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The Importance of Competition for Food Resources in the Interaction Between Brook Trout (*Salvelinus fontinalis*) and Rainbow Trout (*Salmo gairdneri*)

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I am submitting herewith a thesis written by William E. Ensign entitled "The Importance of Competition for Food Resources in the Interaction Between Brook Trout (*Salvelinus fontinalis*) and Rainbow Trout (*Salmo gairdneri*)." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

Richard J. Strange, Major Professor

We have read this thesis and recommend its acceptance:

David A. Etnier, Stephen Moore, Charles Parker

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We have read this thesis
and recommend its acceptance:

Stephen E Moore

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THE IMPORTANCE OF COMPETITION FOR FOOD RESOURCES IN THE INTERACTION BETWEEN BROOK TROUT (*SALVELINUS FONTINALIS*) AND RAINBOW TROUT (*SALMO GAIRDNERI*)

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

William E. Ensign
August 1988

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ABSTRACT

The last 80 years have seen a drastic reduction in the range of the brook trout (Salvelinus fontinalis) the only salmonid native to the Southern Appalachians. Much of this range reduction is directly correlated with increases in the range of the introduced rainbow trout (Salmo gairdneri). The purpose of this study was to determine if competition for food resources plays a significant role in this interaction.

Stomach contents were obtained from sympatric and allopatric populations of brook and rainbow trout during June, July, August and September of 1987. Terrestrials comprised the majority of food items in the stomachs of adult fish from all populations, the mean percentage relative wet weight ranging from 59% in sympatric rainbow trout to 74% in sympatric brook trout. Comparisons using Schoener's Index of Dietary Overlap indicated that there was significant dietary overlap between all populations during the majority of the sampling dates. Analysis of variance indicated that there were no significant differences in the mean relative weight of stomach contents of adult brook trout in sympatry or allopatry, or between adult brook trout and adult rainbow trout living in sympatry. However, the mean relative weight of stomach contents in adult rainbow trout in allopatry was significantly lower than that in adult rainbow trout in sympatry or adult brook trout in allopatry. Calculated caloric intake using the mean observed stomach values was never sufficient to meet the estimated metabolic demands of adult fish at any of the sites during any of the sampling periods, despite the fact that there seemed to be sufficient food resources in the stream drift. Fulton-type condition factors of sympatric and allopatric brook trout were not significantly different, but condition factors of sympatric rainbow trout were significantly higher than the condition factor of allopatric rainbow trout. Population estimates taken in July and October indicated all populations suffered losses in biomass as standing crops decreased from 48% in allopatric rainbow trout populations to 24% in sympatric rainbow trout populations.

In summary, despite data that seemed to indicate that these populations were food limited, there was no evidence to support competition for food resources in areas where the two species coexist.

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CHAPTER I

INTRODUCTION

Competition Theory

In ecology, one of the major underlying or unifying themes is the search for pattern and process in the structure and formation of communities (May, 1986). Stimulated by the discoveries of Darwin and the developing theory of evolution, Shelford, Clements, Elton and many other early ecologists spent much of their time describing the patterns that they saw in the world around them. As patterns became apparent in communities (i. e. limiting similarity between species) the role taken by competitive interactions in structuring communities quickly became one of the most important and also the most lively points of controversy in the field of ecology. Although competition had been a main concern to ecologists before the early 1960's (Lotka, 1925; Gause, 1934), a seminal paper by Hairston, Smith and Slobodkin (1960) thrust the theoretical importance of these types of interactions firmly into the limelight. Their general conceptualization stated that, with the exception of herbivores, all trophic levels should be resource limited and the major force exerting this density-dependent control was interspecific competition. Since that time various community, population and even ecosystem ecologists have argued for all of the following points: that competition is of overriding importance in structuring the species occurence patterns that we find today (Diamond, 1978); competition is sporadic in its occurence pattern and therefore may not be an important force in structuring the majority of communities (Schroder and Rosenzweig, 1975; Wiens, 1977); competition is only important for certain trophic levels (Hairston et al., 1960) or types of communities (Menge and Sutherland, 1976).

Much of the theory underlying different approaches to competition has its base in the concept of the niche. Although the term was originally coined by Grinnell (1924), its present form owes much to the works of Robert MacArthur and G. E. Hutchinson. Although variously defined as the distribution of a species (Grinnell, 1924), the range of food resources used by a species (Elton, 1927), the "profession" of a species (Odum, 1971), or an $\underline{n}$-dimensional hypervolume with $\underline{n}$ axes corresponding to the various utilization functions of a species (Hutchinson, 1957), the best working concept relates the niche to the subset of resources or habitat variables most important to the survival of a given species in a given place. Competition supposedly occurs when two species with very similar niches occupy the same area and one or more of the resources critical to the survival of the species is in short supply.

Perhaps the greatest shortcoming associated with the study of competition is that ecologists often attempt to invoke the "ghost of competition past" (Connell, 1980) to explain present-day distribution or resource utilization patterns. If two or more species exhibit non-overlapping, mutually exclusive distribution patterns and it is determined that they are or appear to be ecological equivalents, there has been a tendency to make the assumption that the pattern is due to competition at an earlier point in time. Conversely, there has been a tendency to point to similar species (especially congeners) living in sympatry as examples of character displacement resulting from a prior competitive interaction, especially if their resource utilization patterns change in the absence of the competitor (Diamond, 1973). Unfortunately, all of these examples assume process by looking only at pattern, a point that has been raised by skeptics a number of times (see for example Connor and Simberloff, 1979). It is possible that other factors are responsible for the observed distribution patterns. Unfortunately, researchers are rarely able to dictate the time or the place that such interactions may occur, and are thus forced to formulate ex post facto hypotheses.

The types of interactions that have been lumped under the umbrella of competition all have at least one thing in common. The effect of one of the organisms on the other is detrimental, with the affected organism suffering some loss of fitness as a direct result of the interaction. Organism is used here rather than species, since the effect of competition between the members of a population (intraspecific competition) may be as important as the effects of competition between populations of two different species (interspecific competition) (Abrams, 1980). The magnitude of the loss in fitness can range anywhere from slightly decreased growth rates to mortality.

Competition may take one of two forms. Species may interact aggressively, fighting over territory, food, or some other critical resource. The loser is either expelled or prevented from reaching the necessary item. Such an interaction is termed "interference competition". The second generally recognized pattern is termed "exploitative competition". Rather than the competitors physically engaging each other, there is an attempt to preempt the usage of the needed resource by using it first.

Competition and Salmonids

Although arguments over the appropriate form, structure and relative importance of competition have dominated the ecological literature over the past fifteen to twenty years, there is a practical side to the controversy as well. Man's proclivity for moving other organisms from one place to another has resulted in the juxtaposition of a number of plants and/or animals that could be considered to be "ecological equivalents". The individuals that carry out these transplants are usually well-meaning, but the community into which the exotic is introduced generally has another organism that is already filling the role (occupying the niche) of the newcomer. This results in changes in the composition of the community in terms of the abundance and types of species present.

The field of fisheries has a long history of such moves, dating back to the Romans (Moyle, 1985). Fishes in the family Salmonidae, and in particular members of the genus _Salmo_, _Salvelinus_ and _Onchorhynchus_ have been frequent travelers, and since the ecological requirements of most of these fishes overlap extensively, it is not uncommon for one species of the family to be stocked into waters inhabited by another member of the family. This has led to a voluminous literature on the interactions of varying salmonid species in different places, times and habitats. A paper by Chapman (1965) has dominated current thought on the interrelationships of salmonids in general and stream salmonids in particular. His basic premise is that salmonid population densities are regulated primarily by space limitations. Aggressive displays, hierarchical social structures and other "contest" (interference) forms of competition have been substituted for "scramble" (exploitative) forms of competition. Except under conditions of relatively high resource (food) abundance, the spatial demands of salmonids would seem to be set at an evolutionarily determined level. This view of population regulation pervades much of the later work on salmonid interactions.

Implicit in this view of stream salmonid population regulation is the assumption that even though interference competition for space has been substituted for exploitative competition for food, the end result is the same. By preventing a subordinate fish from occupying a preferred feeding position, the dominant fish is decreasing the energy available to the subordinate, thus decreasing the inferior competitor's fitness and diminishing the probability of survival. Although the information on habitat preference is exhaustive (Hearn, 1987), studies that attempt to correlate habitat preference with energy intake, fitness or survival are lacking with a few exceptions. For example, Fausch (1984) was able to relate specific growth rate of brook trout, brown trout (Salmo trutta) and coho salmon (Onchorhynchus kisutch) to the water velocity of the holding position of the fish in stream aquaria.

Studies of communities which contain native and introduced salmonids living in sympatry, as well as studies of naturally occurring sympatric populations of salmonids have focused on determining differences in microhabitat utilization, i.e. preferences for higher or lower current velocities, shallower or deeper water, association with cover, etc. These differences can occur either due to interactive segregation (segregation resulting from behavioral interactions) or selective segregation (segregation resulting from innate differences in morphology or life history characteristics) of the species in question (Hearn, 1987). In many cases, it has been possible to explain or at least correlate instances of naturally co-occurring populations with differences in microhabitat preference (Jones, 1975; Egglishaw and Shackley, 1977). Unfortunately, the evidence for instances of co-existence of introduced species and native species is not as clear-cut. In some cases, it is possible to observe changes in microhabitat choice with the introduction or removal of a purported competitor (Fausch and White, 1981) and to correlate these shifts in habitat not only with changes in population density (Waters, 1983), but in caloric intake, energy expended in metabolism, and fitness as well (Fausch, 1984; Fausch and White, 1986). Other studies have demonstrated differences in microhabitat preference between a native form and an introduced form which would seemingly allow coexistence and yet the native form is slowly being forced out (Griffith, 1972).

Brook and Rainbow Trout: A Case Study in Salmonid Competition?

Perhaps the most puzzling incidence of the effect of an introduced salmonid on a native fish involves the interaction between the eastern brook trout (*Salvelinus fontinalis*) and the rainbow trout (*Salmo* gairdneri). Salvelinus fontinalis was the only stream resident salmonid native to the streams of eastern North America prior to the late 1800's (MacCrimmon and Campbell, 1969). The original range of the species extended southward from the Hudson Bay region to the tip of the Appalachian mountain range in northeastern Georgia and northwestern South Carolina. The expansion of "civilization" westward in North America resulted in a relatively drastic loss of stream mileage inhabited by the species as logging, farming and industrialization took its toll. The populations in the southern Appalachians were perhaps the most heavily impacted. Uncontrolled logging practices made miles and miles of trout stream unfit, leaving undisturbed headwater reaches as the only available habitat (King, 1937). As streams slowly recovered from the insults of the lumber companies, demand for recreational opportunities increased. In an effort to meet the need for fisheries resources, the rainbow trout was stocked into the streams of the southern mountains, and as the streams began to recover, the exotic flourished. It quickly became obvious that the brook trout was failing to re-establish populations in streams occupied by the rainbow, and subsequent studies indicated that the native was actually losing range (King, 1942; Lennon, 1967). Since the turn of the century, brook trout have lost over 70% of their original range. Approximately 45% of that range reduction has occurred in the period from the early 1950's until the late 1970's (Kelly et al., 1980; Bivens et al., 1985).

The reason for the brook trout's failure to re-establish itself in those streams that it had previously occupied has been attributed to a number of factors at different points in time. The most commonly cited theory by far is that the rainbow trout is competitively excluding the brook trout from its former territory (King, 1937; Lennon, 1967; Whitworth, 1980; Larson and Moore; 1985). A circumstancial argument for competitive exclusion can be formulated from available information. The two species can be viewed as ecological equivalents on the basis of similarities in trophic position, life history parameters and environmental requirements. Stream mileage lost by the brook trout in the southern mountain portion of the native's range can be directly correlated with increases in range by the rainbow trout (Lennon, 1967; Kelly et al., 1980). If rainbow trout are removed from a section where the two occur in sympatry, there is a subsequent increase in the density and the biomass of the native species (Moore et al., 1983). This shift is similar in many ways to that observed by Hairston (1980) in his investigation of competition in plethodontid salamander populations. Rose (1986) detected changes in the size of food particles ingested, as well as differences in growth rates of age 0+ brook trout during the period when age 0+ rainbow trout occupied the same microhabitats. Despite these fairly convincing bits of evidence pointing towards competitive exclusion, as of yet there is no evidence for the mechanism. In fact, there is an equally convincing body of evidence that seems to indicate that the brook trout should be able to coexist with the rainbow trout. Since the two species did not coevolve, and they do seem to be occupy the same ecological niche in their native waters, there should be no innate behavioral characteristics that would influence microhabitat segregation when the two occur together. Therefore if the two species are to partition the available space in the stream as suggested by Chapman (1965), some form of interactive segregation would be expected. The competitive exclusion paradigm suggests that the rainbow trout should be dominant in agonistic interactions, displacing the brook trout to suboptimal habitats. However, the results of controlled laboratory studies do not support this conclusion, as brook trout do as well as and in many cases are able to dominate in the large majority of interspecific interactions with rainbow trout when the fish involved in the interaction are of equal size (Newman, 1956; Helfrich et al., 1982). This is true for a fairly wide range of water temperatures, including both species "preferred" temperature, as well as for different age classes (Cunjak and Green, 1983, 1986). Field studies on habitat preference between the two species also suggest that coexistence is possible. Brook trout have a marked propensity for holding areas in lower velocity water than do rainbow trout and also tend to associate with cover to a much greater degree than do the exotic (Cunjak and Green, 1983). Based on this information and Chapman's theory, there is no reason why sympatric populations should not be established.

Since the evidence for some sort of interference competition over preferred habitat resources seems to be lacking, another alternative is that exploitative competition for food resources may be occurring. A number of authors have suggested that this may indeed be the case, pointing especially to the high degree of dietary overlap between the two species as evidence (King, 1937; Rose, 1986). The purpose of this study is to determine if there is evidence to support this proposition.

If competition for food resources is occurring, it may be manifested in a number of different ways. At the crudest level, the average energy intake of brook trout in the area of sympatry may be less than the average energy intake of rainbow trout, resulting in a concommitant loss in fitness by the native fish. At a finer level, competition from rainbow trout might result in a shift in the types of food resources used by the brook trout, with resultant changes in foraging behavior and energy expenditure. By looking at sympatric and allopatric populations of brook and rainbow trout in the same stream during the same time period, detection of such changes should be possible if they are indeed occurring.

CHAPTER II

STUDY AREA

Sampling for this study was conducted on Sams Creek, a second and third order montane stream located in the Tremont section of the GSMNP in Blount and Sevier counties, Tennessee. The stream is a tributary to Thunderhead Prong which joins with Lynn Camp Prong to form Middle Prong of Little River. The watershed is bounded to the east by Davis Ridge, to the west by Sam's Ridge and to the south by the State Line Ridge. Total area of the watershed is approximately 1088 hectares. Vegetation is mature second growth forest with the canopy consisting primarily of tulip poplar (Liriodendron tulipifera), hemlock (Tsuga canadensis), buckeye (Aesculus spp.), various maples (Acer spp.) and birches (Betula spp.). The dominant shrub and understory vegetation includes dogwood (Cornus florida), silverbell (Halesia carolina) and various ericacious shrubs including dog hobble (Leucothoe fonterosa), Rhododendron spp. and Kalmia spp.. Although the area was logged in the early 1900's, the forest canopy has been reestablished and the surrounding vegetation is slowly returning to a mature state.

Three study sites were selected along the stream which typified allopatric brook trout populations, sympatric populations and allopatric rainbow trout populations. The selection of the study sites was based on distribution records (Kelly et al., 1980; Steve Moore, personal communication), which were then verified by early season sampling. The allopatric brook trout site is located in a second order reach of the stream at an elevation of 990 m. The lower boundary of the site is approximately 500 m. above the confluence of Sams Creek with Starkey Creek, another second order stream. The sympatric site and allopatric rainbow trout site are both in third order sections of the stream at elevations of 900 m. and 820 m., respectively. Two 100 m. sampling sections were established at each site from which fish for stomach content analysis were obtained. To reduce the possibility of fish moving from one section into the other between samples during the same sampling period, the two sampling sections within each site were separated by a "buffer" zone of approximately 60 m.

CHAPTER III

METHODS

Field Collections

Four separate sets of field collections were carried out during the course of the study. Each field date involved the collection of stomach content data as well as data on the availability of invertebrate drift. With the exception of the first sampling date, the following sampling regime was followed on each date at each site. Two drift nets were set in the buffer zone between the upstream and downstream sections in the afternoon approximately five hours before sundown and allowed to remain in the stream for three hours. After the nets were pulled, fish for stomach samples were obtained from the downstream sampling section. The following morning, drift nets were once again set at the same site approximately two hours before sunrise and allowed to remain in the water for three hours. Waters (1962) noted a marked nocturnal periodicity in stream drift in fertile streams in Minnesota. Studies in southern Appalachian streams (Cada et. al, 1987) failed to find this pattern so the sampling design used in this study seems justified. Trout for stomach samples were obtained from the upstream sampling section after the nets had been pulled. In all cases, the allopatric brook trout site was sampled on the first evening and first morning, the sympatric site was sampled on the second evening and the second morning and the rainbow trout on the third evening and the third morning. Field samples were carried out during the last week of June, July, August and

September during 1987. Thunderstorms during the first sampling period resulted in rising water levels, preventing morning sampling at the sympatric site and all samples at the allopatric rainbow trout site.

Fish for stomach samples were obtained using a 700-volt AC backpack electroshocker. An attempt was made to collect a minimum of twenty fish in each section. In the sympatric section, equal numbers of both species were obtained whenever possible. After the fish were collected with the electroshocker, they were anesthetized using tricaine methanosulfonate (MS-222). All fish were weighed with hand-held spring scales, adults to the nearest gram, young of the year to the nearest tenth of a gram. The fish were then measured to obtain maximum total lengths in millimeters.

Stomach samples were obtained using a stomach lavage method similar to that described by Light et al. (1983). The design of the stomach pumping apparatus called for the attachment of a piece of surgical tubing to a 500 ml. Nalgene wash bottle. The fish were placed in a vee-shaped trough with a small circular opening at one end through which a short piece of three-quarter inch PVC pipe extended. The tubing was inserted through the oral cavity of the fish, down through the esophagus and into the stomach. Water forced from the wash bottle then flushed the contents of the stomach out through the mouth. A piece of cotton fabric secured around the PVC pipe retained the stomach contents. The entire piece of fabric, with stomach contents included, was then placed into an individually numbered 60 ml Nalgene sample bottle containing 30 ml of Kahle's solution, along with a piece of waterproof paper which recorded the species of the fish, its length, weight, and the date, site and time of the sample. The trout were then placed in a bucket of fresh water to allow them to revive sufficiently before being returned to the stream. After the fish had recovered, they were redistributed throughout the section to insure that fish densities in any given portion of the section remained relatively unchanged.

Drift nets were set in the buffer zone between the fish collection sections to avoid disrupting the normal feeding behavior of the trout. The nets were one meter long with a mesh size of 375 microns. The mouth of the nets were rectangular measuring 41 cm. by 31 cm. The nets were suspended in the thalweg of the stream with two one meter pieces of reinforced iron bar which had been driven into the substrate. The lower edge of the nets were placed as close to the bottom of the stream as possible to insure that the entire water column from surface to substrate was sampled. Water velocity at the mouth of the net was measured with a Teledyne-Gurley Pygmy Current Meter at the time that the nets were set, at the midpoint of the sample and when the nets were pulled. The depth of the water column passing through the net was measured to the nearest centimeter at the same points in time. This allowed calculation of the total volume of water passing through the net during the sampling period.

After the nets were pulled, all contents were washed into a coarse kitchen strainer suspended over a white plastic tray which retained the wash water. Larger invertebrates, leaves and other debris retained by the strainer were placed in an individually labelled container containing Kahle's solution. The tray was then visually inspected and all invertebrates removed from the tray were also placed into the container. The trays were sorted for a minimum of five minutes or until no other invertebrates were found for a period of one minute. The nets were inspected and any invertebrates found clinging to the nets were removed and placed in preservative. A piece of waterproof paper giving the sampling date, time of the sample, sampling site and location of the net (upper or lower) was placed in each container.

Initial population estimates were obtained during the second sampling period in the upstream section of each site. The sampling technique employed was the three-pass removal depletion method (Moore et al., 1983). Fish obtained with the electroshocker during the first two passes were placed in holding nets outside the section. After the third pass, all fish were redistributed through the section. Lengths, weights and species identification were recorded. Although no block nets were placed at the upper or lower ends of the sections, each section was bounded at both ends by natural obstructions which limited movement of fish into or out of the section during sampling. Final population sampling was carried out at the same sites on October 30 in the same manner. Estimates were calculated using the MICROFISH 2.2 software package (Van Deventer and Platts, 1985).

Water temperature, pH and stream discharge measurements were collected for each site during each sampling period. An Orion Model 211 pH meter was used to obtain pH values. Stream discharge measurements were obtained using the method described by Armour et al. (1983). Water velocities for these measurements were obtained with a Teledyne-Gurley Pygmy Current Meter. During the July sampling date, a number of physical stream characteristics were measured at each section, including mean width, pool-riffle ratios and percent gradient. Mean stream width and percent gradient were obtained by taking measurments at 10 m. intervals throughout each section and averaging the individual measurements.

Laboratory Analysis

All stomach and drift samples were returned to the lab for sorting, identification, and enumeration of individual items using a dissecting microscope. Immature aquatic invertebrates in the orders Diptera, Ephemeroptera, Plecoptera and Trichoptera were identified to family using Brigham et al. (1982) and Merritt and Cummins (1978). The aquatic groups Coleoptera, Amphipoda, Odonata and Salvelinus were lumped into an "Other aquatics" group. All terrestrial invertebrates, including adult aquatic forms were classified simply as terrestrials. Other categories included Decapoda, Urodela and a group of unidentifiable items. "Blotted" wet weights were obtained for all representatives of a given taxa from each stomach by placing the food item on a Kimwipe absorbent tissue and lightly pressing with a second tissue to remove excess moisture. The items were then weighed to the nearest tenth of a milligram on a Mettler Analytical Balance. Dry weights were obtained by placing the food items in individually numbered porcelain crucibles and drying in an oven at 85 degrees C for 48 hours. At the end of the drying period, the crucibles were removed from the oven and immediately placed in a dessicator to cool. After cooling, the contents were transferred to an aluminum weighing pan and weighed to the nearest tenth of a milligram. Since many of the items were extremely small, it was necessary to combine all the stomach contents from a given date, site and time for a given taxon to avoid undetectable weights.

The contents of the drift sample bottles were placed in a white enamel sorting pan and carefully hand-picked. Each pan was sorted for a minimum of thirty minutes or until no additional items were found for a period of one minute. Items from the drift nets were identified, enumerated, weighed, dried and re-weighed in the same manner as the stomach items. The items in the drift samples were placed in the same taxa categories as the stomach contents. Again, to avoid undetectable dry weights for the smaller items, taxa from all four nets at each site were combined.

Data Analysis

Initially, two descriptive measures, the mean percentage relative weight contributed by each taxon to the stomach contents for both species in all samples in which the species occurred and the frequency of occurrence of each taxon in all samples, were calculated to provide a rough comparison of the food habits of the two species. Relative weights were calculated as the total wet weight of stomach contents in milligrams divided by the weight of the fish in grams. Using relative weights allowed comparisons of fish of differing sizes by correcting for differences in total stomach volume. The assumption of a linear relationship between stomach volume and total weight is probably not .pa entirely accurate, but it should provide a more precise and realistic estimate of average food intake than using the uncorrected weights.

To determine the degree of similarity between the diets of populations of the two species at the different sites, Schoener's Index of Dietary Overlap was calculated for the following pairs of comparisons for each sample (evening and morning) on each date: allopatric brook trout (ABKT) x sympatric brook trout (SBKT), ABKT x sympatric rainbow trout (SRBT), SBKT x SRBT, SBKT x allopatric rainbow trout (ARBT), SRBT x ARBT. The values of the index range from 0 to 1 and the overlap between pairs is generally considered to be significant if the value is greater than 0.6. The formula for Schoener's index is as follows:

$$\text{Index of Overlap} = 1 - 0.5\left(\underset{i = 1 \text{ to } n}{\overset{\text{Sum of } i}{\text{for}}} \; |p_{xi} - p_{yi}| \right)$$

where: p_{xi} = proportion of food category i in the diet of species x

p_{yi} = proportion of food category i in the diet of species y

In calculating the index, the average percentage relative weight contributed by each taxon was used as suggested by Wallace (1981). The index was calculated using the lowest possible taxonomic category. In the case of immature aquatic insects, identification was usually to the family level. All adult aquatic forms and obligate terrestrial forms were simply identified as terrestrial. Empty stomachs were eliminated from these calculations as were all unidentifiable items.

In order to investigate possible shifts in prey utilization, Ivlev's Electivity Index was calculated for all species in all samples. The index measures the tendency for an organism to "elect" or feed selectively on a certain prey type. Values of the index range from 1 (strongly selected for) to -1 (strongly selected against). Values close to zero indicate the prey item is taken in relation to its abundance in the environment. The formula for this index is:

$$\text{Electivity Index for food item } i = \frac{pD_i - pR_i}{pD_i + pR_i}$$

where: pD_i = the proportion of food item i in the diet

and pR_i = the proportion of food item i in the environment

The proportion of the food item in the diet was calculated using relative wet weights. As with Schoener's Index, empty stomachs and nonidentifiable food items were not included. The average wet weights of items from the drift net samples were used to estimate the proportion of the food item in the environment. The index was calculated by lumping the lower taxonomic categories into eight major groups. These were the aquatic orders Ephemeroptera, Trichoptera, Plecoptera, Diptera, a miscellaneous group classified simply as Other aquatic, Decapoda, Urodela and Terrestrials, once again including adult aquatic forms in this group.

In an effort to determine if the presence of one species has any effect on the weight of stomach contents of the other species, a two factor analysis of variance was performed, using sample date (second, third and fourth) and species distribution (ABKT, SBKT, SRBT and ARBT) as main effects. All relative weights were log transformed when initial analyses indicated that the means of the various effects were positively correlated with their variances (Sokal and Rohlf, 1981). The first sample date was not included in this analysis because no data were available for either of the allopatric rainbow trout samples or for the morning sample at the sympatric site. The Tukey-Kramer Honest Significant Difference test was used to compare main effects means if the overall F-statistic was significant at the .10 level.

Differences in the average weight of stomach contents, indices of overlap and indices of prey selection are all commonly utilized methods of looking at competition for food resources and while they do provide some information about the relationship between competitors, they are indirect measures of the effects of competition. Demonstrating that a loss in "fitness" has occurred in the presence of a competitor would be more direct evidence that competition is occurring. To investigate this, Fulton-type condition factors (K) were calculated for all fish at all sampling dates, including the final population estimate in October. The equation for the condition factor is as follows:

$$K = \frac{W \times 10^5}{L^3}$$

where: W = weight in grams
L = length in millimeters

Since differences in body conformation between species can affect the value markedly (Anderson and Gutreuter, 1983), comparisons between species were not carried out. However, to determine if there were differences in allopatric and sympatric populations of the same species over the course of the summer, a ANOVA was carried out, once again using sampling date and distribution (sympatric or allopatric) as main effects. If the overall F-statistic was significant at the .10 level for a given factor and there were no interactions, Tukey's HSD test was used to compare main effect means. If the interaction term F-statistic was significant at the .10 level, multiple pairwise comparisons of allopatric and sympatric populations by date were carried out.

Finally, an attempt was made to determine if the mean observed food intake was sufficient to meet the energetic demands of the average fish of each species at each site on each sampling date. The energy intake required to fulfill all of the maintenance requirements in the energy budget (C_{main}) for both species was calculated using the equation formulated by Elliott (1976) for brown trout. The equation takes the following form:

$$C_{main} = aW^{b1}e^{b2T}$$

where: C_{main} = maintenance energy intake in calories per day

W = fish weight in grams

T = water temperature in degrees C

This equation calculates the energy intake necessary to provide enough calories for metabolism with no change in the energy content of the fish (i.e. increase in biomass). It accounts for energy lost in waste products and feces as well as taking into account assimilation efficiencies.The constants a, b1 and b2 take on different values for different ranges of water temperature. Anything above this level of energy intake represents an increase in biomass (growth).

The most commonly employed method of calculating food consumption in field studies has been the "serial slaughter" method (Davis and Warren, 1971; Elliott, 1973; Mann, 1978). Fish are captured every few hours and returned to the lab where the stomach contents are removed. Stomach fullness is estimated to determine feeding patterns. Based on the feeding patterns and rates of gastric evacuation determined from laboratory studies, total food consumption for a given time period is estimated. A variation of this method was used to estimate total food consumption for each species distribution in this study. The assumption was made that the fish fed continously, exhibiting no distinguishable feeding pattern. Stomach weight is thereby maintained at an average value for an entire twenty-four hour period. The total food consumption is then obtained using the following formula (Elliott, 1972; Allan, 1981):

$$C(24) = 24 * S * R$$

where: $C(24)$ = estimate of daily food consumption
S = estimate of average stomach contents
R = exponential rate of gastric evacuation

Estimates of the exponential rate of gastric evacuation for salmonids were obtained from Elliott (1972). Although there is some discussion as to the proper form for the evacuation equation (Windell, 1978) use of the exponential model has received strong support (Persson, 1984; Persson, 1986). Obviously, the greater the frequency of sampling during the 24-hour period used to estimate the average stomach contents, the more precise the estimate of consumption. Since only two samples were taken during the 24 hour period, three different estimates of food consumption were calculated for each species distribution at each sampling date. The estimates used were the mean relative stomach weight, mean relative weight plus one standard deviation, and the maximum relative weight observed during the sampling period Caloric values were obtained by converting the consumption estimates into energetic equivalents using caloric values taken from Cummins and Wuychek (1971) and Davis and Warren (1971). For adult fish all consumption data were standardized to the the amount consumed by a 25 gram fish and then compared to the caloric intake necessary to support maintenance metabolism for a fish of that size. For Y-O-Y fish, all values were standardized to represent the consumption of a 5 gram fish.

Since there is ample evidence that there are differences in food habits and habitat utilization between Y-O-Y fish and adult fish, all of the above analyses of stomach sample were separated into these categories on the basis of length-frequency histograms. Fish less than 90 mm total length (TL) were considered to be Y-O-Y, fish greater than 90 mm TL were considered to be age 1+ or older.

Data obtained from the drift nets were used as an estimate of the resources available to the populations. Dry weights for individual taxa were converted to caloric values using data from Cummins and Wuychek (1971) and Davis and Warren (1968). Calories per cubic meter of water was then calculated for each net and the mean caloric value per cubic meter of water was obtained by averaging the values for the four nets at each site for each sampling date. Estimates of total cubic meters of water flowing by a given point in the stream were obtained for each date and site by multiplying the discharge estimate by the number of minutes in a 24 hour period. This figure was multiplied by the calories per cubic meter of water to provide an estimate of the calories moving past a given point in the stream over the course of a 24 hour period for a given date and site which was then compared to the calories necessary to support a 25 gram trout.

In addition to comparison of the stomach values to the drift net values, a two factor analysis of variance was carried out to determine if there were any differences in the resources available in the drift between the different dates and sites. Since each net sampled different volumes of water during a given sampling period, all values were converted to average wet weight per 100 cubic meters of water. Once again, means were positively correlated with variances so log transformations were carried out. If the overall F-test for a given factor was significant at the .10 level and there were no significant interactions between factors, Tukey's HSD was carried out on the means for that factor.

CHAPTER IV

RESULTS

Physical stream characteristics measured on each sampling date for each sampling site, including water temperature, stream discharge, and pH are presented in Appendix 1. Physical characteristics measured in July including mean stream widths and gradients and pool/riffle ratios are also presented in Appendix 1. As has been previously noted, all samples were carried out in full with the exception of the June sampling date.

Stomach composition data by mean percentage relative wet weight for adult fish are presented in Table 1. The information for percent composition by major food categories is presented in Figure 1. The combined frequency of occurrence data for adult fish is presented in Table 2. Monthly totals for percent composition are presented in Appendix 2. Monthly totals for frequency of occurrence are presented in Appendix 3. In general, terrestrial items were the most important prey item for all distributions, both in terms of mean percent relative weight and frequency of occurrence. The percent contribution of this group ranged from 59% of the mean relative weight of stomach contents in SRBT to 74% in SBKT. The frequency of occurrence of terrestrial items was greater than 90% for all distributions. Ephemeropterans made up slightly more of the percent relative weight in SBKT, SRBT and ARBT stomachs than in the ABKT stomachs as well as occurring with a greater degree of frequency in those populations. The only other obvious difference between the populations was the greater percent contribution

Table 1. Stomach composition for adult fish for all sampling dates combined expressed as mean percent relative wet weight.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	0.4	0.9	0.3	1.4
Ephemerellidae	2.5	0.2	2.7	0.7
Heptageniidae	2.0	6.2	10.6	4.6
Leptophlebiidae	0.1	0.0	0.1	< 0.1
TOTAL	5.0	7.3	13.7	6.7
TRICHOPTERA				
Brachycentridae	0.0	0.0	< 0.1	< 0.1
Glossosomatidae	0.0	0.0	0.7	1.0
Hydropsychidae	3.6	1.2	2.9	4.9
Limnephilidae	0.1	0.0	0.3	0.2
Odontoceridae	0.7	0.0	0.4	0.8
Polycentropodidae	0.2	0.3	0.1	0.0
Rhyacophilidae	0.2	0.0	0.1	0.2
Sericostomatidae	0.4	0.7	0.3	0.1
TOTAL	5.2	2.2	4.8	7.2
PLECOPTERA				
Capnidae	0.0	0.0	0.1	0.0
Leuctridae	0.1	0.0	0.4	1.4
Peltoperlidae	< 0.1	0.0	0.3	0.6
Perlidae	0.9	0.0	1.3	0.6
Perlodidae	0.3	0.0	< 0.1	0.9
TOTAL	1.3	0.0	2.1	3.5
DIPTERA				
Ceratopogonidae	< 0.1	0.0	< 0.1	0.0
Chironomidae	1.2	0.2	0.3	< 0.1
Dixidae	1.4	< 0.1	3.4	0.1
Simuliidae	0.9	0.0	0.7	0.8
Tanyderidae	< 0.1	0.0	0.0	0.0
Tipulidae	1.8	2.6	0.2	0.4
TOTAL	5.3	2.8	4.6	1.3
OTHER AQUATICS				
Amphipoda	0.2	0.0	0.0	0.0
Coleoptera	0.9	0.3	0.2	0.5
Gomphidae	0.0	0.0	0.4	0.0
Salvelinus	0.0	0.0	2.1	0.0
TOTAL	1.1	0.3	2.7	0.5
DECAPODA	5.4	4.6	1.0	0.7
URODELA	2.6	2.6	1.5	2.3
TERRESTRIAL	63.8	74.0	58.9	63.9
NO IDENTIFICATION	9.5	6.2	10.5	12.4

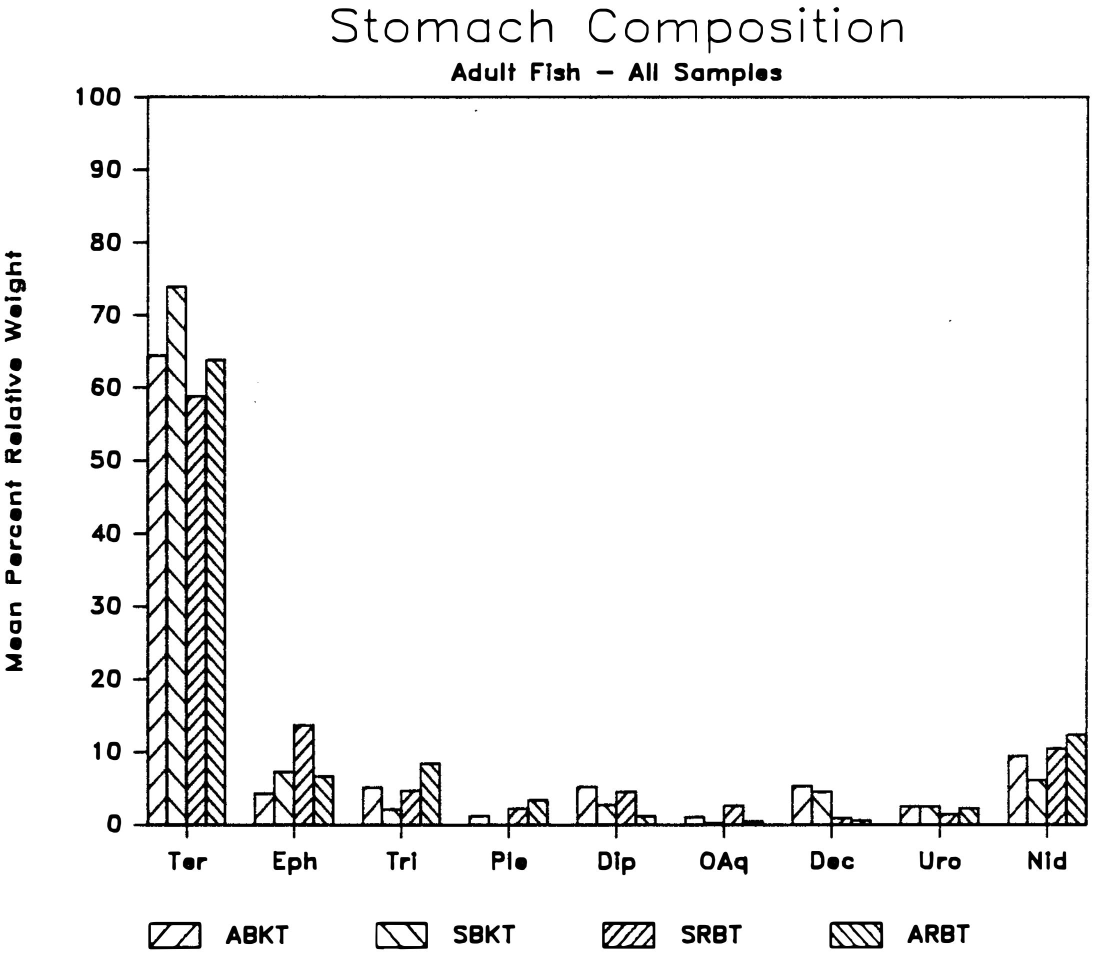


Figure 1. Stomach composition by major food groups for adult fish for all sampling dates. Ter = Terrestrial, Eph = Ephemeroptera, Tri = Trichoptera, Ple = Plecoptera, Dip = Diptera, OAq = Other Aquatics, Dec = Decapoda, Uro = Urodela, Nid = No identification.

Table 2. Frequency of occurrence of prey items in the stomachs of adult fish for all sampling dates.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	3.9	18.9	12.8	14.1
Ephemerellidae	15.7	2.7	17.0	8.2
Heptageniidae	15.0	21.6	40.4	23.5
Leptophlebiidae	1.6	0.0	2.1	1.2
TRICHOPTERA				
Brachycentridae	0.0	0.0	2.1	1.2
Glossosomatidae	0.0	0.0	4.3	5.9
Hydropsychidae	16.5	8.1	27.7	20.0
Limnephilidae	1.6	0.0	4.3	8.2
Odontoceridae	3.1	0.0	4.3	5.9
Polycentropodidae	5.5	2.7	8.5	4.7
Rhyacophilidae	3.1	0.0	4.3	3.5
Sericostomatidae	4.7	2.7	2.1	1.2
PLECOPTERA				
Capnidae	0.0	0.0	0.0	0.0
Leuctridae	2.4	0.0	6.4	4.7
Peltoperlidae	1.6	0.0	6.4	4.7
Perlidae	5.5	0.0	8.5	2.4
Perlodidae	0.8	0.0	2.1	3.5
DIPTERA				
Ceratopogonidae	0.8	0.0	2.1	0.0
Chironomidae	13.4	8.1	21.3	1.2
Dixidae	12.6	2.7	17.0	8.2
Simuliidae	11.8	0.0	19.1	8.2
Tanyderidae	0.8	0.0	0.0	0.0
Tipulidae	7.9	5.4	4.3	2.4
OTHER AQUATICS				
Amphipoda	0.8	0.0	0.0	0.0
Coleoptera	4.7	2.7	4.3	2.4
Gomphidae	0.0	0.0	4.3	0.0
Salvelinus	0.0	0.0	2.1	0.0
DECAPODA	14.2	10.8	8.5	2.4
URODELA	3.9	2.7	2.1	3.5
TERRESTRIAL	92.1	91.9	95.7	90.6
NO IDENTIFICATION	41.7	40.5	55.3	45.9

of Decapoda in the ABKT and SBKT stomachs and the comparative lack of crayfish in the rainbow trout stomachs.

Stomach composition data by mean percentage relative wet weight for Y-O-Y fish is presented in Table 3, data based on major food categories is summarized in Figure 4, and the frequency of occurrence data appears in Table 4. Monthly data for percent composition appears in Appendix 2 and for frequency of occurrence in Appendix 3. Terrestrial prey items made up the bulk of the stomach contents in Y-O-Y fish in both brook trout populations. In the SRBT populations, terrestrials and ephemeropterans were of equal importance, each group contributing approximately 45% of the mean relative weight of stomach contents in those populations. Although not of equal importance to the terrestrials, ephemeropterans also contributed 32% of the mean relative weight in ARBT populations. The same trend was evidenced in the frequency of occurrence data for the SRBT population as the three ephemeropteran familes Baetidae, Ephemerellidae and Heptageniidae occurred in 47%, 23% and 53% of the stomachs respectively. The Y-O-Y populations exhibited a great deal of similarity in their utilization of other prey taxa.

Values calculated for Schoener's Index of Dietary Overlap are presented in Table 5 for adult fish and Table 6 for Y-O-Y fish. For adults there was significant overlap in all but three of the comparisons. In the evening samples during the June sampling date, SBKT did not overlap significantly with either ABKT or SRBT. During the July sampling date, SRBT did not overlap significantly with ARBT, ABKT or SBKT during the morning samples. The remaining comparisons at all dates

Table 3. Stomach composition for Y-O-Y fish for all sampling dates combined expressed as mean percent relative wet weight.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	9.5	7.7	14.7	21.1
Ephemerellidae	0.0	0.0	9.8	0.6
Heptageniidae	5.2	8.0	19.7	10.6
Leptophlebiidae	0.0	2.7	0.3	0.0
TOTAL	14.7	18.4	44.5	32.3
TRICHOPTERA				
Glossosomatidae	0.0	2.9	0.0	0.0
Hydropsychidae	4.0	1.9	1.4	1.2
Limnephilidae	0.4	0.2	0.0	0.9
Polycentropodidae	0.1	0.5	0.0	0.0
Rhyacophilidae	0.0	1.5	0.0	0.4
Sericostomatidae	0.0	0.2	0.2	0.1
TOTAL	4.5	7.2	1.6	2.6
PLECOPTERA				
Capnidae	0.0	0.6	0.5	0.0
Leuctridae	0.0	0.1	0.0	0.0
Peltoperlidae	0.0	0.1	0.0	1.8
Perlidae	2.9	0.0	0.0	0.2
TOTAL	2.9	0.8	0.5	2.0
DIPTERA				
Blephariceridae	0.0	0.0	0.0	0.1
Ceratopogonidae	0.0	0.3	< 0.1	0.0
Chironomidae	1.0	3.2	0.2	0.4
Dixidae	5.9	0.1	0.2	0.0
Simuliidae	0.0	0.2	0.9	0.5
Tanyderidae	0.0	3.7	0.0	0.4
Tipulidae	0.0	0.0	5.2	2.7
TOTAL	6.9	7.5	6.5	4.1
OTHER AQUATICS				
Coleoptera	4.9	0.2	0.0	0.0
TOTAL	4.9	0.2	0.0	0.0
TERRESTRIAL	55.2	56.5	43.7	51.9
NO IDENTIFICATION	10.9	9.4	3.2	6.3

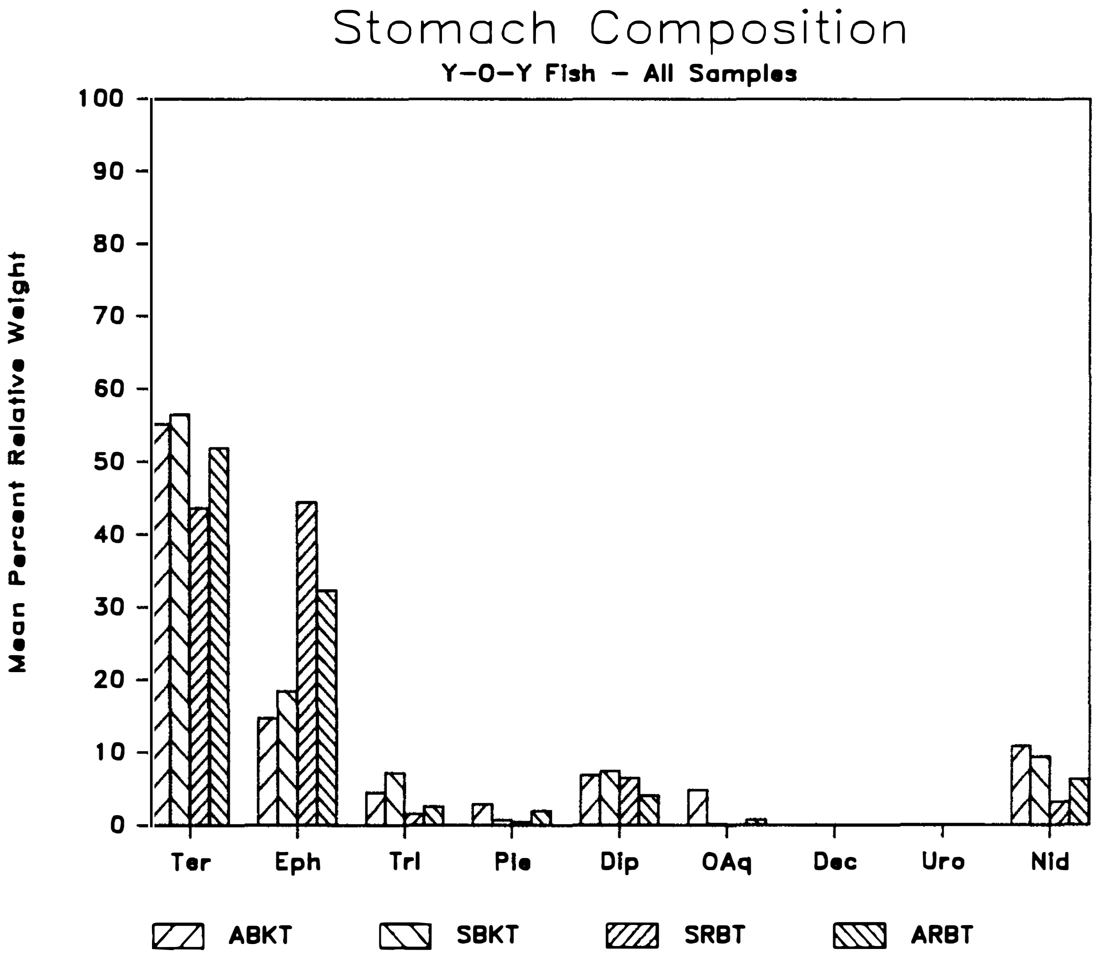


Figure 2. Stomach composition by major food groups for Y-O-Y fish for all sampling dates. Ter = Terrestrial, Eph = Ephemeroptera, Tri = Trichoptera, Ple = Plecoptera, Dip = Diptera, OAq = Other Aquatics, Dec = Decapoda, Uro = Urodela, Nid = No identification.

Table 4. Frequency of occurrence of prey items in the stomachs of Y-O-Y fish for all sampling dates.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	13.6	11.4	47.1	48.3
Ephemerellidae	0.0	0.0	23.5	3.4
Heptageniidae	18.2	25.7	52.9	41.4
Leptophlebiidae	0.0	5.7	5.9	0.0
TRICHOPTERA				
Glossosomatidae	0.0	2.9	0.0	0.0
Hydropsychidae	22.7	5.7	17.6	10.3
Limnephilidae	4.5	5.7	0.0	10.3
Polycentropodidae	4.5	5.7	0.0	0.0
Rhyacophilidae	0.0	5.7	0.0	3.4
Sericostomatidae	0.0	2.9	11.8	3.4
PLECOPTERA				
Capnidae	0.0	5.7	5.9	0.0
Leuctridae	0.0	2.9	0.0	0.0
Peltoperlidae	0.0	2.9	0.0	3.4
Perlidae	4.5	0.0	0.0	3.4
DIPTERA				
Blephariceridae	0.0	0.0	0.0	3.4
Ceratopogonidae	0.0	5.7	5.9	0.0
Chironomidae	18.2	11.4	17.6	10.3
Dixidae	22.7	8.6	11.8	0.0
Simuliidae	0.0	5.7	11.8	6.9
Tanyderidae	0.0	11.4	0.0	6.9
Tipulidae	0.0	0.0	5.9	10.3
OTHER AQUATICS				
Coleoptera	9.1	2.9	0.0	0.0
TERRESTRIAL	77.3	77.1	76.5	69.0
NO IDENTIFICATION	40.9	31.4	29.4	24.1

Table 5. Schoener's Index of Dietary Overlap for adult fish from all sampling dates.

EVENING SAMPLE

	SAMPLE DATE			
COMPARISON	JUNE	JULY	AUGUST	SEPTEMBER
ABKT X SBKT	.345	.768	.639	.751
	(20,3)	(19,6)	(16,4)	(15,5)
ABKT X SRBT	.672	.699	.816	.685
	(20,10)	(19,9)	(16,5)	(15,5)
SBKT X SRBT	.398	.818	.781	.677
	(3,10)	(6,9)	(4,5)	(5,5)
ARBT X SBKT	-	.691	.792	.865
		(13,6)	(13,4)	(14,5)
ARBT X SRBT	-	.634	.802	.709
		(13,9)	(13,5)	(14,5)

MORNING SAMPLE

	SAMPLE DATE			
COMPARISON	JUNE	JULY	AUGUST	SEPTEMBER
ABKT X SBKT	-	.704	.680	.829
	-	(16,8)	(13,6)	(14,5)
ABKT X SRBT	-	.556	.719	.698
		(16,6)	(13,5)	(14,7)
SBKT X SRBT	-	.529	.614	.722
		(8,6)	(6,5)	(5,7)
ARBT X SBKT	-	.691	.672	.764
		(15,8)	(15,6)	(14,5)
ARBT X SRBT	-	.578	.752	.732
		(15,6)	(15,5)	(14,7)

Values greater than .6 are considered to indicate significant overlap. Numbers in parenthese indicate the sample size for the first and second member of the pair, respectively.

Table 6. Schoener's Index of Dietary Overlap for Y-O-Y fish from all sampling dates.

EVENING SAMPLE

COMPARISON	SAMPLE DATE JUNE	JULY	AUGUST	SEPTEMBER
ABKT X SBKT	.500 (3,6)	.395 (1,4)	.472 (2,5)	.536 (3,6)
ABKT X SRBT	-	.270 (1,2)	.471 (2,5)	.522 (3,4)
SBKT X SRBT	-	.529 (4,2)	.746 (5,5)	.710 (6,4)
ARBT X SBKT	-	.500 (5,4)	.745 (5,5)	.756 (6,5)
ARBT X SRBT	-	.743 (5,2)	.852 (5,5)	.595 (5,4)

MORNING SAMPLE

COMPARISON	SAMPLE DATE JUNE	JULY	AUGUST	SEPTEMBER
ABKT X SBKT	-	.667 (3,3)	.621 (6,5)	.685 (4,7)
ABKT X SRBT	-	.525 (3,2)	.145 (6,3)	.166 (4,1)
SBKT X SRBT	-	.442 (3,2)	.426 (5,3)	.167 (7,1)
ARBT X SBKT	-	.663 (5,3)	.725 (4,5)	.745 (5,7)
ARBT X SRBT	-	.537 (5,2)	.559 (4,3)	.068 (5,1)

Values greater than .6 are considered to indicate significant overlap. Numbers in parentheses indicate the sample size for the first and second member of the pair, respectively.

and times indicated that there was significant overlap between species.

In contrast, the results for Y-O-Y fish were not as consistent. During July, ARBT and SRBT showed significant overlap during the evening. During the morning in the same month, SRBT exhibited significant overlap with both allopatric populations. During the evening sample in August, SBKT, SRBT and ARBT all overlapped significantly. During the morning sample, the overlap between SBKT and ABKT and the overlap between SBKT and ARBT was significant. In the September evening sample, SBKT overlapped significantly with SRBT and ARBT. The morning sample in September showed significant overlap between SBKT and ABKT as well as SBKT and ARBT.

The information obtained from the calculation of Ivlev's Electivity Index for the adult fish is presented in Figures 3 through 6. In these figures a value of 1 indicates the taxa occurred in the stomachs but not in the drift samples, a value of -1 indicates that the taxa occurred in the drift but not in the stomachs and no value indicates that the taxa occurred in neither the stomachs or the drift (there were no values of 0, which would have indicated that the taxa was consumed in direct proportion to its abundance in the drift). ABKT and SBKT generally consumed terrestrials in proportion to their abundance in the drift with the exception of the morning sample during the August sampling period when SBKT showed positive selection for terrestrials. With the exception of the morning sample in September, ABKT and SBKT also exhibited a great deal of similarity in their selectivity of ephemeropterans. The pattern for trichopterans was not as consistent as the evening samples in June and July and the morning sample in August showed marked differences in

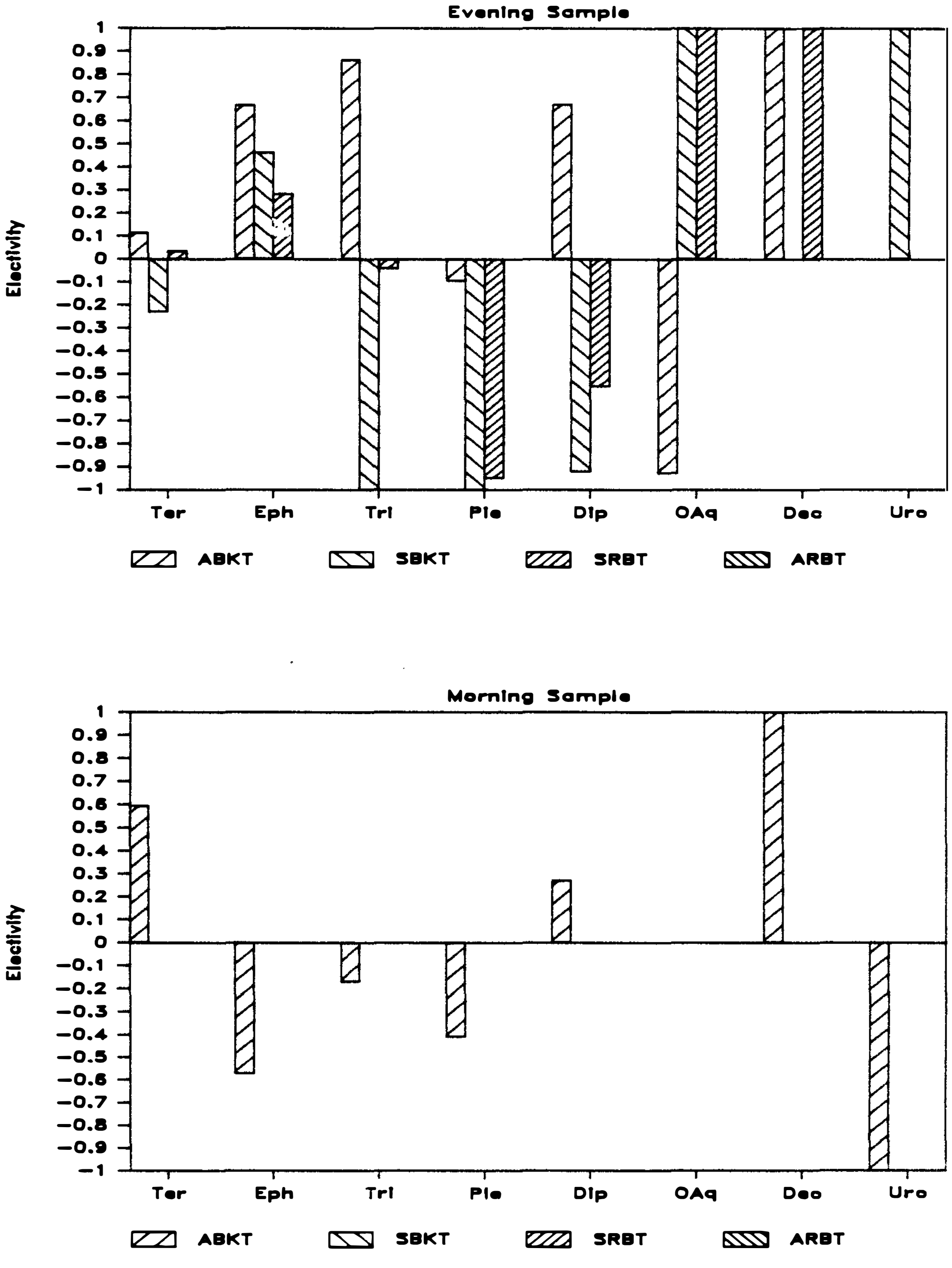
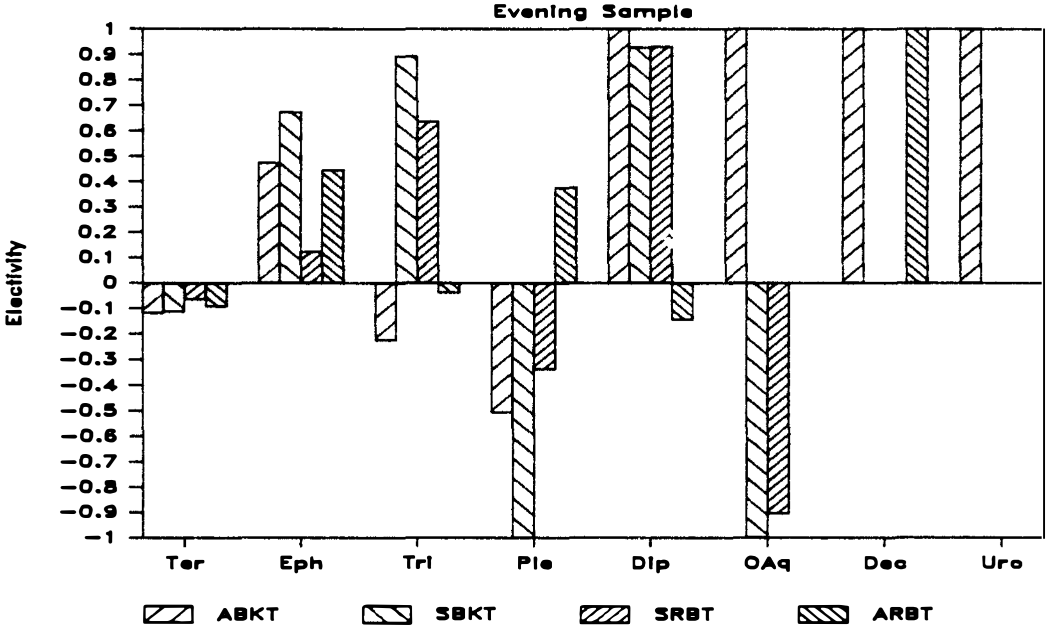


Figure 3. Ivlev's Electivity Index for adult fish from evening and morning samples during June. Ter = Terrestrial, Eph = Ephemeroptera, Tri = Trichoptera, Ple = Plecoptera, Dip = Diptera, OAq = Other Aquatics, Dec = Decapoda, Uro = Urodela.



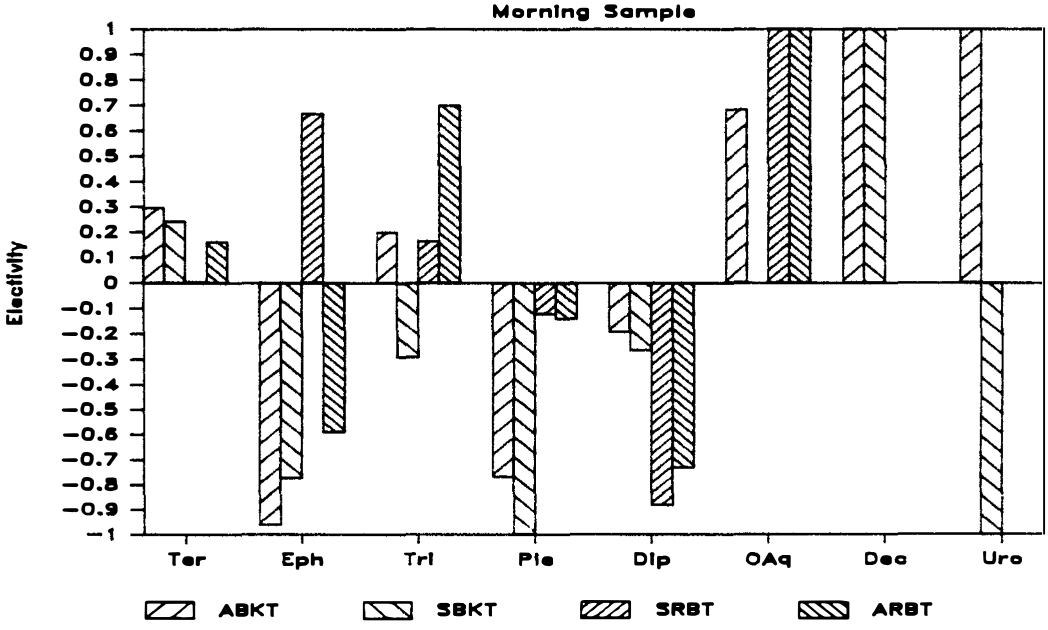


Figure 4. Ivlev's Electivity Index for adult fish from evening and morning samples during July. Ter = Terrestrial, Eph = Ephemeroptera, Tri = Trichoptera, Ple = Plecoptera, Dip = Diptera, OAq = Other Aquatics, Dec = Decapoda, Uro = Urodela.

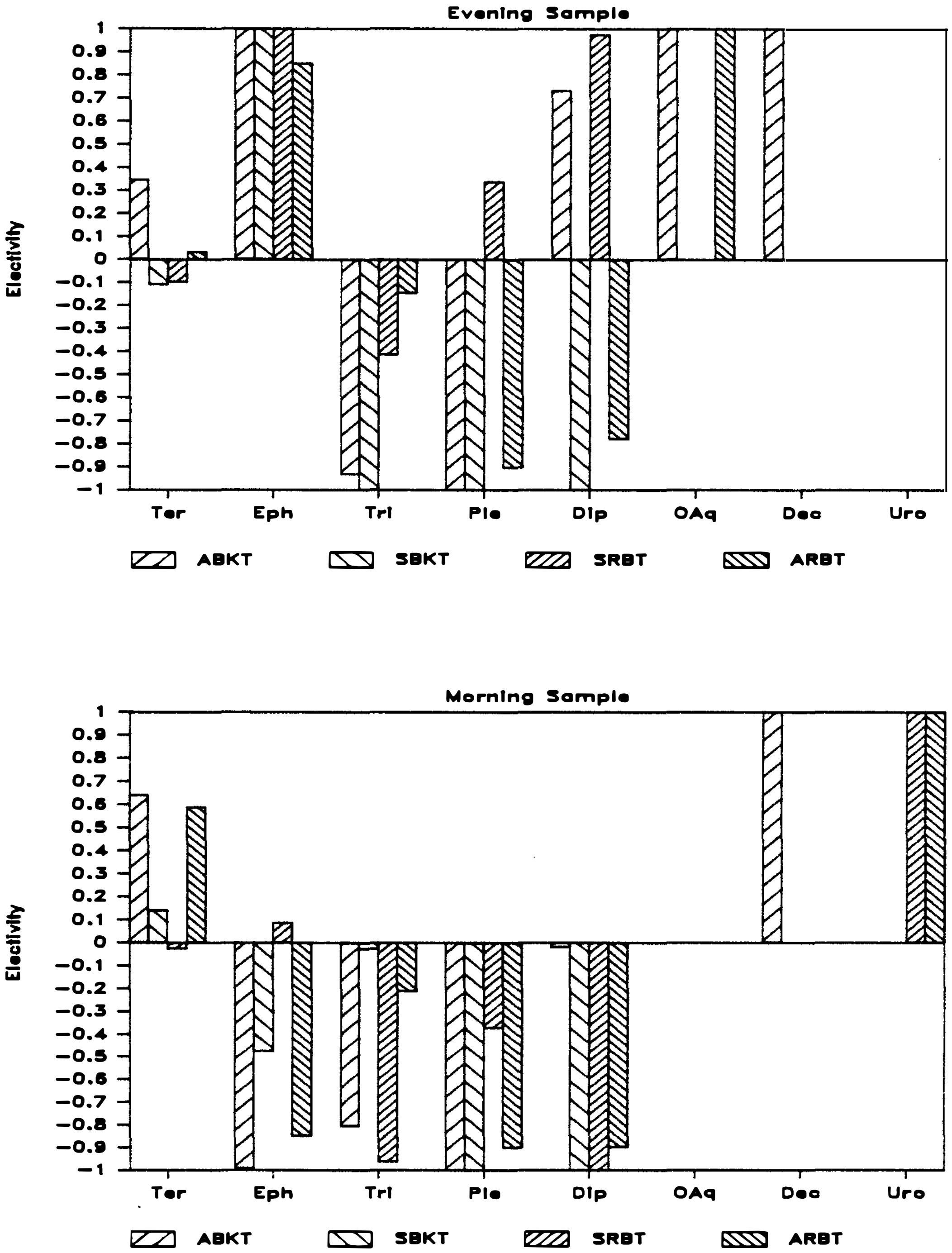


Figure 5. Ivlev's Electivity Index for adult fish from evening and morning samples during August. Ter = Terrestrial, Eph = Ephemeroptera, Tri = Trichoptera, Ple = Plecoptera, Dip = Diptera, OAq = Other Aquatics, Dec = Decapoda, Uro = Urodela.

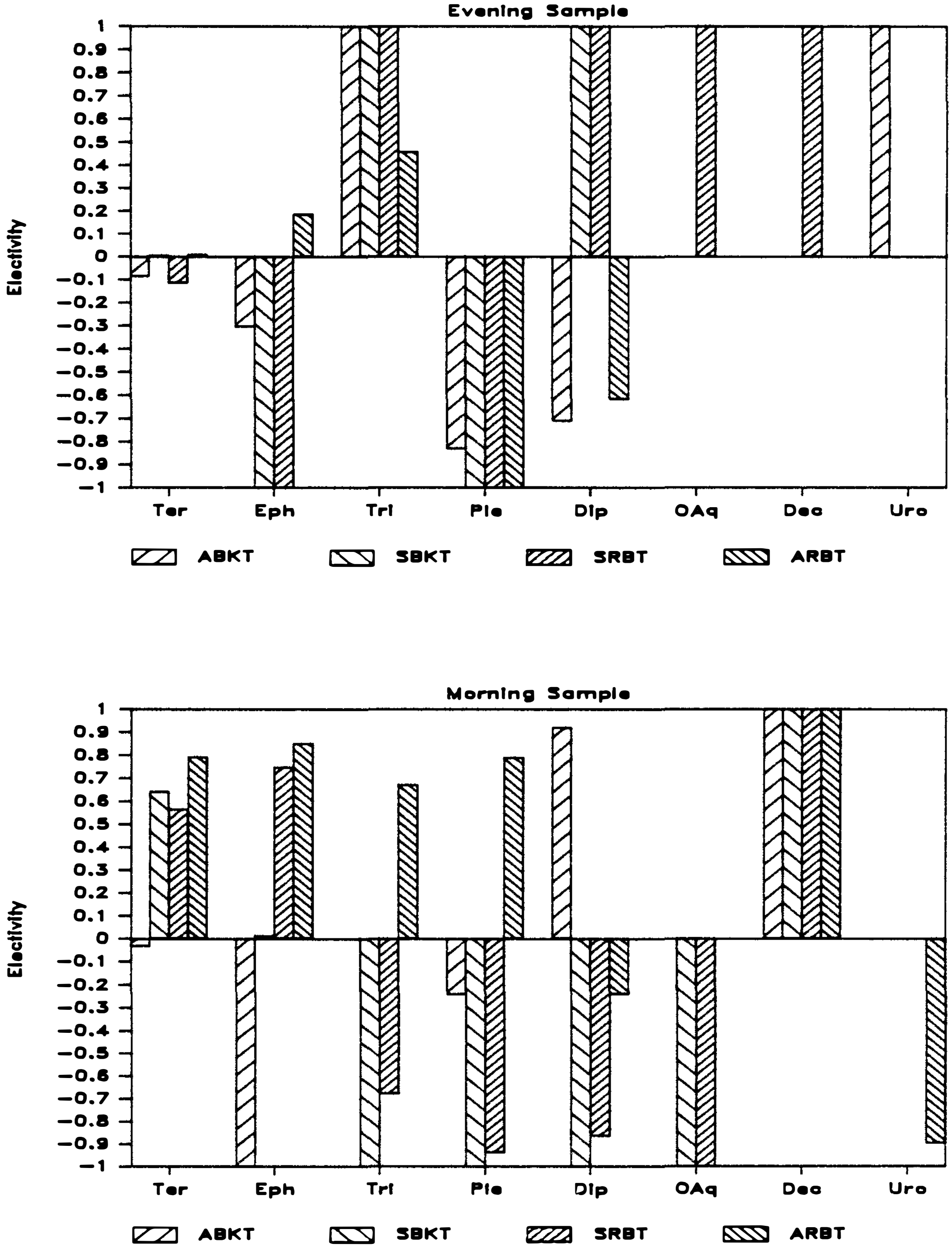


Figure 6. Ivlev's Electivity Index for adult fish from evening and morning samples during September. Ter = Terrestrial, Eph = Ephemeroptera, Tri = Trichoptera, Ple = Plecoptera, Dip = Diptera, OAq = Other Aquatics, Dec = Decapoda, Uro = Urodela.

electivity for that group. Both brook trout populations exhibited negative selection for plecopterans. Electivity for dipterans was highly variable but overall there was not a great deal of similarity in the utilization of this group by ABKT and SBKT.

For most of the sample dates, SRBT and ARBT did not consistently exhibit similar patterns of electivity for any taxa other than terrestrials. There were exceptions to this trend though, as both populations exhibited positive selection for ephemeropterans during the evening sample in August and the morning sample in September. SRBT and ARBT displayed positive selection for trichopterans during the evening sample in September. Plecopterans were taken in proportion to their abundance in the morning sample in July and strongly selected against in the evening in September. Both SRBT and ARBT selected against dipterans during the morning sample in July and August.

The information obtained from the calculation of Ivlev's Electivity Index for the Y-O-Y fish is presented in Figures 7 through 10. The results were highly variable, but one consistent pattern emerged. If the three "miscellaneous" categories (Other aquatics, Decapoda and Urodela) are eliminated, there are a total of 30 possible pairwise comparisons of electivity. SBKT and SRBT showed similar electivities in 26 of these 30 possible comparisons. The only exceptions were for terrestrials during the morning sample in August and September and trichopterans during the morning and evening sample during August.

Mean relative stomach weights, standard errors and the number of fish per sample are presented in Table 7 for adult fish. Similar information is presented in Table 8 for Y-O-Y fish. F-tests indicated

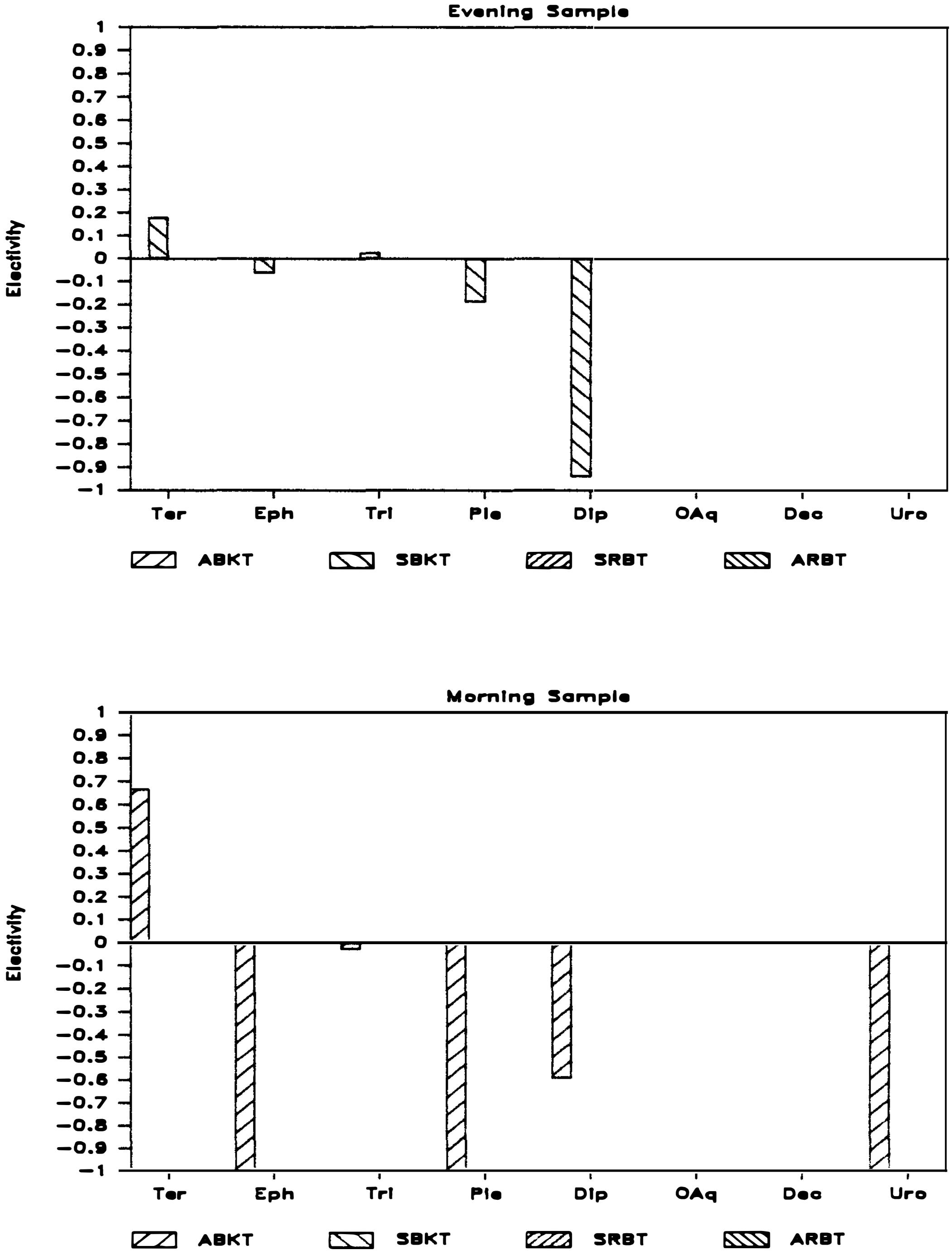


Figure 7. Ivlev's Electivity Index for Y-O-Y fish from evening and morning samples during June. Ter = Terrestrial, Eph = Ephemeroptera, Tri = Trichoptera, Ple = Plecoptera, Dip = Diptera, OAq = Other Aquatics, Dec = Decapoda, Uro = Urodela.

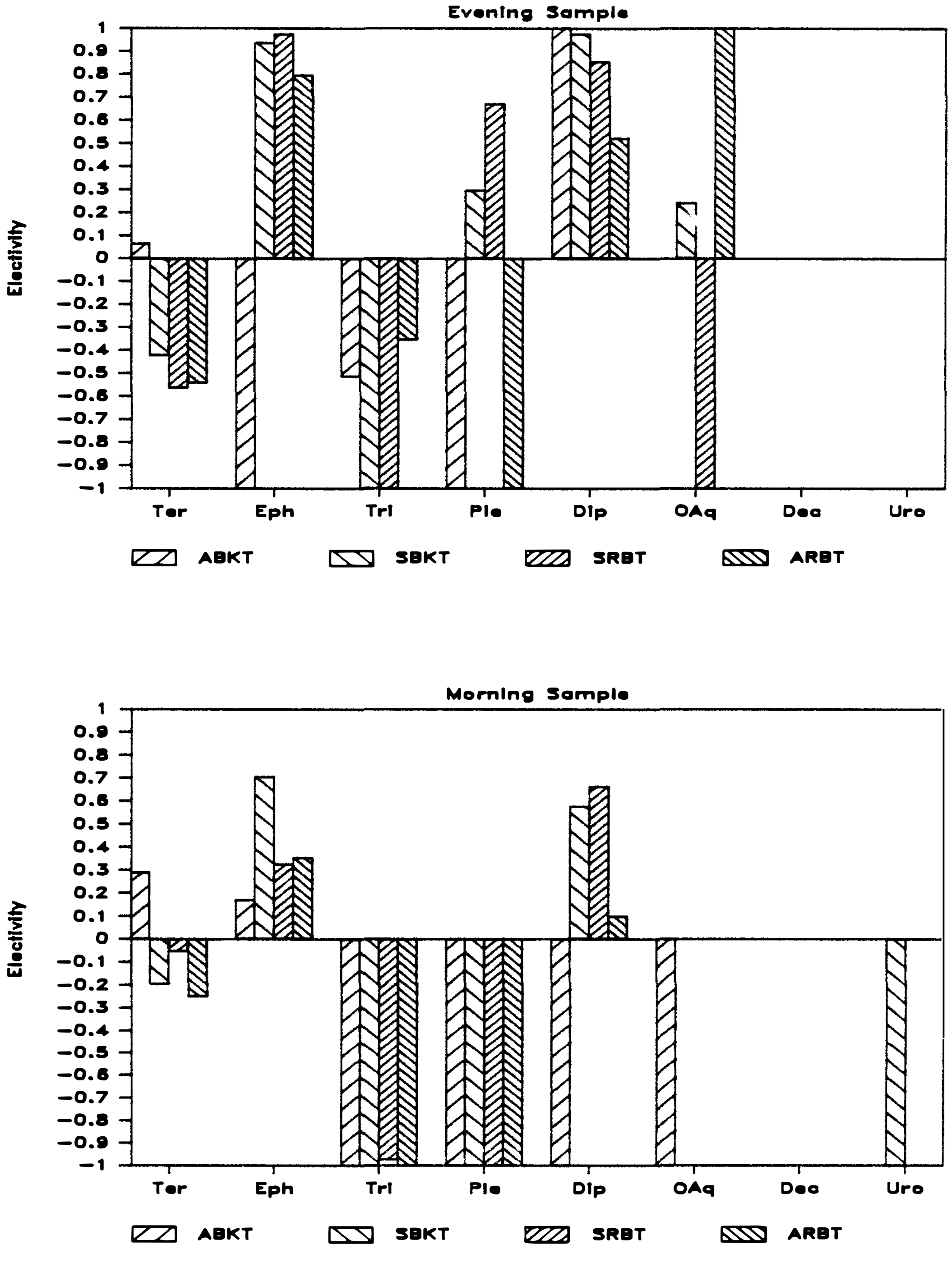


Figure 8. Ivlev's Electivity Index for Y-O-Y fish from evening and morning samples during July. Ter = Terrestrial, Eph = Ephemeroptera, Tri = Trichoptera, Ple = Plecoptera, Dip = Diptera, OAq = Other Aquatics, Dec = Decapoda, Uro = Urodela.

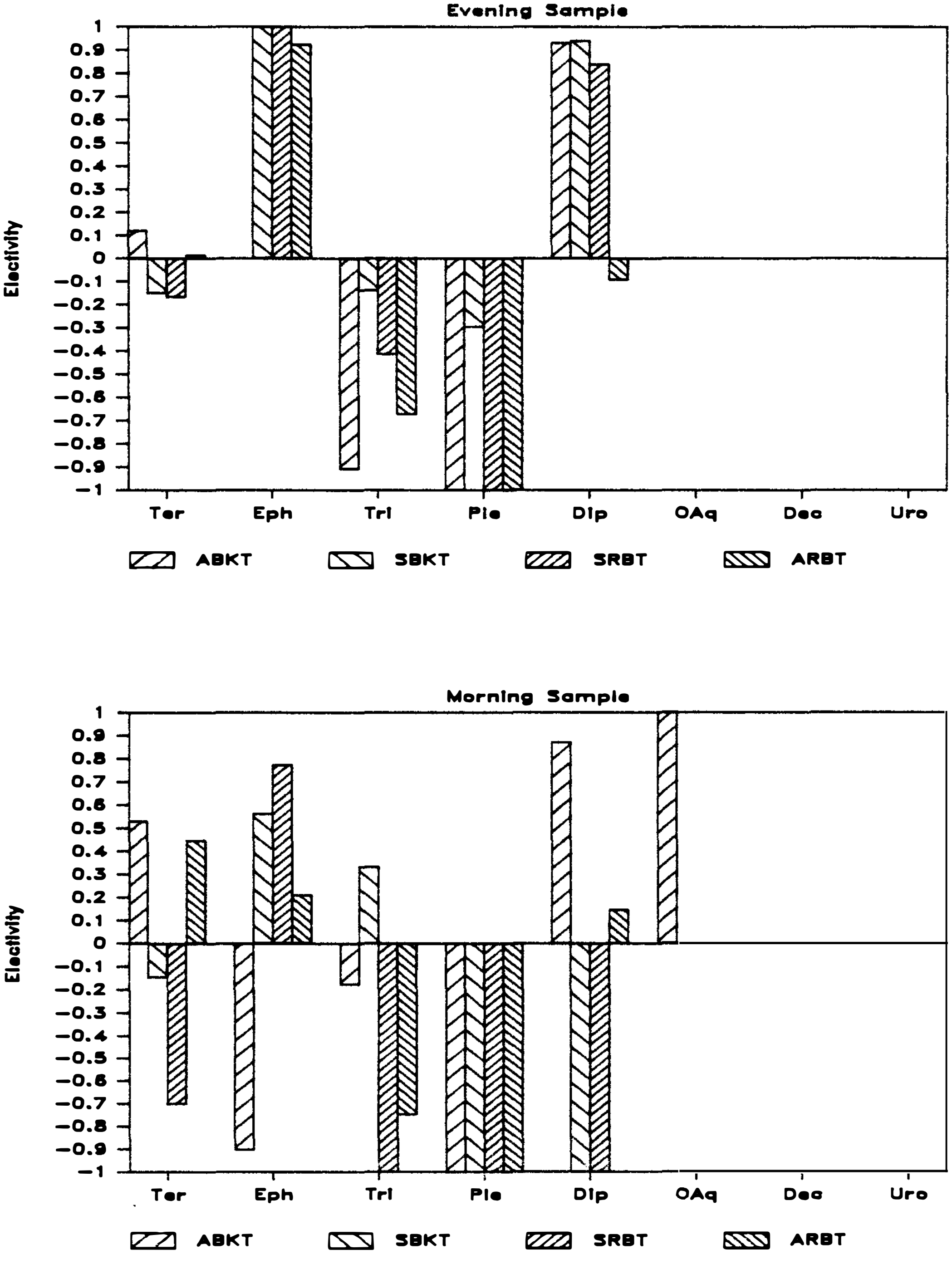


Figure 9. Ivlev's Electivity Index for Y-O-Y fish from evening and morning samples during August. Ter = Terrestrial, Eph = Ephemeroptera, Tri = Trichoptera, Ple = Plecoptera, Dip = Diptera, OAq = Other Aquatics, Dec = Decapoda, Uro = Urodela.

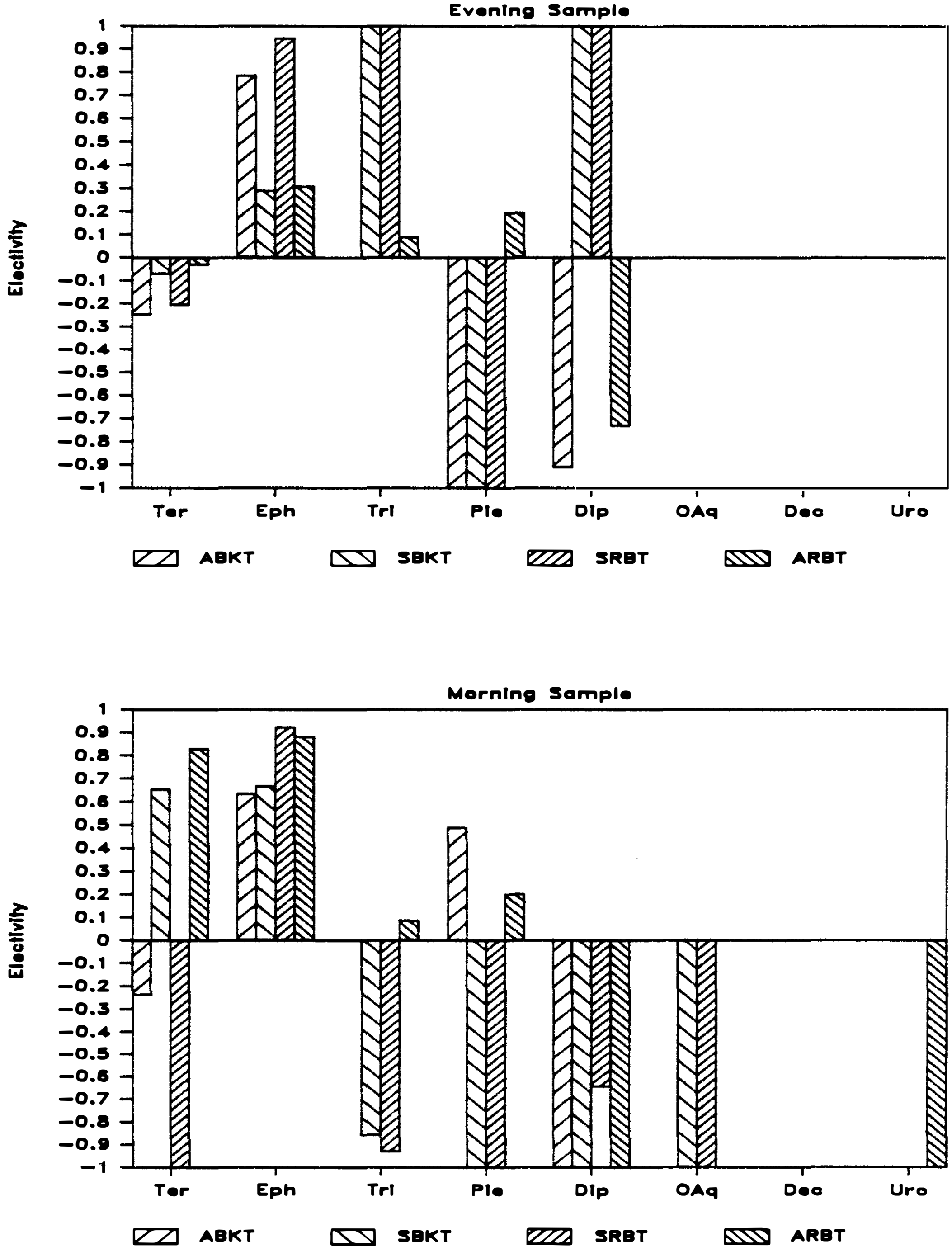


Figure 10. Ivlev's Electivity Index for Y-O-Y fish from evening and morning samples during September. Ter = Terrestrial, Eph = Ephemeroptera, Tri = Trichoptera, Ple = Plecoptera, Dip = Diptera, OAq = Other Aquatics, Dec = Decapoda, Uro = Urodela.

Table 7. Mean relative wet weight of stomach contents for adult fish from all sampling dates.

SAMPLE DATE	SPECIES DISTRIBUTION	MEAN (mg. wet weight/ gram fish weight)	STANDARD ERROR	N
JUNE	ABKT	2.40	0.58	37
	SBKT	2.70	2.36	3
	SRBT	2.29	1.15	10
	ARBT	-	-	-
JULY	ABKT	1.44	0.48	36
	SBKT	0.99	0.33	14
	SRBT	1.16	0.51	15
	ARBT	0.60	0.11	28
AUGUST	ABKT	1.31	0.26	32
	SBKT	2.22	1.39	11
	SRBT	3.45	1.41	10
	ARBT	1.56	0.42	31
SEPTEMBER	ABKT	2.83	0.67	33
	SBKT	2.52	0.78	10
	SRBT	2.18	0.59	12
	ARBT	0.92	0.20	30

Table 8. Mean relative wet weight of stomach contents for Y-O-Y fish from all sampling dates.

SAMPLE DATE	SPECIES DISTRIBUTION	MEAN (mg. wet weight/ gram fish weight)	STANDARD ERROR	N
JUNE	ABKT	9.06	1.57	3
	SBKT	6.24	1.90	5
	SRBT	-	-	-
	ARBT	-	-	-
JULY	ABKT	1.43	1.31	4
	SBKT	1.25	0.44	9
	SRBT	7.97	6.14	4
	ARBT	1.55	0.26	10
AUGUST	ABKT	7.87	2.88	8
	SBKT	3.37	1.52	10
	SRBT	4.57	1.98	9
	ARBT	2.95	1.67	9
SEPTEMBER	ABKT	2.20	0.64	7
	SBKT	5.72	1.42	13
	SRBT	2.49	0.64	5
	ARBT	3.36	1.31	10

that there was a significant difference in the mean values both between dates ($P < .0060$) and between distributions ($P < .0637$) in the mean relative stomach weights of adult fish. Multiple pairwise comparisons indicated that stomach contents in July were significantly lower than stomach contents in September ($P < .1$). There were no significant differences between July and August or August and September. Multiple pairwise comparisons indicated that both SRBT and ABKT had significantly higher stomach contents than ARBT over the course of the summer ($P < .1$). There were no significant differences between any of the other pairwise comparisons. ANOVA indicated that there were no significant differences either by date or distribution for Y-O-Y fish.

The results of the food consumption calculations for adult fish are presented in Table 9. The level of caloric intake needed to meet 24 hour maintenance requirements for a 25 gm. fish during June, July and August was 769 calories. Declining water temperatures in September reduced the required intake to 479 calories. The mean caloric values were never adequate to meet maintenance requirements for any of the species distributions during any of the dates. Mean caloric values plus one standard deviation were sufficient to meet maintenance requirements for SBKT in August and September and for SRBT in August. Maximum caloric values met the maintenance requirements for ABKT in June, July and September, for SBKT in August and September, for SRBT in June, July and August, and for ARBT in August.

Food consumption calculations for Y-O-Y fish are presented in Table 10. The 24 hour maintenance requirement for a 5 gm. fish in June, July and August was 235 calories. In September, that requirement dropped to

Table 9. Calculated caloric intake for a 25 gram adult fish. All values are in calories.

Allopatric Brook Trout	Mean	Mean +1 Std. Dev.		Maximum	
June	262.6	619.8		1596.9	*
July	191.7	543.6		2033.6	*
August	129.6	279.7		585.5	
September	165.7	366.2		744.6	*
Sympatric Brook Trout					
June	269.2	647.0		700.6	
July	139.5	313.6		582.6	
August	286.4	886.7	*	2012.6	*
September	246.8	489.0	*	887.7	*
Sympatric Rainbow Trout					
June	276.2	602.8		1139.8	*
July	172.4	468.5		1169.1	*
August	464.4	1067.0	*	1773.2	*
September	166.8	321.8		457.5	
Allopatric Rainbow Trout					
June	-	-		-	
July	69.1	128.2		232.5	
August	176.2	443.5		951.5	*
September	86.0	186.7		403.0	

(*) indicates caloric intake sufficient to meet maintenance metabolic requirements.

Table 10. Calculated caloric intake for a 5 gram Y-O-Y fish. All values are in calories.

Allopatric Brook Trout	Mean		Mean +1 Std. Dev.		Maximum	
June	167.1		214.0		199.9	
July	43.3		119.1		156.9	
August	201.5		403.1	*	594.4	*
September	45.0		80.6		97.4	
Sympatric Brook Trout						
June	160.5		269.9	*	178.1	*
July	43.2		90.8		126.6	
August	92.7		222.1		427.4	*
September	78.9		147.6		220.2	*
Sympatric Rainbow Trout						
June	-		-		-	
July	296.7	*	783.9	*	1027.2	*
August	131.5		298.5	*	473.4	*
September	38.0		59.2		59.6	
Allopatric Rainbow Trout						
June	-		-		-	
July	44.3		70.4		84.5	
August	74.8		198.9		399.2	*
September	64.2		143.4		260.8	*

(*) indicates values that are sufficient to meet maintenance metabolic requirements.

146 calories. Mean caloric values were sufficient to meet maintenance metabolic requirements for SRBT during July. Mean caloric values plus one standard deviation were sufficient for ABKT in June, SBKT in June and September and for SRBT in July and August. Maximum caloric values met maintenance metabolic requirements for ABKT during August, for SBKT during June, August and September, for SRBT during July and August and for ARBT during August and September.

Condition factors for adult brook trout are presented in Figure 11 and Y-O-Y brook trout are presented in Figure 12. ANOVA indicated that condition factors of adult sympatric and allopatric brook trout were not significantly different. Comparison of all fish by date indicated that at least one of the samples was significantly different from the others ($P < .0039$). Multiple pairwise comparisons using Tukey's HSD indicated that the condition factor of adult brook trout during June was significantly higher than all other sampling dates, including the population estimate taken during October ($P < .05$). The analysis of variance for Y-O-Y brook trout indicated that at least one of the sample dates was significantly different from the others ($P < .0551$). Multiple pairwise comparisons showed that Y-O-Y brook trout had significantly higher condition factors in June then they did in July ($P < .05$), but there were no other significant differences between any of the other sampling dates. ANOVA also indicated that there was no significant difference between sympatric and allopatric populations of Y-O-Y brook trout.

Figure 13 presents the condition factors for adult rainbow trout and Figure 14 for Y-O-Y rainbow trout. ANOVA indicated that there were

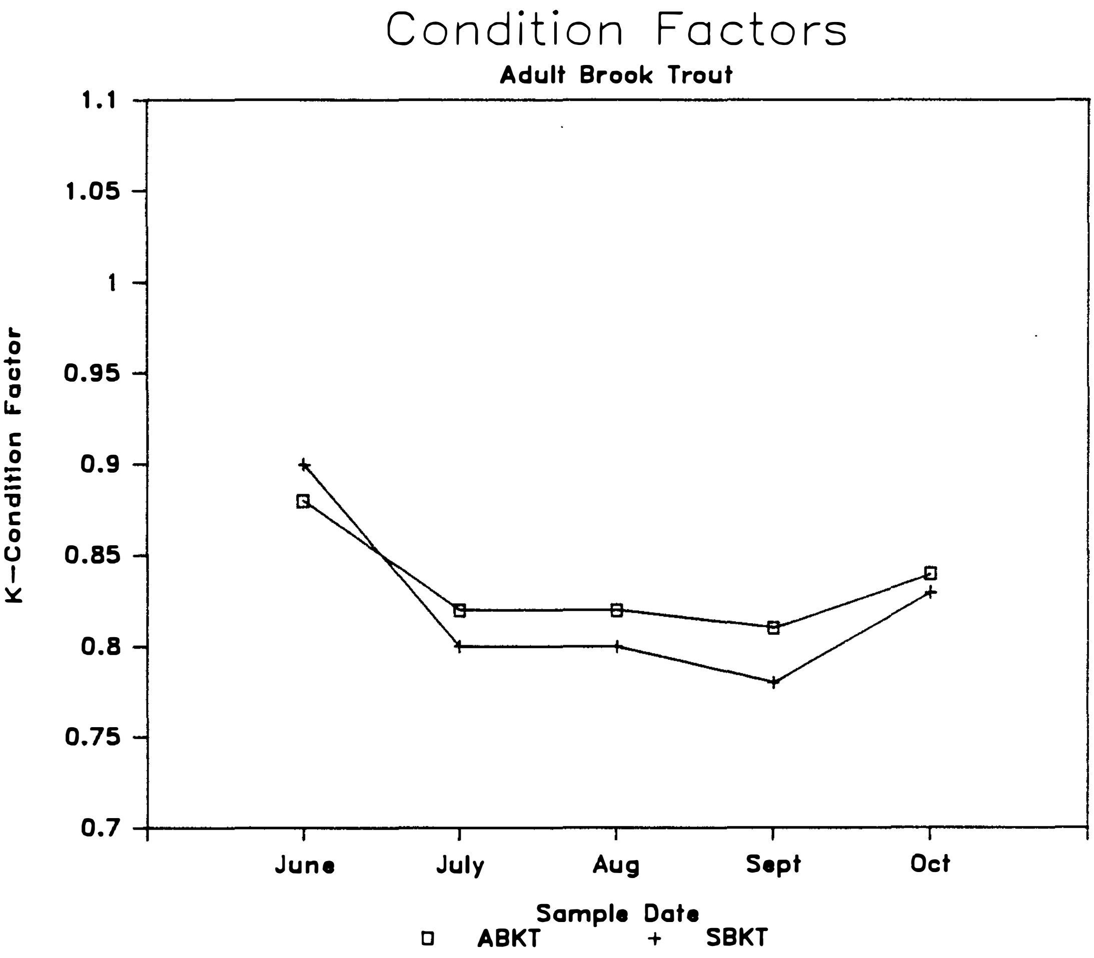


Figure 11. Condition factors for sympatric and allopatric population of adult brook trout from all sampling dates.

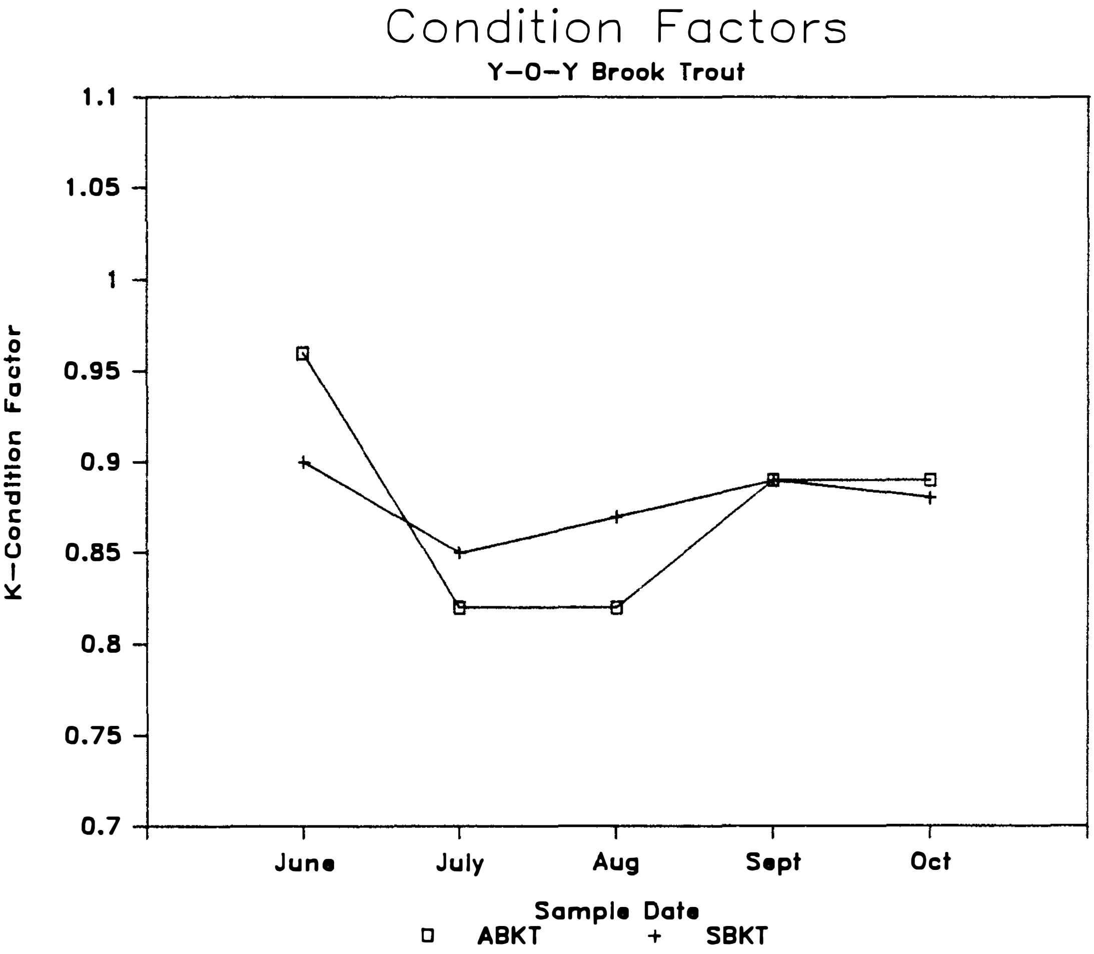


Figure 12. Condition factors for sympatric and allopatric population of Y-O-Y brook trout from all sampling dates.

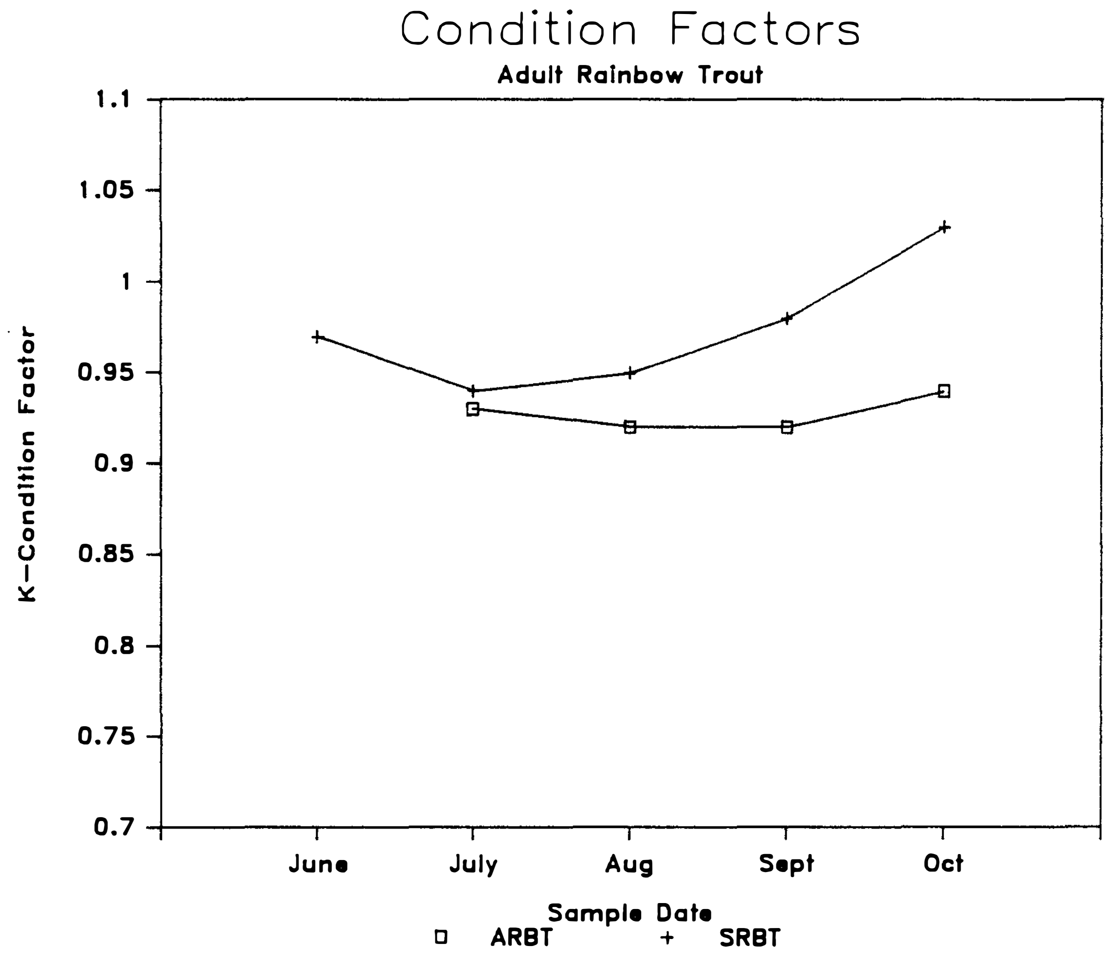


Figure 13. Condition factors for sympatric and allopatric population of adult rainbow trout from all sampling dates.

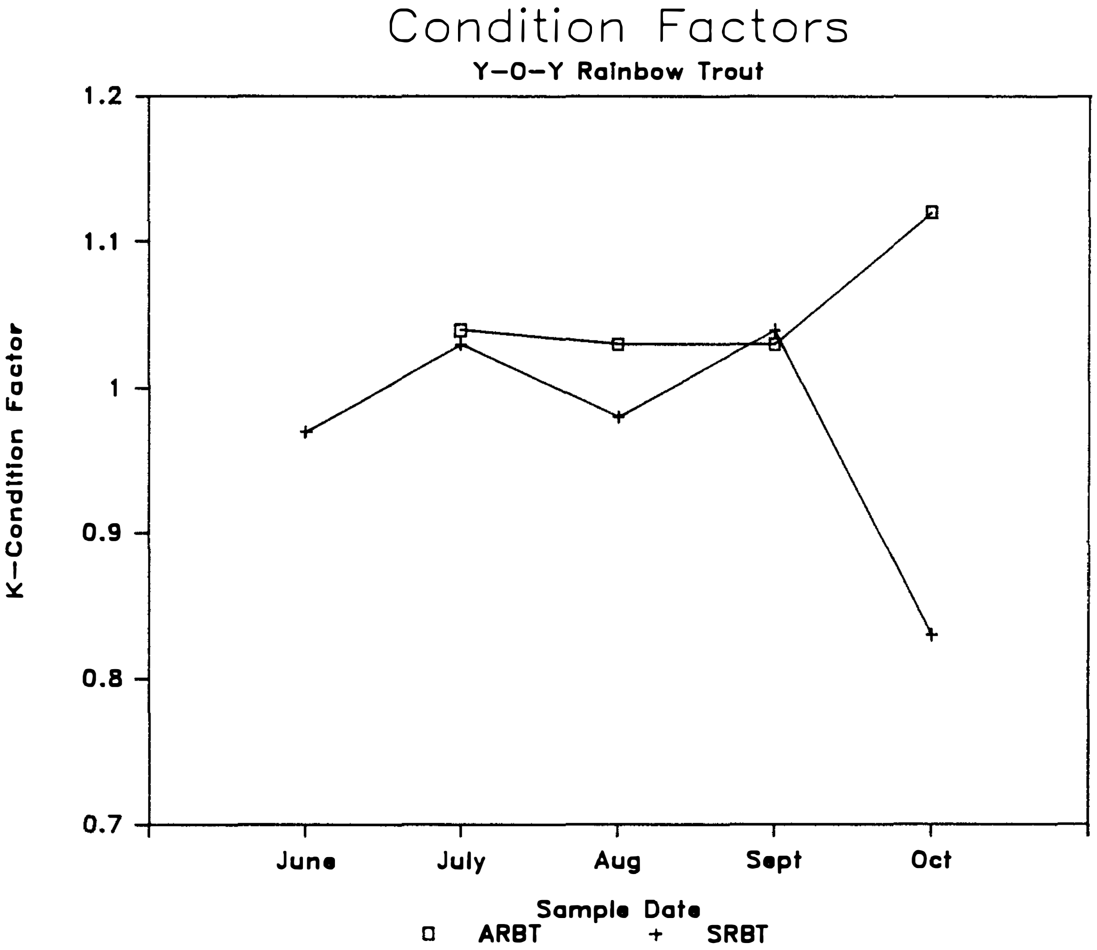


Figure 14. Condition factors for sympatric and allopatric population of Y-O-Y rainbow trout from all sampling dates.

no significant differences between adult rainbow trout during any of the sampling dates, however sympatric adult rainbow trout had significantly higher condition factors than did allopatric adult rainbow trout ($P < .0063$) over the course of the summer. ANOVA for Y-O-Y rainbow trout showed no significant differences by date or by distribution.

Comparison of average caloric values obtained from the drift nets to the the intake requirements of a 25 gm. fish are presented in Table 11. With the exception of the August sampling date at the ABKT site, the calories in the drift passing by a given point in the stream were always far above the level necessary to meet the intake requirements of a 25 gm. fish feeding at that point in the stream.

The mean wet weight per 100 cubic meters of water sampled from the drift collections are presented in Table 12. Analysis of variance indicated that there were significant differences both between sample dates ($P < .0152$) and between sites ($P < .0771$). The mean wet weight of drift net samples taken in August was significantly lower than those in July and September ($P < .05$). The mean wet weight of collections from the sympatric site were significantly higher than the mean wet weight of collections from the allopatric brook trout site ($P < .1$).

Results obtained from the July and October population estimates appear in Table 13. Salmonids were the only fish species obtained during the population estimates. With the exception of SRBT, all populations experienced a dramatic reduction in both numbers and biomass during the course of the study. SBKT and ARBT biomass declined by 48% and 47% respectively, while ABKT biomass declined by 29%. The SRBT figures are somewhat deceiving and may not be directly comparable to the other

Table 11. Comparison of mean 24 hour caloric values moving past a a given point in the stream to the caloric intake necessary for maintenance metabolic requirements of a 25 gram fish.

DATE	SITE	MEAN CALORIC VALUE	
JUNE	Allopatric Brook Trout	15715	*
	Sympatric	11996	*
	Allopatric Rainbow Trout	-	
JULY	Allopatric Brook Trout	2780	*
	Sympatric	17703	*
	Allopatric Rainbow Trout	26097	*
AUGUST	Allopatric Brook Trout	470	
	Sympatric	2402	*
	Allopatric Rainbow Trout	2898	*
SEPTEMBER	Allopatric Brook Trout	1550	*
	Sympatric	6359	*
	Allopatric Rainbow Trout	19365	*

(*) indicates values sufficient to support maintenance metabolic requirements for a 25 gram fish.

Table 12. Mean adjusted wet weights from drift nets for all sampling dates.

DATE	SITE	MEAN (mg. wet weight/ 100 cubic meters water)	STANDARD ERROR
JUNE	Allopatric Brook Trout	187.83	114.70
	Sympatric	145.27	28.57
	Allopatric Rainbow Trout	-	-
JULY	Allopatric Brook Trout	174.93	103.07
	Sympatric	718.76	700.92
	Allopatric Rainbow Trout	754.39	303.20
AUGUST	Allopatric Brook Trout	89.84	90.07
	Sympatric	220.49	165.23
	Allopatric Rainbow Trout	156.85	77.83
SEPTEMBER	Allopatric Brook Trout	295.14	167.31
	Sympatric	628.45	374.26
	Allopatric Rainbow Trout	801.57	1315.13

Table 13. Estimates of numbers and biomass from population estimates in July and October.

SAMPLE DATE	SPECIES DISTRIBUTION	POPULATION ESTIMATE	BIOMASS (kg/ha)
JUNE	ABKT	76	36.37
	SBKT	29	8.67
	SRBT	8	8.60
	ABKT	69	45.56
OCTOBER	ABKT	50	25.66
	SBKT	16	4.48
	SRBT	8	6.49
	ABKT	39	24.20

populations. While SRBT did experience a 25% reduction in biomass, numbers remained constant from July to October. During the July population estimate, only 5 adult fish were obtained during the three pass removal depletion. During October, 7 adult fish were obtained, indicating that there was movement into the section by adult rainbow trout during the intervening four month period, or that the sampling in July failed to obtain all rainbow trout from the sampling section.

CHAPTER V

DISCUSSION

The purpose of this study was to determine if there was evidence that competition for food resources played an important role in the interaction between rainbow and brook trout in a southern Appalachian stream. The starting point for any attempt at determining the possiblity of a competitive interaction is to ascertain whether the species in question utilize the same resource(s). Based on the information obtained from Schoener's Index of Dietary Overlap, comparisons of the percentage composition data, and Ivlev's Electivity Index, it seems clear that adult rainbow and brook trout do indeed utilize the same types of food resources. Both are apparently "opportunistic" feeders, utilizing whatever food resources are available. The only exception would seem to be that brook trout tend to consume a higher proportion of crustaceans than do rainbow trout. These findings are comparable to a number of other studies comparing the food habits of brook and rainbow trout (Tebo and Hassler, 1963; Lohr, 1985; Habera, 1987).

The information for Y-O-Y fish is not quite as clear-cut. Overlap as determined by Schoener's index was highly variable and no consistent pattern was apparent. This may be due in part to the relatively small sample sizes, especially in the case of SBKT where the morning sample in September consisted of a single fish. There was a tendency for overlap between pairs to increase with increasing sample size, indicating that comparisons using smaller sample sizes are not entirely valid. One pattern which was apparent from the stomach composition by percent relative wet weight data and the frequency of occurrence data was the increased importance of smaller prey taxa when compared with adult fish, specifically the ephemeropteran family Baetidae, early instar heptageneids and all dipterans with the possible exception of the family Tipulidae. Also of importance is the high degree of similarity between the prey electivity of SBKT and SRBT at all sample dates. Comparisons between sites may have been confounded by differences in the availability of prey items that were not immediately apparent to the researcher. While it is not possible to determine if Y-O-Y brook trout were shifting their feeding behavior in the presence of rainbow trout, it is possible to state that there was a high degree of similarity between the diets of the two species when they occurred together.

Overlap is of little importance in determining whether or not competition is occurring unless the resource in common is in short supply (Abrams, 1980; Hurlbert, 1978). Overall, the resource data obtained in this study do not present a clear answer as to the availibility of food resources. The drift net data indicate that with the exception of the August sampling date at the allopatric brook trout site there are sufficient food resources available in the stream drift to support the caloric intake requirements of a 25 gram fish. The analysis carried out in this study assumes that a trout uses the entire width of the stream from one bank to the other as a feeding area, an assumption which overestimates the foraging area used by a stream salmonid and thus the resources available to a given fish. Jenkins (1969), in a study involving a series of observations on stream salmonids, found that the majority of feeding forays were limited to the area immediately above, in front of and to either side of the trout's holding position. Although forays of up to one meter were observed, these were relatively infrequent. McNicols et al. (1985) found that young-of-the-year brook trout limited their feeding to a similar area, the length of feeding forays usually being less than three body lengths from the holding position of the fish. Another assumption implicit in this analysis is that all food items in the drift are equally available to a feeding fish. Stream salmonids are often characterised as being visual predators and there is strong evidence which indicates larger prey items are selected to a greater degree than are smaller items (Allan, 1978; Allan, 1981; Ringler, 1979). No attempt was made in the present study to determine availabilities of prey in the drift on the basis of prey size, once again raising the possibility that using uncorrected drift values may lead to an overestimation of the resources available to the trout. Even when these points are taken into account, there would still seem to be an abundance of food resources available in the drift. Other studies have suggested that despite the seeming abundance of invertebrates in stream drift, food resources are insufficient to support maximal feeding rates due to behavioral, physical or perceptual constraints (Jenkins et al., 1970; Tippets and Moyle, 1978; Allan, 1981).

The abundance of food resources in the drift is in direct contrast to the information obtained from the consumption calculations. The apparent inability of adult fish to meet maintenance intake requirements except under optimal assumptions (calculations utilizing the maximum observed stomach value) indicate that these populations are food limited. Although Y-O-Y trout did marginally better, none of the species distributions were able to consistently meet their caloric requirements. The dramatic decline in biomass in all but one of the populations in the study would also seem to support the assumption that food resources are limiting. In a study examining salmonid production in a second order stream in Appalachia, Whitworth and Strange (1983) noted a similar decline in biomass, as well as decreased production during the summer months. Cada et al. (1987) observed similar reductions in biomass in salmonid populations in 5 third and fourth order southern Appalachian streams and attributed this decline to decreasing availability of food resources as the summer progressed. It should be noted that the present study was carried out during the third consecutive summer of below normal precipitation. Low water levels may have resulted in abnormally high population densities, a concomittant increase in demand for available food resources, and an overall reduction in fitness.

Comparison of the condition factors obtained during the course of this study with data from other studies in other years indicates that the trout in Sam's Creek had lower condition factors than similar populations in GSMNP streams. Bivens (1984) in a survey of all brook trout streams in Tennessee obtained an average condition factor of 1.12 for brook trout longer than 100 mm. The range of means from the different populations surveyed was from a low value of .81 to a high value of 1.49. Cada et al. (1987) observed declines in salmonid condition factors in southern Appalachian streams as the summer progressed and, as was the case with the observed reductions in biomass, attributed these declines to decreasing availability of food resources. Again, the effects of lower than normal water levels no doubt contributed to the low condition factors observed during the present study.

It is possible that extrapolation of mean stomach values from two samples during the course of a 24 hour period may not truly typify the feeding by the populations in question. Elliott (1973) has shown that salmonids in highly productive streams exhibit daily feeding patterns, consuming enough in two or three meals to meet minimum requirements for energy intake during a 24 hour period. Average stomach contents therefore show periods of maximum "fullness" over the course of a day, with decreasing volume over a period of time until another meal is consumed. Conversely, Allan (1981) has shown that trout in relatively high elevation streams in Colorado with low productivity apparently feed continously with minimal evidence of "peaks" in stomach fullness. Jenkins et al. (1970) reached a similar conclusion. Appalachian streams have often been characterized as being relatively "sterile" and therefore it seems reasonable to assume that feeding patterns of trout in Sams Creek would show little if any pattern in stomach fullness. The assumption of continous feeding does not seem unwarranted given this information.

The information presented to this point seems to favor the detection of competition for food resources if it is indeed occurring. Despite the fact that food resources would appear to be limiting and resource utilization patterns by the two species are similar, there is no evidence that brook trout are changing the types of food resources that they are using in the presence of rainbow trout or that they are consuming less. The fact that there are no significant differences between the condition factors of sympatric and allopatric brook trout strengthens the argument that the presence of rainbow trout had little if any detectable effect on the fitness of sympatric adult brook trout.

If competition for food resources is not occurring, what is the mechanism driving the exclusion of brook trout by rainbow trout in southern Appalachian streams? Although no significant differences were found in the food consumption or condition factors of adult sympatric and allopatric populations of brook trout, there were significant differences between sympatric and allopatric populations of rainbow trout. Allopatric rainbow trout consumed significantly less food, had significantly lower condition factors and were able to obtain enough energy to meet maintenance metabolic requirements only once under the most liberal assumptions in the stomach calculations. In contrast, sympatric rainbow trout showed an increase in condition factor over the course of the summer, had consistently higher stomach contents and were able to exceed maintenance metabolic requirements by a large margin in three out of four of the samples under the same liberal assumptions. In the sample in which the sympatric rainbow trout failed to meet maintenance intake levels, they fell short by only 20 calories. High population densities in allopatric rainbow trout sections would insure that all sites with the preferred combination of microhabitat variables (i. e. water velocity, water depth, substrate composition, cover) would be occupied by dominant trout. The remaining sites in the allopatric rainbow trout section would present some combination of suboptimal conditions. It has been shown that salmonids forced into suboptimal microhabitats exhibit decreases in growth rate and overall fitness (Fausch, 1984). When a rainbow trout moves from allopatry into an area of sympatry with brook trout, it is possible that the introduced species may experience some degree of ecological release from the intraspecific competition downstream. This is supported by studies which indicate that adult rainbow and brook trout may utilize different microhabitats (Cunjak and Green, 1983). Sites preferred by rainbow trout would either be unoccupied in an area of sympatry, or occupied by subdominant brook trout that had been forced into areas that would be less than optimal for the native species. If this is the case, than all stream positions with microhabitats suitable for the two species should be occupied and the combined standing crop of brook and rainbow trout in areas of sympatry should be higher than the standing crop of either species in allopatry. Moore et. al (1983) observed such a pattern in GSMNP streams when rainbow trout were removed from areas of sympatry. Although brook trout populations exhibited a marked increase in biomass in these areas, the total standing crop of the native species was consistently below that of the same sites under symaptric conditions. Unfortunately, experiments where brook trout have been removed from areas of sympatry have not been carried out and therefore no data concerning the response of rainbow trout populations under similar circumstances is available.

While this scenario accounts for the initial invasion of allopatric brook trout sections by rainbow trout, it does not explain why brook trout populations have completely disappeared from streams that they formerly occuppied. While the data from this study seems to indicate that the presence of rainbow trout has little negative effect on brook trout, it should be noted that the sympatric site used in this study had relatively low densities of rainbow trout. As the density of rainbow trout in sympatric areas increases, the microhabitats preferred by the exotic will become saturated. Subdominant rainbow trout will then be forced into utilizing those areas preferred by the native species. This could be the critical stage in the interaction between the two species and it is at this point that one would expect to find the negative effects associated with competition.

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APPENDIXES

APPENDIX 1

PHYSICAL STREAM CHARACTERISTICS

Table 14. Selected physical characteristics of the three study areas on Sam's Creek.

	SITE		
CHARACTERISTIC	ALLOPATRIC BKT	SYMPATRIC	ALLOPATRIC RBT
Mean Width (m)	4.08	4.81	5.44
Pool/riffle ratio			
Pool (%)	55	57	56
Riffle (%)	45	43	44
Gradient (%)	10.8	5.5	7.4
Discharge (cubic meters/minute)			
June	5.18	6.41	-
July	0.97	1.39	2.16
August	0.48	0.76	1.43
September	0.39	0.59	1.38
Temperature (C)			
June	17	17	17
July	17	17	17
August	17	17	17
September	12.5	12.5	12.5
pH			
June	6.9	6.9	6.9
July	7.1	7.1	7.1
August	7.0	7.0	7.0
September	7.0	7.0	7.0

APPENDIX 2

STOMACH PERCENT COMPOSITION DATA

Table 15. Stomach composition for adult fish for the June sampling date expressed as mean percent relative wet weight.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	1.4	0.1	0.9	
Ephemerellidae	4.5	3.0	12.3	
Heptageniidae	2.0	33.8	9.0	
Leptophlebiidae	0.3	0.0	0.4	
TOTAL	8.2	36.9	22.3	
TRICHOPTERA				
Brachycentridae	0.0	0.0	0.2	
Glossosomatidae	0.0	0.0	3.5	
Hydropsychidae	5.0	0.0	7.0	
Limnephilidae	0.4	0.0	1.2	
Polycentropodidae	0.4	0.0	0.3	
Rhyacophilidae	0.7	0.0	0.0	
Sericostomatidae	0.8	0.0	0.0	
TOTAL	7.3	0.0	12.2	
PLECOPTERA				
Leuctridae	0.1	0.0	0.0	
Peltoperlidae	0.1	0.0	0.0	
Perlidae	1.4	0.0	0.1	
TOTAL	1.6	0.0	0.1	
DIPTERA				
Chironomidae	2.4	0.6	1.1	
Dixidae	0.0	0.0	0.8	
Simuliidae	3.0	0.0	2.6	
Tipulidae	0.3	0.0	0.0	
TOTAL	5.7	0.6	4.5	
OTHER AQUATICS				
Coleoptera	0.9	3.6	0.0	
Gomphidae	0.0	0.0	0.7	
Salvelinus	0.0	0.0	9.8	
TOTAL	0.9	3.6	10.5	
DECAPODA	6.8	0.0	2.9	
URODELA	0.0	31.8	0.0	
TERRESTRIAL	61.2	21.2	40.7	
NO IDENTIFICATION	8.5	5.9	6.6	

Table 16. Stomach composition for adult fish for the July sampling date expressed as mean percent relative wet weight.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	2.9	1.3	0.4	4.1
Ephemerellidae	3.5	0.0	0.4	1.9
Heptageniidae	3.7	0.7	10.8	3.9
Leptophlebiidae	0.0	0.0	0.0	0.1
TOTAL	10.1	2.0	11.6	10.0
TRICHOPTERA				
Glossosomatidae	0.0	0.0	0.0	1.1
Hydropsychidae	4.4	3.1	4.3	3.6
Odontoceridae	2.1	0.0	0.9	0.4
Polycentropodidae	0.3	0.8	0.0	0.4
Rhyacophilidae	0.0	0.0	0.1	0.5
Sericostomatidae	0.2	0.0	0.0	0.0
TOTAL	7.0	3.9	5.3	6.0
PLECOPTERA				
Capnidae	0.0	0.0	0.2	0.0
Leuctridae	0.3	0.0	0.0	0.0
Peltoperlidae	0.1	0.0	0.7	1.7
Perlidae	0.0	0.0	2.3	1.5
Perlodidae	1.1	0.0	0.0	2.7
TOTAL	1.5	0.0	3.2	5.9
DIPTERA				
Ceratopogonidae	0.1	0.0	0.1	0.0
Chironomidae	1.8	0.4	0.1	0.0
Dixidae	0.6	0.0	6.9	0.1
Simuliidae	0.0	0.0	0.0	0.2
Tanyderidae	0.1	0.0	0.0	0.0
Tipulidae	6.3	6.9	0.1	1.2
TOTAL	8.9	7.3	7.2	1.5
OTHER AQUATICS				
Amphipoda	0.8	0.0	0.0	0.0
Coleoptera	1.9	0.0	0.1	1.3
Gomphidae	0.0	0.0	0.8	0.0
TOTAL	2.7	0.0	0.9	1.3
DECAPODA	2.8	4.9	0.0	0.2
URODELA	3.4	0.0	0.0	0.0
TERRESTRIAL	63.0	74.8	66.7	57.6
NO IDENTIFICATION	3.4	7.0	5.3	17.5

Table 17. Stomach composition for adult fish for the August sampling date expressed as mean percent relative wet weight.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	0.0	0.9	0.0	0.0
Ephemerellidae	0.9	0.0	0.0	0.2
Heptageniidae	0.6	10.7	7.2	5.6
TOTAL	1.5	11.6	7.2	5.8
TRICHOPTERA				
Glossosomatidae	0.0	0.0	0.0	1.8
Hydropsychidae	0.7	0.0	0.1	10.6
Odontoceridae	0.0	0.0	0.3	0.0
Polycentropodidae	0.0	0.0	0.1	3.5
Sericostomatidae	0.4	2.4	0.0	0.4
TOTAL	1.1	2.4	0.5	16.3
PLECOPTERA				
Leuctridae	0.0	0.0	1.5	0.7
Peltoperlidae	0.0	0.0	0.2	0.0
Perlidae	0.0	0.0	2.6	0.0
TOTAL	0.0	0.0	4.3	0.7
DIPTERA				
Chironomidae	0.0	0.0	0.1	0.0
Dixidae	5.6	0.0	4.6	0.1
Simuliidae	0.0	0.0	0.0	0.1
TOTAL	5.6	0.0	4.7	0.2
OTHER AQUATICS				
Coleoptera	0.8	0.0	0.0	0.3
TOTAL	0.8	0.0	0.0	0.3
DECAPODA	9.0	0.0	0.0	0.0
URODELA	0.0	0.0	7.1	4.6
TERRESTRIAL	63.1	84.2	63.9	65.5
NO IDENTIFICATION	18.9	1.8	12.6	6.6

Table 18. Stomach composition for adult fish for the September sampling date expressed as mean percent relative wet weight.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	0.0	0.6	0.1	0.1
Heptageniidae	1.5	1.2	14.6	4.2
Leptophlebiidae	1.5	1.8	14.7	4.3
TOTAL	1.5	1.8	14.7	4.3
TRICHOPTERA				
Brachycentridae	0.0	0.0	0.0	0.1
Hydropsychidae	3.3	0.1	0.2	0.4
Limnephilidae	0.0	0.0	0.0	0.6
Odontoceridae	0.7	0.0	0.0	2.1
Polycentropodidae	0.0	0.0	0.1	0.7
Rhyacophilidae	0.0	0.0	0.5	0.1
Sericostomatidae	0.1	0.0	1.3	0.0
TOTAL	4.1	0.1	2.1	4.0
PLECOPTERA				
Leuctridae	0.0	0.0	0.4	3.6
Perlidae	2.2	0.0	0.1	0.2
Perlodidae	0.0	0.0	0.7	0.0
TOTAL	2.2	0.0	1.2	3.8
DIPTERA				
Chironomidae	0.0	0.0	0.3	0.1
Dixidae	0.2	0.1	0.1	0.1
Simuliidae	0.3	0.0	0.6	2.0
Tipulidae	0.0	0.0	0.5	0.0
TOTAL	0.5	0.1	1.5	2.2
OTHER AQUATICS				
Coleoptera	0.0	0.0	0.7	0.0
TOTAL	0.0	0.0	0.7	0.0
DECAPODA	3.3	10.0	1.4	1.8
URODELA	7.1	0.0	0.0	2.4
TERRESTRIAL	71.6	78.4	60.2	68.6
NO IDENTIFICATION	9.6	9.7	18.3	13.2

Table 19. Stomach composition for Y-O-Y fish for the June sampling date expressed as mean percent relative wet weight.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	0.0	0.9		
Heptageniidae	0.0	11.3		
TOTAL	0.0	12.2		
TRICHOPTERA				
Glossosomatidae	0.0	20.0		
Hydropsychidae	8.9	2.0		
Limnephilidae	3.2	0.0		
Polycentropodidae	0.0	3.6		
TOTAL	12.1	25.6		
PLECOPTERA				
Capnidae	0.0	2.7		
Peltoperlidae	0.0	0.4		
TOTAL	0.0	3.1		
DIPTERA				
Chironomidae	0.5	0.0		
Simuliidae	0.0	0.5		
TOTAL	0.5	0.5		
OTHER AQUATICS				
Amphipoda				
Coleoptera				
Gomphidae				
Salvelinus				
TOTAL	0.0	0.0		
DECAPODA	0.0	0.0		
URODELA	0.0	0.0		
TERRESTRIAL	78.8	58.7		
NO IDENTIFICATION	8.6	0.0		

Table 20. Stomach composition for Y-O-Y fish for the July sampling date expressed as mean percent relative wet weight.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	25.0	23.8	26.9	41.4
Ephemerellidae	0.0	0.0	0.0	1.7
Heptageniidae	0.0	4.4	10.1	13.9
TOTAL	25.0	28.2	37.0	57.0
TRICHOPTERA				
Hydropsychidae	0.0	0.0	0.1	1.8
Polycentropodidae	0.7	0.0	0.0	0.0
TOTAL	0.7	0.0	0.1	1.8
PLECOPTERA				
Capnidae	0.0	0.9	2.2	0.0
TOTAL	0.0	0.9	2.2	0.0
DIPTERA				
Ceratopogonidae	0.0	0.0	0.1	0.0
Chironomidae	0.0	14.7	0.0	0.0
Dixidae	0.5	0.0	0.0	0.0
Simuliidae	0.0	0.0	2.7	0.0
Tanyderidae	0.0	18.5	0.0	1.1
Tipulidae	0.0	0.0	22.0	7.6
TOTAL	0.5	33.2	24.8	8.7
OTHER AQUATICS				
Coleoptera	0.0	0.9	0.0	2.2
TOTAL	0.0	0.9	0.0	2.2
DECAPODA	0.0	0.0	0.0	0.0
URODELA	0.0	0.0	0.0	0.0
TERRESTRIAL	68.5	36.0	34.3	27.5
NO IDENTIFICATION	5.4	0.9	1.6	2.6

Table 21. Stomach composition for Y-O-Y fish for the August sampling date expressed as mean percent relative wet weight.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	1.1	10.0	17.8	18.4
Ephemerellidae	0.0	0.0	6.9	0.0
Heptageniidae	0.6	6.9	24.3	12.2
Leptophlebiidae	0.0	9.4	0.6	0.0
TOTAL	1.7	26.3	49.6	30.6
TRICHOPTERA				
Hydropsychidae	7.6	0.0	0.0	1.7
Rhyacophilidae	0.0	4.2	0.0	1.4
Sericostomatidae	0.0	0.7	0.4	0.3
TOTAL	7.6	4.9	0.4	3.4
PLECOPTERA				
Leuctridae	0.0	0.4	0.0	0.0
TOTAL	0.0	0.4	0.0	0.0
DIPTERA				
Ceratopogonidae	0.0	0.1	0.0	0.0
Chironomidae	2.5	0.8	0.3	1.2
Dixidae	15.9	0.4	0.5	0.0
Simuliidae	0.0	0.3	0.0	1.7
TOTAL	18.4	1.6	0.8	2.9
OTHER AQUATICS				
Coleoptera	13.5	0.0	0.0	0.0
TOTAL	13.5	0.0	0.0	0.0
DECAPODA	0.0	0.0	0.0	0.0
URODELA	0.0	0.0	0.0	0.0
TERRESTRIAL	50.0	54.8	44.1	57.6
NO IDENTIFICATION	8.7	11.8	5.1	5.5

Table 22. Stomach composition for Y-O-Y fish for the September sampling date expressed as mean percent relative wet weight.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	14.3	0.0	0.0	3.3
Ephemerellidae	0.0	0.0	22.2	0.0
Heptageniidae	15.6	9.6	19.8	5.9
TOTAL	29.9	9.6	42.0	9.2
TRICHOPTERA				
Hydropsychidae	0.0	4.5	4.9	0.0
Limnephilidae	0.0	0.6	0.0	2.7
Rhyacophilidae	0.0	0.8	0.0	0.0
TOTAL	0.0	5.9	4.9	2.7
PLECOPTERA				
Peltoperlidae	0.0	0.0	0.0	5.3
Perlidae	9.1	0.0	0.0	0.7
TOTAL	9.1	0.0	0.0	6.0
DIPTERA				
Ceratopogonidae	0.0	0.6	0.0	0.0
Chironomidae	0.0	0.0	0.2	0.0
Dixidae	0.1	0.1	0.0	0.0
Simuliidae	0.0	0.0	1.0	0.0
Tipulidae	0.0	0.0	0.0	0.2
TOTAL	0.1	0.7	1.2	0.2
OTHER AQUATICS				
TOTAL	0.0	0.0	0.0	0.0
DECAPODA	0.0	0.0	0.0	0.0
URODELA	0.0	0.0	0.0	0.0
TERRESTRIAL	43.4	68.1	50.6	71.2
NO IDENTIFICATION	17.4	15.7	1.4	10.7

APPENDIX 3

STOMACH FREQUENCY OF OCCURRENCE DATA

Table 23. Frequency of occurrence of prey items for adult fish for the June sampling date.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	10.8	33.3	30.0	
Ephemerellidae	27.0	33.3	60.0	
Heptageniidae	18.9	66.7	50.0	
Leptophlebiidae	5.4	0.0	10.0	
TRICHOPTERA				
Brachycentridae	0.0	0.0	10.0	
Glossosomatidae	0.0	0.0	20.0	
Hydropsychidae	32.4	0.0	60.0	
Limnephilidae	5.4	0.0	20.0	
Polycentropodidae	10.8	0.0	30.0	
Rhyacophilidae	10.8	0.0	0.0	
Sericostomatidae	2.7	0.0	0.0	
PLECOPTERA				
Leuctridae	2.7	0.0	0.0	
Peltoperlidae	2.7	0.0	0.0	
Perlidae	13.5	0.0	10.0	
DIPTERA				
Chironomidae	29.7	66.7	50.0	
Dixidae	0.0	0.0	10.0	
Simuliidae	32.4	0.0	60.0	
Tipulidae	8.1	0.0	0.0	
OTHER AQUATICS				
Coleoptera	5.4	33.3	0.0	
Gomphidae	0.0	0.0	10.0	
Salvelinus	0.0	0.0	10.0	
DECAPODA	18.9	0.0	10.0	
URODELA	0.0	33.3	0.0	
TERRESTRIAL	91.9	66.7	100.0	
NO IDENTIFICATION	54.1	33.3	50.0	

Table 24. Frequency of occurrence of prey items for adult fish for the July sampling date.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	2.9	28.6	13.3	35.7
Ephemerellidae	23.5	0.0	13.3	17.9
Heptageniidae	20.6	14.3	46.7	10.7
Leptophlebiidae	0.0	0.0	0.0	3.6
TRICHOPTERA				
Glossosomatidae	0.0	0.0	0.0	7.1
Hydropsychidae	17.6	14.3	26.7	21.4
Odontoceridae	8.8	0.0	6.7	3.6
Polycentropodidae	8.8	7.1	0.0	7.1
Rhyacophilidae	0.0	0.0	6.7	7.1
Sericostomatidae	8.8	0.0	0.0	0.0
PLECOPTERA				
Capnidae	0.0	0.0	13.3	0.0
Leuctridae	5.9	0.0	0.0	0.0
Peltoperlidae	2.9	0.0	13.3	14.3
Perlidae	0.0	0.0	6.7	3.6
Perlodidae	2.9	0.0	0.0	10.7
DIPTERA				
Ceratopogonidae	2.9	0.0	6.7	0.0
Chironomidae	17.6	7.1	13.3	0.0
Dixidae	14.7	0.0	20.0	7.1
Simuliidae	0.0	0.0	0.0	7.1
Tanyderidae	2.9	0.0	0.0	0.0
Tipulidae	20.6	14.3	6.7	7.1
OTHER AQUATICS				
Amphipoda	2.9	0.0	0.0	0.0
Coleoptera	8.8	0.0	6.7	3.6
Gomphidae	0.0	0.0	6.7	0.0
DECAPODA	17.6	21.4	0.0	3.6
URODELA	5.9	0.0	0.0	0.0
TERRESTRIAL	94.1	92.9	86.7	92.9
NO IDENTIFICATION	17.6	42.9	46.7	64.3

Table 25. Frequency of occurrence of prey items for adult fish for the August sampling date.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	0.0	10.0	0.0	0.0
Ephemerellidae	7.7	0.0	0.0	6.9
Heptageniidae	7.7	20.0	40.0	27.6
TRICHOPTERA				
Glossosomatidae	0.0	0.0	0.0	10.3
Hydropsychidae	3.8	0.0	10.0	27.6
Odontoceridae	0.0	0.0	10.0	0.0
Polycentropodidae	0.0	0.0	10.0	6.9
Sericostomatidae	3.8	10.0	0.0	6.9
PLECOPTERA				
Leuctridae	0.0	0.0	20.0	10.3
Peltoperlidae	0.0	0.0	10.0	0.0
Perlidae	0.0	0.0	10.0	0.0
DIPTERA				
Chironomidae	0.0	0.0	20.0	0.0
Dixidae	34.6	0.0	20.0	6.9
Simuliidae	0.0	0.0	0.0	3.4
OTHER AQUATICS				
Coleoptera	3.8	0.0	0.0	3.4
DECAPODA	15.4	0.0	0.0	0.0
URODELA	0.0	0.0	10.0	6.9
TERRESTRIAL	96.2	100.0	100.0	89.7
NO IDENTIFICATION	57.7	30.0	70.0	34.5

Table 26. Frequency of occurrence of prey items for adult fish for the September sampling date.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	0.0	10.0	8.3	7.1
Heptageniidae	10.0	20.0	25.0	32.1
TRICHOPTERA				
Brachycentridae	0.0	0.0	0.0	3.6
Hydropsychidae	6.7	10.0	16.7	10.7
Limnephilidae	0.0	0.0	0.0	25.0
Odontoceridae	3.3	0.0	0.0	14.3
Polycentropodidae	0.0	0.0	8.3	7.1
Rhyacophilidae	0.0	0.0	8.3	3.6
Sericostomatidae	3.3	0.0	8.3	0.0
PLECOPTERA				
Leuctridae	0.0	0.0	8.3	3.6
Perlidae	6.7	0.0	8.3	3.6
Perlodidae	0.0	0.0	8.3	0.0
DIPTERA				
Chironomidae	0.0	0.0	8.3	3.6
Dixidae	6.7	10.0	16.7	10.7
Simuliidae	10.0	0.0	25.0	14.3
Tipulidae	0.0	0.0	8.3	0.0
OTHER AQUATICS				
Coleoptera	0.0	0.0	8.3	0.0
DECAPODA	3.3	10.0	25.0	3.6
URODELA	10.0	0.0	0.0	3.6
TERRESTRIAL	86.7	90.0	100.0	89.3
NO IDENTIFICATION	40.0	50.0	58.3	39.3

Table 27. Frequency of occurrence of prey items for Y-O-Y fish for the June sampling date.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	0.0	20.0		
Heptageniidae	0.0	40.0		
TRICHOPTERA				
Glossosomatidae	0.0	20.0		
Hydropsychidae	66.7	20.0		
Limnephilidae	33.3	0.0		
Polycentropodidae	0.0	40.0		
PLECOPTERA				
Capnidae	0.0	20.0		
Peltoperlidae	0.0	20.0		
DIPTERA				
Chironomidae	33.0	0.0		
Simuliidae	0.0	20.0		
TERRESTRIAL	100.0	80.0		
NO IDENTIFICATION	66.7	0.0		

Table 28. Frequency of occurrence of prey items for Y-O-Y fish for the July sampling date.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	25.0	28.6	75.0	100.0
Ephemerellidae	0.0	0.0	0.0	10.0
Heptageniidae	0.0	14.3	25.0	50.0
TRICHOPTERA				
Hydropsychidae	0.0	0.0	25.0	20.0
Polycentropodidae	25.0	0.0	0.0	0.0
PLECOPTERA				
Capnidae	0.0	14.3	25.0	0.0
DIPTERA				
Ceratopogonidae	0.0	0.0	25.0	0.0
Chironomidae	0.0	28.6	0.0	0.0
Dixidae	25.0	0.0	0.0	0.0
Simuliidae	0.0	0.0	25.0	0.0
Tanyderidae	0.0	57.1	0.0	20.0
Tipulidae	0.0	0.0	25.0	20.0
OTHER AQUATICS				
Coleoptera	14.3	0.0	0.0	10.0
TERRESTRIAL	75.0	57.1	75.0	50.0
NO IDENTIFICATION	25.0	14.3	25.0	20.0

Table 29. Frequency of occurrence of prey items for Y-O-Y fish for the August sampling date.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	12.5	10.0	62.5	22.2
Ephemerellidae	0.0	0.0	25.0	0.0
Heptageniidae	12.5	30.0	75.0	33.3
Leptophlebiidae	0.0	20.0	12.5	0.0
TRICHOPTERA				
Hydropsychidae	37.5	0.0	0.0	11.1
Rhyacophilidae	0.0	10.0	0.0	11.1
Sericostomatidae	0.0	10.0	25.0	11.1
PLECOPTERA				
Leuctridae	0.0	10.0	0.0	0.0
DIPTERA				
Ceratopogonidae	0.0	10.0	0.0	0.0
Chironomidae	37.5	20.0	12.5	33.3
Dixidae	37.5	20.0	25.0	0.0
Simuliidae	0.0	10.0	0.0	22.2
OTHER AQUATICS				
Coleoptera	25.0	0.0	0.0	0.0
TERRESTRIAL	75.0	80.0	75.0	77.8
NO IDENTIFICATION	50.0	50.0	37.5	33.3

Table 30. Frequency of occurrence of prey items for Y-O-Y fish for the September sampling date.

TAXA	ABKT	SBKT	SRBT	ARBT
EPHEMEROPTERA				
Baetidae	14.3	0.0	0.0	20.0
Ephemerellidae	0.0	0.0	40.0	0.0
Heptageniidae	42.9	23.1	40.0	40.0
TRICHOPTERA				
Hydropsychidae	0.0	7.7	40.0	0.0
Limnephilidae	0.0	15.4	0.0	30.0
Rhyacophilidae	0.0	7.7	0.0	0.0
PLECOPTERA				
Peltoperlidae	0.0	0.0	0.0	10.0
Perlidae	14.3	0.0	0.0	0.0
DIPTERA				
Ceratopogonidae	0.0	7.7	0.0	0.0
Chironomidae	0.0	0.0	40.0	0.0
Dixidae	14.3	7.7	0.0	0.0
Simuliidae	0.0	0.0	20.0	0.0
Tipulidae	0.0	0.0	0.0	10.0
TERRESTRIAL	71.4	84.6	80.0	80.0
NO IDENTIFICATION	28.6	38.5	20.0	20.0

VITA

William Edward Ensign was born in Knoxville, Tennessee on February 20, 1959. He attended elementary school in Chattanooga, Tennessee and graduated from Brainerd High School in June, 1977. He then attended Wake Forest University from September, 1977 until December, 1978. He began studies at George Washington University, and in May, 1982 received a Bachelor of Arts degree in Zoology.

After working as a library research assistant in private law firm libraries in Washington, D. C., he was admitted to The Graduate School at the University of Tennessee, Knoxville in the winter of 1985 and began study for a Master's degree. During the period that he was working on his Master's degree, he served as a teaching assistant in the General Biology program at the University. He received the Master of Science degree with a major in Ecology in August, 1988.