

AN ABSTRACT OF THE THESIS OF

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Date thesis is presented May 5, 1966 \_\_\_\_\_

Title Influence of Competition on the Food Consumption and Production  
of Animals in Laboratory Stream Communities \_\_\_\_\_

Abstract approved Redacted for privacy \_\_\_\_\_  
(Major professor)

The growth rates, production, and bioenergetic relationships of animals in laboratory streams were studied at the Pacific Cooperative Water Pollution and Fisheries Research Laboratories, Oregon State University, from September, 1963, through December, 1965. These studies were concerned with the rates of food consumption and production of carnivorous fish and insects as influenced by intraspecific and interspecific competition. The impact of the carnivores on prey density and the relationships between food density and rates of consumption, growth and respiration of fish were also studied.

Six laboratory streams, each having a 1.25 square-meter productive area that was covered with rubble and gravel, were provided with light from fluorescent tubes and were equipped for exchange flows of filtered stream water. Plant communities developed in the streams from algal cells that passed through the filter. Small populations of herbivorous insects became established in much the same way, but additional seeding of these forms was usually necessary to obtain

population levels capable of supporting large carnivore biomasses. Herbivorous snails, Oxytrema silicula, naiads of two carnivorous stoneflies, Acroneuria pacifica and A. californica, sculpins, Cottus perplexus, and cutthroat trout, Salmo clarki, were added to the streams in different biomasses and combinations of biomasses for the various experiments. The production of the snails and carnivores was estimated directly from changes in biomass, since mortality was usually not an important factor. The consumption rates of these animals in the streams were estimated by comparing their growth rates with the growth rates of similar animals fed known rations in aquaria or in laboratory streams in which no communities were allowed to develop. Food assimilation efficiencies and oxygen consumption rates were determined in other aquarium experiments.

Production of the snails was influenced by the amount of light energy to which the stream communities were subjected and by water temperature. Production was low at low light levels as a result of the low algal production. Snail production was highest during the colder winter experiments.

Total carnivore production and total carnivore food consumption was found to be a function of total carnivore biomass, both being low at low biomasses, highest at intermediate biomasses, and again low at the highest biomasses. These relationships were due at least in part to the stocking ratios employed, and had the stocking ratios been different, the relationships could have been greatly altered. Food consumption of the sculpin and stonefly declined at high biomass of these carnivores, whereas trout food consumption usually did not decline with increases of trout biomass.

Using the food habits and feeding behavior of the different carnivores as bases for further analysis, sculpins and stoneflies were found to consume mainly larval forms of insects associated with the periphyton. The trout, on the other hand, appeared to subsist on larvae, pupae, and adult insects drifting freely in the water. The stonefly naiads and sculpins compete directly with each other and can influence the food consumption and production of the trout through cropping the benthic food organisms, thus reducing the amount of food organisms that could potentially appear in the drift. The trout affected the production of the sculpins and stoneflies very little because their consumption of drifting organisms did not usually materially reduce the benthic population.

Differences in sculpin and stonefly naiad biomasses appeared to have greater effects than did seasonal or other differences on the levels of benthic food organism biomass in the laboratory streams. However, other carnivores and seasonal differences both influenced the relationships between trout biomass and the density of their food organisms.

Growth rate, food consumption rate, and respiration of sculpins and trout in all experiments increased as the density of food organisms increased. Such relationships were apparent only when these parameters were plotted against the appropriate food density.

INFLUENCE OF COMPETITION ON THE FOOD  
CONSUMPTION AND PRODUCTION OF ANIMALS IN  
LABORATORY STREAM COMMUNITIES

by

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A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of  
the requirements for the  
degree of

MASTER OF SCIENCE

June 1966

APPROVED:

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Date thesis is presented May 5, 1966

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## ACKNOWLEDGMENTS

I am indebted to Dr. Charles E. Warren, Professor of Fisheries, for his counsel and leadership during the course of the investigation, and for his editorial assistance in the preparation of this thesis. Special thanks are given to Dr. Gerald E. Davis for the help given me in designing and carrying out selected experiments, and for the encouragement given throughout these studies.

I am grateful to Dr. James D. Hall for reviewing this thesis and offering many constructive criticisms. The helpful instruction given me by Dr. C. David McIntire enabled me to carry out the studies on primary production in the laboratory streams, and is gratefully acknowledged.

Without the assistance and support given me by my wife, Lola, completion of this thesis would have proven much more difficult.

This investigation was supported by National Science Foundation Research Grant No. GB 467.

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INFLUENCE OF COMPETITION ON THE FOOD  
CONSUMPTION AND PRODUCTION OF ANIMALS IN  
LABORATORY STREAM COMMUNITIES

INTRODUCTION

In the 20 and more years since Lindeman (1942) advanced his approach to the trophic dynamic aspect of ecology, many of us have used his ideas in considering community problems. These ideas seemed to provide a general way of seeking some of the underlying similarities of communities. In retrospect, and in spite of the efforts of biologists interested in energy transfer in communities, I am not sure that appreciably more is known now than was in Lindeman's time about the common energetic characteristics of entire communities.

There are reasons why more may not be known. Most natural communities are very complex, and it is difficult to see how hypotheses concerning their overall energetic characteristics can be tested with the information that is now available, or that is likely to be forthcoming in the foreseeable future. Knowledge of the rates of energy intake, production, and respiration of most of the species in the communities studied would be needed. Satisfactory measurements of these processes in nature are difficult to obtain even for a single species. Good measurements have been made for populations and very simple communities in the laboratory, and the production rates and even consumption rates of a few species of animals in nature have been estimated with varying degrees of reliability (Allen 1951; Horton, 1961; Mann, 1965). But, I am not aware of any serious attempts to obtain reliably the necessary information on the species of even one complex natural community.

Lindeman suggested that organisms of like trophic kinds be combined into levels in order to make possible an examination of the overall efficiencies of energy transfer through communities. It is questionable that natural communities can be meaningfully stratified so simply (Peterson and Jensen, 1911; Ivlev, 1945; Darnell, 1958; Warren et al., 1964), but I wonder whether or not it is worthwhile even in communities where it might be possible. Davis and Warren (1965) studied very simple communities consisting primarily of algae, herbivorous insects and snails, and carnivorous insects and fish in laboratory streams. They were able, as I have been, to obtain reasonably satisfactory measurements of the rates of energy intake, production, and respiration of these organisms, and because of the discrete food habits of these organisms in the streams, these measurements can be summed to provide trophic level values. Having data on the energy utilization of the individual species, neither Davis and Warren nor I have added much to our understanding of the trophic relations of this simple community by summing the values for species that may be of similar trophic kind but that differ structurally, bioenergetically, and behaviorally. It has been the examination of the relationships between species and not between trophic levels that has increased our understanding of this community. At the same time, I have been able to obtain insight into the reasons for the success of some of the individual species.

It is difficult to reach very useful conclusions regarding the production of a carnivore even in a very simple system having one predator and one prey species, for the production of the carnivore is

a complex function of the biomass and age structure of the carnivore population and the production and availability of the prey. When competing carnivores of different structure, physiology and behavior are present, summing their consumption and production rates has not proved rewarding, and the analysis of the consumption and production of individual species in relation to their own biomass and the biomasses, consumption, and production rates of the other carnivores for various food resources has been discouraging. In this thesis I will present evidence for the value of considering the consumption, growth, and respiration rates of a predator as a function of the density of its prey, which is the outcome of the production of the prey and whatever fates the prey suffers. Production as a function of growth rate and biomass can then be interpreted in terms of food availability, whatever the complexities of the system. This approach is intuitively appealing and is certainly not new (Ivlev, 1945, 1961; Richman, 1958), but it has not been much exploited. The difficulty of measuring and relating to environmental conditions such parameters as total consumption and production has not prevented attention from being drawn away from the simpler and more direct relationships between food density and consumption, growth, and respiration rates.

These studies of simple communities of plants and animals in six laboratory streams are a continuation of the studies reported by Davis and Warren (1965). The laboratory streams were provided with rubble bottoms and an exchange flow of filtered stream water. Algal communities developed in the streams from cells entering through the filter.

Small populations of herbivorous insects became established in much the same way, but additional seeding of these forms was usually necessary to obtain population levels capable of supporting large carnivore biomasses. A herbivorous snail, Oxytrema silicula, naiads of two carnivorous stoneflies, Acroneuria pacifica and Acroneuria californica, a sculpin, Cottus perplexus, and cutthroat trout, Salmo clarki, were added to the streams in different densities and combinations for the various experiments. The production rates of the snail and the carnivores were estimated directly. The consumption rates of these animals in the streams were estimated by comparing their growth rates with the growth rates of similar animals fed known rations in aquaria or in laboratory streams in which no communities were allowed to develop. Food assimilation and respiration rates were determined in other aquarium experiments.

My results will be interpreted and discussed mainly in terms of the growth and bioenergetics of the species, their food consumption and production as these are influenced by intraspecific and interspecific competition, the impact the carnivores have on prey density, and the relationships between food density and rates of consumption, growth and respiration of the carnivores. Insofar as possible, all of my findings have been related to the structure, bioenergetics, and behavior of the individual species. Davis and Warren (1965) presented and discussed various trophic level and other production efficiencies for communities very similar to the ones I have studied here, and I will not do this since it would add nothing essentially new.

These studies were carried out in a series of experiments conducted from September 1963 through December 1965, at the Pacific Cooperative Water Pollution and Fisheries Research Laboratories, Oregon State University.



## METHODS AND MATERIALS

### Laboratory Stream Apparatus

Six laboratory streams were used in this study (Figure 1). The streams were housed in a small concrete-block building. Each stream consisted of two wooden troughs, 25 cm wide, 20 cm deep, and 3 m long, placed side by side. Openings in the adjacent sides at each end of the troughs permitted circulation of water. Paddle wheels were used to maintain water currents at a velocity of approximately 24 cm per second except during one experiment in which the velocity in three of the streams was increased to approximately 39 cm per second. The bottoms of the laboratory streams were covered with similar amounts and assortments of natural stream rubble and gravel. The water was taken from a small spring-fed stream, filtered to remove most suspended materials, and was exchanged in each laboratory stream at the rate of 2 liters per minute. Banks of fluorescent lights operated through time switches provided controlled illumination for about 12 hours of each day. No attempt was made to control water temperatures; they followed rather closely the diel and seasonal variations of the water supply stream. Analyses of the chemical characteristics of the water supply were made in 1962 by the U. S. Geological Survey, Portland, Oregon, under the supervision of L. B. Laird, District Chemist, and are reported by McIntire *et al.*, (1964).

### Algal Production

Rates of algal production and community respiration in the laboratory streams were estimated on the basis of data on the dissolved



Figure 1. Two of the six laboratory streams used for these studies.

oxygen concentration of the influent and effluent water obtained at regular time intervals. The method of calculating the amounts of oxygen released or utilized has been described in detail by McIntire et al., (1964). The estimates were based upon the overall photosynthesis or respiration reaction  $6\text{CO}_2 + 6\text{H}_2\text{O} + \text{E} = (\text{CH}_2\text{O})_x + 6\text{O}_2$ , and involved the assumption that the photosynthetic quotient was unity for the algal community. The amount of carbohydrate formed or respired was calculated by multiplying the grams of oxygen released or utilized by 0.9375 (one mol carbohydrate divided by six mols of oxygen). The energy in kilocalories was obtained by multiplying the grams of carbohydrate by 3.750, the caloric value of one gram of glucose.

#### Animal Respiration

Experiments were conducted to determine the rates of respiration of sculpins and trout. Snails were graded to size and acclimatized to test temperatures of 10 C and 20 C for a one-week period. A Warburg Manometer equipped with a self-contained thermal-regulation unit was used to obtain estimates of respiration rates. Methods and procedures were standardized according to Umbreit (1949). The snails used for the determinations had a mean wet weight of 0.56 g. The snails were left to respire in the manometer flasks for a period of 3 hours, following a 1 hour acclimatization period. The oxygen uptake was determined by measuring the pressure change within the manometer flasks each hour in millimeters of mercury. The measurements were cumulatively corrected for changes in barometric pressure by

using a control manometer simultaneously. The corrected pressure change for each manometer flask was then multiplied by a previously determined flask constant. Respiration rates of the snails have been expressed in cal/kcal snail/hr. This was done by multiplying the milligrams of oxygen respired by the oxy-calorific coefficient for one milligram of oxygen, 3.38 calories (Ivlev, 1934). The number of calories of respiration was divided by the biomass of snails (kcal), and this quotient was then divided by the number of hours the animal respired.

Stonefly naiads and sculpins were acclimatized to test temperatures of 10 C and 20 C for a one-week period. Individual naiads and sculpins were placed in 250 ml Erlenmeyer flasks which were filled to capacity with aerated well water. The flasks were then fitted with ground glass stoppers and placed in a water bath to maintain the test temperature. Dissolved oxygen determinations were made before the animals were placed in the flasks and again 24 hours later. Initial and terminal determinations were made on water placed in a flask containing no animals and any difference was subtracted from the oxygen change occurring in flasks containing animals. These determinations were made using the Alsterberg (azide) modification of the Winkler method (American Public Health Association, 1955). The corrected difference between the initial and terminal determinations of oxygen in a test flask was the amount of respiration that took place during the 24-hour period. Oxygen utilization was expressed in cal/kcal/hr.

Respiration rates of trout were determined in a flowing water

system at 12 C after an acclimitization period of one week. Individual trout were held in a darkened 2-liter jar through which water was metered at a rate of 1 liter per hour. Periodic measurements were made of the dissolved oxygen content of the influent and effluent water and the differences taken to be the amount being used by the trout in the container. The oxygen uptake was then expressed as a rate in cal/kcal/hr. All measurements of respiration rates were performed using animals which had not fed for 36 hours and these measurements can be considered to approximate routine metabolic rates.

#### Food Assimilation

Preliminary attempts to estimate the assimilation efficiencies of snails, stonefly naiads, sculpins, and trout were largely unsatisfactory when gravimetric methods were employed to determine amounts of fecal material resulting from known amounts of food consumed. In order to obtain more reproducible results, I used a method employing wet combustion of organic material present in water in which animals were held after being fed.

A 15 ml sample of this water was drawn into an evacuated flask containing 5 ml of 0.5 percent potassium iodate. To this was added 45 ml of concentrated sulfuric acid. The mixture was then heated to 190 C and held at this temperature for twenty minutes to insure total digestion of all organic material. After the flask contents were cooled, approximately 375 ml of distilled water and 10 ml of 10 percent potassium iodide were added. The contents were then titrated with 0.2 N thiosulfate to determine the amount of oxygen required for

combustion of the organic materials.

Groups of 15 snails each were held in 45 ml of water and fed known amounts of a specially prepared ration consisting of algae and a small amount of sodium alginate. The snails were held for a sufficient period of time for them to empty their guts, after which the snails were removed from the water. The fecal material and the water in which the snails were held was then frozen and stored until determinations could be made by the wet combustion method.

Individual stonefly naiads were held in 10 ml of water and fed known amounts of midge larvae. The uneaten larvae were removed and weighed, and the stonefly naiads allowed a period of 36 hours to empty their guts. After removal of the naiads, the fecal residues of three stoneflies along with the water were combined and the composite sample was frozen and stored until determinations were made.

Individual sculpins and trout were held in 45 ml and 1 liter of water, respectively, and fed known amounts of midge larvae. After removal of the sculpins, the fecal material and water were treated in the above manner except that the samples were not composited. The trout were left in their containers for 36 hours to empty their guts and then removed. The water in which the trout were held was then metered through a constant flow centrifuge and the fecal material collected. A 15 ml aliquot was then taken from the centrifuged water and used as a sample for determining the amount of dissolved organic material and the water sample was then frozen and stored until determinations were made.

Wet combustion determinations were made on midge larvae and on

the prepared snail ration in order to obtain standard values from which to calculate the total amounts of food fed in terms of milligrams of oxygen. By dividing the milligrams of oxygen required to oxidize the fecal and other organic material in the sample by the milligrams of oxygen required to oxidize the amount of food fed, an approximate value for the percent assimilation was derived.

### Calorimetry

Oxygen bomb calorimetry was employed to determine the caloric values of samples of experimental animals, herbivorous insects, algae, and prepared snail food. A Parr semi-micro oxygen bomb calorimeter No. 1411 was used in making these determinations. The procedures described in Parr Instrument Company Manuals 128 and 130 and in Supplement No. 1 were followed. No special treatment was given the materials combusted in the calorimeter other than to add distilled water to the dried powdered samples in order to prepare the pills for combustion.

Mean percent dry weight and mean caloric values for the materials combusted in the calorimeter are given in Table 1. A series of values is given for cutthroat trout to show how the caloric values of their tissue varied with their nutritional status.

### Food Consumption and Production of Experimental Animals

Estimates of the caloric equivalents of food consumed by the snails, stoneflies, sculpins, and trout in the laboratory streams were made by comparing the growth rates of these animals with those of individuals held in aquaria and fed different food rations of known caloric

value.

Table 1. Mean percent dry weight, range of caloric values, and mean caloric value per gram dry weight of experimental materials.

Material	Number of samples	Mean percent dry weight	Range of caloric values (kcal/g dry wt)	Mean caloric value (kcal/g dry wt)
Trout				
Low ration	7	18.514	4.1362 - 4.4896	4.2152
Medium ration	9	20.503	4.5087 - 4.7200	4.5429
High ration	12	22.427	4.8789 - 5.1743	5.0398
Sculpins	17	23.526	4.7391 - 5.4382	5.2869
Stonefly naiads	19	19.201	4.8359 - 5.4781	5.3644
Snails	10	50.820	0.7940 - 0.9477	0.9104
Tubificid worms	14	16.205	5.3358 - 5.9862	5.4913
Midge larvae	6	14.165	4.9680 - 5.3288	5.2731
Artificial algae	14	23.177	4.0591 - 4.1170	4.0805
Algae	10	-----	0.9863 - 1.3910	1.1501

The aquarium experiments on the food consumption and growth rates of sculpins, snails, and trout were conducted concurrently with the laboratory stream experiments with animals that were similar in age and size to the animals in the streams. Conditions of temperature and light in the aquaria were similar to those in the streams. Data on stonefly naiad food consumption and growth rates were taken from Davis and Warren (1965), and are included in the Results section. Data on food consumption and growth rates of yearling trout were taken from Warren *et al.*, (1964).

Groups of snails were held in glass jars of 1-gallon capacity which were fitted with tubes through which water was continuously exchanged. Individual sculpins were held in 500 ml Erlenmeyer flasks in which a constant flow of water was maintained. Trout were held



separately in individual 5-gallon aquaria fitted with standpipe drains. Water was continuously introduced into the aquaria and the flow was directed in a manner to maintain a circular movement of the water. Some activity of the fish resulted from this water movement.

Sculpins were fed weighed amounts of midge larvae, mainly of the genus Chironomus. Larvae which were not consumed were removed, dried, and weighed in order to estimate the amounts of food consumed. Snails were fed weighed amounts of the specially prepared food described above which remained relatively intact in water. Had natural algal material been fed, losses through the exchange water could not have been adequately evaluated. Uneaten food was removed, dried, and weighed, so that the amounts consumed could be determined.

The changes in biomass of the animals during the time they were held in aquaria were converted to caloric values. Each value so obtained was divided by the caloric value of the mean biomass of the animal for the time interval involved and the quotient was then divided by the number of days in the interval. This permitted the expression of growth rates of the snails, sculpins and trout in terms of calories of growth per kilocalorie of biomass per day. Food consumption rates of the aquarium animals were computed in a like manner by dividing the caloric equivalents of food consumed during each experiment by the caloric value of the mean biomass of the animal, and then dividing the quotient by the number of days in the period.

To check the validity of the assumption that activity levels of the trout held in aquaria were similar to those of trout in laboratory streams, concurrent aquaria and laboratory stream feeding experiments

were conducted. The gravel and rubble in the laboratory streams were scrubbed clean and light levels were reduced to prevent algal production. A stream velocity of 24 cm per second was maintained in three streams, and a velocity of 39 cm per second was maintained in the remaining three streams. Each stream was divided into two parts by placing screens in the openings between the ends of its two troughs. This gave a total of six streams at each velocity. A single under-yearling trout was placed in each stream section and fed different known rations of housefly larvae and adults. Fish held in individual aquaria were fed the same array of rations during the same experimental period. Weight changes were converted to caloric values based upon the condition factor of the individual trout and the relationship between calories per gram of wet weight and condition factor (Warren, et al., 1964). The growth and food consumption rates were computed in the same manner as were those for the snails and sculpins.

Mean growth rates of snails, stonefly naiads, sculpins, and trout stocked in laboratory streams were computed for each experimental period using the same procedure employed in computing growth rates of the aquarium animals. The growth rates thus obtained for animals in the laboratory streams were used to estimate food consumption rates from growth rate-consumption rate curves established in aquaria. The caloric value of the food consumed by all individuals of that species in a stream during a given period was estimated by multiplying the graphically determined rate of food consumption (cal/kcal/day) by the mean caloric value (kcal) of its biomass during the period and then multiplying the product by the number of days in

the period.

Production of each of the species of experimental animals, when no mortality occurred, was estimated directly by measuring its increase or decrease in weight during a given experimental period. When it was determined at the end of an experiment that animals had died or had been lost from a stream, an adjustment of the production value was required. These animals were assumed to have lived in the stream on the average for half of the experimental period, and production was estimated by multiplying the average number of animals of this species by the mean of the mean initial and mean terminal weights. Experimental animals were selected for uniformity of size at the beginning of the experiments in order to reduce errors in estimates made when animals were lost.

Samples of the algal community and herbivorous insects in the benthos were taken from each stream immediately before the experimental animals were stocked, each time primary production estimates were made (usually monthly) and at the conclusion of an experiment. In order to obtain the samples, two water-tight partitions were inserted 20 cm apart between the walls of the streams so as to provide a sample of organisms from a stream area of  $500 \text{ cm}^2$ . After the rocks and gravel were scrubbed in the water and removed, the water containing the benthic organisms was siphoned into a plankton net which concentrated the animals and most of the algal material. A dissecting microscope was used to aid in the removal of the animals from the benthic samples. The biomasses of both plant and animal materials were determined, and samples were retained for caloric analysis.

The small numbers of herbivorous midge larvae and mayfly naiads obtained from the benthic samples were insufficient to permit direct estimates of the production of these organisms based upon number, size, and growth relationships.

Samples of drifting insects were taken from each stream immediately before stocking experimental animals, generally at two-week intervals during the experimental period, and immediately after termination of the experiment. The samples were collected by diverting the water leaving the streams through the overflow drains into plankton nets for a 24-hour period. The overflow drains were located on the side opposite the incoming water, thus allowing for complete circulation of the water in the trough before being recovered in the plankton nets. The samples were then removed from the plankton nets, the insects separated from pupal cases and plant debris, and weighed.

## DESCRIPTION OF STREAM COMMUNITIES

Algal communities were developed in the laboratory streams as a result of colonization by cells that remained in the water entering the streams after filtration. These communities were usually dominated by a species of the filamentous algae Oedogonium and the diatoms Synedra ulna and Melosira varians. Energy values determined for light, gross plant production, community respiration, and mean plant biomass during the fall 1963 and winter 1964 experiments are given in Table 2. Estimates of light energy at the surfaces of the laboratory streams were made using a circular eight-junction Eppley Thermopile. A one millimeter pyrex window was used to filter out most of the energy unavailable for photosynthesis.

Herbivorous insects were the predominant benthic organisms other than the snails and sculpins which were stocked in the streams. The insects either entered the streams with the water as eggs or very small larvae, or were stocked in the streams from collections made at Berry Creek, a small woodland stream approximately 12 miles northwest of Corvallis, Oregon. Of the insect forms present, midge larvae of the genera Chironomus, Calopsectra, and Micropsectra were the most numerous. Mayfly naiads were often present in the streams, but their numbers were small. Extremely small biomasses of cladocerans, copepods and naupliid oligochaetes were found in benthic samples. Although a few specimens of Sialis, a predaceous megalopteran, were observed in the laboratory streams, its occurrence was too rare for it to be considered important as a consumer of herbivorous insects.

Table 2. Energy values determined for the stream communities during the Fall 1963 and Winter 1964 experiments expressed in kilocalories per square meter.

	Stream					
	1	2	3	4	5	6
Fall 1963 Experiment						
Light energy <u>1/</u>	8,160	8,160	8,160	8,160	8,160	4,080
Gross plant production	430	657	432	748	558	342
Community respiration	160	359	349	481	385	275
Mean plant biomass	2,782	4,778	5,560	4,616	5,130	2,577
Winter 1964 Experiment						
Light energy <u>1/</u>	7,320	7,320	7,320	7,320	3,660	3,660
Gross plant production	679	239	714	631	562	454
Community respiration	301	86	321	345	287	335
Mean plant biomass	18,594	11,716	11,499	8,956	5,059	1,170

1/ Estimates of light energy were made at the water surface and are believed to be reasonable estimates of absorbed light as most of the periphyton was on rocks a few inches from the water surface.

The selection of the species of snails, stoneflies, sculpins, and trout used in the laboratory stream studies was based upon some general knowledge of the food habits of each species.

Snails of the species used in the study were found by Ching (1959) to feed well in the laboratory on a variety of food plants, and she suggests that the digestive system of this snail is adapted to a diet rich in carbohydrates. Davis and Warren (1965) calculated the ratio of algal biomass to food organism biomass in two laboratory streams and found the animal material in the streams to be approximately 0.10 percent of the plant material. In considering what is known of the food habits of the snails and the likelihood of snails contacting animals suitable for food during normal feeding activity, they concluded that snails did not play an important role as consumers of the herbivorous insects in the laboratory streams.

Analyses of stomach contents of sculpins and stonefly naiads reported by Davis and Warren (1965) indicated that these species in nature and in the laboratory streams consumed primarily chironomid larvae and less frequently small mayfly naiads. Although diatoms were frequently observed in the guts of sculpins, the frustules were usually intact and the chloroplasts retained their integrity even in the posterior part of the gut. Diatoms were found only when animal materials were present, and these investigators concluded that either the plant materials were ingested accidentally, or that they were contained in the guts of herbivores that were consumed.

Analyses of the contents of stomachs of trout living in the laboratory streams indicated that the trout subsisted almost entirely on

herbivorous insects. Chironomid pupae were the dominant forms observed in the trout stomachs and the numbers of larvae were usually quite low. This appeared to be related to the feeding behavior of the small trout which appear to rely mainly on drifting food organisms. Chironomid larvae, being associated with the periphyton, were probably less available to the drift-feeding trout than were the pupae and adults. The proportion of larvae found in samples of the food organisms being exported from the streams was low, and this would also indicate that differences in availability existed. Estimates of the density of drifting food organisms are expressed in calories per cubic meter of water, whereas estimates of the density of food organisms in the benthos are expressed in kilocalories per square meter of bottom area (Table 3).

The effect of competition on the food consumption and production of cutthroat trout was studied in stream experiments performed during the fall 1963, winter 1964, summer 1965, and fall 1965. Because of the many stocking levels and combinations of different species, this information is presented in tabular form (Table 4). Water temperatures varied between different experiments and are given in Table 5.

During the fall 1963 and winter 1964 experiments, varying biomasses of sculpins and stonefly naiads were stocked in combination with trout (Table 4). Snails were added to the streams to utilize part of the algal production in competition with the herbivorous insects. The effects of reduced light intensity on the laboratory stream communities were also studied during these experiments. Light intensity was reduced over one stream during the fall 1963 experiment by one-half



Table 3. Mean density of food organisms in the drift and benthos.

Experimental period	Stream	Food animals in drift in calories per cubic meter		Food animals in benthos in kilocalories per square meter	
		Initial sample included 1/	Initial sample not included 2/	Initial sample included 1/	Initial sample not included 2/
Fall, 1963	1	3.06	3.09	1.50	2.04
	2	2.50	2.94	1.44	1.96
	3	4.82	4.85	1.44	1.90
	4	3.06	3.24	1.63	1.79
	5	1.33	1.47	0.81	1.89
	6	1.74	1.91	0.59	1.53
Winter, 1964	1	8.81	1.13	2.54	0.94
	2	5.07	5.08	3.28	1.08
	3	10.71	10.16	3.21	2.66
	4	2.58	1.15	2.87	1.15
	5	2.96	7.21	3.02	2.29
	6	1.14	0.97	1.02	0.41
Summer, 1965	1	7.54	4.14	1.95	1.73
	2	9.10	8.28	2.25	0.83
	5	11.01	6.19	3.97	0.38
	6	1.23	6.90	3.28	2.90
Fall, 1965 #1	1	0.12	0.35	0.41	0.37
	2	1.91	0.73	0.62	0.63
	3	2.35	2.24	0.21	0.19
	4	0.56	0.22	0.39	0.32
	5	2.47	0.62	0.70	0.41
	6	1.23	0.05	0.59	0.29
Fall, 1965 #2	1	0.50	0.58	0.52	0.54
	2	0.36	0.66	0.59	0.51
	3	0.18	0.08	0.29	0.31
	4	3.24	0.60	0.72	0.43
	5	3.72	0.68	0.67	0.51
	6	2.53	0.49	0.37	0.25

1/ Values listed in this column are means of all food density samples taken during the experiment for each laboratory stream.

2/ Values listed in this column are means of only those food density samples taken after animals were stocked in the laboratory streams.

Table 4. Mean biomass and numbers of animals stocked and recovered in laboratory streams.

[illegible]

Table 5. Mean weekly water temperatures during the experimental periods showing the mean and the range in degrees centigrade.

Experimental Period	Date	Water temperature (C)	
		Mean	Range
Fall, 1963	10/21 - 10/27	10.9	8.9 - 12.5
	10/28 - 11/3	9.6	8.6 - 11.1
	11/4 - 11/10	9.9	8.6 - 11.1
	11/11 - 11/17	10.6	8.9 - 11.7
	11/18 - 11/24	9.1	6.7 - 11.7
	11/24 - 12/1	7.7	4.5 - 11.7
	12/2 - 12/8	6.8	5.6 - 8.3
	12/9 - 12/15	6.3	4.5 - 8.6
	12/16 - 12/22	7.9	6.4 - 9.5
	12/23 - 12/29	8.8	6.9 - 10.6
	12/30 - 1/5	8.1	5.8 - 10.8
Winter, 1964	2/10 - 2/16	7.1	5.6 - 8.9
	2/17 - 2/23	7.9	6.1 - 9.7
	2/24 - 3/1	8.0	5.0 - 9.5
	3/2 - 3/8	6.9	4.7 - 8.9
	3/9 - 3/15	7.7	6.1 - 10.3
	3/16 - 3/22	8.0	6.1 - 9.5
	3/23 - 3/29	8.5	6.1 - 11.1
	3/30 - 4/5	8.9	6.4 - 10.6
	4/6 - 4/12	9.6	7.8 - 11.7
	4/13 - 4/19	9.7	6.1 - 13.1
Summer, 1965	7/12 - 7/18	15.7	13.9 - 17.8
	7/19 - 7/25	14.9	12.8 - 18.9
	7/26 - 8/1	15.5	13.9 - 19.5
	8/2 - 8/8	15.5	13.9 - 18.9
	8/9 - 8/15	16.6	15.0 - 18.9
Fall, 1965 #1	9/22 - 9/28	14.0	11.1 - 16.7
	9/29 - 10/5	13.3	11.1 - 15.0
	10/6 - 10/12	13.3	11.1 - 16.7
	10/13 - 10/19	11.4	10.0 - 13.9
	10/20 - 10/29	11.8	10.6 - 13.3
Fall, 1962 #2	11/11 - 11/17	10.5	9.5 - 11.1
	11/18 - 11/24	9.9	8.3 - 11.1
	11/25 - 12/1	7.9	6.7 - 9.5
	12/2 - 12/8	9.4	8.3 - 10.6
	12/9 - 12/15	7.9	6.7 - 8.9

of that employed for the other streams, and two streams were exposed to these reduced light levels during the winter 1964 experiment (Table 2).

Snails and stonefly naiads were not used in experiments performed during the summer 1965. Stonefly naiads of the proper size and age were unavailable in local streams, so sculpins were stocked with trout alone. Biomasses of under-yearling sculpins ranging from  $5.45 \text{ kcal/m}^2$  to  $18.45 \text{ kcal/m}^2$  were stocked in combination with yearling trout biomasses ranging from  $7.43 \text{ kcal/m}^2$  to  $21.98 \text{ kcal/m}^2$ .

The fall 1965 experiments were designed to illustrate the effects of increased trout biomass on trout food consumption and production. Biomasses of under-yearling trout ranging from  $2.68 \text{ kcal/m}^2$  to  $25.51 \text{ kcal/m}^2$  were stocked in the six streams during two experiments.

## RESULTS AND INTERPRETATION

Food Consumption, Growth and Bioenergetics of Snails,  
Stonefly Naiads, Sculpins and Trout

The relationship found between snail growth rate and food consumption rate (Figure 2) is generally similar to those reported by Davis and Warren (1965). At the higher consumption rates, however, the snails I fed appeared to be more efficient in food conversion than were the snails fed by Davis and Warren. Activity was probably lower during the experiment I conducted due to colder water temperatures, thus leaving a greater proportion of the food consumed available for growth. Efficiencies of assimilation of groups of snails fed a specially prepared ration ranged from 57.2 to 61.0 percent (Table 6). Because the proportion of sodium alginate added to the ration fed to the snails was small, the assimilation efficiency of the snails was probably not greatly different than it would have been had the snails been fed a ration of pure algae. The results of experiments to determine directly snail respiration rates show the rates to be lower at 10 C than at 20 C as might be expected, the snails being more active at higher temperatures (Table 7).

Figures 3 and 4 showing the results of aquarium experiments performed by Davis and Warren (1965) with stonefly naiads have been used to estimate the food consumption of these animals in my laboratory streams experiments. The curves relating stonefly growth and food consumption rates were fitted to quite variable data, and estimates based on them must be considered tentative.

Groups of stonefly naiads fed midge larvae in 12 experiments

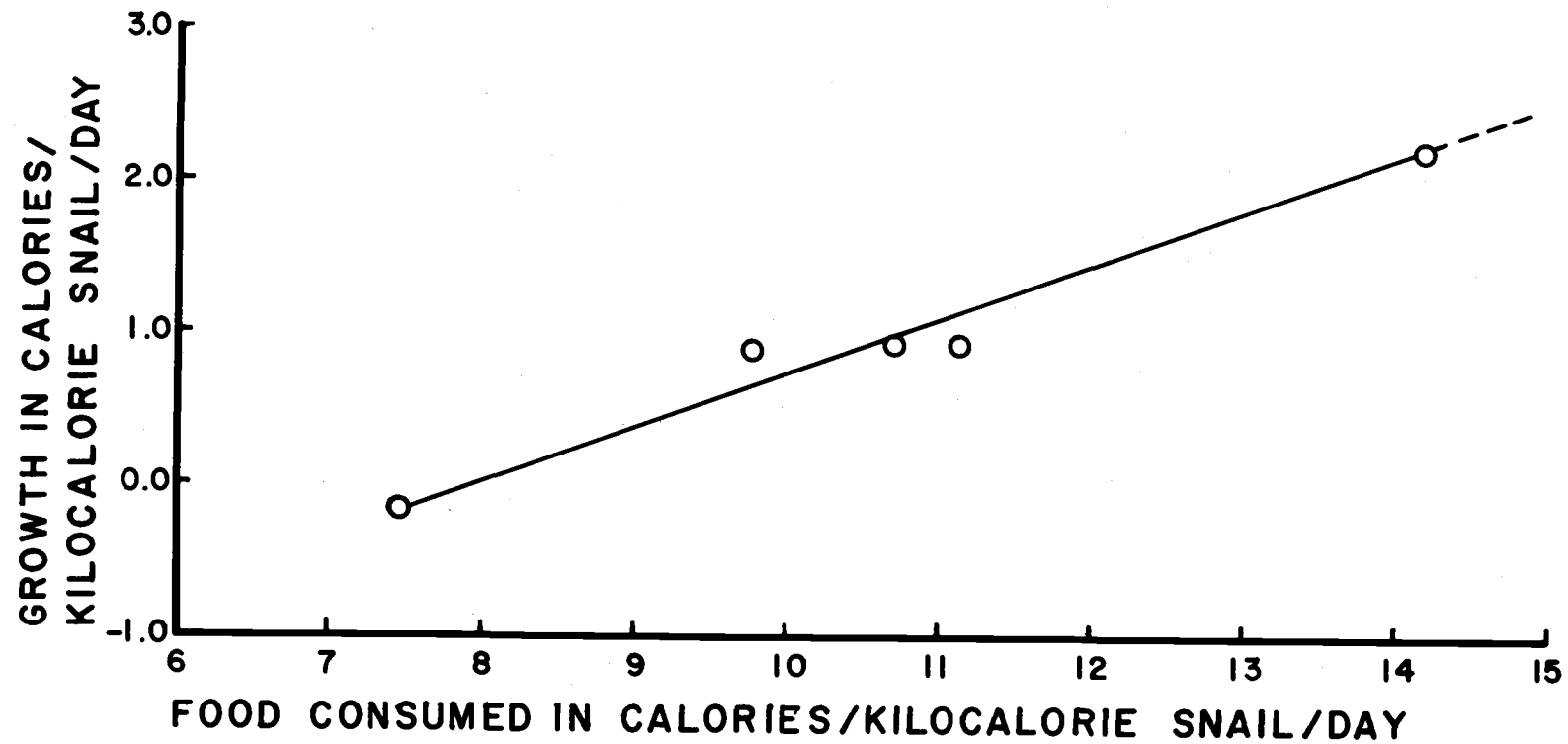


Figure 2. Relationship between snail food consumption rate and growth rate for the fall 1964 aquarium feeding experiment.

Table 6. Percent of food consumed that was assimilated by individual trout and sculpins, and groups of stonefly naiads and snails held at 10 C.

Snails	Stonefly naiads	Sculpins	Trout
57.2	82.7	83.7	86.1
60.3	80.1	78.4	85.2
61.0	82.3	79.8	85.2
58.5	83.3	82.0	84.9
60.0	82.0	84.4	85.6
60.5	82.0	84.4	85.9
	83.0	82.8	
	83.4	80.7	
	85.6	81.6	
	82.5		
	83.0		
	83.0		
Mean	59.6	82.8	81.9
			85.5

showed a range of assimilation efficiencies from 80.1 to 85.6 percent, the mean being 82.8 (Table 6). It was necessary to combine the fecal material of three stonefly naiads to employ the wet combustion method, and, thus, each assimilation value obtained was a mean. Respiration rates for stonefly naiads were lower when experiments were conducted at 10 C than when experiments were conducted at 20 C (Table 7). The high respiration rates of stonefly naiads, as compared to those of the other experimental animals, are similar to those reported by Dewitt (1963). These values tend to confirm the high estimates of total respiration of stonefly naiads determined by difference for the fall 1963 laboratory stream experiment, which will be discussed later.

The relationship between food consumption rate and the new growth rate of under-yearling sculpins (Figure 5) was not greatly different

Table 7. Routine metabolic rates for stonefly naiads and snails held at 10 C and 20 C.

Stonefly naiads			
10 C		20 C	
Biomass (kcal)	Oxygen consumption (cal/kcal/hr)	Biomass (kcal)	Oxygen consumption (cal/kcal/hr)
0.068	1.51	0.077	1.78
0.097	0.98	0.091	1.90
0.105	0.71	0.140	1.46
0.135	0.92	0.142	1.17
0.287	0.53	0.215	1.17
0.291	0.71	0.319	0.85

Snails			
10 C		20 C	
Biomass (kcal)	Oxygen consumption (cal/kcal/hr)	Biomass (kcal)	Oxygen consumption (cal/kcal/hr)
0.230	0.32	0.230	0.60
0.251	0.31	0.251	0.60
0.268	0.27	0.268	0.59
0.272	0.33	0.272	0.53
0.273	0.32	0.273	0.56
0.307	0.29	0.307	0.56



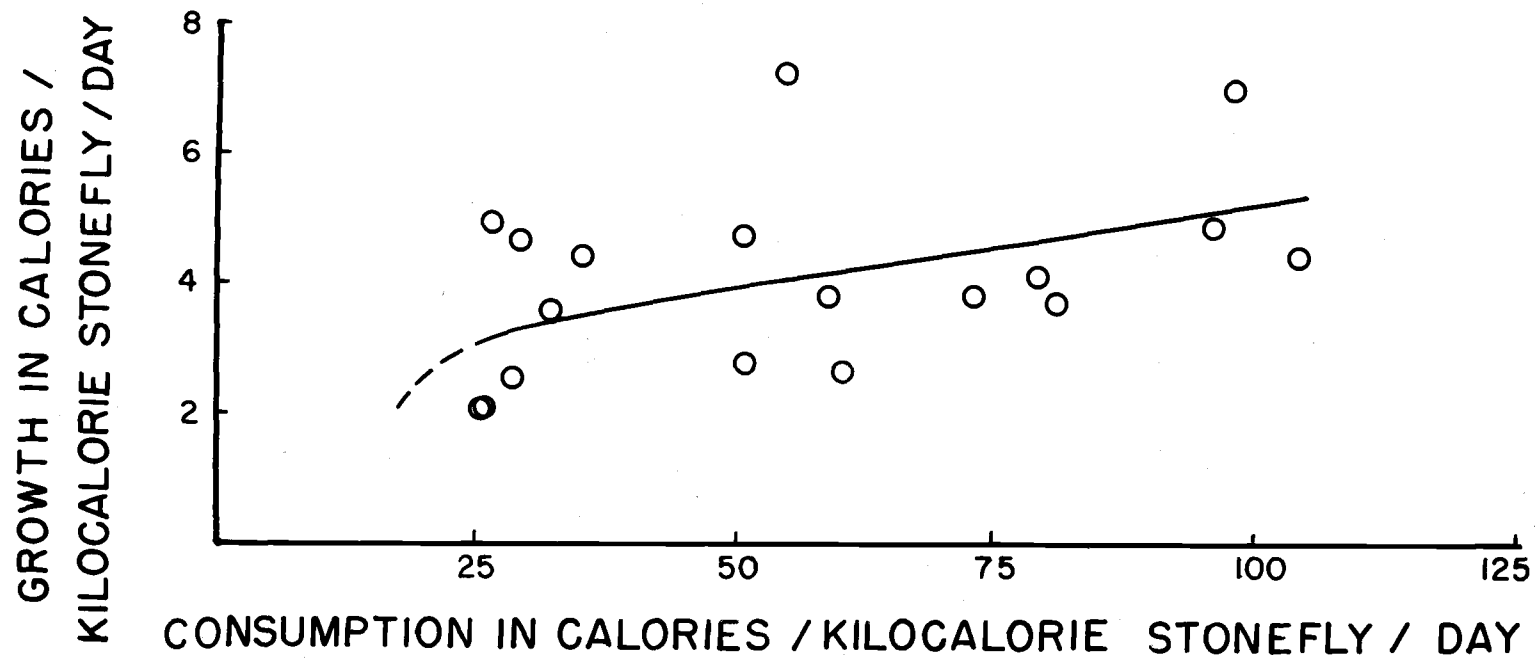


Figure 3. Relationship between stonefly naiad food consumption rate and growth rate for the fall 1961 aquarium feeding experiment. This figure is from Davis and Warren (1965:856, Fig. 4).

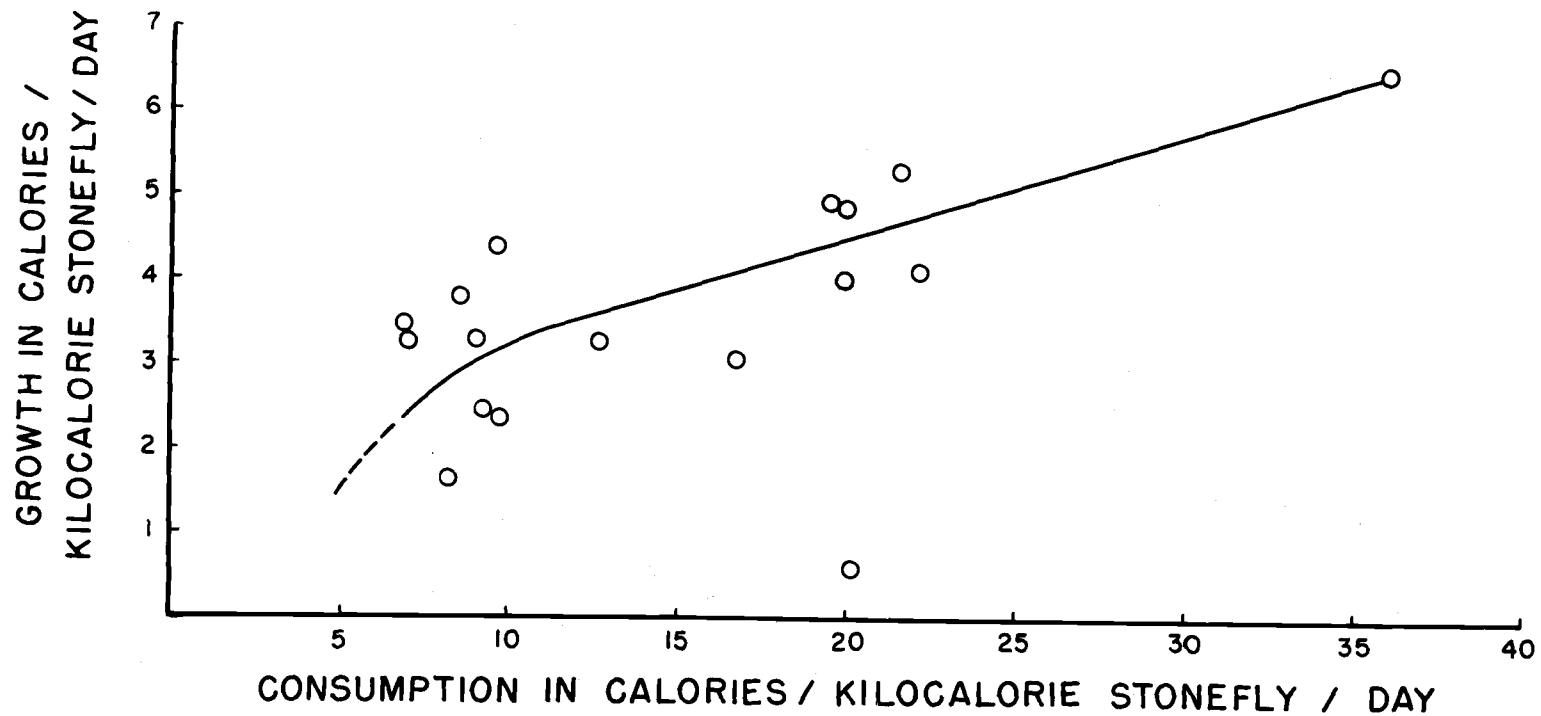


Figure 4. Relationship between stonefly naiad food consumption rate and growth rate for the winter 1962 aquarium feeding experiment. This figure is from Davis and Warren (1965:856, Fig. 5).

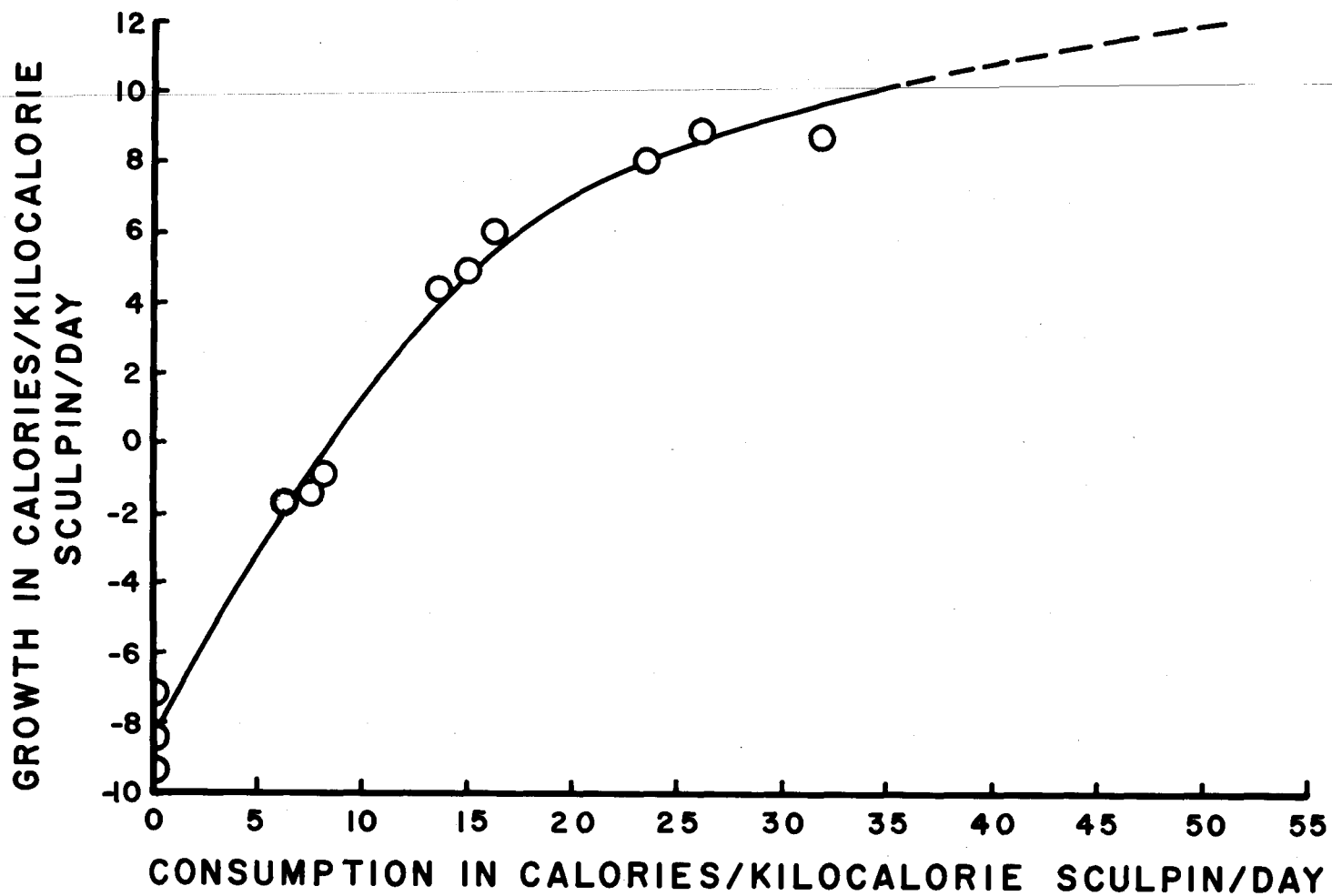


Figure 5. Relationship between under-yearling sculpin food consumption rate and growth rate for the winter 1964 aquarium experiment.

than that derived by Davis and Warren (1965) for yearling sculpins during the fall of 1961. When higher growth rates were obtained in the stream experiments than in the aquarium experiment, it was necessary to extrapolate the curve (dotted portion) relating consumption and growth rates to obtain an estimate. The under-yearling sculpins were more efficient in converting food to tissue than were the yearling sculpins fed by Davis and Warren (1965). Because I used yearling sculpins in one stream during the fall 1963 experiment, I have taken a value for food consumption rate from the fall 1963 sculpin growth rate-consumption rate curve derived by Davis and Warren (1965). This value (5.53 cal/kcal sculpin/day) has been used in calculating the total food consumed by these sculpins in this experiment.

Determination of assimilation efficiency for sculpins fed midge larvae had more variability than those for the other test animals (Table 6). It was at first believed that these differences could have been due to retention of fecal material in the digestive tract. However, fish held under the same conditions as the test fish and fed similar amounts of midge larvae retained no fecal material 30 and 36 hours after feeding. The mean rate of respiration of sculpins held at 10 C was 0.17 cal/kcal/hr and that of sculpins held at 20 C was 0.23 cal/kcal/hr (Table 8). As in the case of the other organisms, the respiration rate of the sculpins decreased with increases in size. These rates can be interpreted as routine metabolic rates as the sculpins had not been fed for 36 hours and were disturbed very little.

In order to estimate the food consumption of yearling trout in

stream experiments, I have used a curve relating the growth rates and consumption rates of yearling cutthroat trout derived by Warren et al., (1964) during the months from February to June (Figure 6). Some error may have resulted from use of this curve to estimate food consumed by yearling trout in experiments conducted during seasons different than that at which the relationship was derived. The efficiency of utilization of food for growth may be affected by temperature and other seasonal changes. The results of the experiment in which under-yearling trout were fed rations of known caloric value in aquaria and in laboratory streams in which production of food organisms was not permitted were quite revealing (Figure 7). Trout held in laboratory streams were more efficient in the utilization of food for growth than were trout held in aquaria. Trout in the aquaria exhibited considerable and continuous random activity during the hours of light. The fish in the streams stayed in rather restricted areas of low velocity and moved into faster current only for food. There were no significant differences between the food consumption and growth relationships of fish held in streams with a velocity of 24 cm per second and those of fish held in streams with a velocity of 39 cm per second. This may suggest that the behavior of trout in streams may tend to reduce the respiratory costs of their activity. Trout respiration rates determined at 12 C varied with the size of the fish, the respiration rate declining as body size increased (Table 8).

The study of the food consumption and growth of under-yearling trout held in the laboratory streams and fed rations of known caloric value has made it possible to develop energy budgets for the individual

Table 8. Routine metabolic rate for sculpins held at 10 C and 20 C and trout held at 12 C.

Sculpin			
10 C		20 C	
Biomass (kcal)	Oxygen consumption (cal/kcal/hr)	Biomass (kcal)	Oxygen consumption (cal/kcal/hr)
0.67	0.25	0.69	0.34
0.99	0.21	0.95	0.27
1.08	0.18	1.11	0.25
1.09	0.19	1.14	0.26
1.21	0.13	1.24	0.19
1.31	0.13	1.30	0.17
1.44	0.13	1.33	0.21
1.72	0.12	1.46	0.17

Trout	
12 C	
Biomass (kcal)	Oxygen consumption (cal/kcal/hr)
2.45	0.27
3.01	0.26
3.20	0.26
8.38	0.23
11.29	0.22
13.74	0.19
14.49	0.14?
16.10	0.18



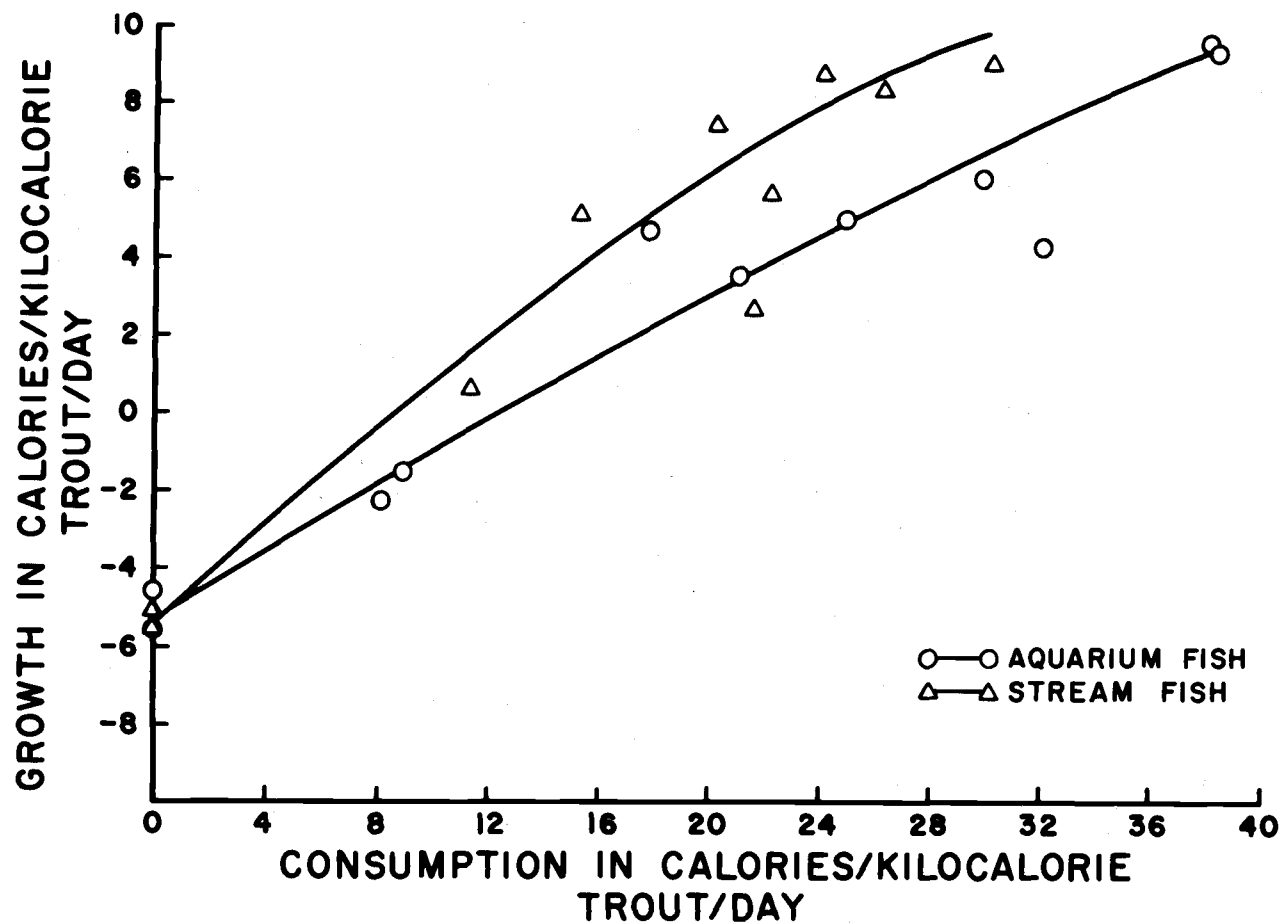


Figure 7. Relationships between food consumption rate and growth rate of under-yearling cutthroat trout held in aquaria and in laboratory streams.



fish (Table 9). Food consumption and growth were the only direct measurements made. The percentage of food consumed not assimilated by the fish has been obtained from the mean value of assimilation efficiency of 85.5 percent found for trout (Table 6). Use of this percentage, because it is a mean of 10 determinations for fish consuming food at different rates, could lead to some error. Efficiency of food assimilation may vary with the rate of food consumption. Also, as discussed in detail by Davis and Warren (1965), a small but variable portion of the energy value of food assimilated by fish is lost through the gills and kidneys in the form of nitrogenous materials. The values for respiration were calculated by difference between food assimilated and growth and are further broken down into respiratory cost of food handling and other respiration. The value for the respiration of the unfed fish was subtracted from the total respiration values for each fish to derive the values for respiratory costs of food handling, which include the costs of digesting, assimilating and storing of food materials. The validity of these values is dependent on the assumption that the activity levels of all the fish fed were the same as the activity level of the starved fish. This assumption has been made on the basis of direct observation of the fish in the streams. As previously mentioned, the fish in all streams chose locations with low water velocity. However, even the starved fish moved into the faster current at times, indicating that activity was approximately the same for all fish.

At the starvation level, there was weight loss, most of the energy involved being utilized through respiration. At low levels of food

Table 9. Energy utilization by under-yearling trout held separately in laboratory streams and fed measured amounts of housefly larvae and adults.

Fish	Fish biomass (cal)	Food consumed (cal)	Food not assimilated (cal)	Food assimilation (cal)	Growth (cal)	Respiration (cal) 1/	Respiratory costs of food handling (cal) 2/	Activity and other respiratory costs (cal) 3/	Growth as percent of food consumed (cal)	Growth as percent of food assimilated (cal)
1	3590	0	0	0	-432	432	0	432	—	—
2	4027	960	139	821	54	767	335	432	5.63	6.57
3	3546	1144	166	978	387	591	159	432	33.83	39.57
4	3282	1542	224	1318	402	916	484	432	26.07	30.50
5	3665	1637	237	1400	208	1192	760	432	12.71	14.86
6	5037	2142	311	1831	792	1039	607	432	36.97	43.26
7	4468	2271	329	1942	837	1105	673	432	36.86	43.10
8	4960	2745	398	2347	878	1469	1037	432	31.99	37.41
9	4560	2897	420	2477	870	1607	1175	432	30.03	35.12

1/ Respiration value is derived by subtracting calories of food not assimilated and calories of growth from calories of food consumed.

2/ Cost of digestion value is derived by subtracting the calories of respiration of the starved fish from the calories of respiration of the individual fish fed different rations.

3/ Activity levels of all fish were assumed to be equal.

consumption, most of the energy available was required for respiration and little growth resulted. As the levels of food consumption increased, growth represented a larger percentage of the food consumed, but more energy was required for respiration. The increased requirement for respiration was due largely to increases in energy utilization for digestion, assimilation, and storage of food. The respiratory cost of food handling at the highest feeding level was nearly three times all other respiratory costs at the level and was three and one-half times the cost of food handling at the lowest feeding level. This is in general agreement with the finding of Davis and Warren (1965) that respiration of yearling sculpins at higher levels of consumption was four times that of sculpins at the lowest level of consumption.

#### Interspecific and Intraspecific Competition, Food Consumption, and Production of Animals

Snail production during the fall 1963 experiment, in which biomasses approximately equivalent to  $100 \text{ kcal/m}^2$  were added to five of the streams at high light levels, was not as high as was production during the winter 1964 experiment in two streams which were stocked with about  $140 \text{ kcal/m}^2$  at high light levels. During the winter 1964 experiment, snail production in streams containing biomasses of approximately  $40 \text{ kcal/m}^2$  at high light levels was somewhat greater than the production in the streams stocked at the higher biomass levels during the fall 1963 experiment. The greater snail production at high light levels during the winter experiment than during the fall experiment was not due to food availability but probably due to the

snails using consumed food more efficiently for growth at the lower winter temperatures.

The sixth stream during the fall 1963 experiment received only one-half as much light energy as the other streams and had a snail biomass only one-third as great. Under these conditions, the snails lost weight and a negative production value resulted, the available food energy being insufficient even for maintaining the snails. A very small snail biomass of 6 kcal/m<sup>2</sup> was added to a stream under similar light conditions during the winter 1964 experiment. Production under these circumstances was greater than was production in the stream receiving the low light level during the fall 1963 experiment, probably because the lower snail biomass required less food for maintenance, and more food was available for growth.

Very similar total biomasses of stonefly naiads, sculpins, and trout were added to the laboratory streams with one exception, during the fall 1963 experiment (Table 4). Since the proportions of different carnivores making up the similar biomasses in these streams varied, the relationships between production, food consumption and biomass could not be conveniently presented in the form of curves. Instead, the results of this experiment are presented in the form of simplified energy transfer diagrams (Figure 8). Stream 6 received only about one-half the light energy as the other five streams, and consequently algal production in this stream was much less than in the other streams. Even though snail biomass in this stream was only one-third that in any of the other streams, the snails lost weight resulting in a negative value for production (Figure 8). Though trout were the only

carnivores placed in this stream, and even though trout biomass was reduced to one-half that in any of the other streams, availability of herbivorous food organisms was also insufficient to prevent the trout from losing weight, and a negative value for total production in the stream was obtained (Figure 8). The influence that light levels resulting in little net algal production can have on the animals of a community is strikingly illustrated.

The very low food consumption and production of sculpins in Stream 1 (Figure 8) cannot be explained by low production of food organisms or the presence of trout. Rather, this appears to be poor utilization of the food resource by the sculpins, resulting in low consumption and growth rates in this stream. These sculpins were in their second year of life, while those in the other five streams were in their first year of life.

The larger amounts of food consumed by the stoneflies than by the sculpins or trout, even though stonefly biomasses were always lower than those of either species of fish, indicate the relatively higher efficiency with which the stonefly crops its food resource. As previously mentioned, the variability in the data of the growth rate-consumption rate curves used to estimate stonefly food consumption could account for some of this difference. However, a very large proportion of the food consumed by this organism was utilized in respiration (Figure 8). Observations on the high activity levels and oxygen consumption rates of the stonefly naiads tend to support the high estimates of their energy expenditure for respiration in the laboratory streams.

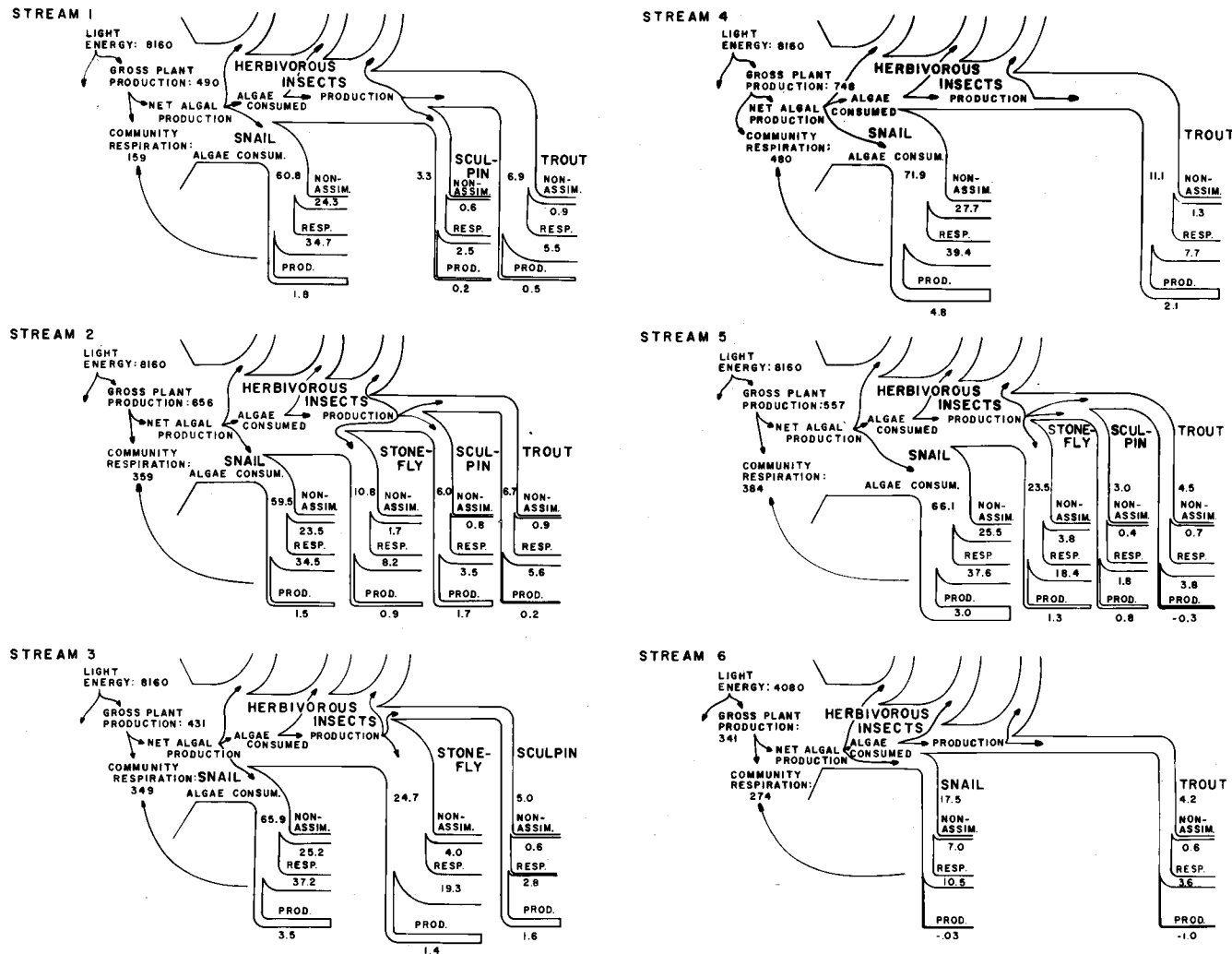


Figure 8. Simplified energy transfer diagrams showing energy utilization by the experimental animals in the six communities during the fall 1963 experiment.

It appears that sculpins and stoneflies reduce the food resource and consequently the food consumption and production of the trout (Figure 8). This can be seen by comparing trout food consumption and production in stream 4 (in which trout were the only carnivore present), with trout food consumption and production streams 1, 2, and 5 (in which sculpins or sculpins and stoneflies were present in addition to trout). Conversely, it appears that trout have relatively little influence on the food resources of the sculpins and stoneflies (Figure 8). This can be seen when the food consumption and production of sculpins and stoneflies are compared between streams 3 (in which no trout were present) and streams 2 and 5 (in which all carnivores were stocked).

Total carnivore production and consumption during the winter 1964 experiment, when plotted against total carnivore biomass, was low at the smallest biomasses, highest at intermediate biomasses, and intermediate at the highest biomasses (Figure 9). This figure bears a striking resemblance to the relationships derived by Davis and Warren (1965) when sculpin production and consumption was plotted against sculpin biomass. Comparison of a curve based on consumption and production relations of one species with a curve based on consumption and production relations of stoneflies, sculpins and trout taken together is not very meaningful. On the basis of the food habits and feeding behavior of the different carnivores, I have made a more detailed analysis below. The trout were found, through examination of stomach contents and from direct observations on their feeding activity, to subsist almost entirely on pupae and adult insects that were

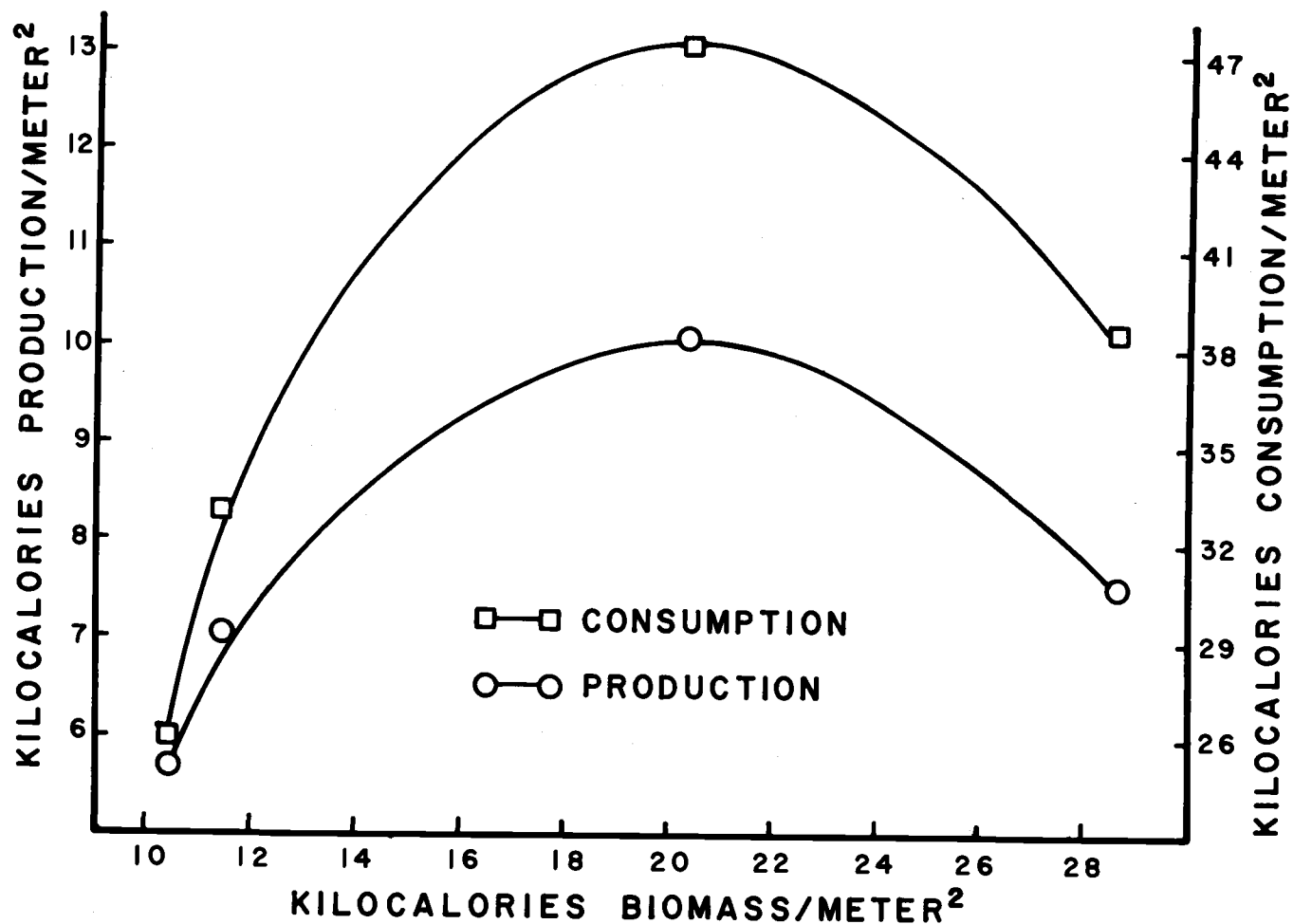


Figure 9. Relationships between total carnivore production and total carnivore biomass, and between total carnivore food consumption and total carnivore biomass at low, intermediate and high total carnivore biomass levels during the winter 1965 experiment.



drifting freely in the water during the winter 1964 experiment. The stonefly naiads and sculpins, on the other hand, appeared to consume mainly larval forms of insects associated with the periphyton.

Increases in the biomasses of stonefly naiads and sculpins in the winter 1964 experiment resulted in increases in the production and food consumption of these carnivores (Figure 10). Low production at the low sculpin and stonefly naiad biomasses resulted not from a shortage of food but from the restriction of the amount of new tissue which could be elaborated by the small sculpin and stonefly naiad biomasses.

Although growth rates of the sculpins and stoneflies were found to be highest at the lowest biomasses, declining markedly with increases of biomass, high growth rates and small biomasses resulted in a low production value. At the intermediate sculpin and stonefly biomasses, the available food was converted to sculpin and stonefly tissue by a more substantial biomass. Although it was not demonstrated in this experiment, further increases in the biomasses of both species would have resulted in declines in both production and food consumption (Davis and Warren, 1965). However, sculpin production was maintained at a high level at even higher biomasses of sculpins alone, and food consumption by the sculpins was markedly lower than the combined consumption of the two forms at lower biomasses. This indicated that the efficiency of utilization of food for growth was less in streams containing both species than in streams stocked with sculpins alone.

Trout production in the winter 1964 experiment was found to be low at low levels of trout biomass, highest at intermediate levels of trout biomass, and again reduced at the highest trout biomass (Figure

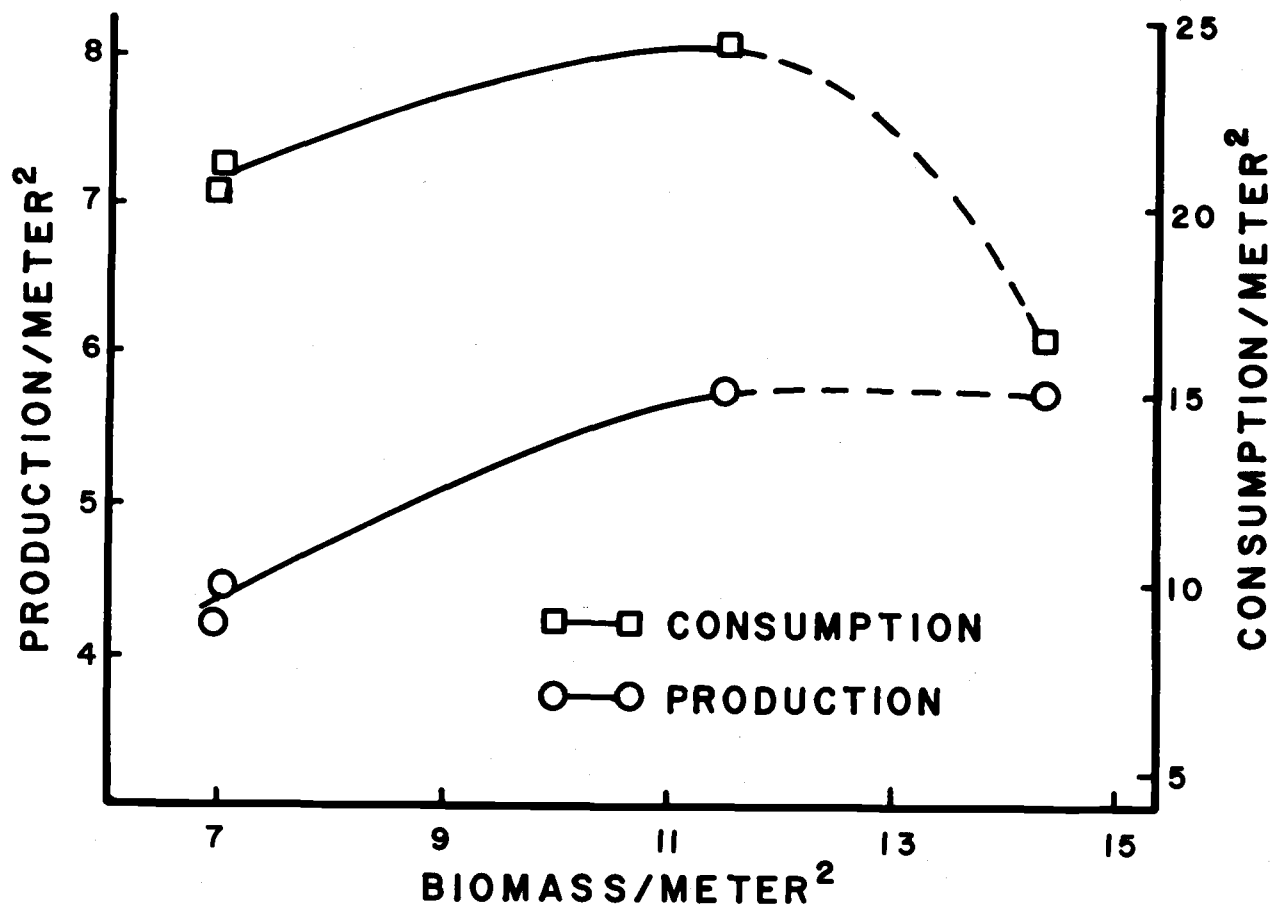


Figure 10. Combined sculpin and stonefly naiad production and combined sculpin and stonefly naiad food consumption (points at low and intermediate biomass levels) and production and food consumption of sculpins alone (points at high biomass level) plotted against biomass of sculpins and stonefly naiads combined or sculpin alone for the winter 1964 experiment.

11). Trout food consumption increased as biomass increased to an intermediate level for the reasons given in the case of the sculpins and stonefly naiads (Figure 10), but remained at a high level even at the highest levels of trout biomass (Figure 11). This relationship between trout food consumption and trout biomass can be explained on the basis of the feeding habits of the trout that were discussed earlier. The trout, feeding mainly on the drifting pupae and emerging adults, were not cropping their food resource directly and therefore were not able to overexploit this resource even with increased biomass. Because of this, the amount of food consumed remained high at the high biomass levels; but, due to the increased biomass and maintenance costs, production decreased. However, had the biomass of sculpins and stonefly naiads stocked in this stream been greater, the amount of food available in the drift would have been lowered through further cropping of the organisms in the benthos from which the drifting animals originated. This would have lowered trout food consumption and production and obscured the relationship shown in Figure 11.

In view of differences in the structure and behavior of the stoneflies, sculpins, and trout, and the relationships that were found to exist between their food consumption and production, there seem to exist differences in the nature of competition between the species. The stonefly naiads and sculpins compete directly with each other and can influence the food consumption and production of the trout through cropping the benthic food organisms directly, thus reducing the numbers drifting. The trout, on the other hand, affect the production of the sculpins and stoneflies very little because their consumption of

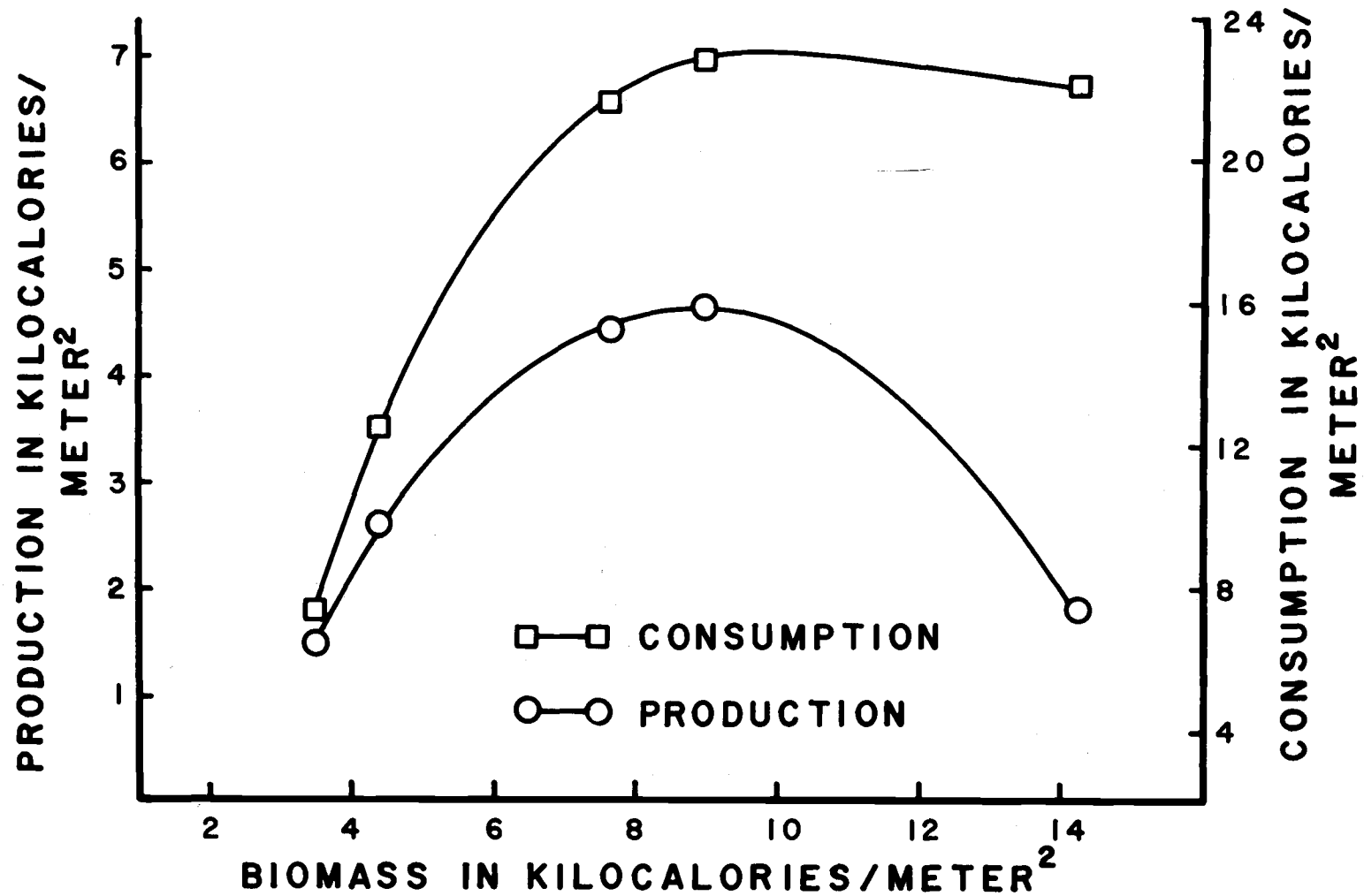


Figure 11. Relationships between trout production and trout biomass and between trout food consumption and trout biomass at low, intermediate, and high trout biomass levels during the winter 1964 experiment.

drifting organisms does not usually materially reduce the benthic population. These relationships were obscured when combined food consumption and combined production of the stonefly naiads, sculpins and trout were plotted against the combined biomasses of these species (Figure 9). The more important competitive relations became apparent, only when the feeding behavior of the sculpins and stonefly naiads and that of the trout were considered so as to make it possible to relate various consumption and production values to more appropriate biomasses. Even these more careful analyses would have failed to demonstrate those relations had the stocking ratios of the carnivores been different.

The results of the summer 1965 experiment tended to confirm previous conclusions regarding sculpin food consumption, production, and biomass relationships. Sculpin production and food consumption was low at low biomasses, highest at intermediate biomasses, and lowest at the highest biomasses (Figure 12). At the highest levels of sculpin biomass, two factors probably became important in reducing food consumption and production. Food organism production was probably reduced due to overcropping by the sculpins; and a greater proportion of the food which was available was required by the sculpins for maintenance. The relationship between trout production and trout biomass in this experiment was essentially the same as that found in the previous experiments. However, the relationship between trout food consumption and trout biomass was different (Figure 13). Trout food consumption was slightly less at the higher biomasses than it was at the next to the lowest biomasses, indicating that under some circumstances the trout were able to reduce their own food resource. The

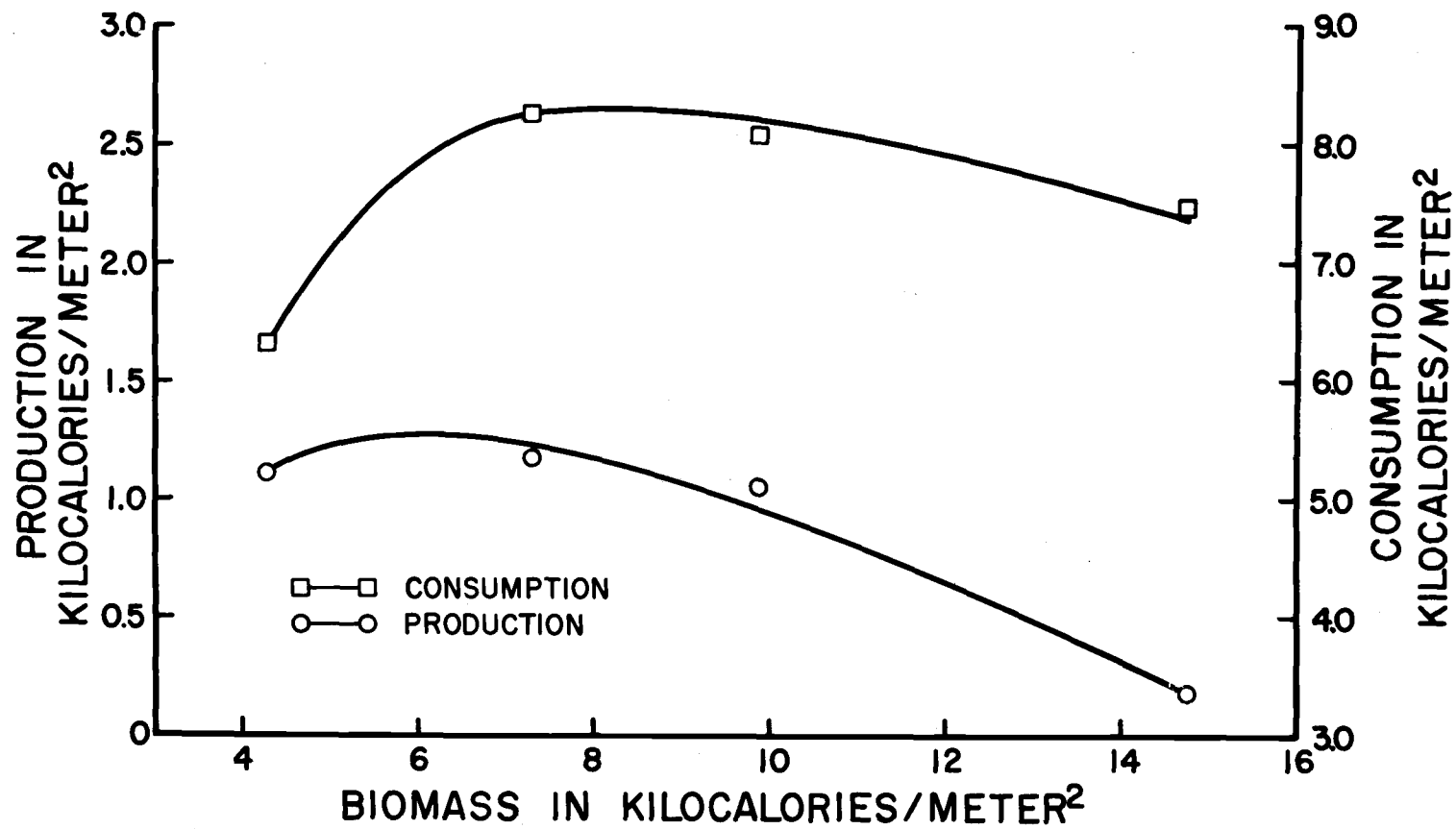


Figure 12. Relationships between sculpin production and sculpin biomass and between sculpin food consumption and sculpin biomass during the summer 1965 experiment.

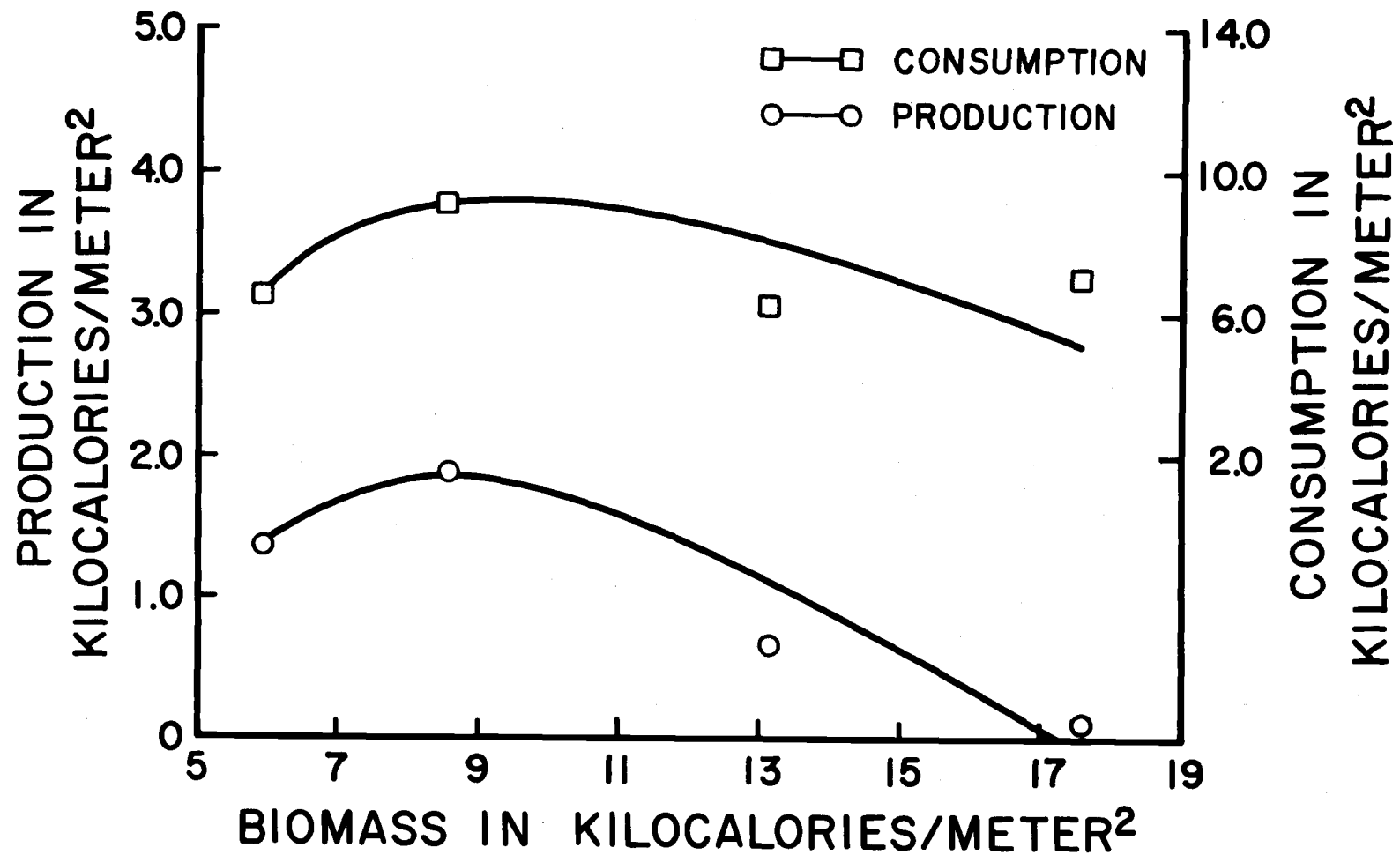


Figure 13. Relationships between trout production and trout biomass and trout food consumption and trout biomass during the summer 1965 experiment.

food source of the trout during this experiment was mainly drifting midge larvae. Larvae not consumed by the trout are not necessarily exported from the system but have the opportunity to reattach to the stream bottom materials as they are passed around the streams in the water being recirculated by the paddle wheels. When the trout feed predominately on immature life history stages or other forms that are not likely to reattach to the bottom, their effect on their food resource would be less. That the relationships shown in Figure 13 were apparent and could be interpreted with some confidence was due to the way in which the sculpin biomasses were stocked in combination with the trout. Had the biomass of sculpins been higher or lower in particular laboratory streams, the relationships between trout food consumption, production, and biomass would probably have been obscured due to the sculpins cropping more or less of the benthic organisms, this resulting in decreases or increases in drifting animals.

In order to study further the influences of the trout on their food resource, I stocked a wide range of trout biomasses (Table 4) in the streams without any other major carnivores during the fall 1965. In the first experiment trout production decreased with increases in trout biomass (Figure 14). Trout food consumption remained fairly constant with these biomass increases. Food consumption remained constant probably because the trout were cropping drifting organisms and did not decrease the biomass or production of their food organisms in the benthic environment. Trout production decreased, however, due to less food being available per unit of trout biomass. Negative production values were obtained because the biomasses and no doubt the



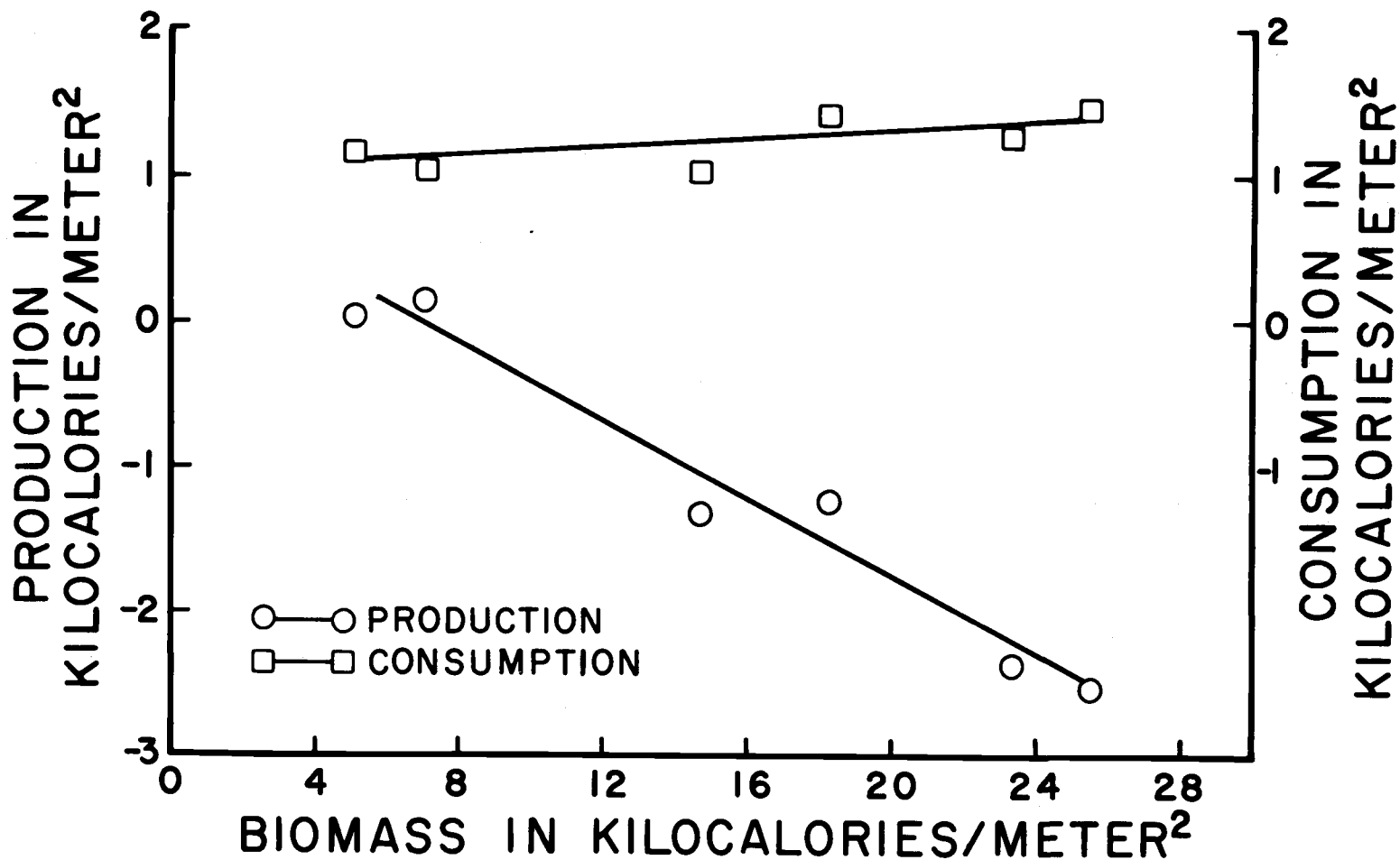


Figure 14. Relationships between trout production and trout biomass, and trout food consumption and trout biomass during the first fall 1965 experiment.

production of herbivorous insects in the streams during this experiment were lower than during other experiments. The low biomass and production of insects in the benthic environment would necessarily reduce the number of drifting organisms.

The relationships between the food consumption, production, and biomass of trout were again studied in a second fall 1965 experiment, in which trout were stocked in increasing numbers in the six streams without any other major carnivores being present (Table 4). These relationships in this experiment (Figure 15) were found to be similar to those of the first fall 1965 experiment (Figure 14). Production of trout was low at all biomasses and decreased with biomass increases. Food consumption increased somewhat with increases in biomass, indicating greater efficiency in cropping the food resource by the trout at the higher biomasses. The larger numbers of trout at the high biomasses, exploiting a relatively more limited food supply, appear to have been able to capture a larger percentage of the drifting organisms than could the fewer trout at the lower biomass levels. When food is relatively less available, ration size decreases, but fewer food organisms escape capture.

Differences in relationships between trout food consumption, production and biomass in different experiments (Figure 11, 13, 14 and 15), were due in part to differences in the levels of food organism production. Examination of the food consumption and production of carnivores in relation to their own biomass is helpful to clarify relations between increases in biomass and increases in food exploitation and in maintenance costs. Such an examination cannot vigorously take

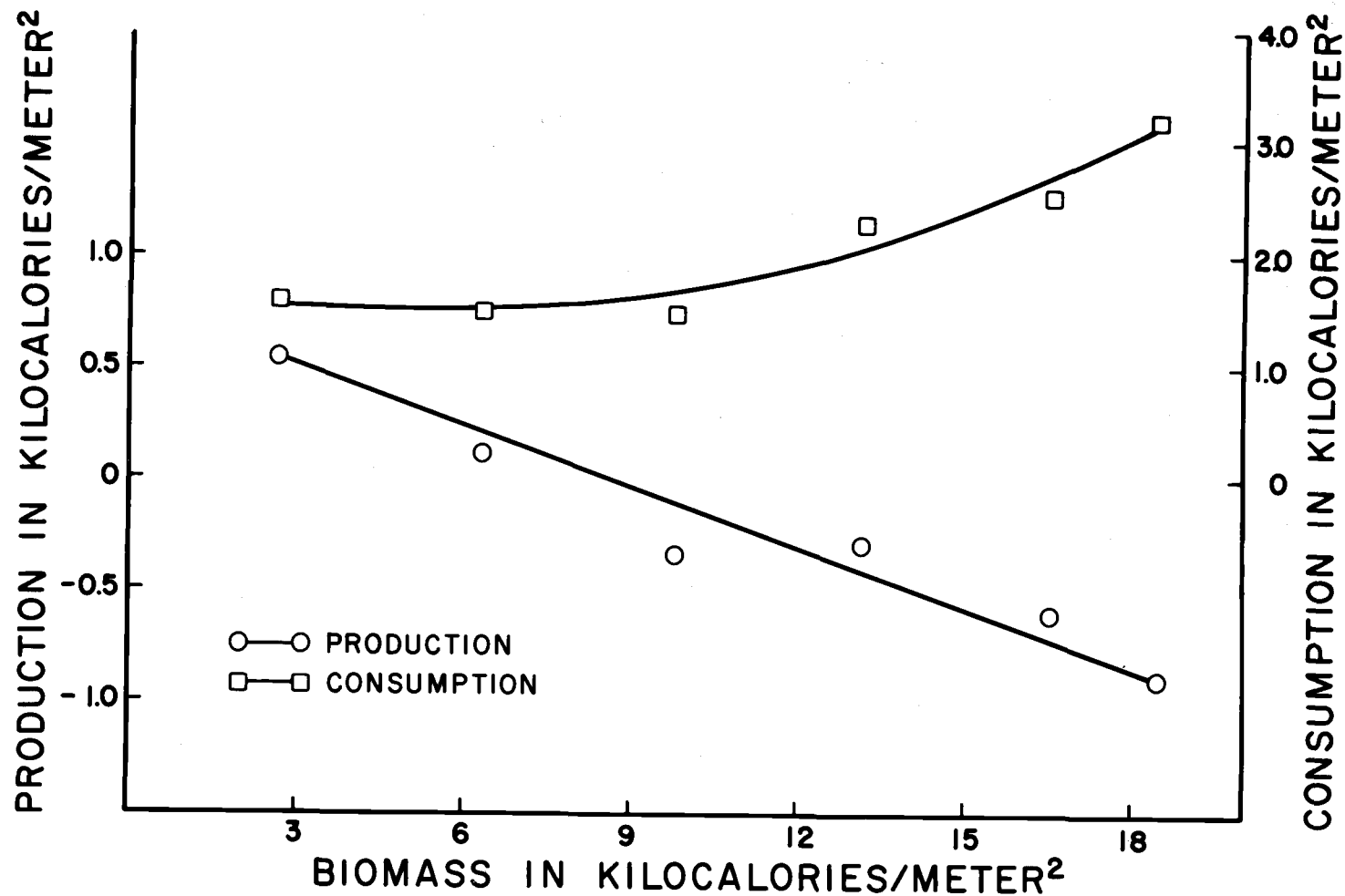


Figure 15. Relationships between trout production and trout biomass, and between trout food consumption and trout biomass during the second fall 1965 experiment.

into account the important influences differences in food organism production will have on the availability of food organisms and their consumption by predators. Such differences may be due to differences in the capacity of the streams to produce food organisms or differences in the effects the carnivores themselves have on the production of their food. Food density might be expected to be influenced in either case and food density is intuitively appealing as a measure of food availability.

The effects that sculpins and stoneflies have on the density of their food organisms can be observed when the biomass of food organisms per square meter ( $\text{kcal/m}^2$ ) is plotted against combined biomasses of these carnivores (Figure 16). These food organism densities are based on means of the biomass samples taken from the streams during the period the carnivores were present. The density of food organisms decreases as combined stonefly and sculpin biomass increases. The points shown at zero carnivore biomass (Figure 16) are means of the food densities present in all streams used in an experiment before any carnivores were stocked. In two cases these points appear near an extrapolation of the curve to zero biomass, but in one case a point is much lower than this. That the mean food organism density when carnivores were present was higher than the initial density indicates production of food organisms was somewhat higher than consumption and other fates during the experiment. That the points should all lie so near to the curve defining the food density-carnivore biomass relationship suggests that the impact of these benthic carnivores on the density of their food organisms is greater than that of seasonal or

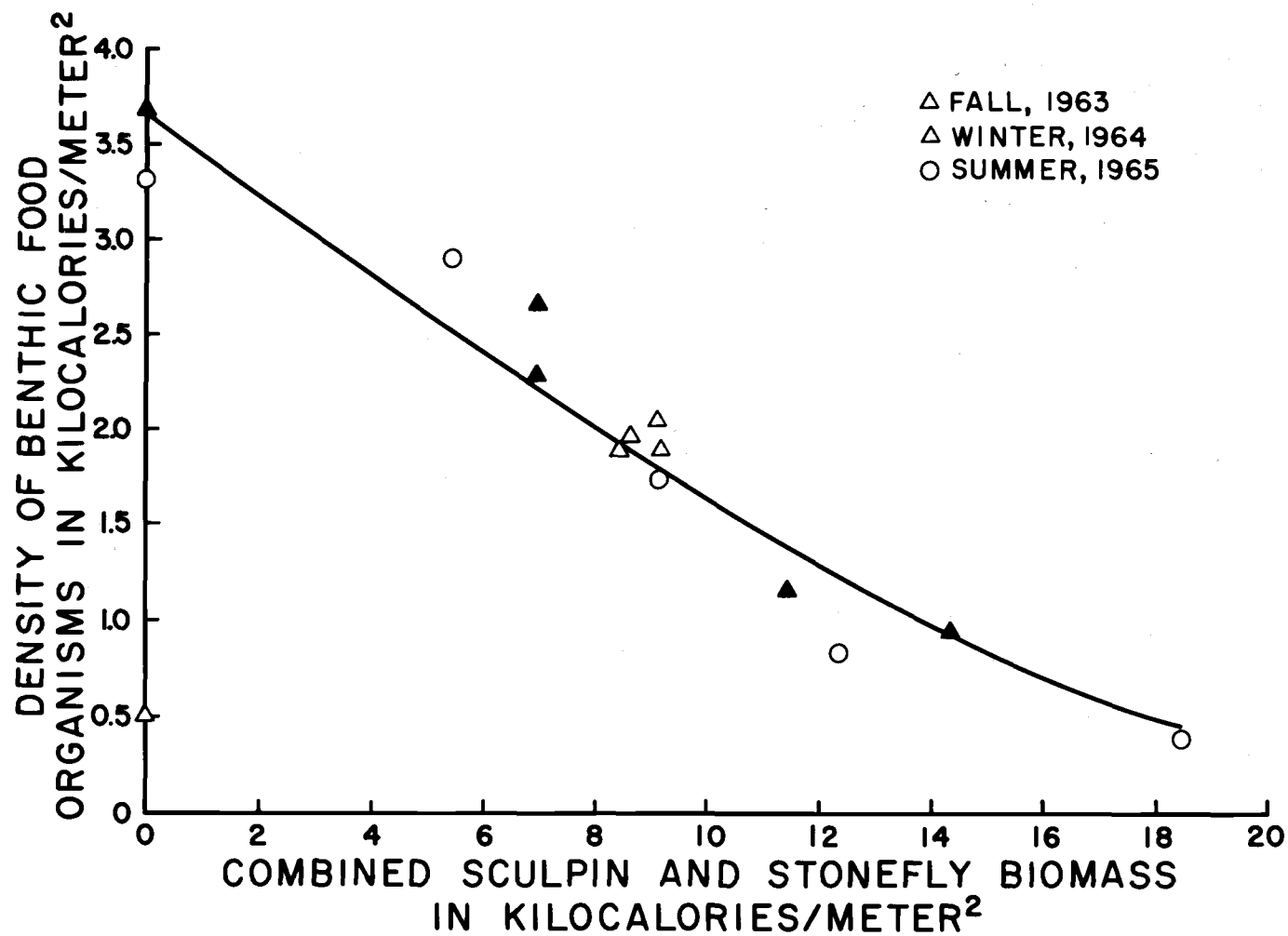


Figure 16. Relationship between combined sculpin and stonefly naiad biomass and density of benthic food organisms for all experiments in which either sculpins or both sculpins and stonefly naiads were present in the stream communities.

other differences in food organism production.

The density of drifting food organisms in  $\text{cal/m}^3$  was plotted against total carnivore biomass (Figure 17) to illustrate the effect of trout and other carnivore biomass on the density of the food resource of the trout. The points at zero biomass are means of the densities of drifting food organisms present in all of the streams used during a particular experiment before any carnivores were stocked. All other food organism densities are means of the densities observed in the streams during the period the carnivores were present. The effect that trout alone have on their food resource is shown (Figure 17) for the two fall 1965 experiments during which trout were the only major carnivores present. Such a graphical analysis is not satisfactory for the other experiments in which stonefly naiads and sculpins were stocked in addition to trout, because it is not possible to separate the effects the trout have on the density of their food from the effects of sculpins, stonefly naiads, and differences in food organism production.

The effects that trout can have on the density of their food can best be shown by plotting the density of drifting food organisms against stonefly naiad and sculpin biomass and by identifying arrays of points representing similar trout biomasses (Figure 18). Lines have been drawn near points at which trout biomasses were similar. The arrows drawn downward connect relationships found during the same experiment at different trout biomasses. Thus in the case of the summer 1965 experiment, trout biomasses for points near the upper curve were approximately  $9 \text{ kcal/m}^2$  and for points near the lower curve were

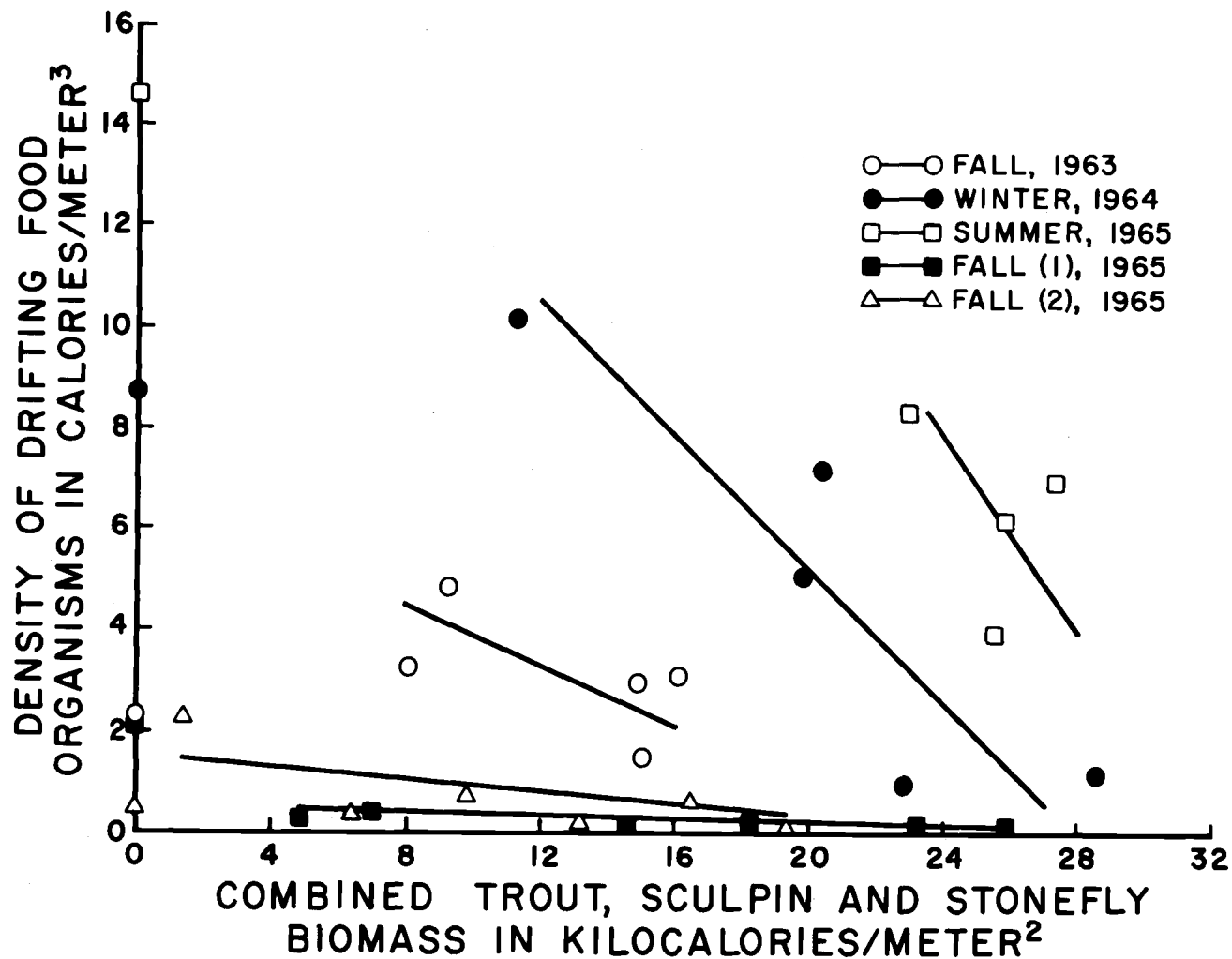


Figure 17. Relationships between density of drifting food organisms and combined stonefly naiad, sculpin and trout biomass for all experiments performed. Only trout were present in the two fall 1965 experiments.

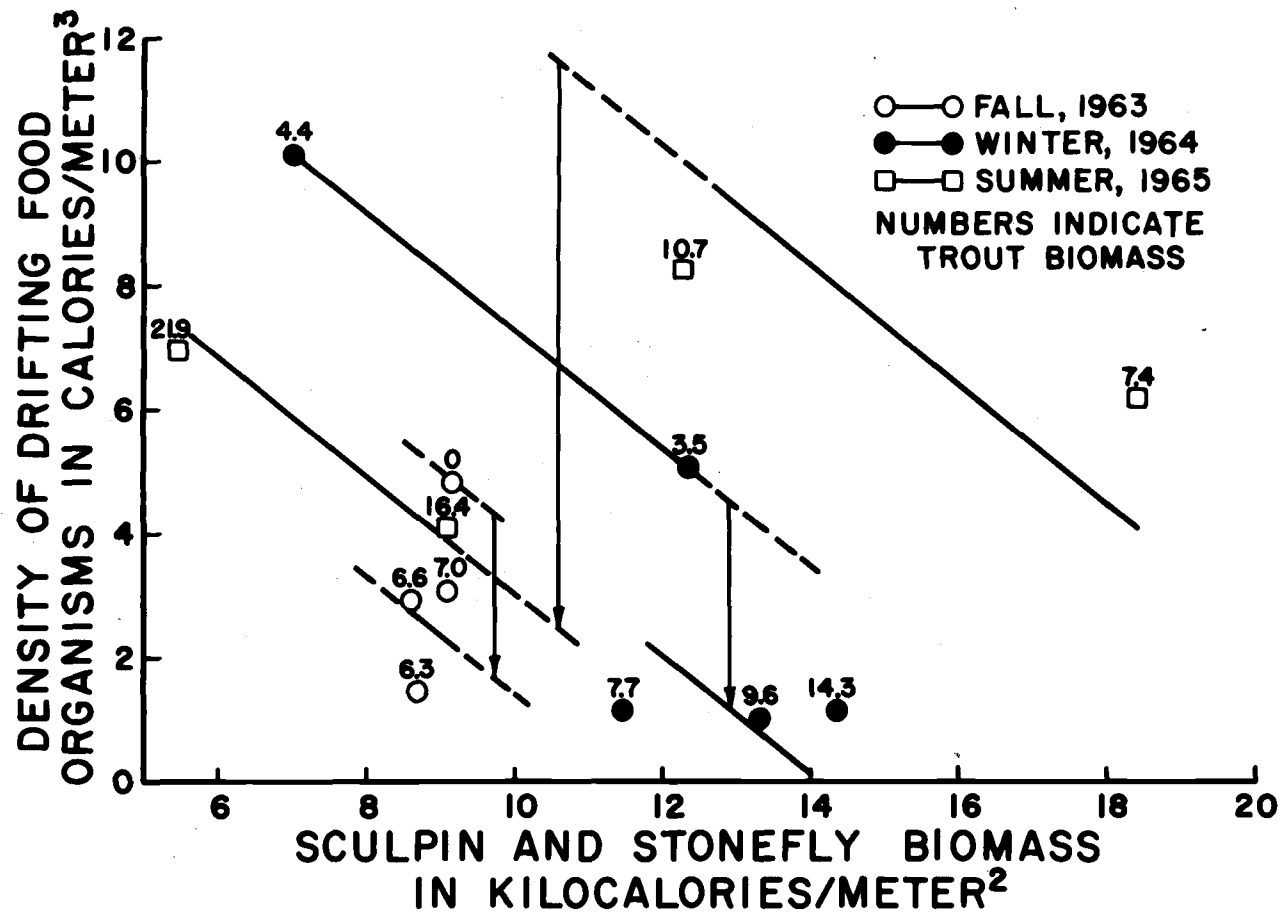


Figure 18. Relationships between density of drifting food organisms and combined sculpin and stonefly naiad biomass showing impact of increased trout biomass on food organism density.



approximately  $19 \text{ kcal/m}^2$ . The distance between the two curves represents an increase of  $10 \text{ kcal/m}^2$  in trout biomass. This biomass increase reduced the density of drifting food organisms by approximately  $9 \text{ cal/m}^3$ . The data I have are insufficient for such a graphical analysis, which I have introduced here only to illustrate a means of separating the effects different carnivores and levels of food organism production have on the density of trout prey. The effects of differences in food organism production are indicated by differences in the density of prey at points where carnivore biomass are similar. The slope of a particular line indicates the effect the sculpins and stoneflies have on the density of trout prey.

Food Density, Food Consumption, Respiration,  
and Growth of Sculpins and Trout

Ivlev (1961), in his studies of the bioenergetics of a population of the bleak, Alburnus alburnus in a hatchery pond attempted to quantify various ecological and physiological parameters which could lead either to the success or failure of the population. After determining values for respiration, growth, and food consumption under one set of conditions, Ivlev computed changes in these quantities as a function of food density by means of a mathematical model. I have made direct measurements of the food concentration and growth of sculpins and trout under different sets of conditions. Food consumption rates have been taken from the appropriate growth rate-food consumption rate curves previously described. Values for respiration have been derived by subtracting energy values for food not assimilated and growth from total food consumed thus giving respiration or energy expended. The

relationships between the food consumption, growth, and respiration of the sculpins and trout and the density of their prey can be examined with the aid of graphs.

The growth rate of the sculpins increased as the density of their food organisms in the benthos increased (Figure 19). This was a result of the increases in food consumption rate which occurred with increased prey density (Figure 20). Respiration of the sculpins increases as food density increases (Figure 21) due primarily to the increased cost of food handling caused by the larger amount of food consumed. Even though respiration increased at the higher food densities, the proportion of the total food consumed that went to respiration at the higher food densities was smaller than the proportion of the food that went to respiration at lower food densities, leaving a greater amount of food available for growth.

Growth rates of the trout, increased as the density of drifting food organisms increased (Figure 22). The rate of food consumption by trout, as in the case of the sculpins, increased as food density increased (Figure 23). Respiration of the trout also increased with increases in food density (Figure 24). Again, the amount of respiration is a smaller proportion of the total food consumed at the higher food densities than it is at the lower food densities, thus allowing for increased growth rates at increased consumption rates.

The variation in the relationships between growth, food consumption, and respiration rates of sculpins and trout and the density of prey organisms is admittedly large. However, this is not surprising as the data I have used are from five separate experiments performed

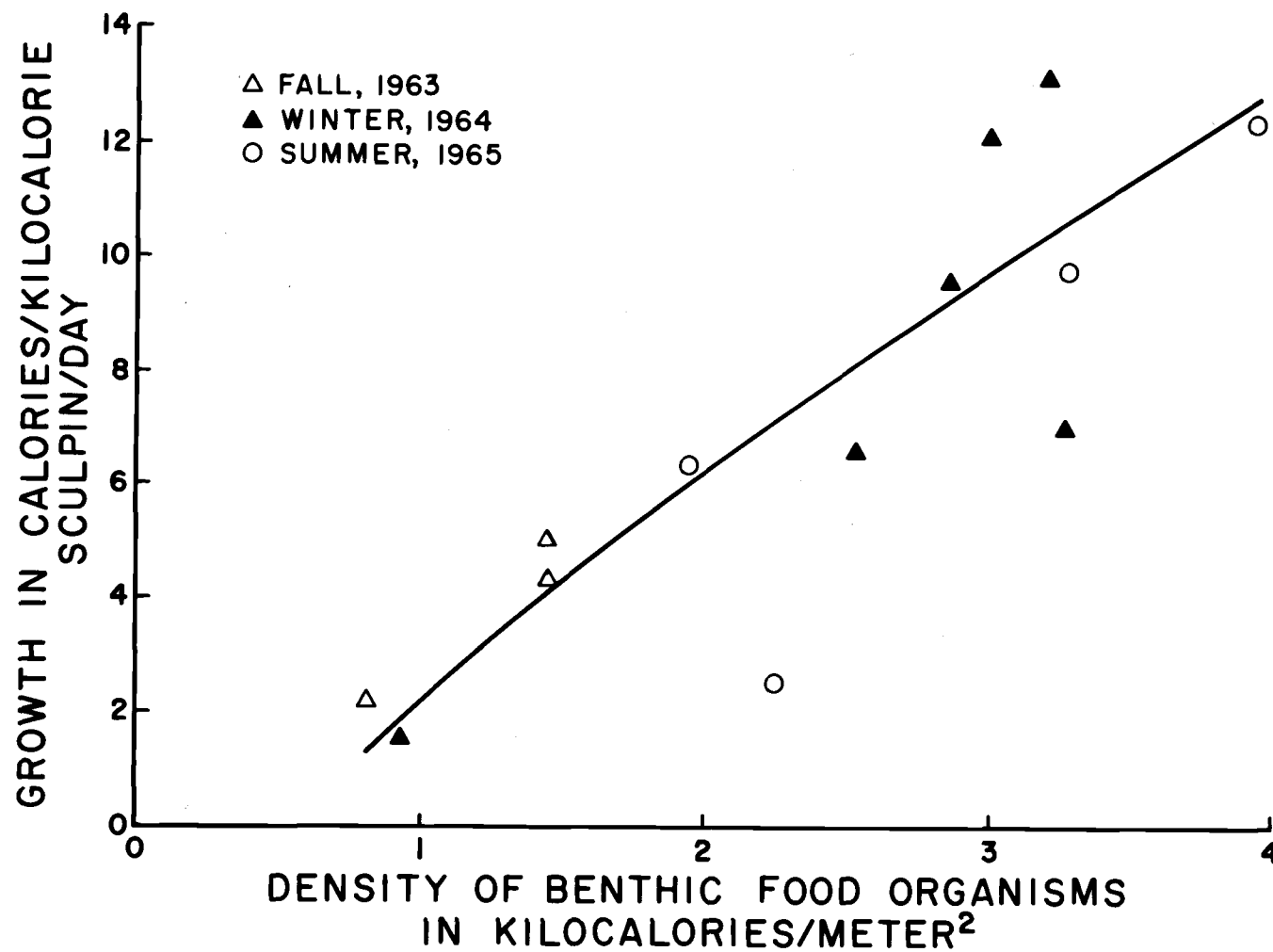


Figure 19. Relationship between density of benthic food organisms and growth rate of sculpins during the fall 1963, winter 1964, and summer 1965 experiments.

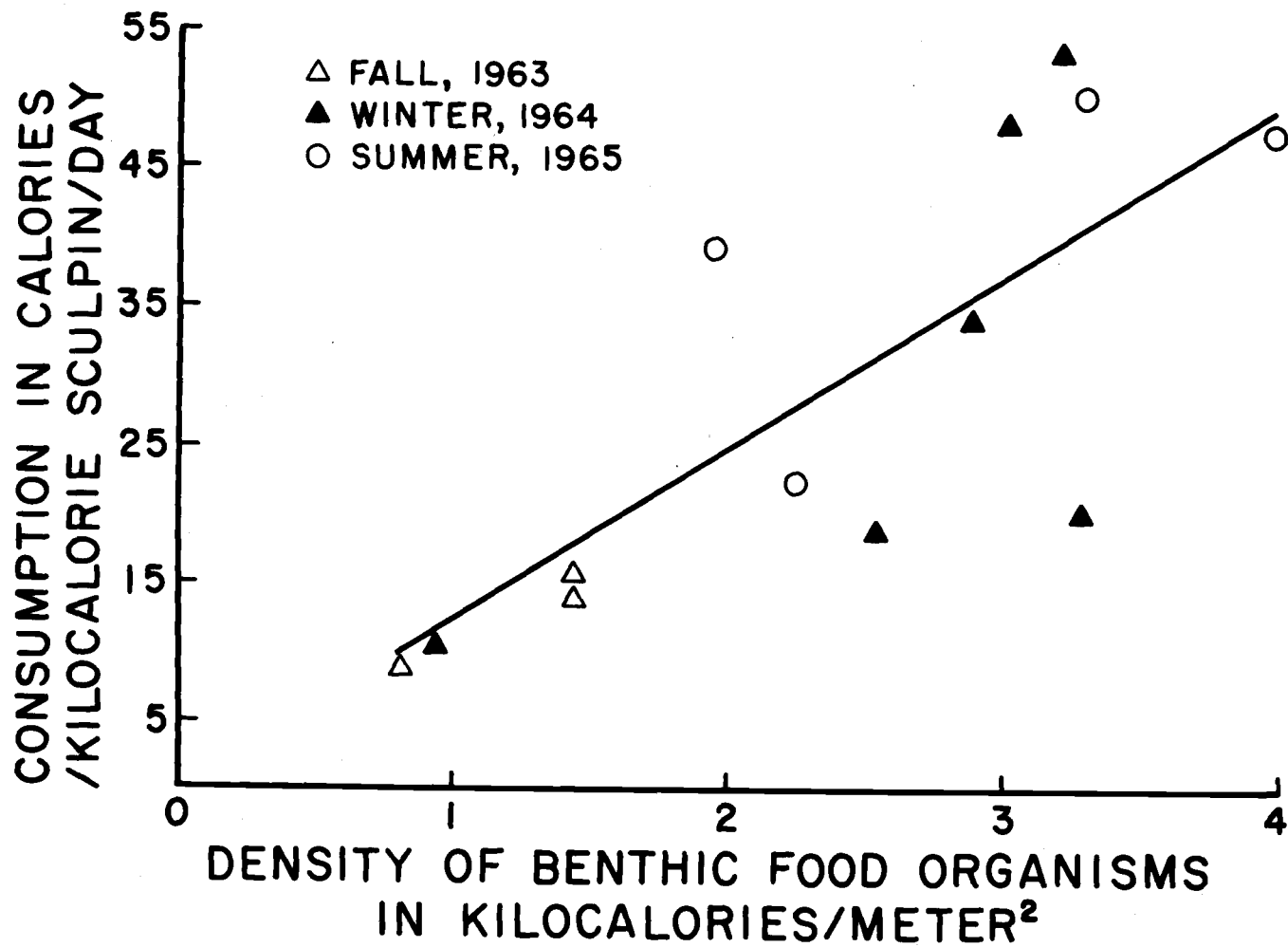


Figure 20. Relationship between density of benthic food organisms and food consumption rate of sculpins during the fall 1963, winter 1964, and summer 1965 experiments.

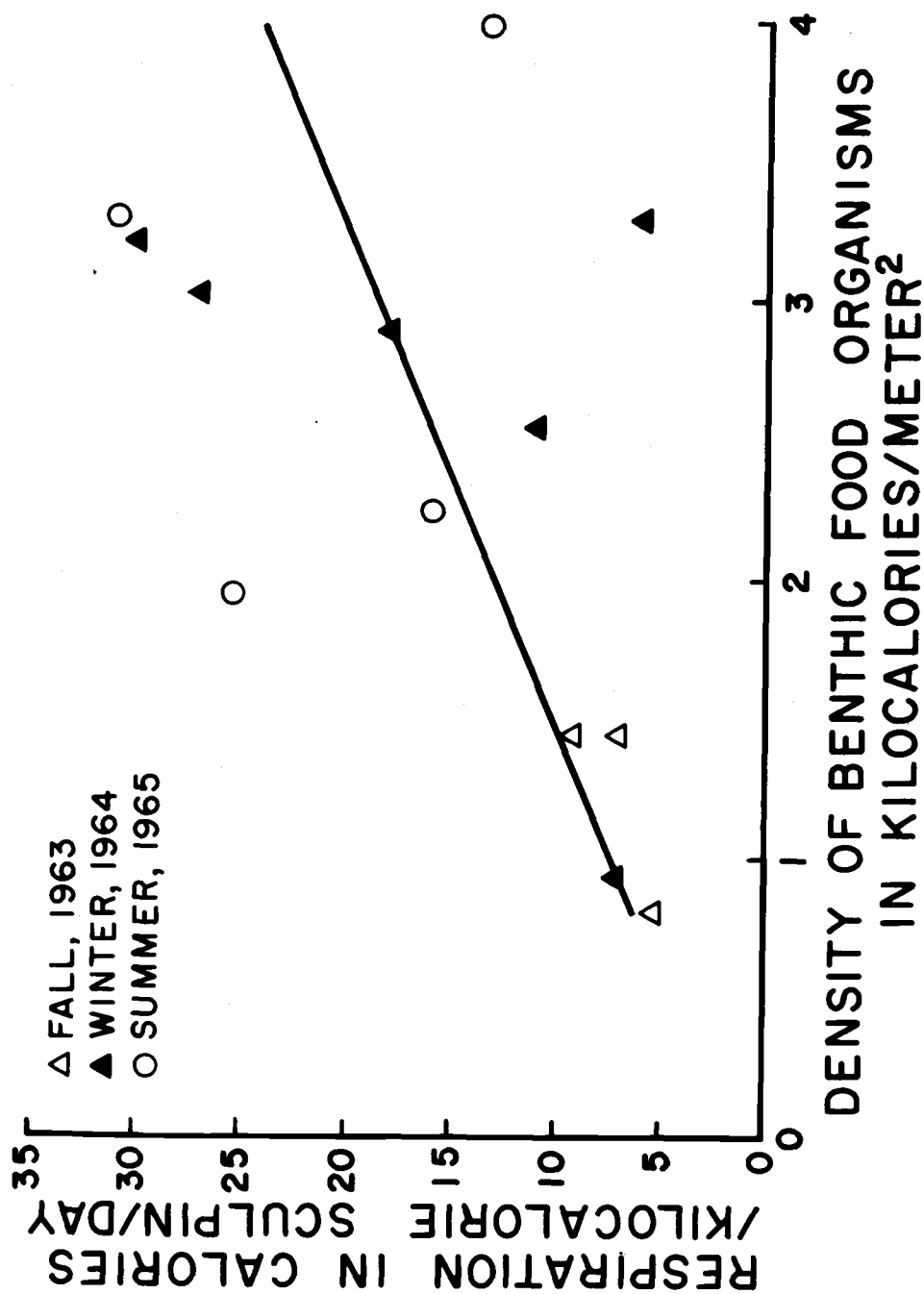


Figure 21. Relationship between density of benthic food organisms and respiration rate of sculpins during the fall 1963, winter 1964, and summer 1965 experiments.

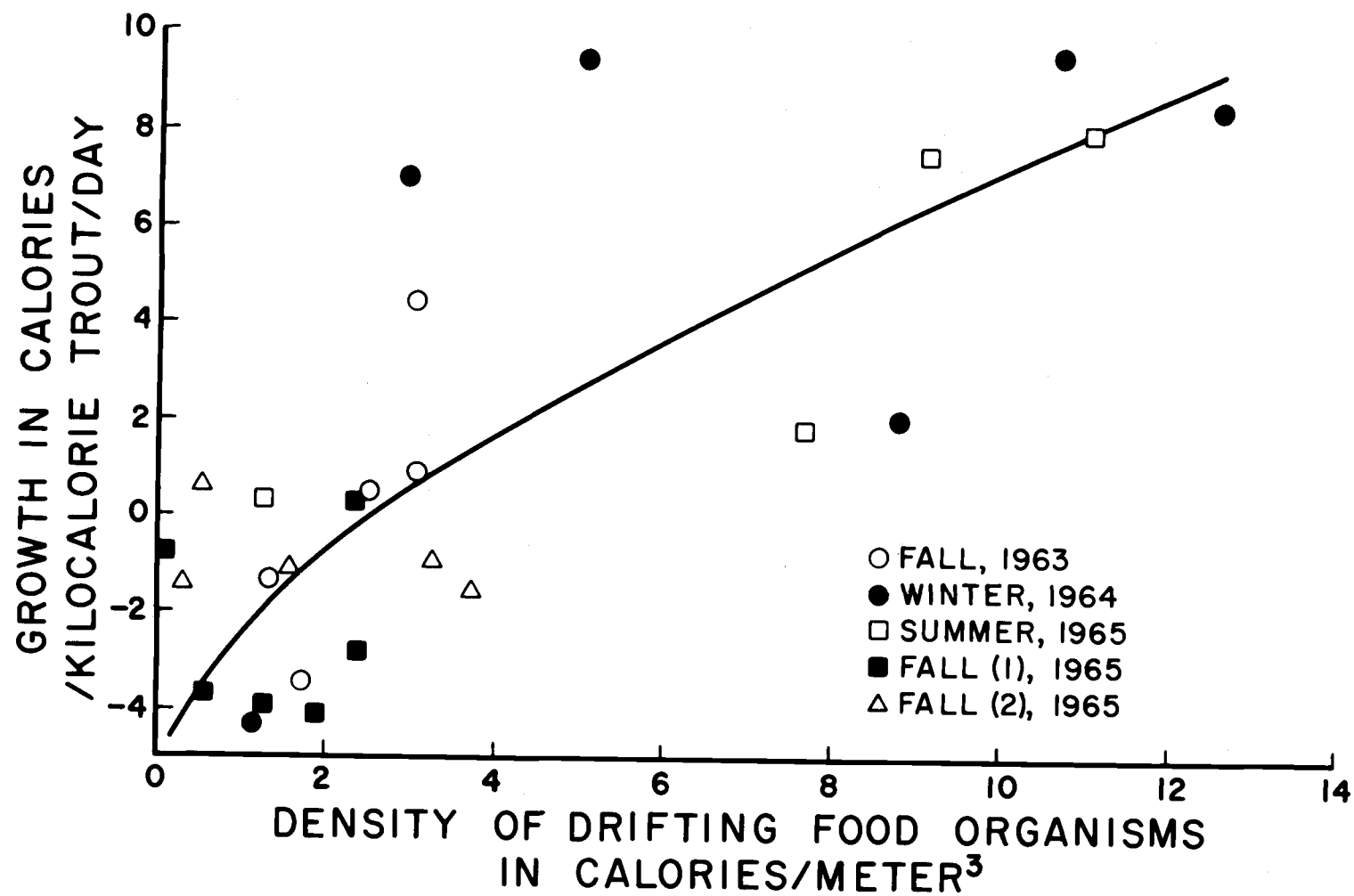


Figure 22. Relationship between density of drifting food organisms and growth rate of trout during all experiments.

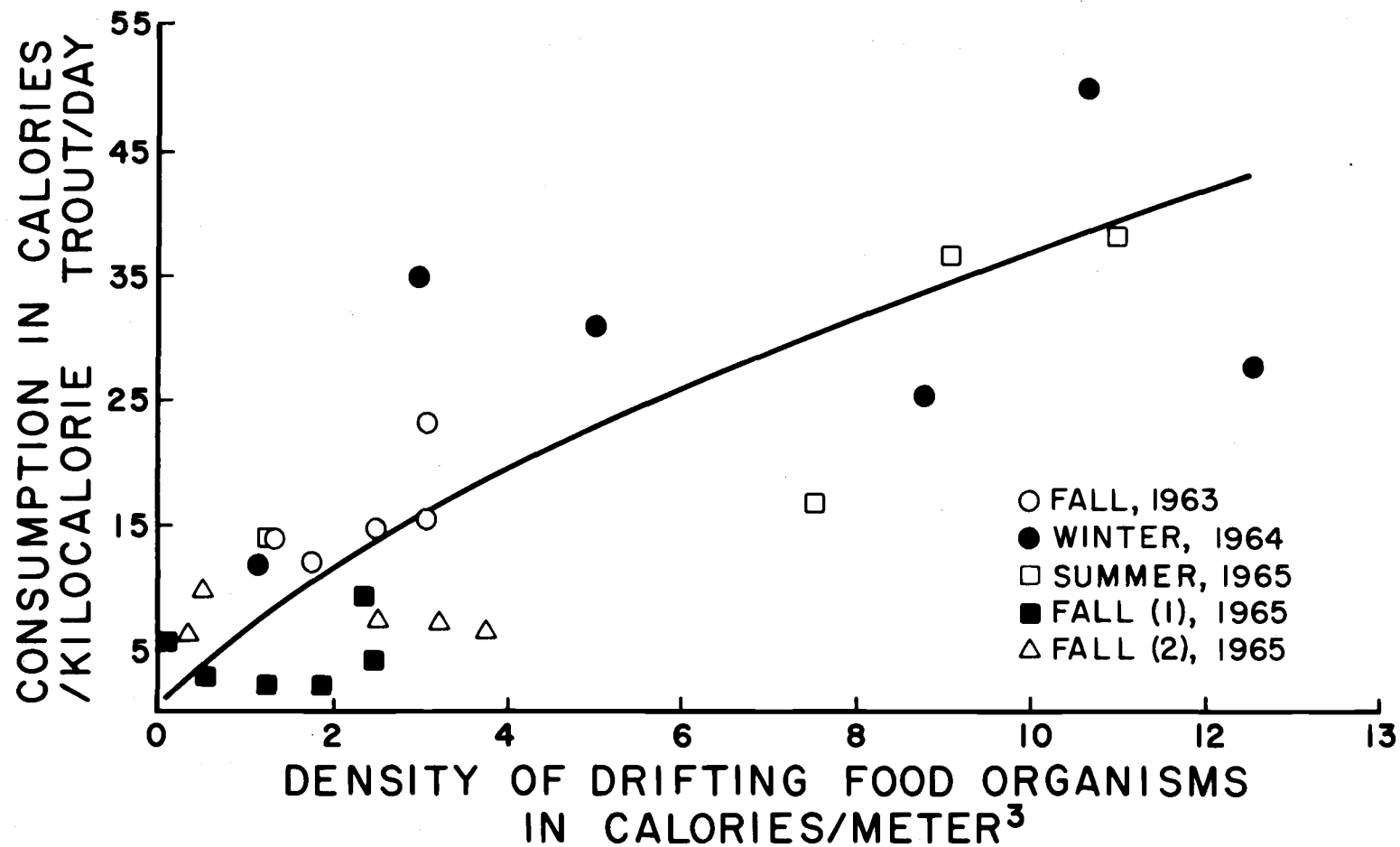


Figure 23. Relationship between density of drifting food organisms and food consumption rate of trout during all experiments.

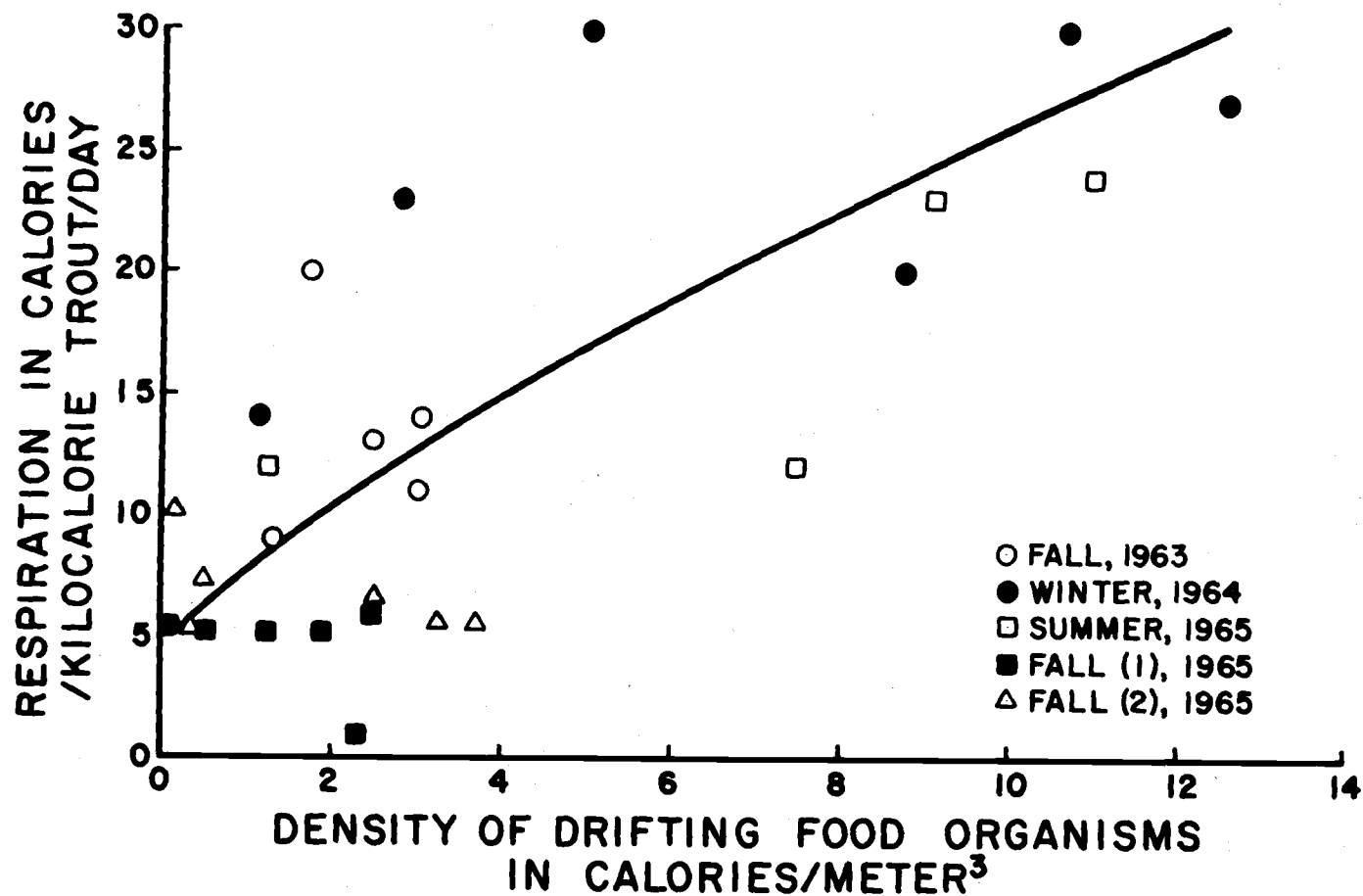


Figure 24. Relationship between density of drifting food organisms and respiration rate of trout during all experiments.



at different seasons of different years with widely varying biomasses of different carnivores. That relationships are apparent indicates food density is a useful parameter for evaluating the food consumption and growth opportunity of a predator, irrespective of the factors influencing this density. Much of the variance is due to experimental error. The measurements that have been used to estimate food organism density were not made for this purpose, and better methods can probably be developed.

## DISCUSSION

## Problems of Defining and Studying Trophic Levels

Probably in no study of an ordinarily complex ecosystem has sufficient information been obtained on the food habits of the different animals to justify assignment of all of these animals to particular trophic levels. If such trophic levels could be defined, and this is doubtful (Peterson and Jensen, 1911; Ivlev, 1945; Darnell, 1958; Warren et al., 1964), the effort required to determine the rates of food consumption, assimilation, production and respiration of the energetically important species would be monumental. In the twenty years since Lindeman (1942) proposed the use of trophic levels, no one has been successful in actually determining trophic level efficiencies for a complex ecosystem. Even in simpler systems, such as the ones I have been studying, where trophic levels are reasonably well-defined, there is some question that totaling food consumption and production by trophic levels leads to any real understanding.

In this thesis the difficulty of analyzing the food consumption and production of even two or three carnivores in relation to either their individual or combined biomasses has been demonstrated. The relationships that appeared to exist between food consumption and total carnivore biomass and between total carnivore production and total carnivore biomass (Figure 9) contributed little to my understanding of the ecosystem being studied. The adding of food consumption and of production values for the carnivores obscured the relationships that existed between the production and food consumption

and the biomass of the individual species (Figures 10 and 11). Even then, these relationships (Figure 10, 11, 12 and 13) were apparent only because I was careful to stock the different carnivores so that the expected relationships would not be obscured. As mentioned previously, had the proportion of stonefly naiads or sculpins been greater in any of the laboratory streams in which trout were present, the relationships between trout food consumption and production and trout biomass could not have been detected (Figure 11). A greater or lesser number of sculpins or stoneflies would have altered the concentration of drifting food organisms available to the trout.

It is useful to examine the relations between the consumption and production and the biomass of a species. Production is a function of biomass, for production is determined by the biomass and growth rate of a species. It is necessary, however, to relate the production of a species to its own biomass. If for example, we plot stonefly production (product of biomass and growth rate) against the combined biomasses of sculpins and stoneflies rather than against the biomass of stoneflies, the resultant relationship, if any, will contribute little to our understanding. Biomass is also an index to competition. In Figure 12 for example, the food consumption and production of sculpins decreased for two reasons as the biomass increased. The increased biomass of sculpins reduced the production of food organisms, and maintenance costs increased with increased biomass. The use of the appropriate biomass is necessary to understand the interrelationships that exist, and the separation of the appropriate biomass is not always possible in a complex system where more than one carnivore is present.

The problems that are inherent in considering various parameters as functions of biomass suggest that more discreet methods of examining data on the trophic relations of animals are necessary if we are to increase our understanding of the reasons for the success of individual species. Such understanding will be required before more general understanding of the organization of ecosystems is possible.

### Characteristics of the Environment and the Structure, Physiology, and Behavior of a Species

We may assume that each species has evolved so as to maintain itself successfully in its particular environment. Each species is adapted in its structure, physiology and behavior to cope with the physical, chemical, and biological factors of its niche. Therefore, any real understanding of the success of a species has to be in terms of how it copes with these factors, an important one of which is its energy resource. It is necessary to understand how a species is adapted to exploit its energy resource, within the limits other factors of the environment place on the species. The sculpins I have studied have a small protractile mouth and no air bladder, and are well-adapted to exploit small benthic organisms as a source of food. The trout, on the other hand, possesses an air bladder and a larger mouth and are better adapted for feeding on drifting organisms. As would be expected, my studies have shown these animals to feed in the manner for which they are best adapted.

We must understand the interactions that exist between species and other competing species because of the way in which they are adapted. For example, I found that the stonefly naiads and sculpins

compete directly with each other in removing food organisms from the benthos and can influence the food consumption and production of the trout by reducing the numbers of organisms entering the drift. Conversely, in the laboratory streams, the trout have little influence on the food consumption and production of the stoneflies and sculpins, presumably because the animals they are removing from the drift do not usually return to the benthic environment. To understand the interactions that exist between a species and its energy resource, complex relationships must be reduced to their simplest possible terms. In simplest terms, the individual fish or other animal is influenced most immediately, so far as its energy resource is concerned, by the density of the food in its surroundings.

#### Relation Between Growth and Food Density

At any given moment of time, it is the density of food that will determine the amount a fish is able to obtain and the respiratory cost of obtaining it, and the amount it obtains will to a considerable extent determine its total metabolic rate. The food density with which we concern ourselves must be the appropriate food density, appropriate in terms of size, availability, and choice of the fish. Even for a single species, which food density determinations are appropriate will vary with the life history stage or age class of the fish. Certainly with different species, the appropriate methods of evaluating their food resources will vary. Thus, for the sculpins, the biomass of insects actually inhabiting the benthic environment was found to be the most appropriate measure of food density. For the trout, the most

appropriate measure of food density appeared to be the biomass of insects drifting in the streams.

In addition to most directly expressing the availability of food for a given predator species, food density most simply reflects the impact that all other competitors have on the availability of food for the given predator. Thus, the influence stonefly naiads and sculpins have on the food availability for trout can most simply be examined in terms of the effects they have on the density of drifting insects. Further, the effects the trout has on its own food availability can most conveniently be examined in this manner. Finally, the appropriate food densities provide a parameter which includes not only the combined effects of intraspecific and interspecific competition on food availability, but also includes the effects of differences in the levels of production of the food organisms involved.

#### Other Studies on the Relationship Between Food Density and Growth of Animals

Biologists have long been aware that some very general relations must exist between food density and the food consumption and growth rates of a predator. That these relationships have been demonstrated in few if any natural ecosystems, as they were demonstrated in my simple ecosystems, may be due in part to the greater complexity of natural systems. A more likely reason for such relationships not having been generally observed in nature may be that the growth of the predators has not usually been measured over sufficiently short periods of time and has not been related to the appropriate food densities. Less attention seems to have been given to questions of food density as

interest in the computation of production of predators and prey has developed. This is surprising in view of the difficulty of determining production values.

Richman (1958), in laboratory studies on the energetics of Daphnia pulex, examined the influence of food density on food consumption, growth, respiration, and reproduction. He found for Daphnia, as I did for sculpins and trout, that food consumption and growth increased with increases in food density.

Ivlev (1961) determined the growth rate of a plankton feeding fish, Alburnus alburnus, at one food density in a hatchery pond. He then attempted to estimate what the food consumption, growth, and respiration of this fish would be at different food densities by means of a mathematical model relating food consumption rate to food density. To do this he needed information on maximum rations and routine and active metabolic rates, which he determined in laboratory studies. The results of Ivlev's analysis seemed to indicate that food consumption and growth rates increase with increases in food density but that respiration rates decline. Ivlev assumed that changes in the respiration of the fish would be due primarily to changes in swimming activity necessary to obtain food, and his results would be expected on the basis of this assumption. He did not take into account increase in respiratory costs of digesting, assimilating, and storing of food materials that would be occasioned by increases in food consumption rates. I have shown that the costs of food handling may be considerably more than the cost of capturing food and that respiration rates, at least in the sculpin and trout, probably increase with increases in food

density. There is another striking difference between my findings and those of Ivlev. Although structural, physiological, and behavioral differences in species make it important that they be compared only with care, both the trout in my streams and the plankton-feeding fish Ivlev studied obtained their food from suspension in the water and were more or less continually active while doing this. It is surprising that the trout were able to maintain an energy balance permitting growth at food densities of about 2.6 calories per cubic meter of water whereas Alburnus alburnus in the hatchery pond appeared to maintain such a balance only at densities higher than 600 calories per cubic meter. Differences between the plankton-feeding minnow and the benthic-feeding sculpin in their structure and feeding behavior make comparison between these two species difficult. It is probably only fortuitous that the density of food organisms per square meter which barely permitted sculpin growth was nearly the same as the density of food organisms per cubic meter that permitted the minnow to grow. We have, perhaps inappropriately, expressed the density of food organisms of the sculpins using a square meter as the unit area even though individual sculpins in our stream undoubtedly exploit a much smaller unit of bottom area.

#### Relationships between Production, Consumption, Decomposition and Density of Food Organisms

The food density surrounding the fish at a moment in time is dependent on the dynamic relationships between the production rates of the different food organisms and the rates at which they are being consumed by different predators, dying and being decomposed, and by



the rates at which they are leaving the limits of the ecosystem. Thus, though density of food organisms may most immediately influence a predator, density itself is the variable outcome of many complex processes going on within the ecosystem. Presumably, for any successful predator population the density of its food organisms must be such as to permit it to maintain an energy balance favorable for growth over an extended period of time.

The production rate of any one species of food organism is a function of the productivity of the ecosystem for that form, the life history of the form, its biomass, and the age structure of its population. The rate at which it is consumed depends on the populations of predators utilizing it and on its own availability. The rate at which it is decomposed as well as the rate at which it leaves the ecosystem depend on its population size and structure and on other factors. It is the outcome of these complex interacting processes that determines the density of the food organism at any point in time. One of the significant findings of my laboratory stream studies is that whatever circumstances result in a particular prey density, it is that density which determines the food consumption and growth rate of the predator at a particular time.

#### Determination of Ecotrophic Efficiencies

Although the food density may provide the simplest means of evaluating the food opportunity of a predator, the extent to which a predator is utilizing its food resource cannot be determined on the basis of density information alone. The extent to which a particular

predator is utilizing its food resource can perhaps best be expressed as the ratio of its food consumption to the production of its food organisms over a period of time. Such an ecotrophic or cropping coefficient not only shows the proportion of the prey production being utilized by a particular predator, but can be compared to similar coefficients for other predators utilizing the same prey resource. The difficulty of estimating an ecotrophic coefficient can hardly be overestimated as it entails not only the estimation of the consumption rate of the predator, but the individual production rates of the various prey organisms.

#### Predictive Value of Food Density-Growth Information

Because production, even of a single species, is not only a function of the growth rate of that species but also of the biomass and age structure of the species, no simple relationship can be expected to exist between food density and production as has been shown to exist between food density and growth rate. Thus, food densities that may permit high levels of production in one ecosystem may not permit high levels of production in another ecosystem. On the other hand, if we consider that a species in itself has common structural, physiological and behavioral characteristics, it is reasonable to suppose that food densities that permit an energy balance favoring a certain growth rate in one ecosystem will approximate the densities that permit the same growth rate in similar ecosystems. If this is so, the food density-growth relationships for an individual species for a particular ecosystem may have considerable value in predicting food densities that will favor growth in similar ecosystems.

I have re-examined some of the data on which Warren et al., (1964) based their paper on the production of trout in an experimental stream enriched with sucrose. During the period of the year from February through June when most of the growth and production of trout occurs in this stream, there was a high correlation between density of drifting animals and the growth rate of the trout. This correlation tended to disappear at other times of the year when temperature and other factors influence the feeding behavior of the trout.

Careful laboratory experiments, though helpful in demonstrating that relationships between food density and growth exist, would not always be necessary to make food density-growth relationships of value. The ideas advanced here are important enough to merit studies being made on wild populations of fish in which the growth rates of particular age classes can be related to the appropriate food densities. If it can be shown that for a particular species in different but similar ecosystems food density-growth relationships are approximately the same, appropriate studies of food densities in similar ecosystems having that species may provide a valuable index to its growth potential at its existing biomass level.

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