209		3	1			5	1			
210-219			3			1	2			
220-229			2			1	3			
230-239			1				1			
240-249			1				3			
250-259							2			
260-269							10			
270-279							5			
280-289							4			
290-299							3	2		
300-309				1			2			
310-319							5	2		
320-329							2			
330-339							1	2		
340-349								1		
350-359								2		
360-369								1		
370-379										
380-389								2		
390-399								2		
≥400	(Lengths of individual fish)							(400)	(423) (446)	(421) (430)
Total	248	87	12	1	41	31	44	15	2	2
Mean length	89	159	206	307	80	180	271	349	435	425

* - smallest age I fish from length-frequency histogram.

Brown trout showed a less truncated age distribution with many fish living to age III and some to age V. In general, age groups of brown trout to age III did not overlap each other greatly in length.

Comparisons of growth calculated from the mean of aged samples are valid between the 2 species, since all fish were captured at the same time from the same stream. Brown trout are, on average, larger than brook trout at every age except age 0. Because few brook trout survived to age III, comparisons with brown trout past age II are not warranted.

Brook Trout Positions

Multivariate comparisons between brook trout position characteristics in sympatry and allopatry provide the main evidence for or against the interspecific competition. Four dependent variables were used in comparisons for 15-20-cm fish: focal point velocity, maximum velocity within 60 cm, water depth and distance to cover. For 20-25-cm fish, the comparisons involved a new dependent variable derived from the difference between focal point and 60-cm velocity, as well as water depth and distance to cover. The means and 95% confidence intervals for all position characteristics are presented in Table 11. These intervals are "multivariate confidence intervals" and are shown only to indicate variability. They cannot be used to determine the significance of differences between the positions. For dependent variables not used in multivariate tests, the standard deviations are

Table 11. Characteristics of resting and feeding positions of brook trout in allopatry and in sympatry with brown trout. Means ± 95% multivariate confidence intervals are shown. Where variables did not enter into calculation of the multivariate confidence intervals, standard deviations are shown in parentheses.

Position type	Population type	Sample size (n)	Water velocity (cm/sec) Focal point	Water velocity (cm/sec) Maximum at 60 cm	Water velocity (cm/sec) Difference	Water depth (cm)	Distance (cm) To bed	Distance (cm) To cover
				15-20-cm Brook Trout				
Resting	Sympatry	16	20.4±7.3	36.4±9.3	16.0 (6.2)*	64.7±16.6	3.0±1.8	0.0 (0.0)*
	Allopatry	27	12.7±6.4	30.3±8.6	17.7 (9.1)	51.7±11.3	2.0±1.1	0.0 (0.0)
Feeding	Sympatry	25	27.2±5.8	43.3±7.5	16.1 (12.1)	66.9±13.0	8.2±6.8	187.8 (58.0)
	Allopatry	19	24.7±5.9	45.6±6.8	20.9 (10.9)	72.7±8.9	5.5±3.1	127.9 (61.6)
				20-25-cm Brook Trout				
Resting	Sympatry	5	19.5 (6.7)*	36.0 (7.6)*	16.5±22.1	61.6±60.0	2.4±9.4	0.0 (0.0)*
	Allopatry	3	13.2 (6.3)	49.8 (8.8)	36.6 (3.1)	62.3 (5.7)	3.0 (0.0)	0.0 (0.0)
Feeding	Sympatry	5	21.3 (8.1)	39.0 (5.0)	17.7±24.1	67.6±49.4	6.8±14.1	172.0 (47.6)
	Allopatry	5	18.3 (6.1)	48.8(19.8)	30.5±94.8	74.2±54.0	7.0±14.8	134.0 (72.0)

*These position characteristics not used in multivariate analysis for this size class.

shown in parentheses. Standard deviations are also shown for the 3 brook trout of 20-25-cm observed resting in allopatry. No confidence intervals could be calculated for these positions because no T^2 value existed for such a small sample. The original data for brook trout positions are shown in Appendix Tables A1 through A5. The positions of the brown trout observed are similarly presented in Table A6. A summary of the results of the statistical tests applied to the data is provided in Table 12.

Ratios of Visible Resting Trout

The ratios of brook to brown trout in visible resting positions was far higher than the brook:brown ratio in the population. For 15-20-cm fish, the chi-square test of the difference between the observed (visible resting positions) and the expected (population) ratios was significant at $p < .05$. For 20-25-cm trout, the significance of the chi-square analysis was $p < .001$.

15-20-cm Brook Trout

Although 15-20-cm brook trout positions provided the most data for judging interspecific competition, positions of these fish were generally similar in sympatry and allopatry. However, there were marked differences between feeding and resting positions in sympatry, as well as in allopatry.

For feeding fish, the multivariate T^2-test showed no overall significant difference between position characteristics when sympatry was compared to allopatry. Multivariate confidence intervals (MCI) for differences between means (as

Table 12. Results of statistical analyses. The level of significance of individual dependent variables determined from multivariate confidence intervals is shown at right.

Comparison (test used)	Overall significance of test	Water velocity (cm/sec): Focal point	Water velocity (cm/sec): Max. at 60 cm	Water velocity (cm/sec): Difference	Water depth (cm)	Distance (cm): To bed	Distance (cm): From cover
15-20-cm Brook Trout							
Sympatry vs allopatry							
For resting fish (multivariate pooled T^2)	$p > .10$	$p = .10$					
For feeding fish (multivariate pooled T^2)	$p \gg .10$						
(univariate t)	$p < .01$						$p < .01$
Resting vs feeding							
When sympatric (multivariate paired T^2)	$p < .01$		$p < .10$			$p < .05$	
When allopatric (multivariate paired T^2)	$p \ll .01$	$p < .01$	$p < .05$		$p < .01$	$p < .05$	
Brook vs brown trout							
Ratio of visible resting fish (chi-square)	$p < .05$						
20-25-cm Brook Trout							
Population and position type (analysis of var.)	population, $p = .02$		position, $p = .52$		interaction, $p = .23$		
Sympatry vs allopatry							
For resting fish (multivariate pooled T^2)	$p < .025$			$p < .025$			
For feeding fish (multivariate pooled T^2)	$p \gg .10$						
(univariate t)	$p < .20$						$p < .20$
Brook vs brown trout							
Ratio of visible resting fish (chi-square)	$p \ll .001$						

opposed to MCI's for individual means shown in Table 9) were 2-4 times greater than the differences. This indicated that the small observed differences were of very little significance.

For resting fish, the position characteristics in sympatry and allopatry again were not significantly different. However, means for the 4 position characteristics used in the comparisons were all less in allopatry than in sympatry. The MCI's for differences between means showed that the difference between focal point velocity means was significant at $p=.10$. This significance is probably further reduced by the inflation of Type I error due to the lack of independence among T^2-tests mentioned in the Methods.

In sympatry, the multivariate T^2-test showed that mean differences between characteristics of feeding and resting positions were highly significant ($p<.01$). The MCI's indicated that mean differences between distance from substrate were significant ($p<.05$), and those between maximum velocity were nearly significant ($p<.10$) for sympatric resting versus feeding fish.

In allopatry, mean differences between resting and feeding fish were very highly significant ($p\ll.01$). The MCI's for allopatric feeding and resting positions showed that mean differences between focal point velocity and between water depth were highly significant ($p<.01$), and those between maximum velocity and between distance from substrate were significant ($p<.05$).

In both sympatry and allopatry, significant differences reflect larger mean values of all position characteristics for feeding fish when compared to resting fish. In allopatry these mean differences were greater than in sympatry. This is largely due to lower mean values for all position characteristics of allopatric resting fish (except velocity difference) when compared to those in sympatry (see above <u>for resting fish</u>).

<u>20-25-cm Brook Trout</u>

Because the sample of 20-25-cm brook trout (n=18) was so small, care was exercised to test only the important differences. However, despite the small sample size, significant differences were detected between allopatric and sympatric positions for resting fish.

The initial univariate analysis of variance of water velocity difference indicated a highly significant difference between population types ($p=.02$). Neither the interaction between independent variables ($p=.23$) nor the difference between position types ($p=.52$) was significant.

<u>For resting fish</u>, the multivariate T^2-test showed a highly significant difference between positions in sympatry and allopatry ($p<.025$). The MCI's for resting fish showed a significant difference only between water velocity difference for sympatric versus allopatric brook trout.

<u>For feeding fish</u>, the multivariate T^2-test showed that differences between sympatric and allopatric positions were of very little statistical significance ($p\gg.10$). The

MCI's were again many times the differences between means.

Distance to Cover

For both 15-20-cm and 20-25-cm feeding brook trout, the mean distance to nearest overhead cover indicated that allopatric fish fed from positions closer to overhead cover than did those in sympatry. This relationship was significant at $p < .01$ for 15-20-cm brook trout, but only significant at $p < .20$ for 20-25-cm fish.

Light

The lighting characteristics of brook trout positions are presented for all fish larger than 15 cm in Figure 5. A large percentage of feeding brook trout in both sympatry and allopatry occupied positions in indirect light. Some fish in both population types fed in direct sunlight, whereas no fish fed from positions in the shade class. In contrast, resting fish in both population types most frequently occupied positions classed as shade. Some resting positions were found in areas of indirect light, but only 2 sympatric resting brook trout occupied positions in direct sunlight.

Resting brook trout occupied a higher percentage of positions in shade after brown trout were removed. In addition, smaller percentages of brook trout rested in positions in direct sunlight or indirect light after the removal. In general, the light data indicate that brook trout occupied resting positions with lower illumination in allopatry than when in sympatry with brown trout.

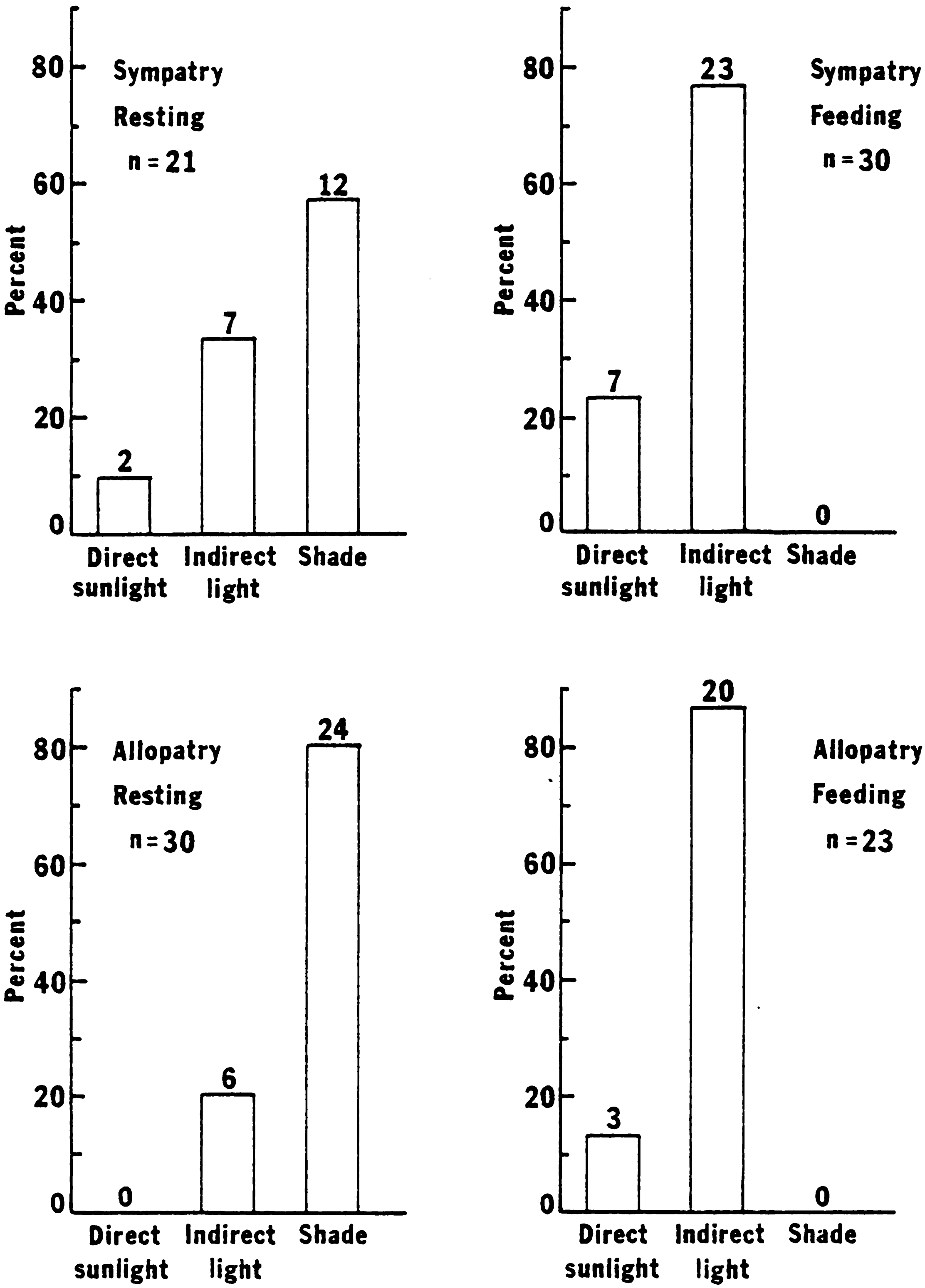


Figure 5. Light characteristics of positions occupied by brook trout larger than 15 cm. Number of positions in each category is above each bar.

Feeding brook trout occupied a slightly higher percentage of positions in indirect light and a lower percentage of positions in direct sunlight after brown trout were removed. In general, feeding positions in allopatry were illuminated less than those occupied when brook trout were in sympatry with brown trout.

DISCUSSION

Interspecific competition is characterized by mutual demand for a resource in short supply. The importance of space in population regulation of salmonids has been a central theme in much of the research on this group. Thus, it is reasonable to consider that suitable living space may be more critical than food, predation, temperature or temporal factors (time of day, season) in the interaction between brook and brown trout. The behavior of trout in the East Branch is further evidence that suitable space is a major limiting resource and helps specify which spatial relationships are most important. The observed microhabitat shift defines the mechanism of interspecific competition between brook and brown trout and pinpoints resting microhabitat as critical to the daytime interaction between the 2 species.

Several limitations of this study are acknowledged. Because observations were restricted to periods of adequate underwater visibility, the study was limited to fairly bright sunny daylight hours. Although underwater observation is one of the best methods of directly viewing trout, it may cause unnatural fish behavior. Limits of mark-and-recapture electrofishing in estimating trout populations are indicated by large confidence intervals for brook trout estimates

(Table 4). The results obtained here may not apply during other seasons, at night, or in stream sections with vastly different physical characteristics.

The standing crop of trout in the study area was generally similar to standing crops in sections of other mid-western streams (Table 9). The standing crop of East Branch brook trout fell within the range of 11 annual standing crops calculated for the Pigeon River, Michigan, containing brook and brown trout, and fell below the range for 9 annual standing crops from Hunt Creek, Michigan, containing only brook trout. The standing crop of East Branch brown trout also fell within the range determined for the Pigeon River, Michigan. When the total standing crops of brook and brown trout were combined, East Branch trout fell within the range of standing crops for all streams presented except 2 in Wisconsin.

Importance of Space to Stream Salmonids

Evidence for the importance of space in the population regulation of stream salmonids was first consolidated by Chapman (1966). Drawing from research on juvenile salmonids in western North American streams, he theorized that population regulation begins each spring with the effects of density independent climatic factors. Chapman proposed that during summer populations are regulated by a space-food or a space-shelter mechanism, with predation, cannibalism, disease and parasites as the agents of mortality. Finally, density of stream salmonids may be regulated during the winter by the limited space suitable as refuge from ice and current displacement. According to A. Lindroth (unpublished in Chapman, 1966), the factor limiting salmonid populations depends on the type of stream. Whether a space-food or space-shelter mechanism operates probably depends on stream morphology and hydrology.

Allen (1969b) also considered space important to stream salmonid production. He pointed out that, for a specific size and species of salmonid, density in a stream section is limited primarily by its minimum space requirement and the suitable habitat. Additionally, he emphasizes that these fish may be further limited by adjacent larger or more aggressive fish of the same or of an interacting species that exclude them from suitable positions.

McFadden (1969) proposed that regulation of salmonid populations could not be attributed to one factor, but that a complex set of interrelated factors that varied throughout the life of the fish was responsible. However, the prevalence of density dependent factors implies the importance of space in the studies he cites concerning regulation for juvenile fish. He states that little is known about the behavior of adult salmonids but acknowledges that their density is related to the amount of cover available.

In the East Branch, and probably in other upper midwestern streams containing brook and brown trout, stream morphology, hydrology and the nature of the 2 species indicate that Chapman's (1966) space-shelter mechanism is most important in the population regulation of adult fish. In this and other studies, space-shelter is simply termed "cover" or "resting microhabitat." The importance of cover to adult brook and brown trout has been demonstrated by research to assess effects of the increase in permanent bank cover on trout populations through habitat management (Shetter, Clark and Hazzard, 1946; Saunders and Smith, 1962; Hale, 1969; Hunt, 1971; White, 1975a; reviewed by White, 1975b). More recently, investigators have established quantitative criteria for suitable cover for adult trout. Measurements of permanent bank cover have been successfully used to explain the variation in adult trout abundance among stream sections (Stewart, 1970; Hunt, 1971; Wesche, 1973; Enk, 1977).

Social Behavior

Having established the importance of suitable space to stream salmonids, observations of daytime behavior of East Branch trout may be used to further clarify the role of space in the interspecific competition between brook and brown trout. Placing emphasis on directly observed behavior also helps to ensure that the statistical comparisons between brook trout positions in sympatry and allopatry are realistically interpreted.

The stereotyped nature and similarity between salmonid behavior signals has been well documented (Newman, 1956; Kalleberg, 1958; Hartman, 1965) and indicates that different species "understand" each other's displays. Thus, brook and brown trout probably have little trouble responding to interspecific agonsitic displays.

Few investigations have dealt with adult trout behavior (Newman, 1956; Butler and Hawthorne, 1968; Jenkins, 1969; DeVore, 1975; Bassett, 1978) and only in those by Newman and Jenkins were any trout observed under natural conditions. However, the feeding behavior of brown trout studied by Bassett (1978) was expected to correlate with those I observed, as he used old hatchery receways supplied with East Branch water and the schedule of insect emergence was similar.

Hierarchical Social Structure

Hierarchical social organization is characteristic of salmonid behavior. Dominance is bestowed on the individual of greatest size and weight. Even in mixed-species groups, the largest fish is most often dominant (Newman, 1956; Jenkins, 1969). Although prolonged observation is usually required to determine dominant-subordinate relationships in groups of trout, the dominant fish in the 3 large East Branch pools was easily identified by its size and in many instances by its position at the head of the pool. Dominant-subordinate relationships could not be defined for feeding and resting fish in other parts of the channel. It was also impossible to distinguish between size-related dominance and dominance related to characteristics of the species, referred to here as "competitive advantage."

Feeding Behavior

Although the 3 large pools offered feeding positions for a few trout, most trout fed in other parts of the stream. These latter feeding positions were typically near the thalweg, beneath principle lines of drift, and were located behind obstructions in the channel bed in areas of low water velocity overlain by water of high velocity. The concept of principle lines of drift was first proposed and tested by Jenkins (1969) who was only able to show indirectly the importance of water velocity difference to feeding positions.

Daytime feeding behavior in the East Branch differed distinctly between small (15-20 cm) and large (>20 cm) trout of both species. Large brook and brown trout were crepuscular and were not usually observed to feed during the day. Large brook trout in the East Branch fed during daylight only when invertebrate drift was very abundant, such as during a hatch of *Tricorythodes* mayflies. Large brown trout were not observed in feeding positions, from which they would probably be easily disturbed during the day. In contrast, small trout of both species often fed during the day whenever sufficient invertebrate drift was available. Bassett (1978) observed similar behavior for brown trout in uniform hatchery channels. He noted that small brown trout fed frequently on abundant small drift items, whereas large fish usually lacked food of proper size, seldom fed and lost weight. Only when Bassett artifically added large drift items (grasshoppers) did his large brown trout feed with regularity.

This behavior can be related to the energy maintenance of trout. Jenkins (1969) stated that trout must maintain a favorable energy balance. By choosing a position where the feeding range encompasses a large range of water velocity ("water velocity difference"), a trout can minimize energy expenditure, while maximizing available invertebrate drift. However, in addition to choosing beneficial positions, large trout must feed on large or very abundant drift items to maintain a favorable energy balance, whereas small fish may efficiently forage on small items of drift. This hypothesis is substantiated by feeding behavior of large East Branch brook trout, and by Bassett's (1978) observations of large fasting brown trout. Both species were induced to feed on the abundant Tricorythodes hatch during the day. In addition, Bassett calculated that most of the energy expended by the brown trout he studied was for feeding.

Although there was a significant sympatry-allopatry difference for distance of feeding brook trout from nearest cover, these fish rarely swam to the closest overhead cover when I disturbed them. In addition, during evening twilight small brook trout moved into relatively shallow, open portions of the channel, and fed even further from cover (K.D. Fausch, personal observation while fishing). However, in the low illumination, they were probably poorly visible to predators even in these exposed positions. Thus, for small brook trout light seems to be a more important factor in choice of feeding positions than distance to nearest cover. Figure 5 indicates that brook trout most often fed from indirectly lit positions. Frequently, positions of small fish were near the edge of shadows of the bank or of bank vegetation and showed little relation to objects in the stream channel. Large brook trout most often chose shaded or indirectly lit positions near some form of lateral cover. Observations while diving indicated that feeding from a shaded area allows maximum visibility of drift in sunlit areas while minimizing the risk of predation from overhead. Even in the clearest streams, reflection from particles in the water hampers visibility in sunlit areas (R.J. White, K.D. Fausch, personal observation while diving).

Several investigators have described increased agonistic behavior of adult trout during feeding (Jenkins, 1969; Butler, 1975; Bassett, 1978). Butler described the movable, defended area ahead of a trout as its "social force field" after McBride (1964), and further stated that this area was largest during feeding when agonistic behavior was highest. Bassett (1978) noted that social force fields expanded when trout fed, so that feeding trout became intolerant of other fish at a greater distance than when resting.

East Branch trout often fed close together, but agonistic behavior was observed only once, by the dominant fish in a hierarchy. Although Bassett found increased agonistic behavior, he also noted little competition for feeding positions among brown trout and attributed this to the uniform cross-sections of his channels. Bassett proposed that this feature precluded principle surface currents and produced a uniform distribution of drift. Competition for feeding positions was also minimal among East Branch brook trout of both size classes, as evidenced by the similarity in feeding position characteristics in sympatry and allopatry (Tables 11 and 12). As in Bassett's channels, the uniform cross-sections in the East Branch apparently prevented principle lines of drift and probably minimized competition because feeding positions were numerous and of about equal quality.

Thus, suitable feeding positions were probably not important to the interaction of East Branch trout. In addition, it is apparent that Chapman's (1966) space-food mechanism was not operating to regulate the existing trout populations in this stream because there is little possibility that feeding positions or invertebrate drift were limiting.

Resting Behavior

In the East Branch, resting positions were more important than feeding positions in the daytime behavior of brook and brown trout. The feeding behavior described above implies that 15-20-cm trout of both species occupied resting positions during daylight unless sufficient drift prompted them to feed. Trout larger than 20 cm rarely left resting positions during the day.

Underwater observations suggested that dominance or competitive advantage permitted occupation of optimal positions. Characteristics of optimal resting positions were:

low water velocity, maximum shade and concealment from overhead and lateral view. Thus, resting positions nearest the bank beneath artificial and natural cover were preferred.

Brook and brown trout were found to be highly cover oriented by Butler and Hawthorne (1968). The brown trout studied remained under cover longer than the brook trout, but as previously mentioned, this relationship was confounded by the disparate lengths of the fish used (see Introduction). Brook and brown trout of equal size probably have similar requirements for resting cover. East Branch brook trout preferred shaded positions over those indirectly lit or in direct sunlight (Figure 5).

Several investigators used uniform channels to study the responses of brown trout to overhead cover that lacked refuge from water velocity. DeVore (1975) showed that brown trout preferred cover 10 cm from the channel bed to that placed higher. Butler and Hawthorne (1968) and Bassett (1978) observed that brown trout occupied the most upstream portions of overhead cover. Although I defined all positions under cover as resting microhabitat, trout probably fed from positions varying from those in the open channel to those under cover, depending on food availability.

Large East Branch trout used resting positions offering little space above or below the fish. Dominant trout also used the most upstream portions of cover, especially under wing deflectors, but this may merely have coincided with their preference for low velocity, shaded positions near the bank that afforded overhead and lateral concealment.

Butler (1975) observed that brown trout showed little agonistic behavior while resting and proposed that their "social force field" was smallest then. Bassett (1978) also reported minimal aggression for resting fish, but noted that dominant fish readily displaced subordinates from optimal positions, even though little agonistic behavior was evident. Perhaps subtle behavior was undetected from Bassett's observation blinds 6 meters above the channel. Dominant trout in the East Branch were presumed to easily displace subordinates from optimal resting positions and probably did so with subtle agonistic behavior.

Assemblages of small brook trout were frequently observed resting close together near the margins of cover. In view of the previous discussion, these fish were probably subordinates prevented from using better resting positions by larger trout. Bassett (1978) observed that the presence of dominant trout inhibited agonistic behavior among subordinates. Thus, these groups of small brook trout in the East Branch may have been able to coexist closely under the same deflector through this agonism-inhibiting mechanism.

In light of the daytime behavior observed for East Branch trout, resting positions are proposed to be the most important microhabitat in the interaction between brook and brown trout. Further evidence for this hypothesis is available from statistical analysis of the microhabitat shift.

Microhabitat Shift

The previous discussion has shown that the parts of the stream which serve as resting microhabitat are likely to be important in the interaction between brook and brown trout. Before considering evidence provided by the microhabitat shift concerning this hypothesis, 2 additional factors that affect space and the interacting populations deserve attention. These factors are flow regime, which governs the amount of suitable living space, and population structure, which specifies how many trout of each species and size are present to compete with each other in stream sections.

Flow Regime

The stream discharge recorded for the days of observation indicates that trout were studied in the East Branch during summer baseflow. Although 1977 baseflow was not significantly lower than normal (Table 3), the study coincided with the summer period of minimum suitable living space for trout in this stream. Therefore, competition for microhabitat in shortest supply should have been greatest during this period.

Population Structure

A striking feature of the East Branch brook trout population was the truncated age structure indicating high mortality (Table 10). However, survival beyond age II or III is rare in exploited brook trout populations, whether in sympatry with brown trout or not. The age structure of the East Branch brown trout population was only slightly truncated. This is also a normal attribute for exploited brown trout populations (see Introduction).

Growth of East Branch brook and brown trout is rapid when compared to other investigations that included lengths at each age (Cooper, 1953; McFadden, 1961; McFadden and Cooper, 1964; Cooper, 1967; McFadden, Alexander and Shetter, 1967). Mean length of East Branch brown trout was greater than brook trout at all ages except age 0. Cooper (1953) accounted for this phenomenon, also found among brook and brown trout in Michigan's Pigeon River, by documenting selective fishing mortality of the larger, faster growing brook trout when they reached creelable size. East Branch brook trout reached creelable size of 178 mm at age I or II.

Of the many other factors besides interspecific competition that affected the interaction between brook and brown trout, differential angling mortality probably had the greatest effect. The numbers of brook and brown trout were of different orders of magnitude in every 5-cm size class except 20-25 cm (Figure 4). The requisites of microhabitat for trout vary with size and age of the fish (White, 1973). In view of this, and because trout abundance in each size class was unequal, the microhabitat shift was analyzed separately for the 2 size classes of adult trout.

Shift of 15-20-cm Brook Trout

For feeding brook trout of 15-20 cm, statistical analysis indicated no shift in feeding position when fish were released from competition with brown trout (Table 12).

This lack of microhabitat shift lends further evidence that high quality feeding positions were not limiting in the relatively uniform East Branch channel. Feeding positions near principle lines of drift were very abundant for 15-20-cm trout, and thus competition for optimal feeding positions was probably minimal. Although statistical analysis showed that feeding positions were similar in sympatry and allopatry, the lighting of positions chosen was different. Figure 5 indicates a small shift of all brook trout larger than 15 cm toward more shaded positions after brown trout were removed.

For resting brook trout in this size class, although the magnitude of the microhabitat shift was not statistically significant, the direction of shift was consistent (Tables 11 and 12). Thus, after release from competition with brown trout, means of all position characteristics except water velocity difference were less, with the reduction in focal point velocity significant at about $p=.10$. In addition, Figure 5 indicates a marked shift by all brook trout larger than 15 cm toward positions in shade after brown trout were removed. Although the shift alone demonstrates interspecific competition between brook and brown trout, the direction of shift may indicate that 15-20-cm brown trout are able to exclude equal-sized brook trout from optimal resting positions.

In contrast to the hypothesis of interspecific competition, the observed shift in brook trout resting positions could have been caused by the reduction in trout density per se. This alternate hypothesis also implies that neither species has a competitive advantage over the other. Evidence to reject reduced population density as the primary mechanism in the microhabitat shift for 15-20-cm fish may be derived from the pre-removal ratio of brook to brown trout observed in visible resting positions. Descriptions of daytime trout behavior in the East Branch (see Results) indicated that brook and brown trout strongly preferred concealed resting positions. These positions are assumed to be optimal. Thus, if brown trout did not exclude brook trout from preferred optimal positions, the brook:brown ratio observed in visible resting positions should coincide with the expected ratio of 15-20-cm trout present in the population. In other words, if neither species had a competitive advantage, brown trout should have occupied their share of the less optimal, more visible resting positions. A chi-square analysis showed that brown trout were observed significantly ($p < .05$) less often than expected (Table 12). Therefore, the 2 species do not appear to be competitively equal, and interspecific competition is a more logical explanation for the resting microhabitat shift.

Shift of 20-25-cm Brook Trout

For feeding brook trout of 20-25 cm, characteristics of feeding positions were very similar in sympatry and allopatry (Tables 11 and 12). Just as for 15-20-cm trout, this implies that feeding positions for 20-25-cm brook trout were not limiting in the uniform East Branch channel.

Although 20-25-cm brook trout were scarce in the East

Branch, position characteristics for resting brook trout provided the most conclusive evidence for the resting microhabitat shift and the proposal of interspecific competition. After the release from brown trout competition, the water velocity difference increased significantly ($p < .025$) for 20-25-cm brook trout positions. In addition, resting positions occupied by all brook trout larger than 15 cm were more often in shade after brown trout were removed (Figure 5). The microhabitat shift alone demonstrates interspecific competition between brook and brown trout of this size class. In addition, the increase in velocity difference implies that 20-25-cm brown trout were capable of excluding equal-sized brook trout from optimal positions in sympatry.

Just as for 15-20-cm trout, it is difficult to separate the effects of reduced density from those of interspecific competition for 20-25-cm fish. For this size class, the reduced density effect is compounded by the removal of 51 brown trout of 25-60 cm in addition to the 21 of 20-25 cm (Figure 4). Although the assumption of no competitive advantage is again implied in this reduced-density hypothesis, 25-60-cm trout of both species would be expected to exclude 20-25-cm trout by virtue of size and weight. However, the ratio of brook to brown trout observed in visible resting positions should have equaled the expected relative abundance of 20-25-cm East Branch trout. Although 21 brown trout of 20-25-cm were captured, only 2 were observed in visible resting positions (Figure 4, Table A). In contrast, 5 of the estimated 16 brook trout inhabiting the study area occupied visible resting positions in sympatry (Figure 4, Table 11). As for 15-20-cm trout, a chi-square analysis showed that 20-25-cm brown trout were observed significantly less often ($p<.001$) than expected (Table 12). Therefore, interspecific competition is again a more logical explanation for the resting microhabitat shift.

Conclusions

The evidence presented above indicates that interspecific competition occurs between adult brook and brown trout in the East Branch. Daytime feeding positions were abundant in the uniform East Branch channel, and feeding microhabitat was probably not important in the interaction between the 2 species. Daytime resting positions appeared to be scarce in the sections studied, and resting microhabitat was found to be the critical resource in the interspecific competition. Further evidence for limited resting microhabitat was provided by stream morphology and hydrology. Not only was the East Branch at baseflow, but the only resting positions provided in the fairly uniform channel were beneath the few habitat improvement devices and sparse natural cover.

There was no evidence, either from observed behavior or from the analysis of position characteristics, that brook trout showed interactive segregation or behavioral plasticity when in sympatry with brown trout. Instead of shifting to a different, optimal strategy, brook trout seemed to merely subsist in marginal resting positions left vacant by brown trout of equal and larger size. Brook trout in sympatry with brown trout faced higher water velocities than those in allopatry, and were probably less efficient at maintaining a favorable energy balance. In addition, the resting positions occupied in sympatry were less concealed, which may have led to higher mortality due to predation.

Although the positions occupied by brook trout in sympatry with brown trout probably were marginal and caused reduced fitness, little direct evidence is available to substantiate this proposal. Alexander (1977) has shown that predatory brown trout consume more young brook trout than young brown trout, but laboratory observations indicated that brown trout would not eat young of their own species. Avian predation also appears to be higher for age-0 and age-I brook trout than for brown trout of these ages, but the evidence is not conclusive (see Introduction).

Most streams containing the 2 species have larger brook trout populations in the headwaters and more brown trout in downstream areas. The longitudinal distribution of the 2 species in streams may be partially controlled by physical factors, and population structures of adult trout can be greatly modified by angling mortality and predation. However, interference competition with brown trout for optimal resting microhabitat probably forces brook trout to subsist in positions which directly reduce the fitness of the species in the stream environment. If this were the case, reduced fitness would lead to reduced reproductive success and would provide a mechanism for the decline of brook trout in sympatry with brown trout.

Implications for Further Research

This study has only begun to offer some tentative answers to questions concerning brook and brown trout interaction. Additional questions provide impetus for further research and point to several areas of productive study.

Much of the competitive advantage of brown trout was obscured in this study by disparate numbers of equal-sized trout. Therefore, the hypothesis that brown trout are able to exclude brook trout from optimal resting positions should be tested using fish of equal size and weight in controlled channels offering limited resting microhabitat. These experiments should be performed using fish of ages 0 through II or older, in order to determine the age at which competition is most intense.

The effects of temperature on competition for optimal microhabitat could be studied for age-0 brook and brown trout. This study would require close control of water temperatures in a laboratory stream. Although the effect of temperature on competition would be difficult to assess for larger trout, study could be concentrated on the age at which competition is most intense.

Though nothing could be inferred from this study concerning the differences between winter mortality for the 2 species, this factor may well be important to the interaction. Salmonid populations may be spatially regulated during the winter by the number of suitable refuges from detrimental effects of current and ice (Chapman, 1966). If brown trout exclude brook trout from refuge positions, brook trout winter mortality may be greater in sympatry with brown trout than in allopatry. This response would be best studied at the population level and under natural conditions.

The effects of selective angling mortality and of hatchery selection seem nearly impossible to test, but gross genetic changes could possibly be assessed from the outcome of brown trout competition with very different strains of brook trout. For example, brook trout from a lower Michigan stream versus those from a remote stream, free from effects of exploitation and of hatchery introductions, would provide an interesting comparison.

SUMMARY

1. In streams where brook and brown trout are sympatric, brook trout usually decline in abundance, and their range appears to shift toward headwater areas, probably owing to competition with brown trout. The objective of this study was to investigate this interspecific competition and to determine the mechanism and critical resource.

2. Daytime positions of adult brook trout were observed by wetsuit diving before and after brown trout were removed by electrofishing. The study was during summer baseflow when suitable living space would be scarcest, resulting in maximum competition for stream positions.

3. The size and age structures of the brook and brown trout populations differed greatly. Only at 20-25-cm was each species about equally abundant.

4. Brook and brown trout of 15-20 cm moved from resting to feeding positions when invertebrate drift became prevalent, even in small amounts. Trout of both species larger than 20 cm rarely emerged from resting positions to feed during the day unless drift was very abundant.

5. Water velocities at feeding positions of trout were low, but were most often overlain by high velocities which constituted principle lines of drift. Preferred resting

positions occurred in areas of low water velocity, low illumination and under cover which offered overhead and lateral concealment.

6. Feeding positions of brook trout were similar in sympatry and allopatry. There was probably little competition for feeding positions among trout because the uniform East Branch channel cross-sections produced a uniform distribution of drift, and therefore, many positions of equal quality.

7. Marked shifts in resting microhabitat of brook trout occurred after brown trout were removed. The brook trout rested in positions which were darker and which had lower water velocity but were close to faster currents. The shift was strongest for brook trout larger than 20 cm. The ratios of brook and brown trout in visible resting positions showed that the microhabitat shift was not due to reduced trout density alone. Instead, the microhabitat shift of brook trout indicated that brown trout had been excluding brook trout from preferred resting positions. This constituted interference competition for a critical resource, resting microhabitat.

8. Brook trout showed no interactive segregation or behavioral plasticity when in sympatry with brown trout.

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APPENDIX

INDIVIDUAL POSITION CHARACTERISTICS

FOR BROOK AND BROWN TROUT

Table A1. Individual position characteristics of 15-20-cm resting brook trout in sympatry.

	Water velocity (cm/sec)			Water depth (cm)	Distance (cm)		Light class*
	Focal point	Max. at 60 cm	Difference		To bed	From cover	
1.	9.1	18.3	9.2	68	6	0	3
2.	9.1	24.4	15.3	56	1	0	2
3.	12.2	27.4	15.2	55	4	0	3
4.	15.2	33.5	18.3	66	0	0	3
5.	15.2	45.7	30.5	50	5	0	2
6.	18.3	30.5	12.2	85	3	0	2
7.	18.3	30.5	12.2	85	3	0	2
8.	21.3	30.5	9.2	53	4	0	3
9.	21.3	33.5	12.2	38	0	0	3
10.	21.3	36.6	15.3	62	5	0	3
11.	21.3	48.8	27.5	60	1	0	3
12.	24.4	48.8	24.4	46	3	0	2
13.	27.4	42.7	15.3	64	3	0	3
14.	27.4	42.7	15.3	64	3	0	3
15.	30.5	42.7	12.2	99	5	0	1
16.	33.5	45.7	12.2	85	2	0	1

*1-direct sunlight, 2-indirect light, 3-shade.

Table A2. Individual position characteristics of 15-20-cm resting brook trout in allopatry.

	Water velocity (cm/sec)			Water depth (cm)	Distance (cm)		Light class*
	Focal point	Max. at 60 cm	Difference		To bed	From cover	
1.	.6	15.2	14.6	28	0	0	3
2.	1.5	1.5	0.0	35	2	0	3
3.	3.0	15.2	12.2	54	3	0	2
4.	3.0	21.3	18.3	42	0	0	3
5.	3.0	21.3	18.3	42	0	0	3
6.	3.0	30.5	27.5	65	2	0	3
7.	4.6	18.3	13.7	41	2	0	3
8.	6.1	30.5	24.4	40	3	0	2
9.	6.1	30.5	24.4	40	5	0	3
10.	6.1	39.6	33.5	67	3	0	3
11.	9.1	18.3	9.2	22	0	0	3
12.	9.1	27.4	18.3	60	2	0	3
13.	9.1	30.5	21.4	44	0	0	3
14.	9.1	39.6	30.5	67	3	0	3
15.	12.2	24.4	12.2	40	0	0	3
16.	15.2	24.4	9.2	44	2	0	3
17.	15.2	24.4	9.2	76	2	0	3
18.	15.2	27.4	12.2	47	2	0	3
19.	15.2	36.6	21.4	55	3	0	2
20.	18.3	30.5	12.2	35	0	0	3
21.	18.3	33.5	15.2	89	3	0	3
22.	18.3	61.0	42.7	59	5	0	2
23.	21.3	39.6	18.3	44	0	0	3
24.	27.4	36.6	9.2	76	5	0	3
25.	27.4	48.8	21.4	43	2	0	3
26.	30.5	36.6	6.1	76	2	0	3
27.	33.5	54.9	21.4	66	2	0	3

*1-direct sunlight, 2-indirect light, 3-shade.

Table A3. Individual position characteristics of 15-20-cm feeding brook trout in sympatry.

	Water velocity (cm/sec)			Water depth (cm)	Distance (cm)		Light class*
	Focal point	Max. at 60 cm	Difference		To bed	From cover	
1.	0.0	61.0	61.0	94	10	150	2
2.	15.2	30.5	15.3	79	4	110	2
3.	21.3	30.5	9.2	85	5	100	2
4.	21.3	33.5	12.2	69	10	300	2
5.	24.4	39.6	15.2	68	10	200	2
6.	24.4	39.6	15.2	68	10	200	2
7.	24.4	39.6	15.2	68	10	200	2
8.	27.4	30.5	3.1	100	10	180	2
9.	27.4	30.5	3.1	100	10	180	2
10.	27.4	30.5	3.1	100	10	180	2
11.	27.4	39.6	12.2	47	5	200	2
12.	27.4	39.6	12.2	50	2	250	2
13.	27.4	39.6	12.2	80	10	125	2
14.	27.4	45.7	18.3	66	12	200	1
15.	27.4	54.9	27.5	57	3	200	2
16.	27.4	54.9	27.5	57	3	200	2
17.	27.4	61.0	33.6	47	4	100	2
18.	30.5	39.6	9.1	54	10	150	1
19.	30.5	42.7	12.2	44	1	300	2
20.	30.5	42.7	12.2	56	5	70	2
21.	30.5	45.7	15.2	54	4	200	1
22.	33.5	48.8	15.3	45	0	200	2
23.	36.6	39.6	3.0	75	50	200	2
24.	36.6	61.0	24.4	55	5	250	1
25.	45.7	61.0	15.3	55	3	250	1

*1-direct sunlight, 2-indirect light, 3-shade.

Table A4. Individual position characteristics of 15-20-cm feeding brook trout in allopatry.

	Water velocity (cm/sec)			Water depth (cm)	Distance (cm)		Light class*
	Focal point	Max. at 60 cm	Difference		To bed	From cover	
1.	9.1	61.0	51.9	76	1	40	2
2.	12.2	48.8	36.6	82	5	175	2
3.	15.2	30.5	15.3	67	10	100	2
4.	18.3	36.6	18.3	60	3	75	1
5.	18.3	54.9	36.6	64	2	75	2
6.	24.4	39.6	15.2	89	6	125	2
7.	27.4	36.6	9.2	78	3	250	2
8.	27.4	39.6	12.2	74	10	175	2
9.	27.4	42.7	15.3	50	5	175	2
10.	27.4	42.7	15.3	64	3	150	2
11.	27.4	42.7	15.3	89	6	125	2
12.	27.4	45.7	18.3	71	7	200	2
13.	27.4	48.8	21.4	86	4	100	2
14.	27.4	51.8	24.4	63	3	200	2
15.	27.4	54.9	27.5	74	5	60	1
16.	30.5	42.7	12.2	79	3	50	2
17.	30.5	48.8	18.3	71	3	75	2
18.	30.5	54.9	24.4	72	15	80	1
19.	33.5	42.7	9.2	72	10	200	2

*1-direct sunlight, 2-indirect light, 3-shade.

Table A5. Individual position characteristics of 20-25-cm brook trout.

	Water velocity (cm/sec)			Water depth (cm)	Distance (cm)		Light class*
	Focal point	Max. at 60 cm	Differ-ence		To bed	From cover	
Resting Fish							
Sympatry							
1.	9.1	24.4	15.3	64	0	0	2
2.	18.3	42.7	24.4	52	1	0	3
3.	21.3	33.5	12.2	48	3	0	2
4.	21.3	36.6	15.3	80	5	0	3
5.	27.4	42.7	15.3	64	3	0	3
Allopatry							
1.	6.1	39.6	33.5	67	3	0	3
2.	15.2	54.9	39.7	56	3	0	2
3.	18.3**	54.9	36.6	64	3	0	2
Feeding Fish							
Sympatry							
1.	9.1	30.5	21.4	72	5	170	1
2.	18.3	42.7	24.4	51	5	90	1
3.	24.4	39.6	15.2	68	10	200	2
4.	24.4	39.6	15.2	68	10	200	2
5.	30.5	42.7	12.2	79	4	200	2
Allopatry							
1.	12.2	30.5	18.3	56	10	200	2
2.	12.2	67.1	54.9	76	5	40	2
3.	18.3	36.6	18.3	87	7	150	2
4.	24.4	36.6	12.2	77	3	200	2
5.	24.4	73.2	48.8	75	10	80	2

* 1-direct sunlight, 2-indirect light, 3-shade.

** 25-30-cm brook trout (see text).

Table A6. Individual position characteristics of brown trout.

	Water velocity (cm/sec)			Water depth (cm)	Distance (cm)		Light classes*
	Focal point	Max. at 60 cm	Differ-ence		To bed	From cover	
				15-20-cm Brown Trout			
Resting Fish							
Sympatry							
1.	21.3	48.8	27.5	60	1	0	3
2.	9.1	21.3	12.2	57	1	0	3
Feeding Fish							
Sympatry							
1.	27.4	30.5	3.1	100	10	180	2
2.	21.3	39.6	18.3	67	5	200	2
3.	24.4	39.6	15.2	68	10	200	2
				25-30-cm Brown Trout			
Resting Fish							
Sympatry							
1.	15.2	51.8	36.6	65	0	0	3
2.	18.3	30.5	12.2	42	0	0	3

* 1-direct sunlight, 2-indirect light, 3-shade.