

AN ABSTRACT OF THE THESIS OF

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Ecologists, whether working at the population or community level, recognize that there are density-dependent factors operating which influence fluctuations in numbers. One such density-dependent factor that influences this fluctuation in numbers is the nutritional base of the population, that is, the food supply. With the use of six laboratory streams in which simple aquatic communities developed and to which fish were added, the interdependence between the nutrient resources of consumers of interest from different trophic levels and the biomasses of these consumers of interest were studied from February 1964 through August 1968.

Growth and production of cutthroat trout (Salmo clarki) and reticulate sculpins (Cottus perplexus) were studied in laboratory stream systems having the same basic capacity to produce their food organisms, and in laboratory stream systems having different basic productive capacities. Density measurements were made on the

herbivorous insects and algae, and utilizable light energy was measured in order to examine density-dependence at different trophic levels.

Relationships were found that show growth rate of carnivores and herbivores to be functions of the density of their nutrient resource, and that the density of nutrient resources are functions of the density of the consuming carnivore or herbivore. Relationships showing the biomass of organic matter present in the streams to be a function of light intensity and current velocity were also shown. Such relationships between species of interest and their nutrient resources existed in systems having the same relative basic capacity to produce food organisms, and between systems having different basic productive capacities. Two types of relationships were found to exist, therefore. A negative correlation between the nutrient resource of a consumer and the consumers biomass was found in a single system or systems having similar basic capacities to produce food organisms. Between systems having different basic productivities however, a positive correlation was found between a consumers nutrient resource and the biomass of the consumer. When relationships can be found that show growth rate of a species of interest to be functions of the density of its nutrient resource, and that the density of nutrient resource is some function of the density of the species of interest, these relationships can be incorporated into simple models permitting prediction of the biomass of the species of interest that would

maximize its production.

Density measurements are being made continuously by ecologists. The application of such measurements in the analysis of trophic processes, however, has usually been limited to their use in estimating production. Examples of data from studies conducted in large lake systems, coupled with comparison of data from the laboratory systems are used to suggest an additional framework with which ecologists can examine the interactive processes within and between trophic levels. If the information on the competitive interactions of a consumer of interest and on intermediate links in the food chain of an ecosystem became available through intensive studies, the expenditure of considerable effort in the manipulation of trophic processes would be warranted. The fact that density-dependent food relationships do exist in nature is documented and their utility in studying ecosystems of varying complexity discussed.

Density Dependent Relationships in Trophic Processes
of Simplified Stream Communities

by

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DENSITY DEPENDENT RELATIONSHIPS IN TROPHIC PROCESSES OF SIMPLIFIED STREAM COMMUNITIES

INTRODUCTION

Early man undoubtedly used his knowledge of the feeding behavior of animals to guide his hunting, and since his earliest husbandry of animals, man's knowledge of the nutritional requirements of the beasts he has kept has increased. By Aristotle's time, knowledge of the food habits of wild animals was appreciable, and the dominating of their activities by the search for food recognized. Over the hundreds of years to the present, naturalists have accumulated considerable knowledge of the food habits of animals. Nevertheless, I am aware of no reasonably extensive and complex ecosystem in which the food habits of even the more abundant animals are known.

Lindeman's (1942) magnificent contribution has, in very general terms, had two effects on the study of trophic relations, both important but not both good. His emphasis on the ecosystem with energy as a common denominator has encouraged a broad view and a search for principles in trophic studies. However, a hurried search for principles coupled with use of his simplifying trophic level assumption has encouraged publication and discussion of trophic level efficiencies when not only the food consumption and production but even the food habits of all of the more abundant species are unknown.

Much of the care of the naturalist has been discarded.

Ivlev's (1945) early warning that the "principle of 'trophic levels' does not, in all its endearing simplicity, correspond to the state of affairs in nature" went unheeded. Even were trophic levels to be a natural reality, the measurements necessary to determine the consumption and production rates of even the most important species in a complex ecosystem would preclude obtaining the data necessary to determine meaningful trophic level efficiencies. After an ambitious and imaginative study of trophic structure and productivity of Silver Springs, Florida, Odum (1957) had to conclude that "in spite of the efforts expended and the constancy and reproducibility of [the] ecosystem a really satisfactory system of measurements of herbivore and carnivore production has not been obtained." Hutchinson (1963), Lindeman's teacher and colleague, has more recently warned:

The original statement of the trophic dynamics point of view (Lindeman, 1942) and many subsequent studies have regarded the matter without much reference to the kinds of organisms involved in each level. At the time such an abstraction led to a great advance in understanding, but now, we must attempt, as always, to reintroduce what was discarded in the earlier effort to get some quantitative elementary understanding of the process.

It is perhaps too early to know whether or not Hutchinson's warning will have any more effect than did Ivlev's.

There is one other point regarding trophic levels that has received entirely too little emphasis. It can be simply stated:

Even in ecosystems where trophic levels might be reasonably defined and where it might be possible to measure the energy and materials obtained by all of the species of organisms and to measure their rates of assimilation, respiration, and production, the reduction of this valuable information to a series of ratios expressing the efficiencies with which energy is transferred from one trophic level to another is not making the highest possible use of this information. This is not to say such ratios would not contribute to our understanding of ecosystems; but it is to say that deeper understanding will come only from knowledge of the many processes that lead to these efficiencies, whatever the efficiencies may be. Were we to have the information necessary to determine trophic level efficiencies, we would have information that, analyzed in other ways, would make this deeper understanding possible.

Though I know of no instance of the production of a consumer and the production of its food organisms having been satisfactorily measured in nature, were this to be done it would be possible to determine a food chain efficiency. But such an efficiency, determined under only one set of conditions, has little intrinsic interest. It has been well established that the growth rate and hence the production of a species in a limited environment is a function of its biomass. The decline of growth rate with increasing biomass leads to production increasing from near zero at very low biomass to a

maximum at an intermediate biomass and then decreasing with further increases in biomass. A food chain efficiency, then, must increase from near zero to some maximum and then decreases with increasing biomass. Thus, an efficiency determined under only one set of conditions is only one value of an array of possible values. We should be interested in the causal relations leading to the array, not in any single value. It has been recognized that for an efficiency value to have any intrinsic interest, the system of food organisms and consumers must be in a so-called steady state; and it has been hinted not only that this condition may exist but that somehow efficiencies are maximized. All that we know about the numbers and biomasses of animal populations refutes the idea that they are constant from year to year. Fluctuations over many generations and years admittedly may be about some mean level, but for our purposes here, this idea has little conceptual or analytical value. We are not likely to conduct the extensive trophic studies necessary over long periods of time to establish either the fact or the values. And, more general biological interest lies in changes from generation to generation and their causes.

Thus, those who have followed Lindeman have quite properly emphasized the importance of considering entire ecosystems, have taken advantage of energy units as a common denominator, and have become aware of the important role of production rate; and they have

been encouraged to seek general principles, to ask big questions. The trophic level assumption, however, has quite improperly lead to a disregard for even the most necessary details of food habits and life histories and to a disregard for the data needed to attain stated objectives.

I believe that during the past 25 years the study of trophic relations has somehow left the mainstream of ecological and evolutionary thought. Perhaps the emphasis on ecosystems has drawn attention away from the trophic relations which are so important in the evolution of the species. We all accept that a species evolves only as a part of an ecosystem in which it comes to occupy a niche. But lumping of species and emphasis on only the dynamic aspects of trophic relations blurs the problem of what an individual faces and the meanings of this to the individual and its population in terms of natural selection. Just as it is hard to conceptualize how species compete for a niche rather than for an existing resource, it is hard to conceptualize how species compete for the production rate of a food resource rather than for existing biomasses of food. Moreover, as valuable as the concepts of niche and production may be, we must try to visualize the immediate problems individuals of coexisting species must face in satisfying their needs.

Ivlev (1945) called attention to the need to focus attention on one "product of interest" at a time rather than to diffuse effort over

many species. The great task of making trophic analyses demanded even by Ivlev's approach has perhaps caused some to dismiss it, but this approach makes clear some of the real problems yet to be faced in the study of energy and material transfer in natural communities. It also provides ecologists a basis for determining how best to apportion their efforts. However, where one considers that most carnivores utilize at least several species of prey organisms, we are left with the problem of determining several prey production rates, even with Ivlev's economical approach. If we are to be able to relate changes in the rates of food consumption, growth, and production of an animal to changes in its food resources, it appears that approaches alternative to the determination of the production rates of prey species are needed.

One such alternative view is that it is prey density and distribution rather than production rate that immediately determine the amount of food a predator can obtain and the energetic cost of its pursuit. It is this alternative view which I intend to develop in this thesis. Density of a food resource is an outcome of its rate of production or introduction into a system and the rates at which it is consumed, decomposed and is leaving the system. Thus, changes in these rates should be reflected in changes in the density of the food resource. The mean density of a food resource over a period of time only sufficiently long for measurable changes to occur in the consumer of

interest would appear to be one useful measure of the resource availability causing such changes. Density measurements can be routinely made whereas production measurements usually cannot. Moreover, summing of biomasses of food organisms of different trophic types does not present the conceptual and analytical difficulties presented by summing the production rates of food organisms of different trophic types.

I intend to present evidence in this thesis that the growth rates of consumers in simplified communities in laboratory streams are often simple functions of the densities or biomasses of their food organisms. Further, I intend to present evidence that the densities of the food organisms are often simple functions of the densities of the consumers. Such evidence will be presented both for systems having similar basic capacities to produce food organisms and for systems having different basic productive capacities.

These studies of simple communities of plants and animals in six laboratory streams are a continuation of studies reported by Brocksen, Davis, and Warren (1968). 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 water-supply filter. Populations of herbivorous insects became established in much the same way, but additional seeding of these forms was sometimes necessary. The cutthroat trout,

Salmo clarki, and the reticulate sculpin, Cottus perplexus, were added to the streams in different densities and combinations for the various experiments. The production rates of the carnivores were estimated directly.

My results will be interpreted and discussed mainly in terms of relationships between biomasses and growth rates of consumers and the densities of their food organisms, relationships which determine the functions which production rates are of biomasses (Brocksen, Davis, and Warren, 1968; 1969). Since publication of Lindeman's paper, those who have studied trophic relations have largely ignored if not belittled the importance of density or biomass except as it has been needed in the estimation of production. It is indeed curious that they should have done so, particularly during this period of time, for publication of papers by Nicholson (1933) and Smith (1935) led to great emphasis in ecological thought on the importance of density-dependent phenomena in population control. Earlier, Howard and Fiske (1911) viewed population regulation much as did Nicholson. And we know the essay by Malthus (1798) on human populations led Verhulst (1838) to formulate the logistic equation and was important in Darwins (1859) conceptualization of natural selection.

The trophic dynamic or production point of view so stimulated by Lindeman has vitalized an important area of ecological thought and has shown its relevance to man's problem of food production. In suggesting

an alternative point of view, or, more properly, an additional point of view that is necessary, I am in no way demeaning the importance of dynamic production processes; they underlie all trophic phenomena we observe and measure. Rather, I am suggesting that we cannot afford to limit our conceptualization of the ways in which these processes function. No one questions the importance of the dynamic aspects of production or the value of this point of view. Likewise, few question the importance of density-dependent relations in ecological systems, but they have fallen into disuse in trophic studies. Both points of view are needed in trophic studies if they are to contribute to the mainstream of ecological and evolutionary thought.

The studies presented in this thesis were conducted from February 1964 through August 1968 at the Pacific Cooperative Water Pollution Laboratories, Oregon State University. Where results of experiments other than my own have been used, they are so cited.

METHODS AND MATERIALS

Laboratory Stream Apparatus

The six laboratory streams used in this study (Figure 1) were housed in a small 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 in all experiments conducted prior to January 1967. At this time, the streams were scrubbed thoroughly and current velocities were maintained at approximately 9 cm per second in three streams and 30 cm per second in the remaining three streams (Table 1). The bottoms of the laboratory streams were covered with similar amounts and assortments of rubble and gravel from a natural stream. Water was taken from a small spring-fed stream, filtered through commercial filtering compound to remove most suspended materials, and was exchanged in each stream at the rate of 2 liters per minute, except during a three month period in the summer of 1967 when the flow was increased to 3 liters per minute. Banks of fluorescent lights operated through time switches provided controlled illumination for about 12 hours of each day. Prior to January, 1967, all streams were exposed

Figure 1. One of the six laboratory streams used
in these studies.



to the same light intensity, approximately 350 foot candles. In experiments after this date, three sets of two streams each were exposed to different light intensities, 630, 350 and 120 foot candles (Table 1). 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. No attempt was made to control water temperatures; these followed rather closely the diel and seasonal variations of the stream from which the water was taken (Figure 2). Daily recordings of the high and low temperatures for each stream were made throughout the entire experimental period, and ten-day means were calculated for each stream. Some variation in temperature between the laboratory streams resulted from the differences in light intensity and current velocity. Gross analyses of the chemical characteristics of the water entering and leaving each stream were made by the United States Geological Survey, Water Quality Section, Portland, Oregon. These are given in Table 6 in Results and Interpretation.

Development of Stream Communities

Algal communities were allowed to develop in the laboratory streams as a result of colonization by cells that remained in the water entering the streams after filtration. The dominant species of algae

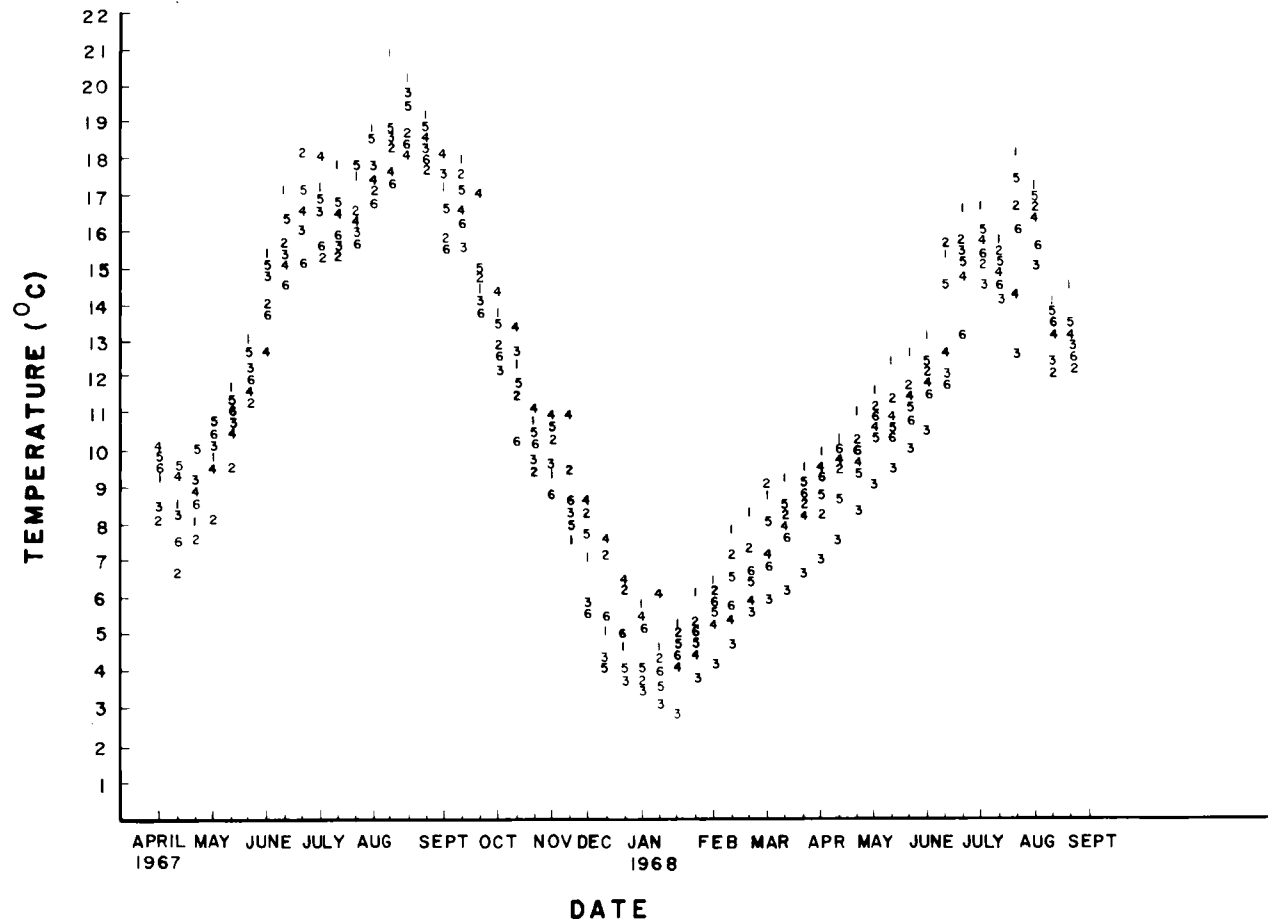


Figure 2. Ten-day mean temperatures for the period from April, 1967, through August, 1968. The numbers identify individual streams and show the range in mean temperatures between streams.

in each stream varied with light intensity and current velocity and will be considered under Results and Interpretation.

Table 1. Light intensity and current velocity to which individual laboratory streams were exposed after January, 1967.

Stream Number	Light Intensity (foot candles)	Current Velocity (cm/sec)
1	630	9
2	630	30
3	350	9
4	350	30
5	120	9
6	120	30

Herbivorous insects were the predominant benthic organisms other than the sculpins that were stocked in the streams. The insects either entered the streams with the incoming 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. Of the insect forms present, midge larvae of the genera Brilla, Micropsectra, and Chironomus were the most numerous. Mayfly naiads were often present in the streams, the general Paraleptophlebia, Leptophlebia, and Cinygma being most prevalent. Ostracods, copepods, and the herbivorous stonefly

Nemoura were occasionally present in small quantities. Although a few specimens of Sialis, a predacious megalopteran, and Acroneuria, a predacious stonefly were observed, their frequency of appearance was rare.

Biomass, Growth, and Production of Sculpins and Trout

Experiments performed during the winter and spring 1961 (Davis and Warren, 1965), in which sculpins were stocked in laboratory streams are included in this thesis. In these experiments, different biomasses of sculpins (Table 2) were stocked in streams having the same basic capacity to produce food organisms, this making it possible to study the effects of intraspecific competition on the growth and production of sculpins. During the winter, 1964, different biomasses and combinations of trout and sculpins were stocked in laboratory streams having the same basic capacity to produce food organisms so that the effects of intraspecific and interspecific competition on the growth and production of trout and sculpins could be studied. In an experiment performed during the fall, 1965, trout were the only carnivores stocked in the laboratory streams (Table 2), only intra-specific competition being studied.

Later experiments were designed to define the effects of intra-specific and interspecific competition in systems having different basic capacities to produce food organisms. Growth and production

Table 2. Mean biomasses and numbers of animals stocked and recovered in laboratory streams.

Experimental Period	Stream Number	TROUT			SCULPINS		
		Mean Biomass (Kcal/M ²)	Number Stocked	Number Recovered	Mean Biomass (Kcal/M ²)	Number Stocked	Number Recovered
Winter 1961 ^{1/}	1				3.27	6	6
	2				6.13	12	11
	3				1.54	2	2
	4				2.78	4	4
	5				4.77	10	10
	6				4.44	8	7
Spring 1961 ^{1/}	1				4.33	6	6
	2				6.95	12	12
	3				1.51	2	2
	4				3.18	4	4
	5				6.25	10	8
	6				5.13	8	7
Winter 1964	1	14.28	2	2	14.35	38	33
	2	7.66	2	2	6.59	15	14
	3	4.39	1	1	3.92	11	9
	4	9.01	2	1	6.92	14	13
	5	3.49	1	1	4.11	9	9
	6	9.58	2	2	13.34	39	33
Fall 1965	1	7.02	4	3			
	2	23.31	12	11			
	3	5.10	2	2			
	4	14.75	6	6			
	5	18.29	9	8			
	6	25.51	16	14			
Summer #1 1967	1	15.76	11	11			
	2	15.11	10	9			
	3	14.76	7	7			
	4	13.61	7	7			
	5	11.21	6	5			
	6	11.61	6	5			
Summer #2 1967	1	11.58	7	7	3.20	16	14
	2	12.58	10	9	3.42	16	15
	3	-	-	-	3.21	16	15
	4	10.80	6	6	2.82	16	12
	5	12.99	6	5	3.40	16	16
	6	13.28	6	6	2.91	19	16
Fall 1967	1	7.76	4	4	5.48	5	5
	2	8.71	3	2	5.22	5	4
	3	7.69	3	3	5.21	5	4
	4	8.81	3	2	5.24	5	4
	5	7.52	3	3	4.90	5	5
	6	6.03			4.04	6	4
Spring 1968	1	25.44	5	5			
	2	21.49	4	4			
	3	22.34	4	4			
	4	19.98	5	5			
	5	22.04	4	4			
	6	19.77	5	5			

^{1/} Data from Davis and Warren (1965).

of sculpins and trout, and the effects these carnivores had on their food resources were studied during the summer and fall 1967, and during the winter and spring 1968. During the first summer 1967 experiment and during the spring 1968 experiment, trout were the only carnivores stocked in the laboratory streams (Table 2), only intraspecific competition being studied. The effects of intraspecific and interspecific competition for food on the growth and production of trout and sculpins in systems having different basic capacities to produce food were studied during the second experiment of the summer 1967 and during the fall 1967. The effects these carnivores had on their food resources in the different systems were also studied. Underyearling sculpins and trout were stocked in most experiments, the only exceptions being the spring 1968 experiment (Table 2). Underyearlings here are considered to be fish less than 12 months of age excluding embryonic and larval development.

Mean growth rates of sculpins and trout stocked in the laboratory streams were computed for each experimental period. The changes in weight of the animals during the time they were kept in the laboratory streams were converted to caloric values. Each value so obtained was divided by the caloric value of the mean weight per animal for the time interval involved, and the quotient was then divided by the number of days in the interval. Growth rates of the sculpins and trout are expressed in terms of calories of growth per kilocalorie of biomass

per day (cal/kcal/day).

Production of each of the fish species in the laboratory streams when no mortality occurred was estimated directly by measuring the total increase or decrease in biomass (kcal/m^2) of each species during a given experimental period. When it was found at the end of an experiment that animals had died or had been lost from a stream, a different method of computing production was necessary. Such 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 estimated average number of animals living in the stream per square meter of area by the difference between the mean initial and mean terminal weights of the animals. Experimental animals were selected for uniformity of size at the beginning of the experiments in order to reduce errors in estimates when animals were lost. Production, as I have measured it, provides an estimate of the total elaboration of new body substance per square meter of stream area (kcal/m^2) by a species during an experimental period and should be differentiated from the growth rate (cal/kcal/day) of that species. A negative production value occurs if the individuals in a population lose weight during an experiment; the rationale for using such negative values has been discussed by Warren et al. (1964).

During the winter, 1968, individual underyearling trout were marked by attaching colored tags with vinyl thread. This was done

to make it possible to relate the growth of individual fish to the feeding station they occupied and to observe any changes in agonistic behavior with changes in food density or availability.

Density Measurements of Herbivorous Insects and Organic Matter

In order to explain changes in growth rates and production of fish with changes in food availability, measurements of the densities of their food organisms were made. Information on the quantity or density of organic matter constituting the food resource of the herbivorous insects was also obtained.

Samples of the herbivorous insects and algal material in the benthos were taken at about two week intervals. When carnivores were stocked in the laboratory streams, samples were taken from the streams immediately before the experimental animals were stocked, at the midpoint in time of an experiment, and at the conclusion of an experiment. In order to obtain a sample, two watertight partitions were inserted 20 cm apart between the walls of a stream, this providing a sample of organisms from a stream area of 500 cm^2 . After the rocks and gravel were scrubbed in the water and removed, the water containing the benthic organisms and algal material was siphoned through a plankton net. A dissecting microscope was used to aid in removing the animals from the samples. The biomasses of both plant and animal materials were determined,

and samples were retained for caloric analysis. The densities of the herbivorous insects in the benthos are expressed in kilocalories per square meter of bottom area (kcal/m^2). The algal material was dried, weighed, and ashed, the latter to determine the percentage of organic matter. Organic matter is expressed as kilocalories per square meter of bottom area (kcal/m^2). Samples of algae were analyzed as described by McIntire (1968) to determine species composition.

Samples of drifting insects were collected from each stream at weekly intervals. This was done by diverting through plankton nets for a 24 hour period the water leaving the streams via overflow drains. The overflow drains were so arranged as to remove water from mid-depth after it had passed around a stream at least once. The samples were removed from the plankton nets, and the insects were separated from pupal cases and plant debris and weighed. Densities of drifting animals are expressed as calories per cubic meter of water (cal/m^3).

Calorimetry

A Parr No. 1411 semi-micro oxygen bomb calorimeter was used to determine caloric values for the smaller samples of experimental animals, herbivorous insects, and algae. When sample size allowed, a Parr No. 13031 macro-oxygen bomb calorimeter was used. No special treatment was given these materials other than to

add distilled water to the dried and powdered samples in order to form the sample pills for combustion. Mean percentages of dry weight and mean caloric values for the material combusted in the calorimeters are given in Table 3.

The caloric value of trout varies widely with their nutritional status (Table 3). When the nutritional state of individual fish could be determined with some degree of objectivity, the appropriate values from Table 3 were used in calculating growth rate and production.

The use of caloric values is convenient because it allows different bioenergetic quantities to be expressed in common units. This is particularly convenient when dealing with the exchange of energy between trophic levels. Because few people commonly think in terms of these units, the following conversion relation may be helpful: One kilocalorie of fish, in an average nutritional state, is approximately equivalent to one gram of wet weight. For organisms other than fish, Table 3 should be consulted.

Table 3. Mean percentages of dry weight, ranges of caloric values, and mean caloric values per gram dry weight of experimental materials.

MATERIAL	No. of Samples	Dry Weight (Percent)	Kcal/Gram Dry Weight	
			Range	Mean
TROUT				
1.0% ration	6	18.97	3.923-4.329	4.245
2.5% ration	6	20.00	4.598-4.897	4.740
3.5% ration	6	19.97	4.829-5.026	4.937
5.0% ration	6	22.56	5.248-5.356	5.291
repletion	6	22.70	5.231-5.401	5.356
SCULPIN	17	23.53	4.739-5.438	5.287
HERBIVOROUS INSECTS	40	16.00	4.324-5.521	5.250
ALGAE	22	-----	0.986-1.391	1.150
Ash-free Organic Matter				4.100

RESULTS AND INTERPRETATION

Nutrient Resources and the Biomass, Growth and Production of Organisms

In any ecosystem in which the limiting resource of a species is food, an increase in the numbers of that species will lead to a reduction in the amount of food each individual can obtain: this in turn will lead to a reduction in individual growth rate. The production of any age class of an animal population in any period of time is usually defined as the product of its mean growth rate and its mean biomass. Thus, with growth rate declining with increasing biomass, production will increase from a low level at some low biomass to a maximum at some intermediate biomass; and, then, with further increases in biomass, production will decline toward zero as growth approaches zero.

The relationship between trout biomass and trout growth rate, and between trout biomass and trout production, in a system where food is the limiting resource are illustrated by the results of the winter 1964 experiment (Figure 3). Similar relationships exist between biomass, growth, and production of sculpins in laboratory streams (Figure 4). For food-limited species, these relationships are not only logically sound, but they have been demonstrated in the pond culture of fish (Walter, 1934; Wolny, 1962) as well as in trout

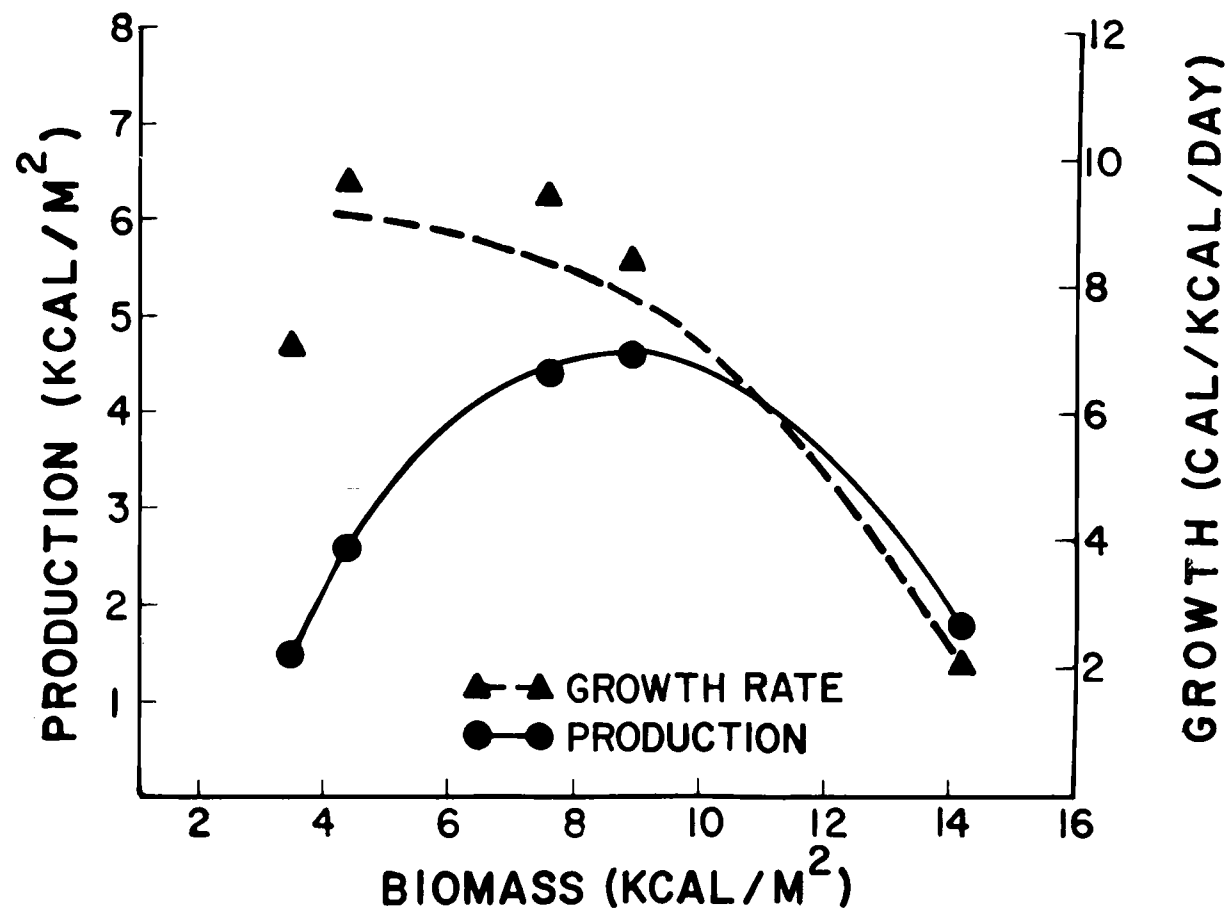


Figure 3. Relationships between trout production and trout biomass and between trout growth rate and trout biomass for the winter 1964 experiment.

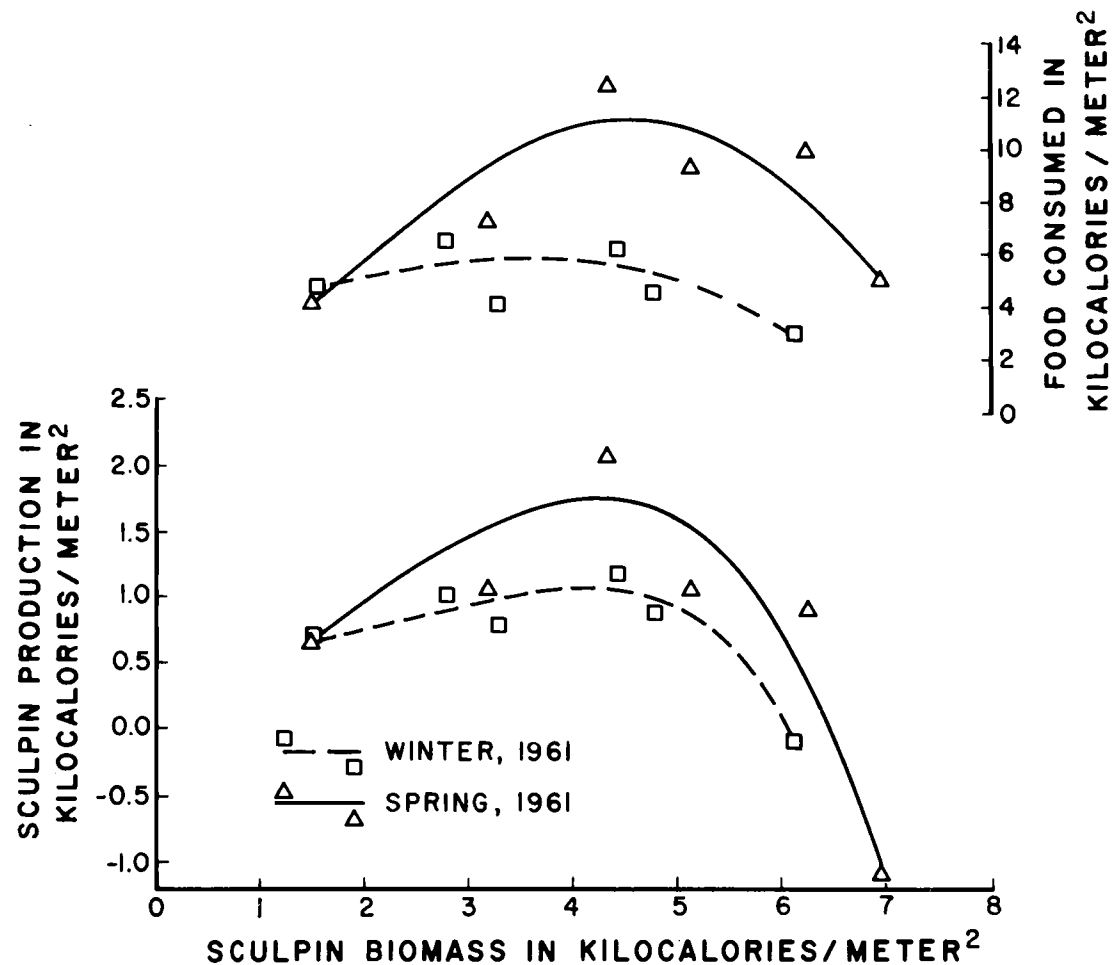


Figure 4. Relationships between sculpin biomass and sculpin production and food consumption determined in laboratory stream experiments conducted during winter and spring 1961. (Data of Davis and Warren, 1965)

streams (Backiel and LeCren, 1968); Ivlev (1947) has provided a mathematical formulation. The biological basis of the superficially simple relationship between biomass and production has been fairly well elucidated in studies of stream communities in which trout and sculpins were the carnivores of interest (Warren et al., 1964; Davis and Warren, 1965; and Brocksen, Davis, and Warren, 1968).

Decline in the growth rate of a consumer with increases in its biomass may result from some controlling influence the consumer exerts on its food resource; but whatever the biological basis of the decline, it should be defined. The first step in the elucidation is perhaps to determine whether or not the growth rate of the consumer is controlled in any definable manner by the availability of its food resource. The question of whether or not the consumer controls, to an important extent, the availability of its food resource will be considered later.

One can reasonably conclude that the density and distribution of an animal's food organisms in its immediate surroundings determine the amount of food the animal can obtain in a short period of time and the energy cost of obtaining this food. When the growth rate of trout stocked in laboratory streams during the winter 1964 experiment is plotted against the density of drifting food organisms in the streams, a strong positive correlation exists (Figure 5). A similar relationship appears when the growth rate of sculpins is plotted against the

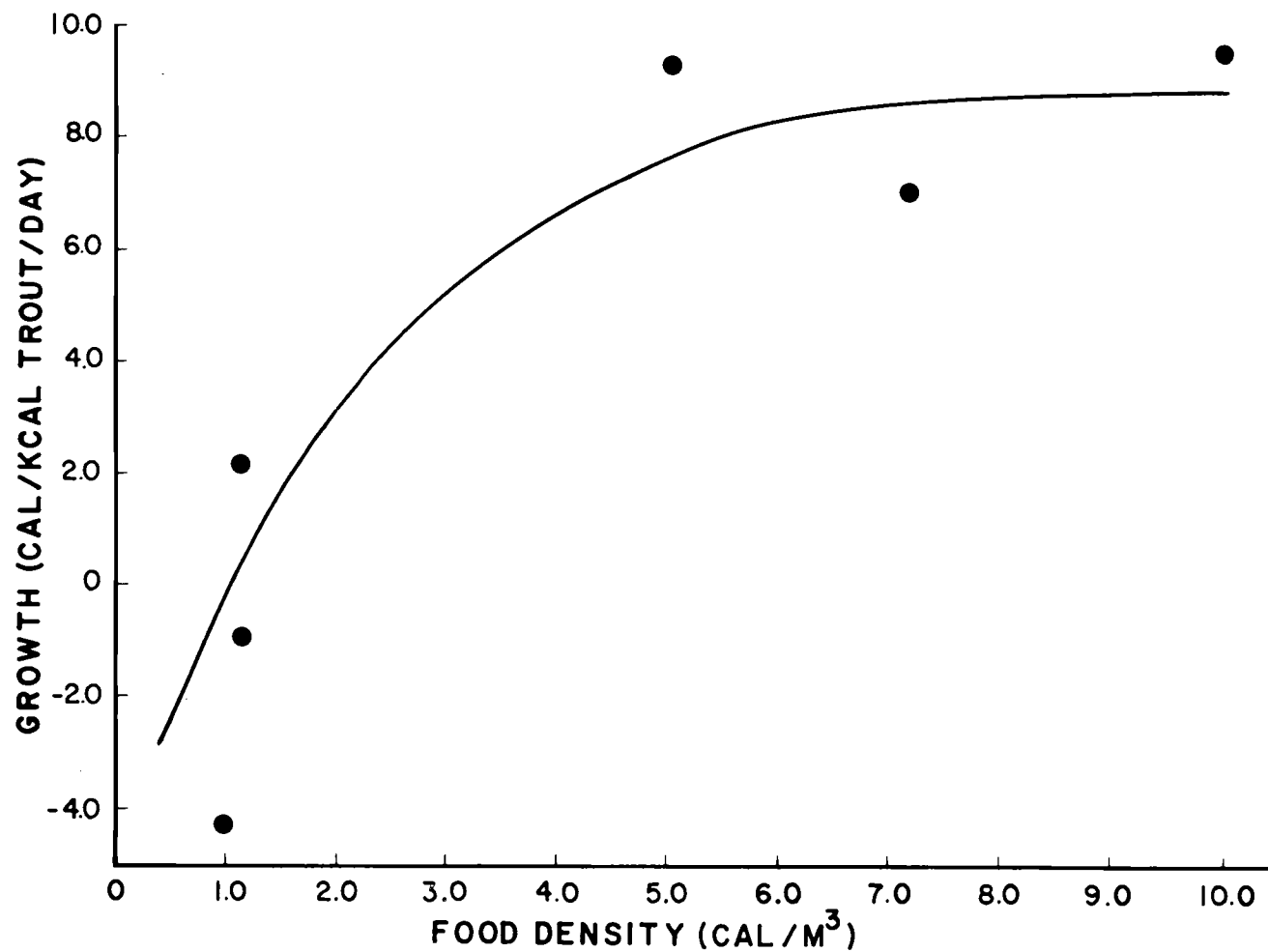


Figure 5. Relationship between growth rate of trout and density of drifting food organisms during the winter 1964 experiment.

density of food organisms in the benthos during this same experiment (Figure 6). There can be little doubt that the growth of the trout and sculpins was limited by the availability of their food resources (Brocksen, Davis, and Warren, 1968). Ivlev (1961a) used zooplankton biomass as a measure of food availability in his examination of the growth of the bleak (Alburnus alburnus). Johnson (1961) has shown that, in a series of seven basins in the Babine and Nilkitkwa lake system in British Columbia, the mean weight of juvenile sockeye salmon (Oncorhynchus nerka) in mid-October exhibits a high positive correlation with the mean dry weight of zooplankton per cubic meter from mid-June to mid-October, the period of the year when nearly all of the growth of the zero age group occurs.

If we now turn to the question of whether or not populations exert controlling influences on the availability of their nutrient resource, we find evidence that under some circumstances they do. When the density of drifting food organisms is plotted against the biomass of trout stocked in the laboratory streams during the fall 1965 experiment, a strong negative correlation exists (Figure 7). Data of Davis and Warren (1965) on the density of benthic food organisms and the biomass of sculpins show the sculpins to be capable of influencing the availability of their food resource (Figure 8). Light intensity and current velocity during these experiments were the same for all six streams; and the streams can be assumed

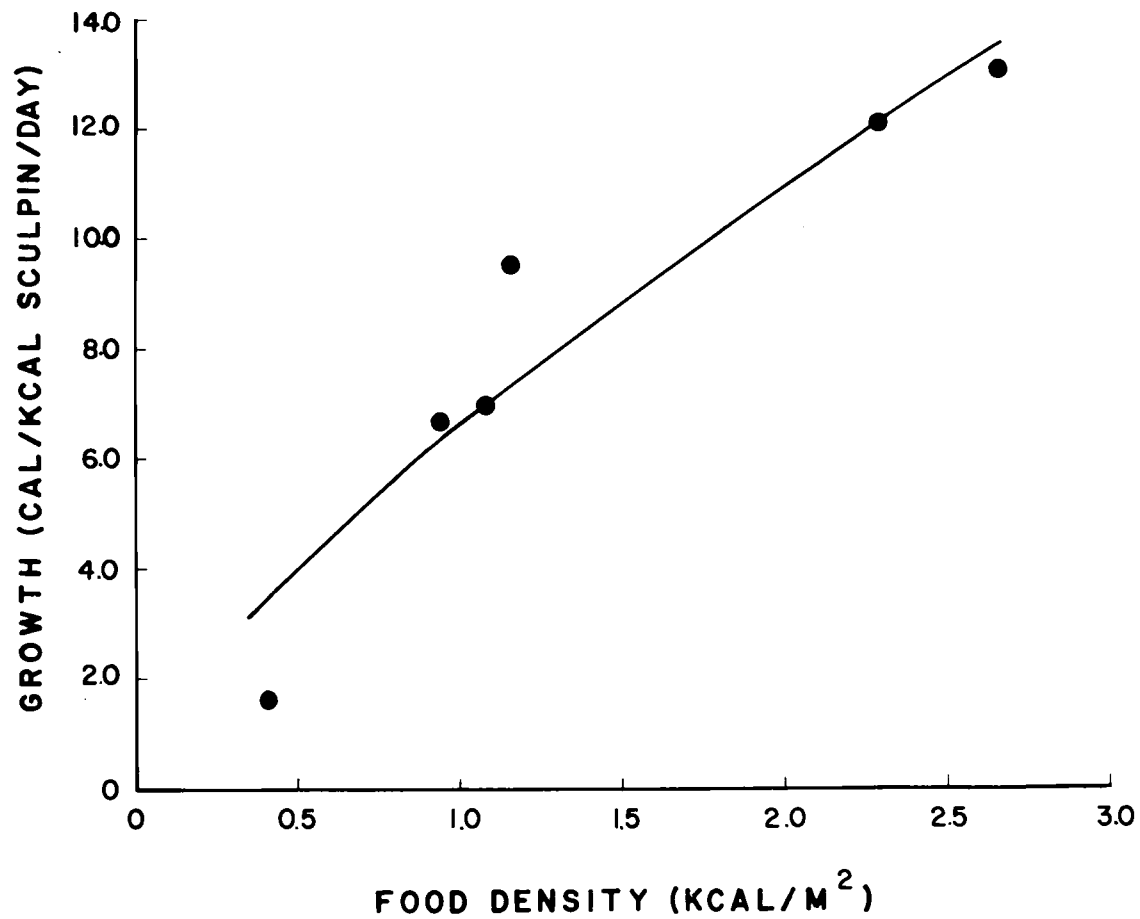


Figure 6. Relationship between growth rate of sculpins and density of benthic food organisms during the winter 1964 experiment.

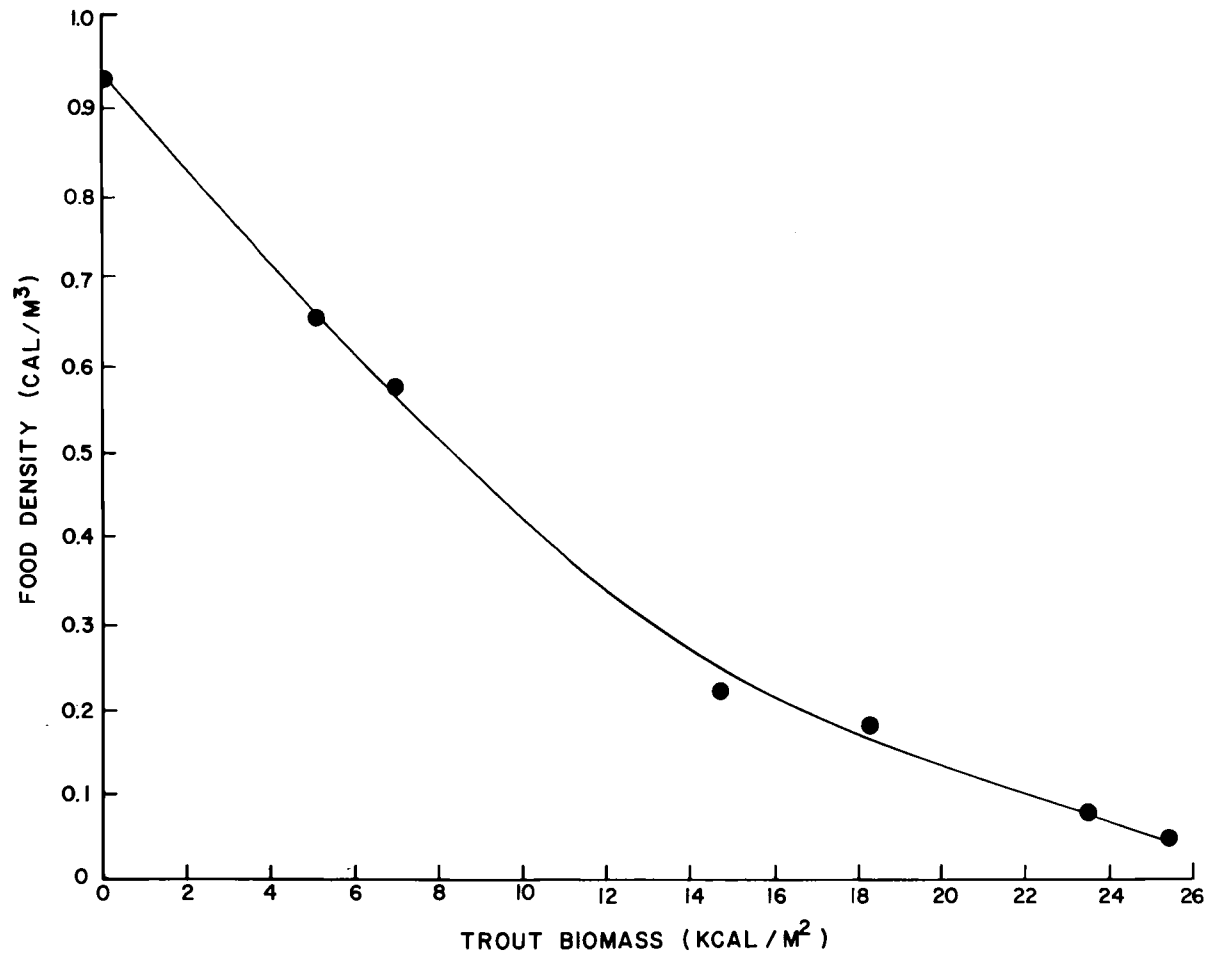


Figure 7. Relationship between the density of drifting food organisms and the biomass of trout stocked in the laboratory streams during the fall 1965 experiment.

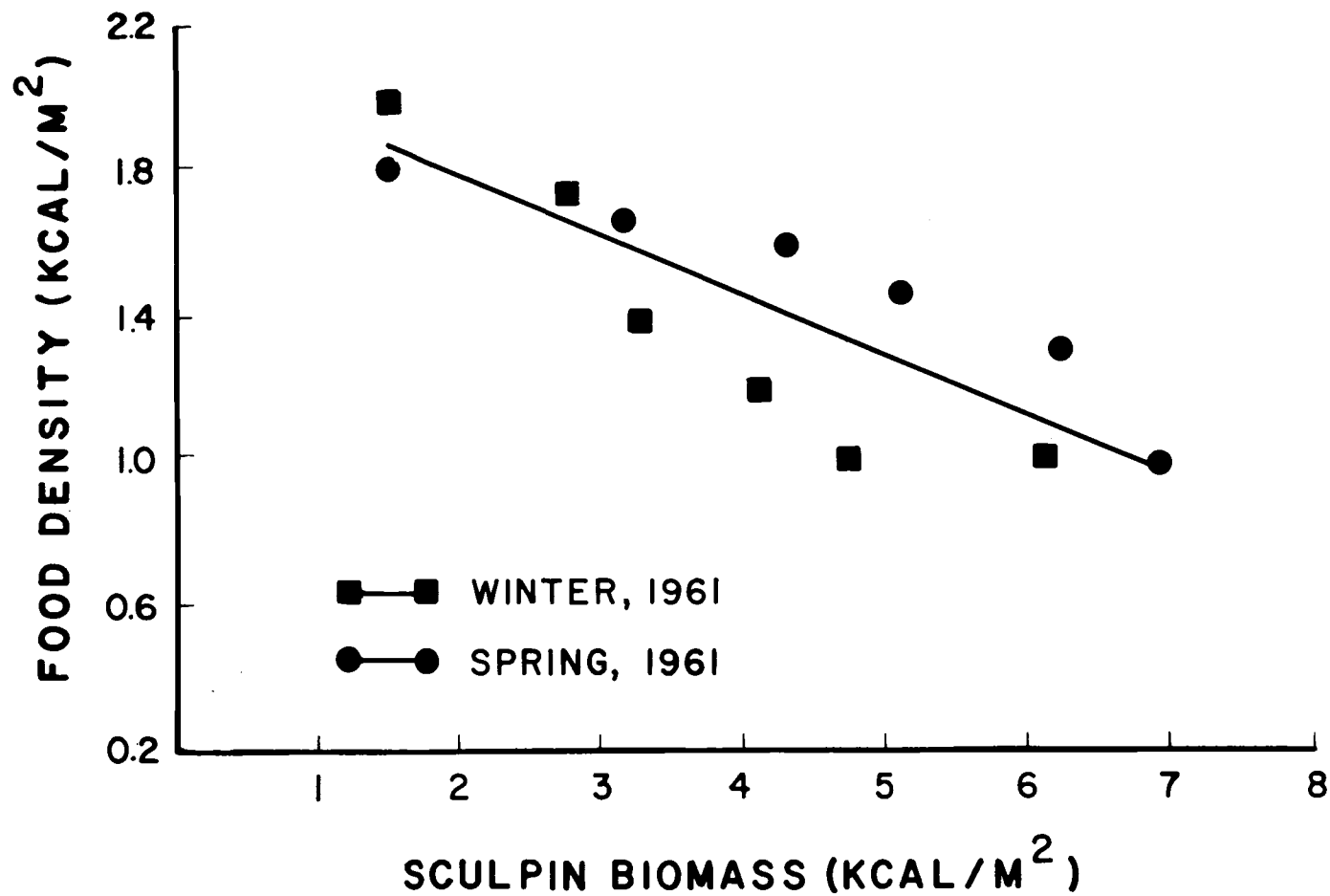


Figure 8. Relationships between the density of benthic food organisms and the biomass of sculpins in the laboratory streams during the winter and spring, 1961, experiments. Data from Davis and Warren (1965).

to be representative of a single system having a fairly constant basic capacity to produce food.

These relationships (Figures 5-8), then, define the predator-prey interactions which determine the form and positions production-biomass curves (Figures 3-4) assume in a single system having a fairly constant basic capacity to produce food. The relationships between food density and the biomass of a particular consumer, and between its growth rate and biomass should be different in ecosystems having different basic capacities for food production so long as food is the limiting resource. Brocksen, Davis, and Warren (1969) using data from three different lake systems in which juvenile sockeye salmon were the dominant carnivore demonstrated this quite graphically by plotting sockeye growth rate against sockeye biomass (Figure 9). The slopes of the resultant curves are all negative, but are positioned quite differently, dependent upon the food base of the system. Thus, relationships between the biomass of a consumer and its production in systems having different basic capacities to produce food can be expected to differ.

It can reasonably be concluded that ecosystems having the highest basic capacity to produce food should maintain the highest biomasses of a consumer, so long as food is the limiting resource. Higher nutrient levels should lead to greater algal production. Greater algal production should lead to increases in herbivore

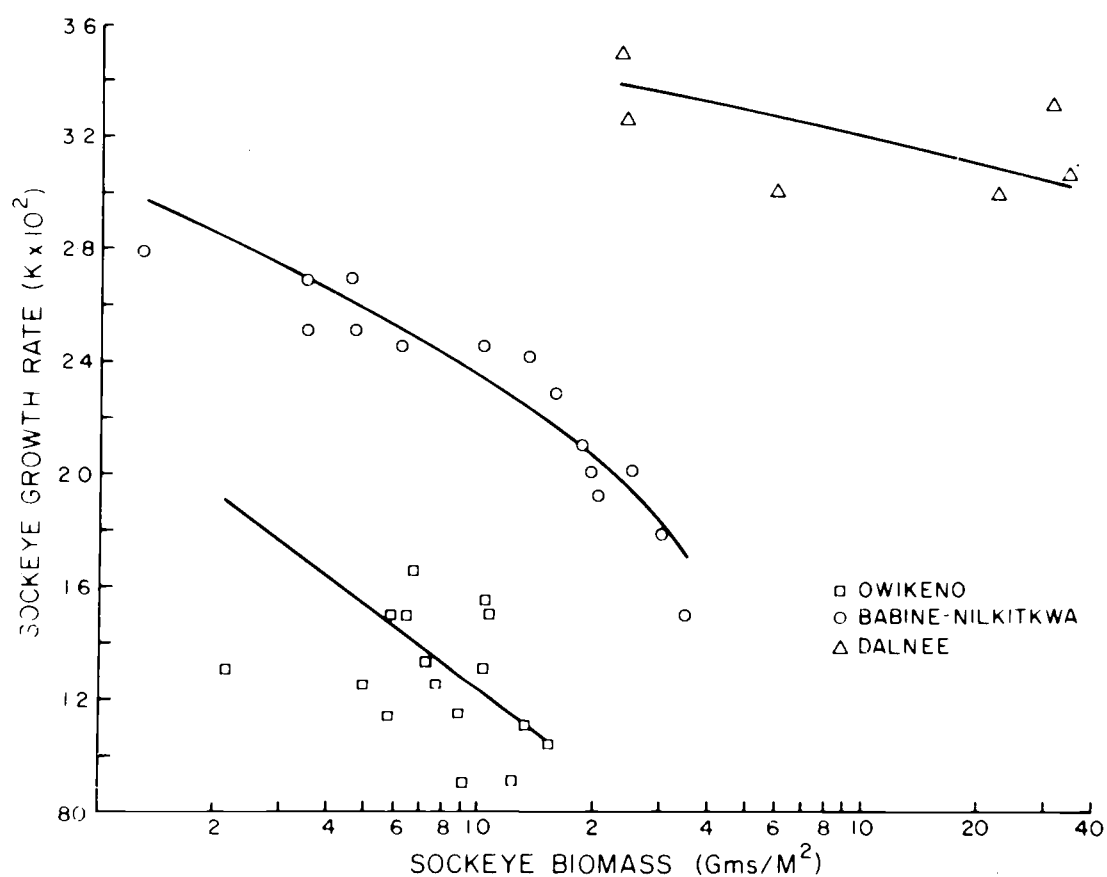


Figure 9. Relationships between mean instantaneous growth rate and mean sockeye salmon biomass for Owikeno Lake, Babine-Nilkitkwa basins, and Lake Dalnee. (Data from Ruggles, 1965; Johnson, 1961; and Krogius and Krokhn, 1948, respectively)

production. These increases would provide higher levels of food organisms for carnivores this resulting in increases in carnivore growth rates and biomasses. Annual or seasonal differences in the capacity of a particular ecosystem to produce food should also lead to annual or seasonal differences in the growth rate and biomass of a consumer that the ecosystem can support. Information from the three sockeye lakes (Figure 10) supports the idea that the relationships between consumer biomass, growth rate, and production differ in systems having different basic capacities to produce food. The impact of increasing biomass on growth rate is markedly less as the basic productivity of the system is increased. This suggests that food resources in the system with the highest basic productivity are much less sensitive to utilization by a consumer than are the food resources in those systems with lower basic productivities. Evidence from the three lakes strongly supports this idea (Figure 10).

It would appear, then, that two kinds of relationships can exist between a consumer's biomass and the density of its food resource. These I have illustrated in Figure 11. Each curve drawn with a solid line represents the decline in nutrient resource occasioned by increasing consumer biomass in an ecosystem having a relatively constant basic capacity to produce a nutrient resource or in systems having the same capacity. The different curves represent ecosystems having different productive capacities and are thus placed higher on

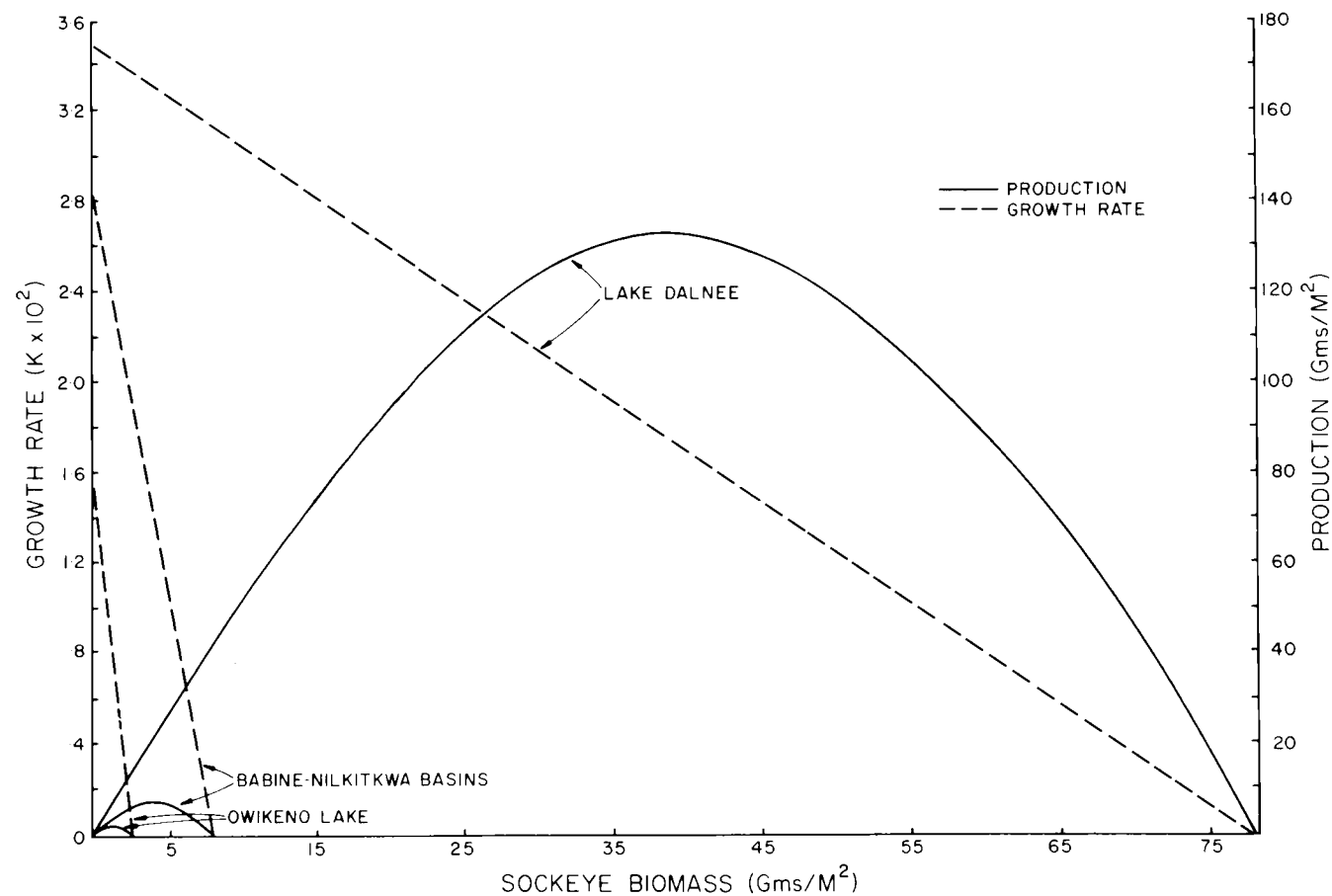


Figure 10. Comparison of growth rate, biomass and production relationships for sockeye salmon in Owikeno, Babine-Nilkitkwa, and Dalnee Lakes. Computed from data shown in Figure 9.

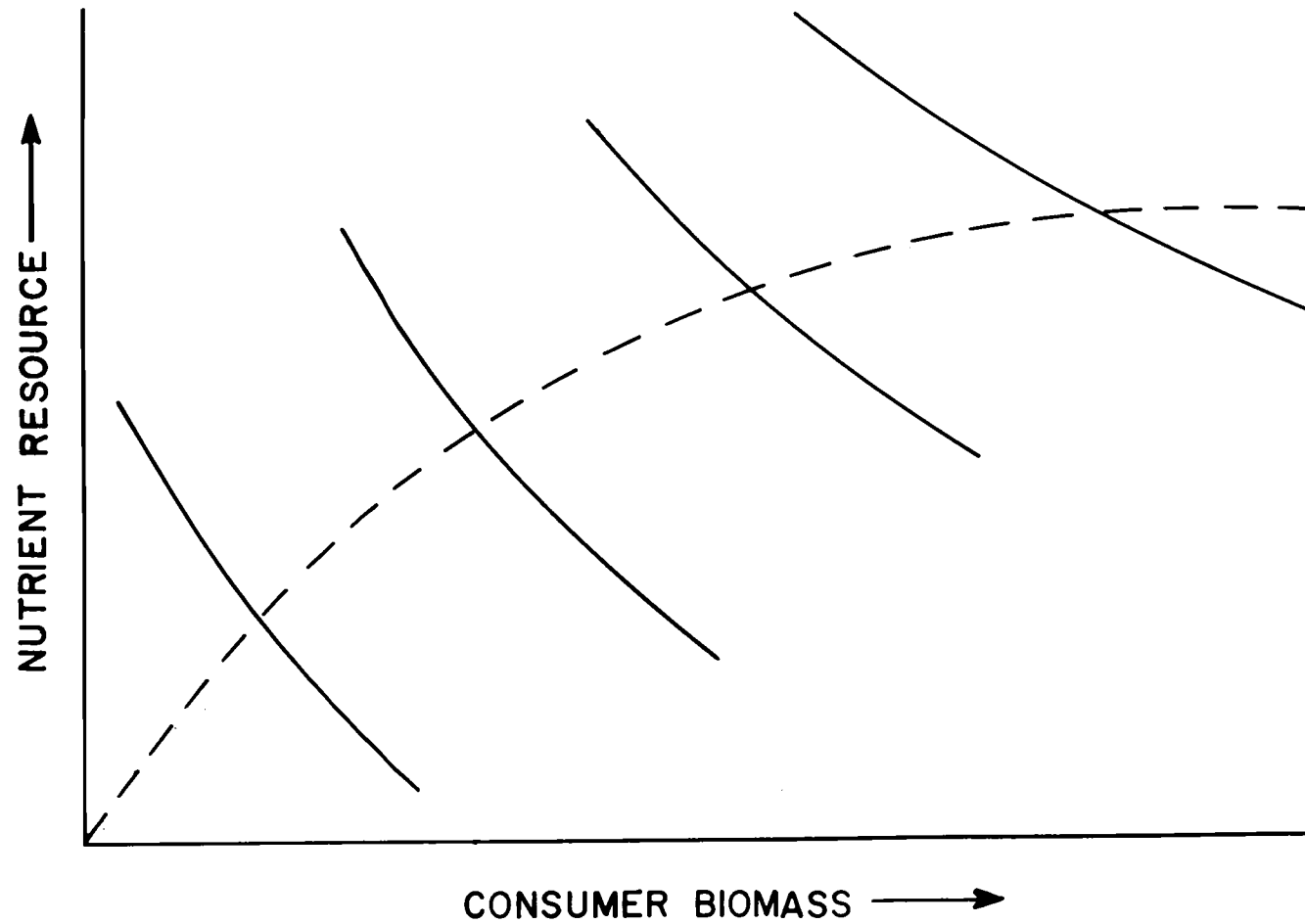


Figure 11. Theoretical relationships between a nutrient resource and the biomass of a consumer of interest within particular systems (solid lines) and between systems (dashed line).

the nutrient resource scale as the ranges of consumer biomasses these systems can sustain are greater. The broken line drawn upward through these curves represents the increase in the consumer biomass that can be supported at higher nutrient resource levels made possible by increased capacity to produce these nutrient resources (Figure 11).

This thesis is mainly concerned with density dependent relationships at all levels of food chains that lead to differences in the capacities of different ecosystems to support consumers. These differences lead to different production-biomass relationships. Though the relationships between consumer biomass and food density and between food density and consumer growth rate that lead to particular production-biomass relationships for systems having the same basic capacity to produce food have been considered elsewhere (Brocksen, Davis, and Warren, 1968), I have here reviewed them. This I have done because explanation of differences in production-biomass relationships between systems having different basic capacities to produce food requires some understanding of relationships within one system or between systems having the same capacity.

In the further development of the ideas I have already introduced regarding systems having different basic capacities to produce food, it will frequently be necessary to introduce systems of curves on the basis of very little information. This has been done only to

suggest probable density dependent relationships of which my observations represent only a very few points. I have reviewed some of the evidence for the existence of such relationships and have presented other evidence elsewhere (Brocksen, Davis, and Warren, 1969). Even though these series of relationships are now rather hypothetical, they are quite necessary to begin to understand how, through density dependent food chain relationships, the production-biomass relationships come to be different in ecosystems having different basic productive capacities.

Carnivore Growth and Production in Ecosystems having Different Productive Capacities

The different light intensities and current velocities to which the six laboratory streams were exposed led to ecosystems having different capacities to produce particular nutrient resources. Relationships between consumers and their nutrient resources suggest that at least three and sometimes up to six distinctly different productive capacities existed among the streams. In later sections, I will consider the algal and herbivore components of these communities and the density-dependent relationships between them. Now, I will consider only the relationships between the carnivores and their food organisms and the carnivore production-biomass relationships to which these lead.

The growth rate of trout, stocked initially at equal biomasses in the six streams during individual experiments, exhibited a strong positive correlation with the density of herbivorous insects present in the streams (Figure 12). The growth rates of trout when plotted against the density of their food organisms form two distinct curves during different seasons of 1967 and 1968. Two factors are important in leading to the distinct relations. The first: the trout stocked in the streams during the June through October experiments were younger and faster growing than those stocked in the streams during the experiments performed from November through April. And the second: there are reasons to believe that the lower temperatures which prevailed during the experiments performed from November through April can have a depressive effect on the growth rate of fish through behavioral or bioenergetic changes (Brocksen, 1966; Averett, 1969). Warren and Davis (1967) have discussed effects of seasonal changes on the bioenergetics of fish.

The relationships between the growth rates of sculpins and the densities of their food organisms when the sculpins were stocked at biomasses initially equal in the six streams were quite similar to those of the trout (Figure 13). The summer and fall 1967 relationships were quite distinct; but in each instance, a strong positive correlation existed. The reasons for the differences in position and slope of the curves are, I believe, the same as those given for

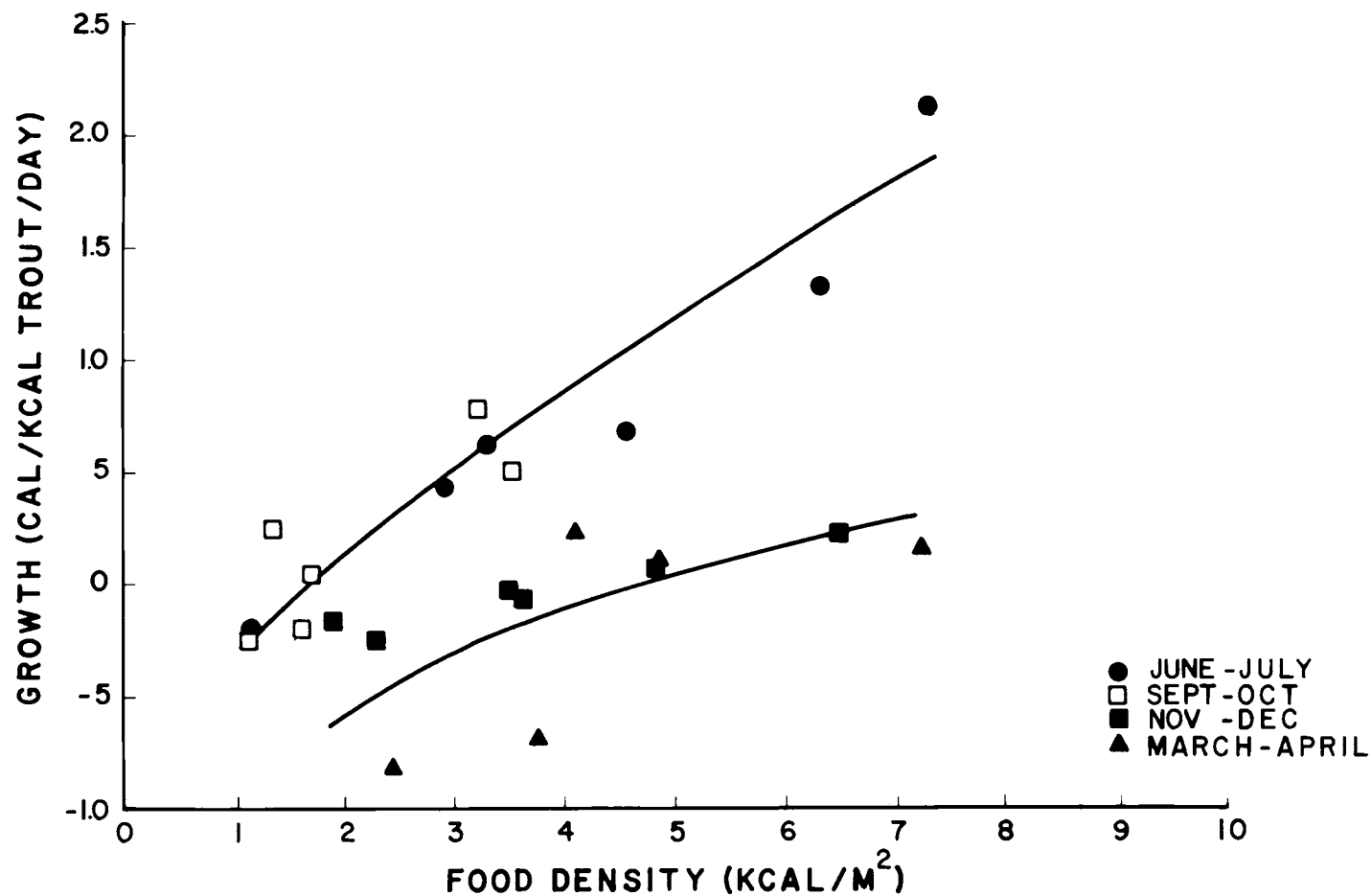


Figure 12. Relationships between trout growth rate and the density of trout food organisms in the benthos of systems with different basic productive capacities during experiments conducted at different seasons of 1967 and 1968.

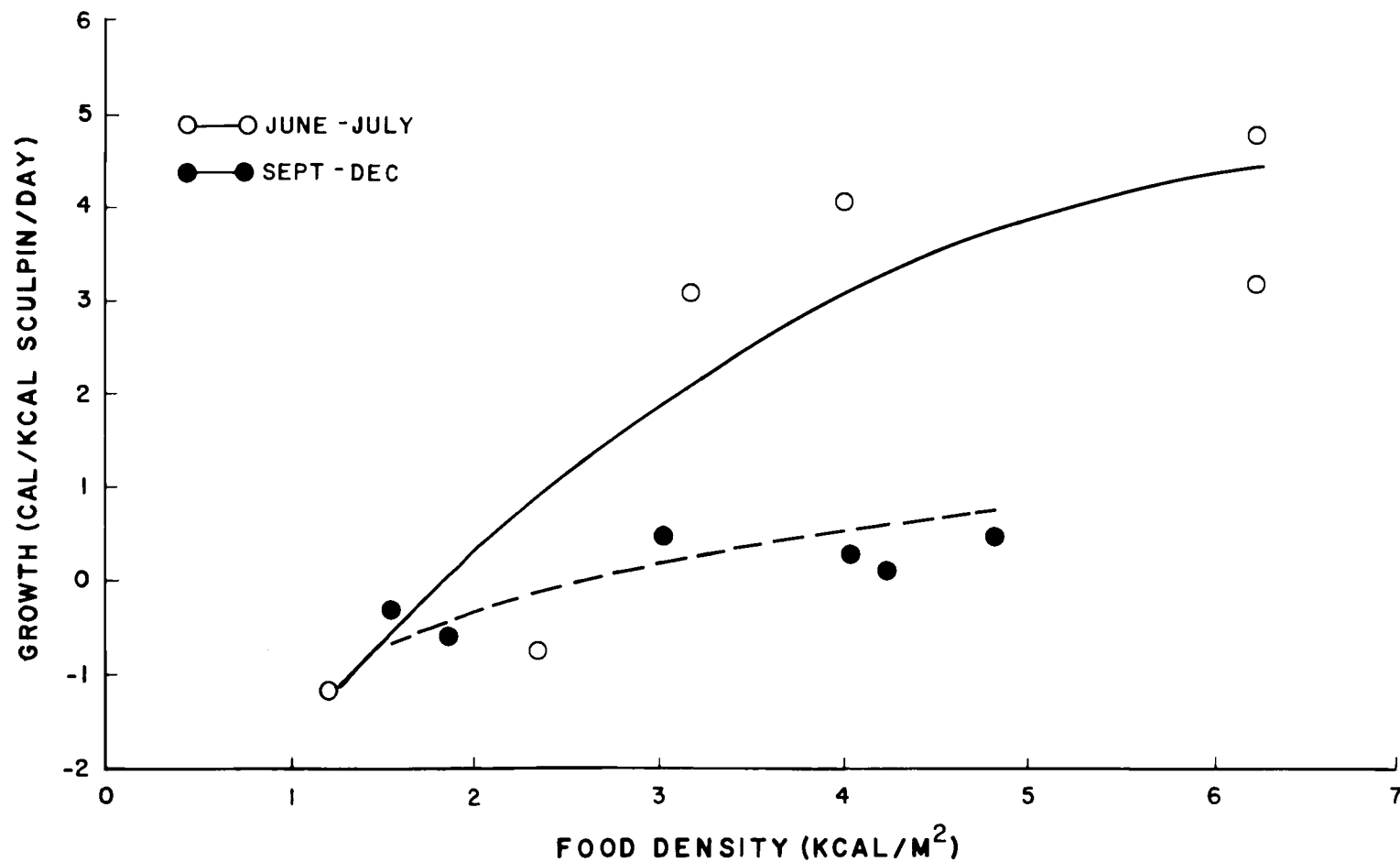


Figure 13. Relationships between sculpin growth rate and the density of sculpin food organisms in systems having different basic productive capacities for experiments conducted during the summer and fall, 1967.

the trout.

The density or biomass of prey at which the growth of the trout or sculpins approaches zero is of considerable biological interest. Such an insect density perhaps approximates the density at which one or the other of these species could not be successful if this density were primarily due to low insect production or intensive interspecific competition. Were this density primarily due to intraspecific competition, the biomass of that species would presumably decline to a level permitting the existence of insect densities more favorable to its growth. There is evidence in Figures 12 and 13 that this indeed was occurring.

During the fall 1967 experiment, interspecific competition may have been more severe in those streams having the lower productive capacities (Table 4). Even though carnivore biomass was approximately the same (and the ratio of trout biomass to sculpin biomass the same) across the six streams, the proportion of insect production that was consumed by sculpins was greater in those streams having the lower capacity to produce food organisms than in those streams having the higher productive capacities (Table 4). This lead to the sculpins having a greater effect on trout growth and production in the least productive systems. Davis and Warren (1965) observed a similar phenomenon between stonefly naiads (Acroneuria pacifica) and sculpins.

Table 4. Turnover rates of insects during the fall 1967 experiment as calculated from estimated consumption by trout and sculpins, other fates, and mean insect biomass. Expressed in kilocalories per square meter.

Stream Number	Trout Consumption	Sculpin Consumption	Other Fates	Estimated Insect Production	Mean Insect Biomass	Turnover Rate
1	8.44	5.13	1.05	14.62	3.64	4.02
2	16.10	4.76	0.72	21.58	3.59	6.01
3	6.82	4.88	0.53	12.23	2.67	4.58
4	11.89	4.66	0.85	17.40	4.26	4.09
5	2.39	3.90	0.42	6.71	2.08	3.23
6	3.06	3.26	0.36	6.68	1.81	3.69

As can be seen in Figures 12 and 13, the mean growth rates of trout and sculpins when plotted against the densities of their food organisms, lie remarkably near the same lines for any given season, even though the productive capacities of the systems in which the fish were stocked differed greatly. This characteristic was also exhibited by the growth rates of juvenile sockeye salmon when plotted against zooplankton densities of the three lake systems having different productive capacities which were considered earlier (Figure 14). These relationships indicate that the growth rates a species can maintain at different densities of food organisms may be more characteristic of the species than of the particular ecosystem. Consideration of the costs of food capture and utilization in the growth process might lead one to the same conclusion; whatever are the production levels and fates of prey that lead to particular prey densities, these densities, insofar as they represent food availability, set limits on the possible growth of a consumer.

As previously postulated, ecosystems having the highest basic capacity to produce food should maintain the highest biomasses of a consumer, so long as food is the limiting resource. This was found to be the case when the mean biomass of benthic herbivorous insects was plotted against the terminal biomass of trout and sculpins for the fall 1967 experiment (Figure 15). Though the biomasses of sculpins and trout stocked in the different streams were initially equal, growth

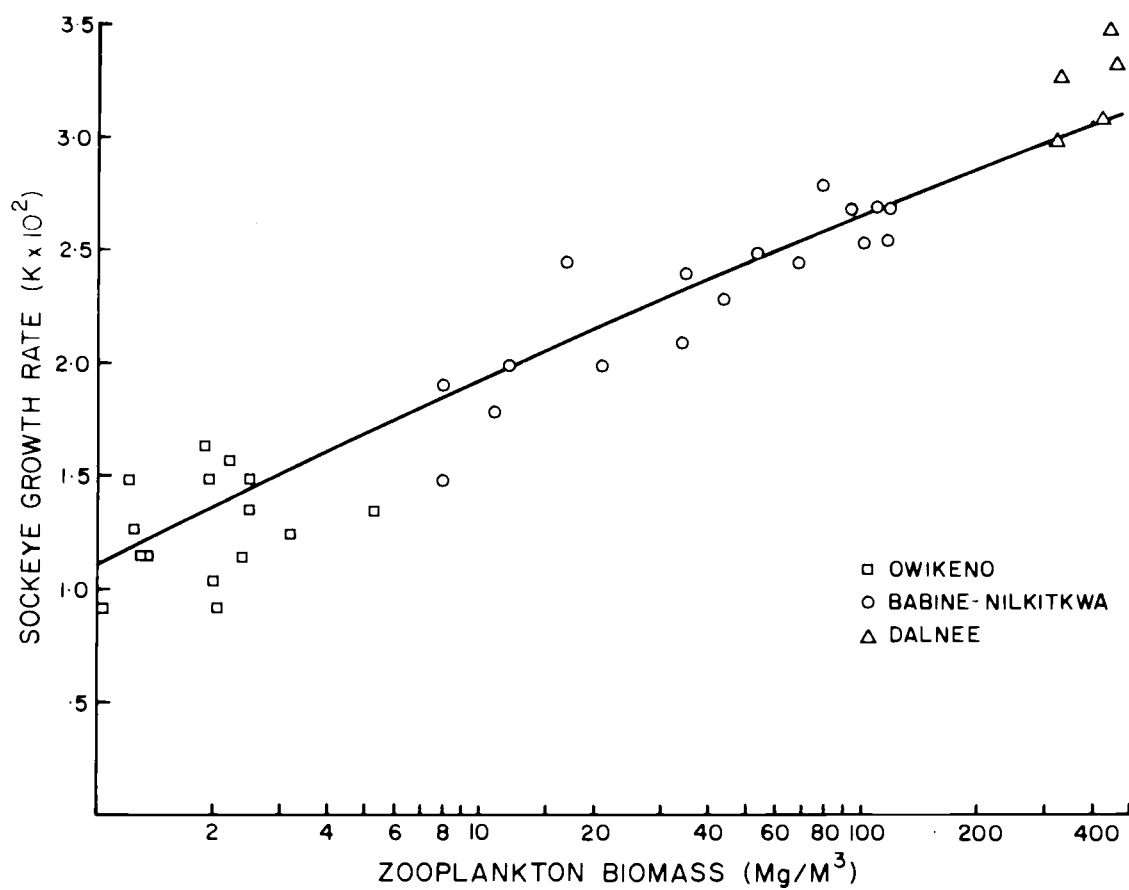


Figure 14. Relationship between mean instantaneous growth rate of sockeye salmon and mean biomass of zooplankton for Owikeno, Babine-Nilkitkwa, and Dalnee Lakes. (Data from Ruggles, 1965; Johnson, 1961; and Krogius and Krokhin, 1948, respectively)

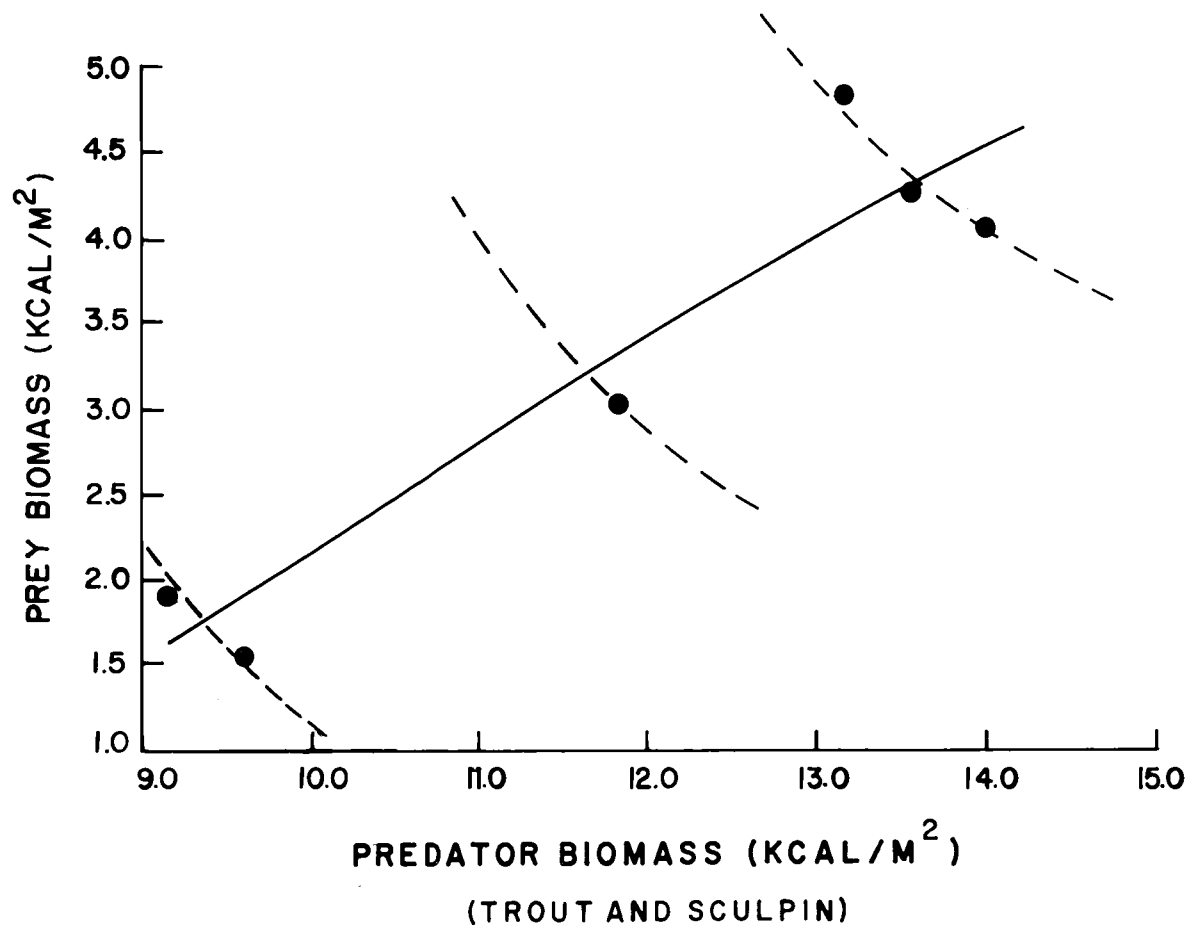


Figure 15. Relationships between prey density and the biomass of predators within a system or systems having a similar basic productive capacity (dashed lines) and between systems with very different productive capacities (solid line), during the fall, 1967, experiment.

was greater in streams having higher food densities and these streams had the highest terminal predator biomasses. The solid line drawn upward through the points in Figure 15 is representative of the increase in capacity of the different systems to maintain higher insect densities at higher densities of trout and sculpins. The dashed lines drawn downward indicate the probable effects on prey densities of increasing trout and sculpin biomass in individual systems of a given productive capacity. This was the effect of increasing sockeye biomass on zooplankton densities within and between lake systems (Figure 9).

One might reason that higher rates of food production would lead to higher food densities and these to higher consumer growth rates and biomasses. The results of the fall 1967 experiment support this view, a view supported by the results of other experiments. Trout growth rate when plotted against the terminal biomass of trout exhibits a strong positive correlation (solid line) in Figure 16. Growth rate and biomass of trout are lowest in the least productive streams and highest in those streams having the highest capacity to produce food. Within a particular system however, we would expect that with increases in trout biomass, the growth rate would decrease (dashed lines, Figure 16). My earlier work with laboratory streams having the same productive capacity demonstrated this negative correlation (Brocksen, Davis, and Warren, 1968), Figure 3 being an example.

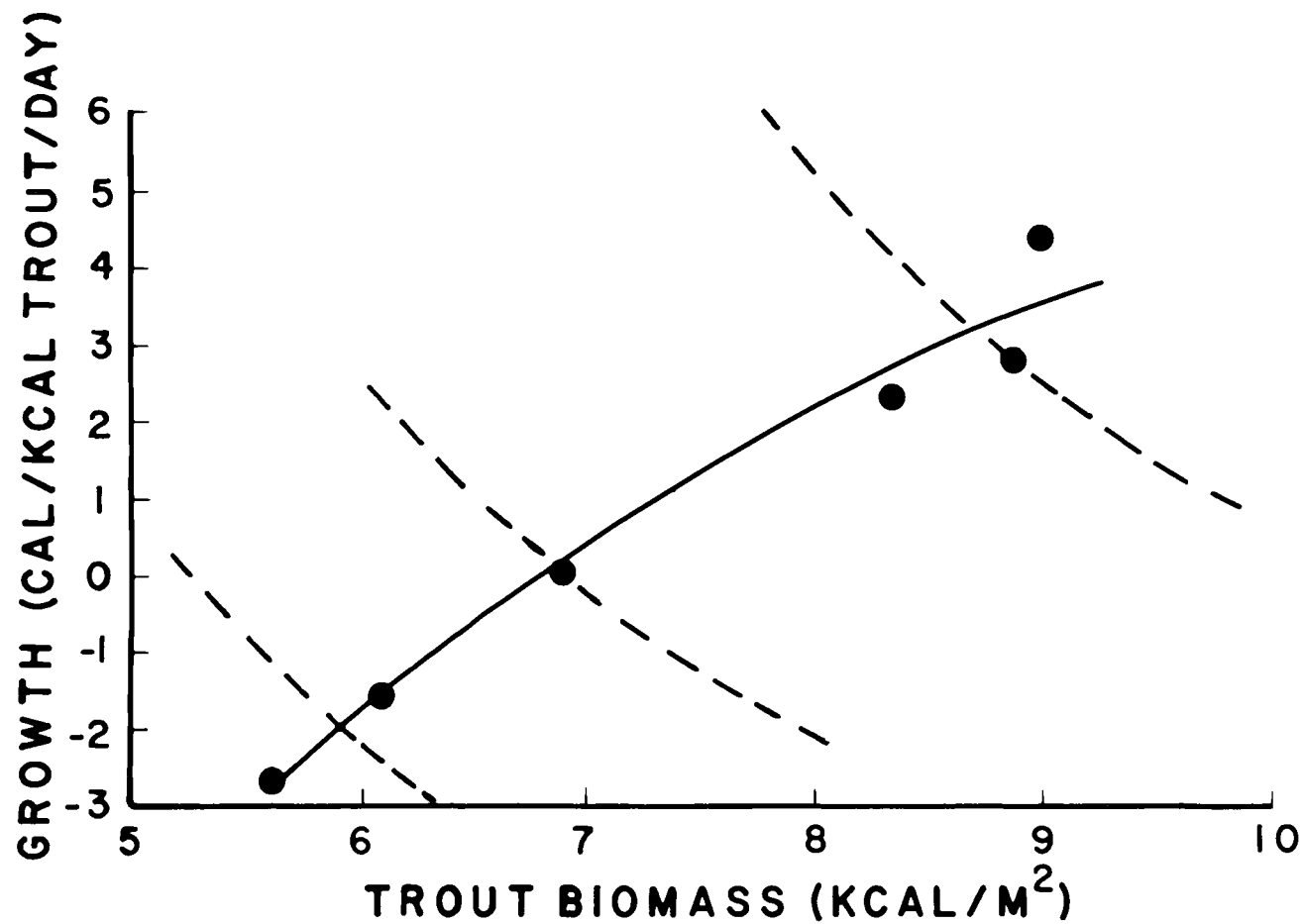


Figure 16. Relationship between trout growth rate and biomass within a system or systems having similar basic productive capacities (dashed lines) and between systems with very different basic productive capacities (solid line), during the fall, 1967, experiment.

The relationship between sculpin growth rate and sculpin biomass for the fall 1967 experiment (Figure 17) is much the same as that shown for the trout. Growth rate increases with increases in sculpin biomass between systems (solid lines), but within a system sculpin growth rate may be expected to decrease with increasing biomass of sculpins (dashed lines, Figure 17). The negative correlation between the growth rate and biomass of sculpins in systems having the same productive capacity has been demonstrated (Brocksen, Davis, and Warren, 1968), Figure 8 being an example.

It appears from the evidence on predator biomass and growth rate, the six laboratory streams constitute three rather than six systems with very different capacities to produce food organisms (Figures 12, 13, 14). The two points in Figure 15, 16, and 17 representing the lowest biomasses and growth rates are those streams that were subjected to the lowest levels of light energy. The intermediate points on these curves are from one of the streams subjected to the intermediate light energy level, the stream having the low current velocity (9 cm/sec). As will be shown later, current velocity appears to be an important factor in the capacity of the streams to produce food organisms. The three highest points on the curves are for the two streams at the highest level of light energy and for the stream having the intermediate light energy level and a current velocity of 30 cm per second. The character of the algal material in

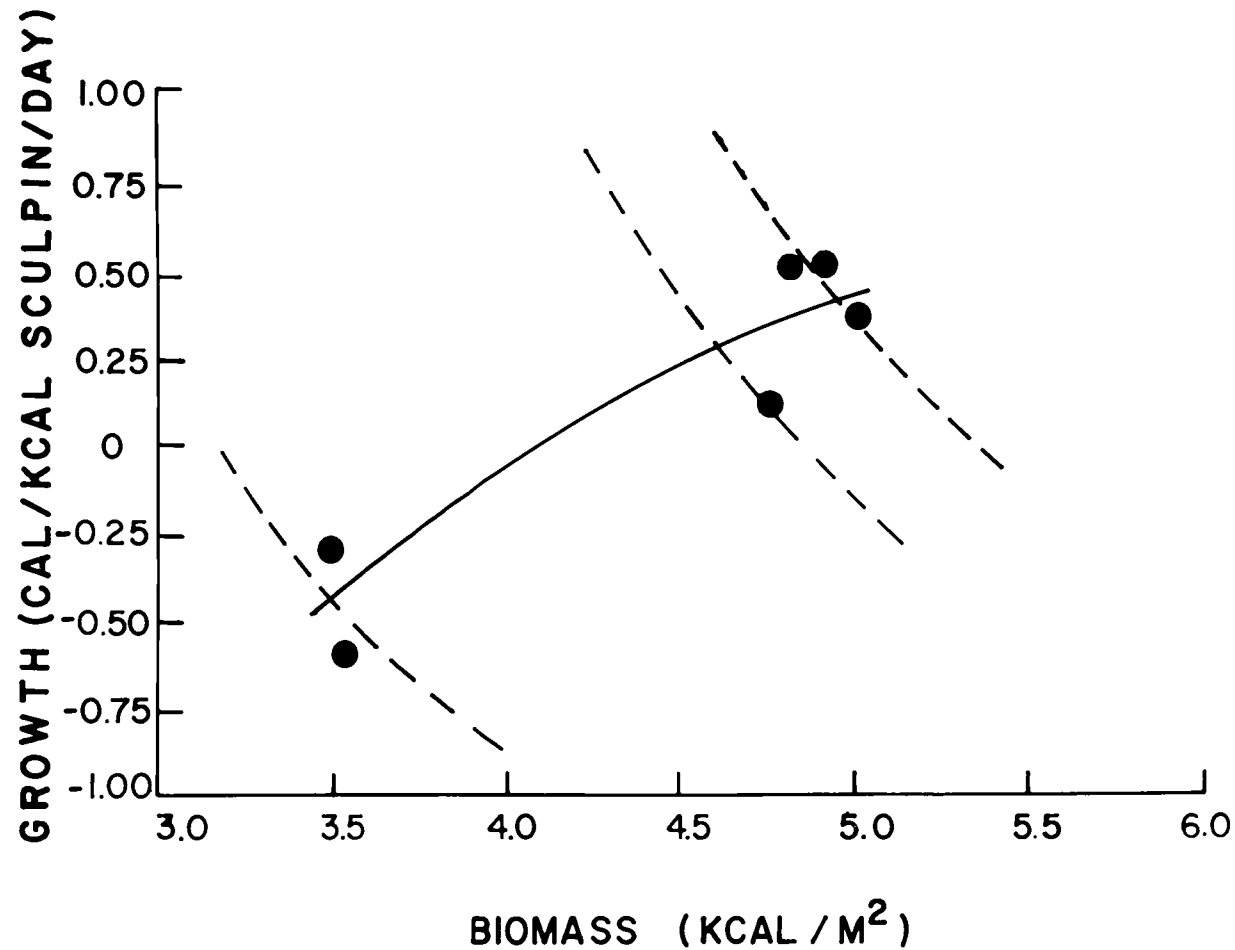


Figure 17. Relationships between sculpin growth rate and biomass within a system or systems having similar basic productive capacities (dashed lines) and between systems with very different basic productive capacities (solid line), during the fall, 1967, experiment.

these three streams differed and affected both the production of food organisms and their availability to the fish. There is evidence that in at least one stream space and not food was the factor limiting growth rate. Observations were made on the feeding location and behavior of trout during the spring, 1968, experiments, and the results of the observations reinforce these conclusions. A more detailed discussion of these factors follows in another section.

Because only one level of biomass of sculpins and trout was stocked in the different streams, it is possible to calculate only one production value for each species in each stream. We must, however, assume that if it were possible to obtain production values for different biomasses in each stream, or for different biomasses in different streams having the same capacity to produce food organisms, production-biomass curves resembling those drawn for illustrative purposes in Figures 18 and 19 would be demonstrated. It is difficult to interpret the meaning of individual production values from different ecosystems without visualizing a system of production biomass curves. Streams maintaining the highest levels of production at the highest biomasses must have the highest capacities for food production. Production must be zero at zero biomass and zero where growth reaches zero at a high biomass. With these ideas in mind, and with the one measured production value, I have subjectively drawn a production biomass curve for each system. This may give some

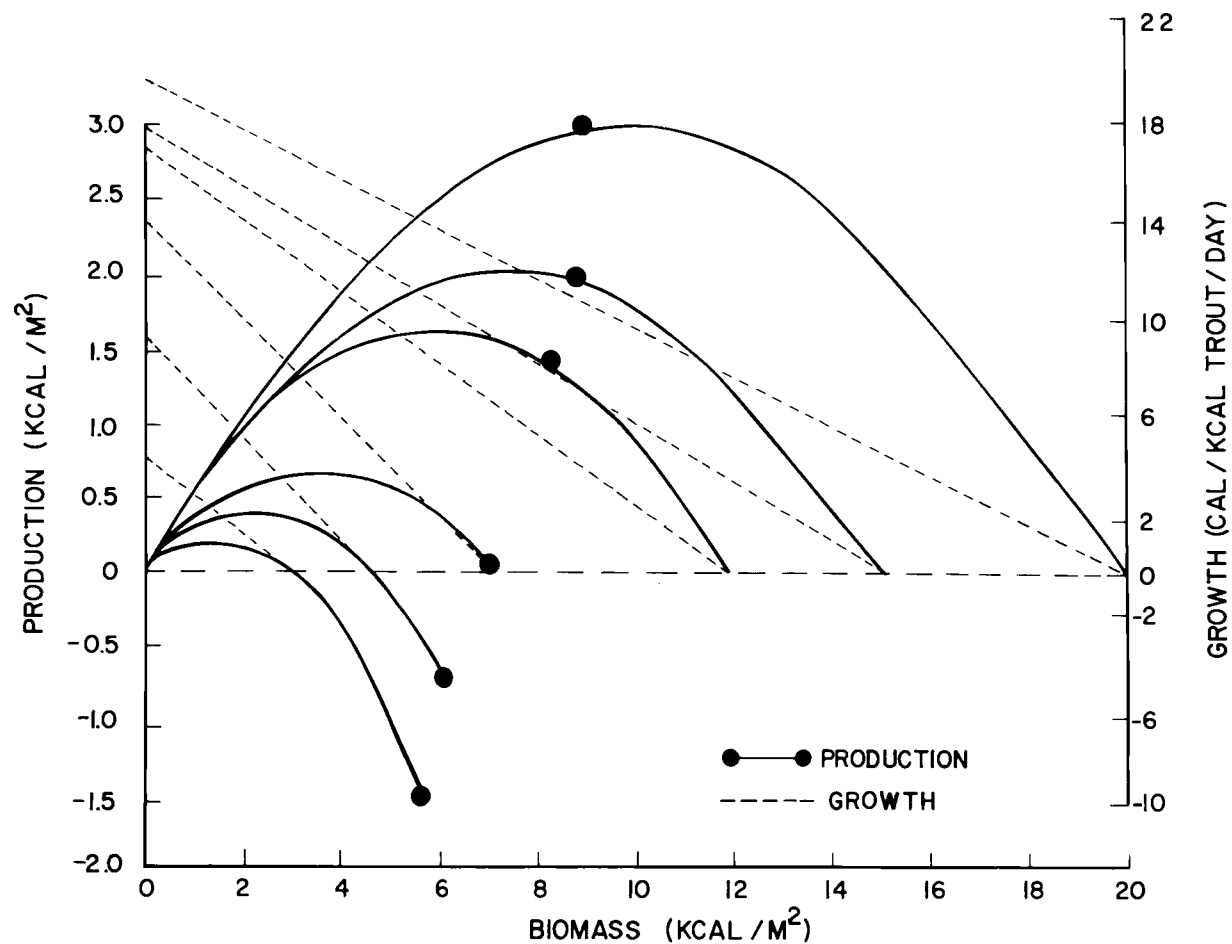


Figure 18. Comparison of trout growth rate, biomass, and production relationships for the six laboratory streams during the fall, 1967, experiment.

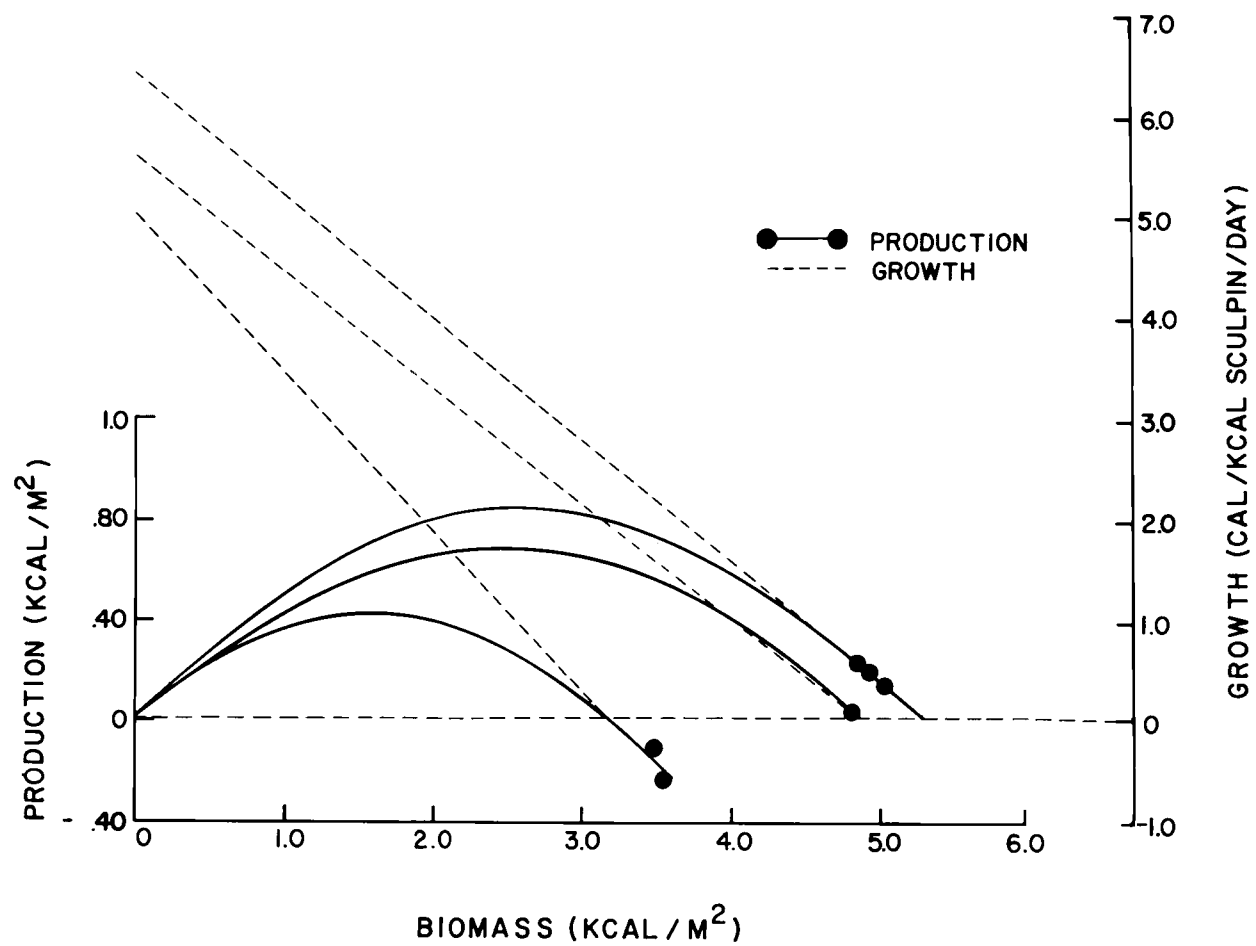


Figure 19. Comparison of sculpin growth rate, biomass, and production relationships for the six laboratory streams during the fall, 1967, experiment.

general indication of the differences in the productive capacities of the different systems. The dashed lines represent the growth rate curves and are based on the one calculated mean growth rate and calculations from the production curve. As was illustrated in Figure 10, the steepness of the growth curve determines the magnitude of the production curve and provides a graphic picture of the effects of increased biomass on the growth of a species. Again, there appears to be three systems with differing capacity to maintain sculpin biomass rather than six. It would appear that food availability was relatively the same for the three streams represented by the production curve with the greatest magnitude (Figure 19). The reasons for this have been discussed briefly and will be treated in greater detail in the discussion.

In this section, I have treated in detail the effects particular carnivores can have on their food resource and the effects the density and availability of a food resource can have on the carnivores. I will now attempt to clarify some of the density-dependent relationships that are involved in the production of the food organisms themselves (herbivorous insects).

Herbivore Biomass and Production and the Density of Algae

In the preceeding attempt to provide a conceptual framework for considering the trophic interactions that may lead to the growth and

production of a species of interest, I have referred to the differences that existed in the basic capacity of the six laboratory streams to produce food organisms. Higher densities of the herbivorous food organisms in some streams suggest these streams to have a greater capacity to produce food organisms. Some examination of the probable levels of insect production in the different streams is warranted. And, any possible elucidation of processes leading to differences in production of these insects is of value. Here, again, evidence of density-dependent relations between consumers, now insects, and their food organisms, now algae, exists. These density-dependent relations may help to explain differences in insect production within and between ecological systems.

It can be reasonably argued that consumption by herbivorous insects is often a principal fate of algal production. When this is true, it follows that growth and production of herbivorous insects may be functions of algal density. Using the turnover rates calculated for herbivorous insects during the fall 1967 experiment (Table 4) as a crude estimate of growth, I have plotted growth of insects (turnover rate) against the mean density of algal material present expressed as organic matter per square meter (Figure 20). Growth rate is found to be positively correlated with food density, as it was for sculpins and trout (Figure 5, 6, 12, 13). Such a relationship should be true not only for systems having the same capacity to produce algae but

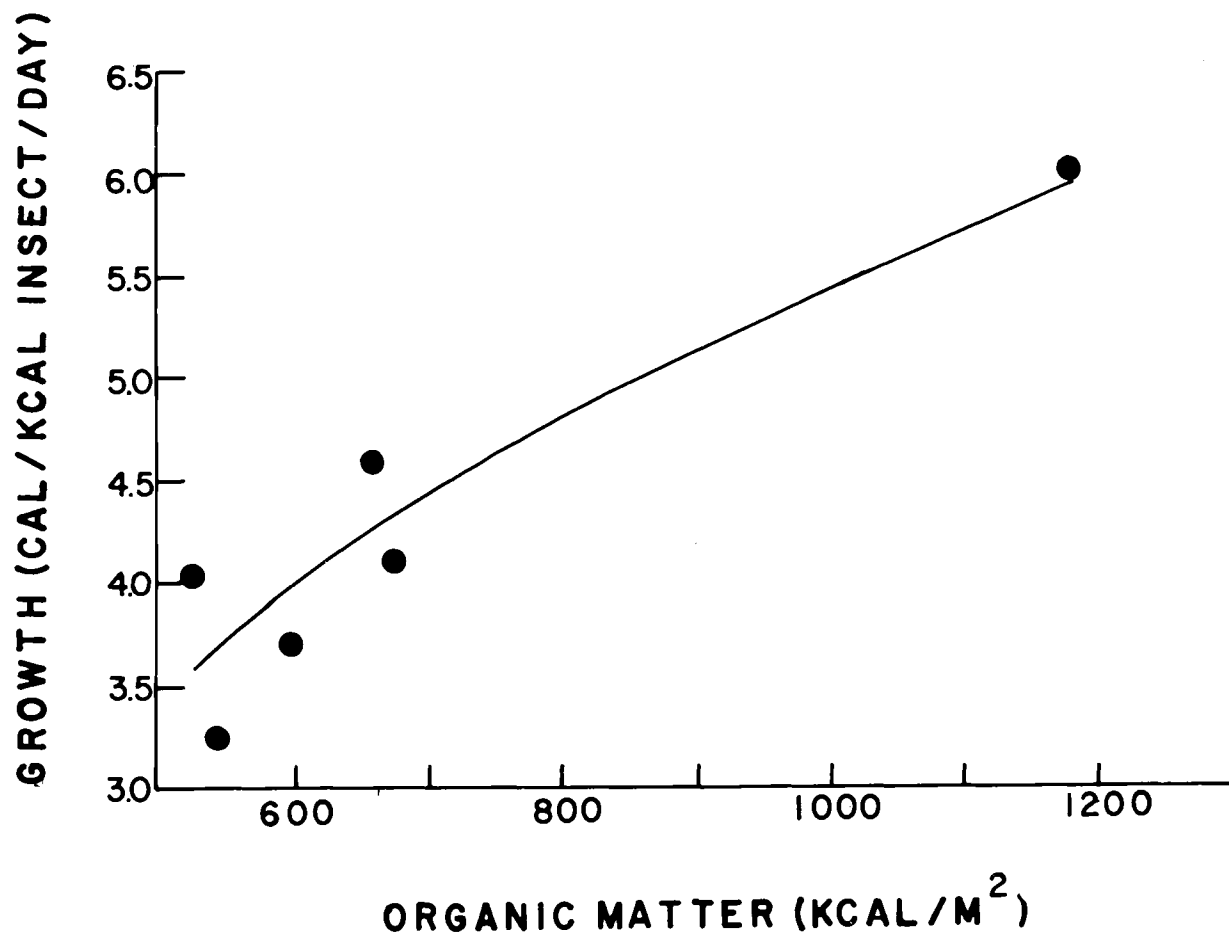


Figure 20. The relationship between herbivorous insect growth rate (turnover rate) and the amount of organic matter present during the fall, 1967, experiment.

between systems having different capacities.

If we consider the series of ecosystems having different basic capacities to produce algae, those systems having the highest algal production rates should maintain higher algal densities at higher insect densities. There should, then, exist a positive correlation between the biomass or density of algae and the biomass of insects when comparing systems with different productive capacities. But as I have explained for trout, sculpins, and sockeye salmon, a negative correlation should exist within the same system or between systems having the same capacity to produce algae. The different symbols in Figure 21 represent ecosystems having different capacities to produce algae. Even the same streams will be different during different seasons of the year, as can be seen by the location of like symbols. The three broken lines drawn downward through the points represent the decrease in food density (organic matter) with increasing insect biomass that would be expected in a single system or in systems having similar capacities to produce algae. The solid line drawn upward through the points represents the increase in insect biomass supported by the increased capacity of the different systems to produce and maintain increased algal densities (Figure 21). The broken lines were drawn rather subjectively and serve only to illustrate the principle hypothesized in Figure 11 and shown in Figures 9 and 15. Seasonal differences in the amount of algal material present occurred

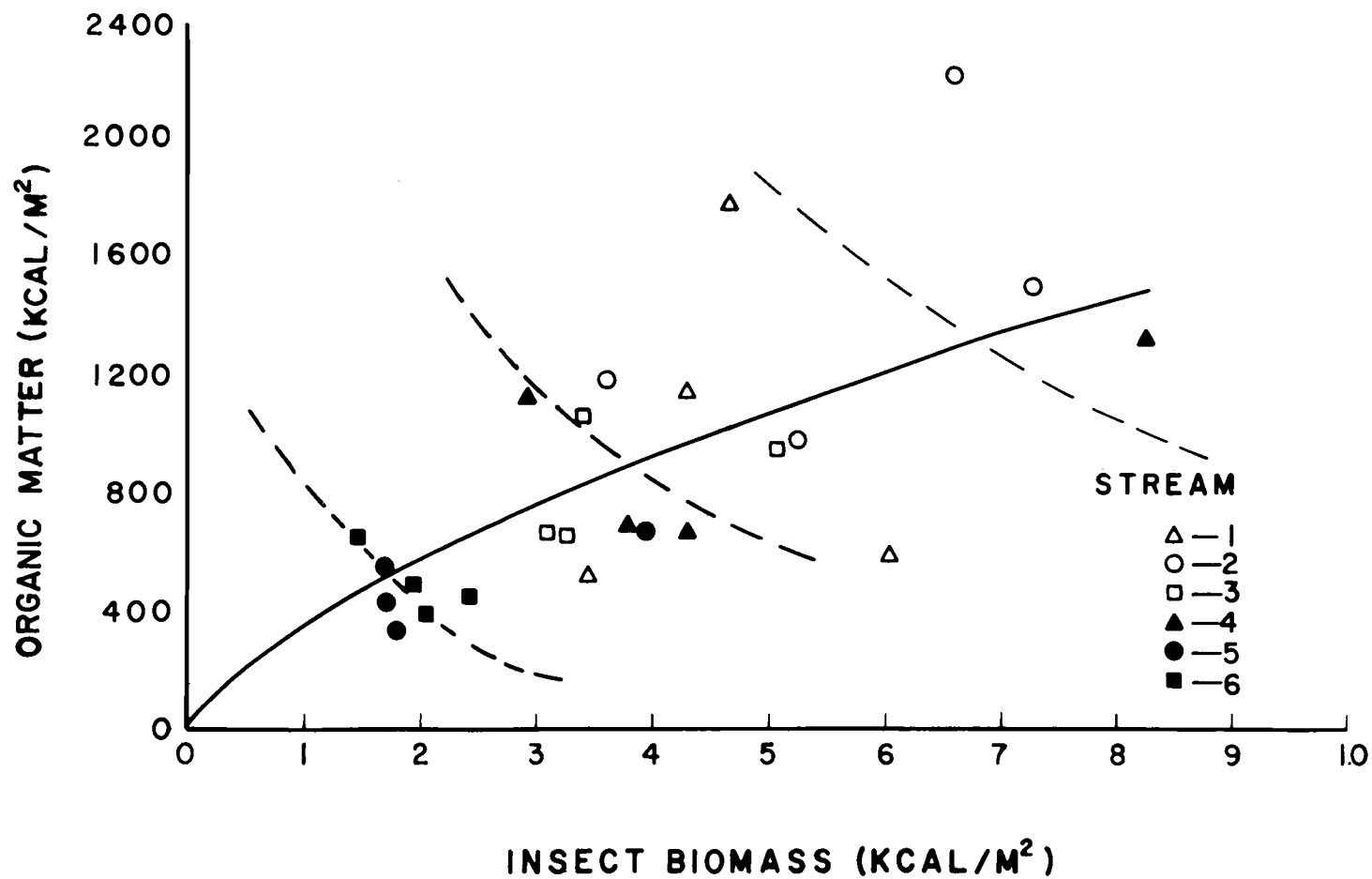


Figure 21. Relationships between mean organic matter (food density) and mean herbivorous insect biomass during the four seasons of the year, within systems having similar basic productive capacities (dashed lines) and between systems having very different basic productive capacities (solid lines).

within each system and this may help explain the apparent contradictory interpretation of Figure 21. While it may appear that a positive relationship existed within a particular system, the seasonal fluctuations account for this, and during the different seasons a negative correlation existed.

In seeking density-dependent relationships between consumers and their food organisms, it is important to be as specific as possible as to the organisms actually being utilized for food and their densities. When the food organisms are algae, this can be difficult. I did investigate species composition differences in the algal material between the six streams communities (Table 5). The ten species of algae that appeared most frequently in the examination of 30 microscope fields for each stream are listed in Table 4. Such an analysis was made for samples taken in June 1967 and in June 1968. Table 5 suggests that although the same species were present in the different streams, the frequency with which they appeared was quite different. Examination of the gut contents of insects from the different streams failed to establish differences in food habits.

The species composition of the algae in the different streams did, however, have implications beyond the feeding of herbivorous insects. Certain species which were dominant in particular streams afforded an increase in cover for the insects, making them less available for consumption by fish, either directly from the benthos

Table 5. The ten most important algal species in each stream during the months of June 1967 and June 1968. The species are listed for each stream in order of decreasing frequency of appearance.

JUNE 1967

<u>Stream:</u>	1	2	3	4	5	6
<u>Algal Species:</u>	Anabaena variabilis	Anabaena variabilis	Fragilaria vaucheriae	Anabaena variabilis	Oscillatoria retzii	Oscillatoria retzii
	Fragilaria vaucheria	Fragilaria vaucheriae	Nitzschia linearis	Fragilaria vaucheriae	Achnanthes lanceolata	Achnanthes lanceolata
	Achnanthes lanceolata	Oscillatoria retzii	Achnanthes lanceolata	Achnanthes lanceolata	Schizothrix calcicola	Nitzschia lanceolata
	Oscillatoria retzii	Achnanthes lanceolata	Anabaena variabilis	Nitzschia lanceolata	Nitzschia lanceolata	Nitzschia lanceolata
	Navicula bryophila	Nitzschia lanceolata	Nitzschia lanceolata	Oscillatoria retzii	Fragilaria vaucheriae	Fragilaria vaucheriae
	Nitzschia lanceolata	Nitzschia linearis	Oscillatoria retzii	Synedra ulna	Navicula minima	Navicula cryptocephala
	Nitzschia linearis	Navicula minima	Synedra ulna	Gomphonema accuminata	Nitzschia linearis	Rhoicosphenia curvata
	Schizothrix calcicola	Achnanthes minutissima	Navicula tuntula	Nitzschia linearis	Navicula cryptocephala	Synedra ulna
	Synedra ulna	Schizothrix calcicola	Gomphonema accuminata	Navicula tuntula	Navicula tuntula	Navicula bryophila
	Navicula tuntula	Navicula bryophila	Navicula minima	Schizothrix calcicola	Navicula miniscula	Navicula radiosa

JUNE 1968

<u>Stream:</u>	1	2	3	4	5	6
<u>Algal Species:</u>	Fragilaria capuceria	Oedogonium sp.	Rhoicosphenia curvata	Rhoicosphenia curvata	Rhoicosphenia curvata	Rhoicosphenia curvata
	Rhoicosphenia curvata	Schizothrix calcicola	Schizothrix calcicola	Achnanthes lanceolata	Achnanthes lanceolata	Achnanthes lanceolata
	Oedogonium sp.	Rhoicosphenia curvata	Fragilaria virescens	Fragilaria vaucheriae	Nitzschia oregona	Schizothrix calcicola
	Anabaena variabilis	Fragilaria virescens	Achnanthes lanceolata	Achnanthes minutissima	Phormidium retzii	Gomphonema rhombicum
	Schizothrix calcicola	Melosira varians	Melosira varians	Navicula minima	Schizothrix calcicola	Nitzschia brustulum
	Fragilaria virescens	Synedra ulna	Oedogonium sp.	Cocconeis placentula	Nitzschia dissipata	Navicula minima
	Cocconeis placentula	Fragilaria vaucheriae	Cocconeis placentula	Synedra ulna	Navicula minima	Oedogonium sp.
	Melosira varians	Tribonema minus	Fragilaria vaucheriae	Melosira varians	Cocconeis placentula	Calothrix parientina
	Gomphonema rhombicum	Achnanthes lanceolata	Gomphonema herculeanum	Fragilaria virescens	Navicula cryptocephala	Anabaena variabilis
	Fragilaria vaucheriae	Cocconeis placentula	Spirogyra sp.	Gomphonema rhombicum	Navicula radiosa	Cocconeis placentula

or from the drift. Further, the effective feeding area of the fish was reduced in some streams, increasing agonistic behavior and competition for food. The implications of these differences will be treated in detail in the discussion.

If, then, the density of algal material can influence the growth of herbivorous insects, and that herbivorous insects exert some controlling influence on the density of their food organisms, an examination of production relationships between streams is in order. With the crude estimate of insect production calculated for the fall 1967 experiment (Table 3), an illustration of the production-biomass relationships that could conceivably exist within systems having a constant capacity to produce can be made. These production-biomass relationships can then be compared with systems having different productive capacities (Figure 22). Again, the effect an increase in consumer biomass (in this case insects) can have on its production appears to be dramatically different in systems with different basic capacities to produce food organisms (Figure 22).

What, then, are the factors that contribute to the basic capacity of a system to support more or less biomass of a species of interest? In most insect communities, perhaps, the upper limits of insect production are set by the levels of algal production possible with existing plant nutrient resources. An examination of these and other questions involving the environmental factors leading to differences

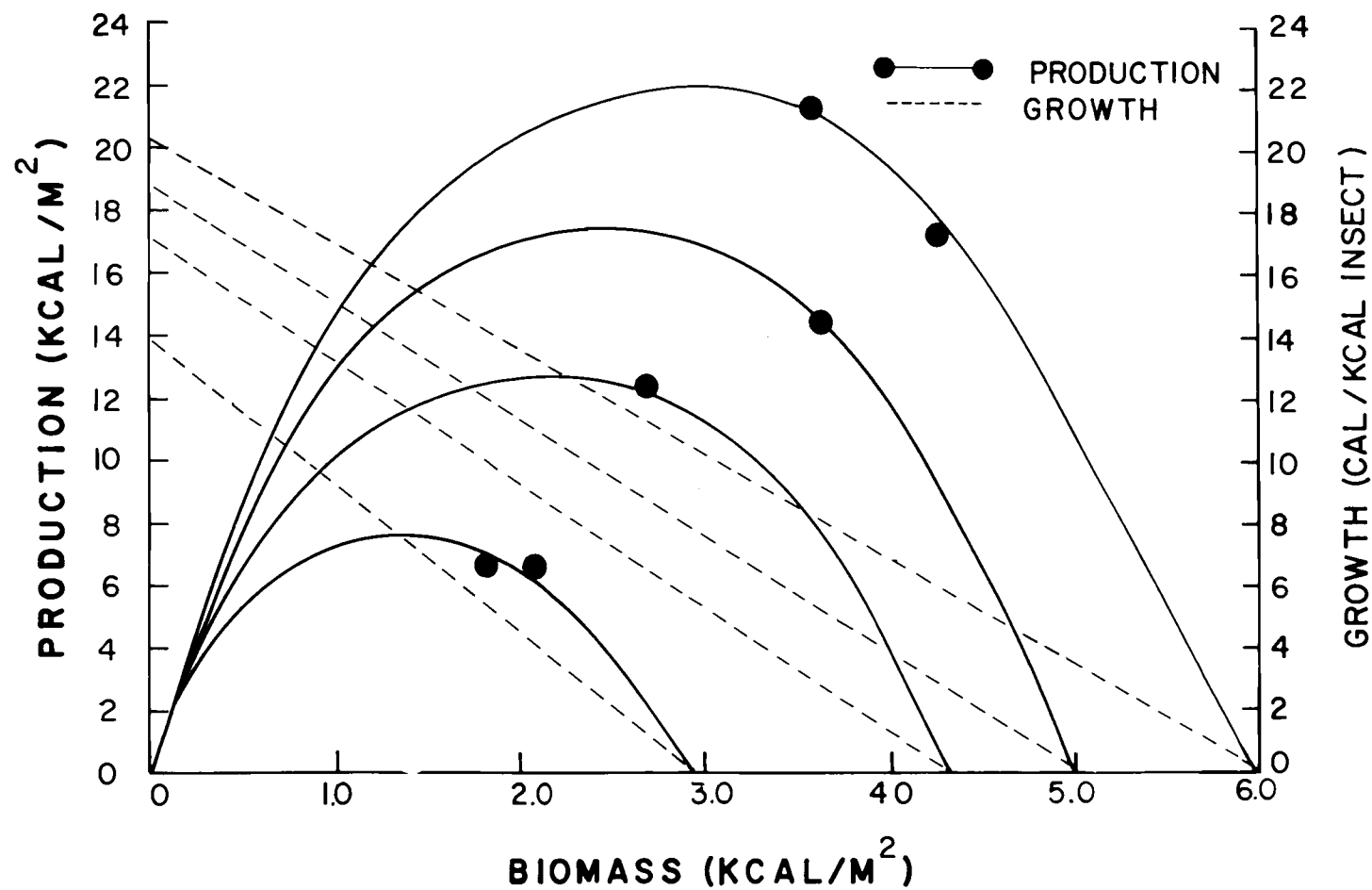


Figure 22. Comparison of estimated herbivorous insect biomass and production relationships for the six laboratory streams during the fall, 1967, experiment. (Data from Table 3)

in basic productive capacities between the six laboratory streams is therefore necessary.

Biomass of Algae and Light Intensity, Current Velocity, and Nutrients

Over much of the year in temperate and arctic regions, light may be one of the important factors exerting a controlling force on the production of algae. Within limits set by plant nutrients, an ecosystem will produce more or less plant material, dependent upon the amount of light energy to which a system is exposed and the amount which is absorbed. This material is then available for consumption by the herbivorous organisms within that community.

In my attempt to develop six different ecosystems, light energy was assumed to be a controlling factor (McIntire, 1966; Brocksen, Davis, and Warren, 1968). Three sets of two laboratory streams were exposed to light levels of 630, 350 and 120 foot candles respectively. The effects of this on the plant communities is best illustrated graphically by plotting mean biomass of organic matter per square meter against the utilizable light energy to which the plant communities were exposed during the different seasons of the year (Figure 23). The mean biomass of organic matter was usually higher during a given period of time at the higher light energy levels. There appeared to be a gradual increase in organic matter from the

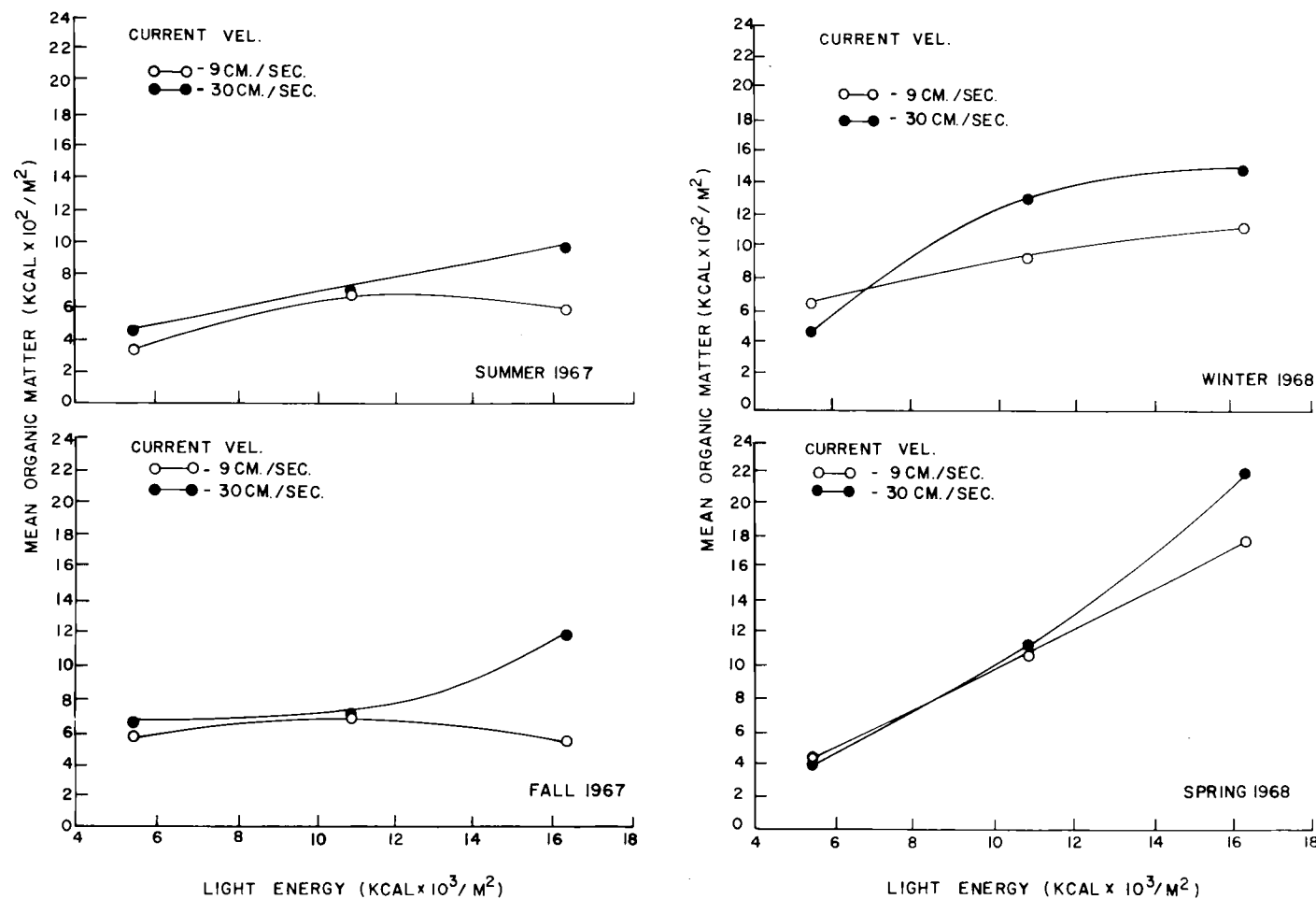


Figure 23. Relationships between mean biomass of organic matter and the utilizable light energy to which the six laboratory stream communities were exposed during different seasons at two current velocities.

summer 1967 through the spring 1968 (Figure 23) except at the lowest light level. This was probably due to both an increase in production and a build-up of detritus on the bottom of the streams from dead and decaying algal cells.

As stated, in most cases the biomass of organic matter produced exhibited a positive correlation with increasing light energy. There were, however, differences at particular light levels between streams having current velocities of 9 cm/sec and 30 cm/sec (Figure 23). Those streams having the higher current velocity were more productive, as indicated by biomass of organic matter, except at the lowest light level during the winter and spring 1968. McIntire (1966) has reported similar current velocity relationships. The relationship between organic matter, light intensity, and current velocity did not remain the same throughout the entire year (Figure 23) seasonal and successional changes apparently being involved (Table 5). At the highest light intensities, the communities were dominated by long, flowing filaments which resembled the aggregations of green filamentous algae often found in ponds.

For an ecosystem having a given resource of plant nutrients, increases in phytoplankton biomass can be expected to decrease the concentration (density) of the limiting nutrient and its availability to the growing, reproducing plant cells (Brocksen, Davis, and Warren, 1969). We should expect, then, the mean growth rate of an algal

population (production/biomass) to decline with algal density increasing over some range. However, between ecosystems having different levels of plant nutrients, we must suppose that, other conditions being similar, those ecosystems having the highest levels of plant nutrients will sustain the highest biomasses of algae.

In the laboratory stream systems, the concentrations of plant nutrients entering the streams were the same (Table 6). Because of the time the water was retained in the laboratory streams and differences in the character of the plant communities under the different conditions of light and current, it would be possible for varying levels of plant nutrients to exist in the different streams. An analysis of Table 6, however, does not make apparent any appreciable differences in the chemical components of the water in the different streams. The rather gross analyses performed on water quality is not, however, sufficient for the purposes of defining limiting nutrients in the laboratory streams. The analyses were made only with the objective of being able to identify any great differences in nutrient base between laboratory streams. As I have stated, any such large differences were not apparent.

Conceptually, density-dependent relationships should exist between plants and nutrient resources, as discussed in the preceeding paragraphs. In kind, the decline in algae growth rate that could be expected with declining density of nutrients is really not different

Table 6. Concentrations of important elements or compounds in the water flowing into all streams and in the water flowing out of each stream.

Element or Compound	Concentration in mg/l							
	Incoming Water	Outflowing Water:	Stream Number					
			1	2	3	4	5	6
Silica (SiO ₂)	40		39	39	39	40	41	40
Iron (Fe)	0.08		0.08	0.07	0.11	0.10	0.07	0.07
Calcium (Ca)	23		23	23	23	23	24	22
Magnesium (Mg)	8.7		8.8	9.1	9.1	8.8	8.9	8.8
Sodium (Na)	9.1		9.0	9.0	9.0	9.1	9.1	9.2
Potassium (K)	0.7		0.7	0.7	0.7	0.7	0.7	0.7
Bicarbonate (HCO ₃) ^{1/}	129		129	125	129	128	130	129
Sulfate (SO ₄)	0.2		0.0	0.0	0.2	0.2	0.2	0.2
Chloride (Cl)	5.5		6.0	6.0	5.5	5.5	5.5	5.5
Flouride (F)	0.1		0.1	0.1	0.1	0.1	0.1	0.1
Nitrate (NO ₃)	0.1		0.0	0.0	0.1	0.1	0.1	0.1
Total phosphate (PO ₄)	0.15		0.16	0.12	0.17	0.17	0.15	0.14

^{1/} pH in all streams was 8.2

from the decline in the growth rate of trout, sculpin or insect populations with decline in the density of their food resource (Figures 5, 6, 12, 13, and 20). The outcome, then, of these two density-dependent relationships--the decline in nutrient concentration with increasing algal biomass, and the decline in mean algal growth rate with limiting nutrient concentration decline--should, in theory at least, be no different from that of animal populations (Figure 3). That is, with algal biomass increasing from zero to some relatively high level, algal production should first increase from zero to some maximum, and then it should decline toward zero with further increases in biomass. This is for an ecosystem having a given resource of plant nutrients. As previously stated, however, among ecosystems having different levels of plant nutrients, those systems having the highest levels of plant nutrients will sustain the highest biomasses of algae. For a given system, then, the relationship between nutrients and algal biomass can be expected to be positive. This should lead to herbivore consumption having less effect on the production and biomass of algae in ecosystems having the higher levels of plant nutrients (Figures 11, 15, 21).

DISCUSSION

Ecologists have recognized the importance of energy relations to individual organisms, to the success of populations, and to the stability of communities. The intake of materials and energy, the respiration, and the growth of the individual organism in the laboratory have been rigorously studied for some species. Some studies of the energetics of laboratory populations have utilized sound bioenergetic principles. There have been attempts to describe energy relationships in complex natural communities, but these have been based on little or no knowledge of the food consumption, respiration, and production of most of the species present. Considering the complexity of these systems and the objectives of community ecologists, this is understandable; nevertheless, under these circumstances, energy budgets for complex natural communities remain unconvincing. The results of studies of laboratory populations may well be applicable to the analysis of complex community relationships, but such applications can be made with more confidence if it can be shown that laboratory results can be relied upon to correctly interpret relations in at least some simple communities.

Autotrophic plants more nearly represent a discrete trophic level than do the herbivores or the carnivores present in a community.

Neither herbivores nor carnivores have so common an energy source as green plants. Studies of the production of animals are rendered more difficult in that measurements must be made separately for each species. The production of autotrophic plants can be estimated by measurement of their combined photosynthetic activity. No doubt these were some of the considerations that led Ivlev (1945) to suggest that studies of animal production be oriented around some product of interest. He suggested that understanding of this product be sought through studies of its utilization of the production of its most important food species. Ultimately, understanding of the production of food species would also be sought through studies of their utilization of energy resources. However, measurement of the energy utilization and production of more than a few species of prey organisms would be a formidable task, one that has yet to be accomplished for any ecosystem. Ivlev (1961a, 1961b) based his own studies of predator utilization of prey organisms on the density of prey, not the production of prey. Measurements of the production of prey organisms are not only difficult to obtain, but are less useful measures of prey availability to a particular predator than is generally thought. The production of any prey organism passes into many trophic pathways, all of which would need evaluation before the proportion of prey production available for a particular predator could be assessed. It is the density of a particular prey organism that, at any point in time,

determines the quantity of prey a particular predator can consume and the metabolic cost of its capture and utilization. The density of prey surrounding a predator is one of the outcomes of prey production; and, of all the fates of that production, it is perhaps the most significant to the predator.

The most generally important and useful of my findings regarding animals and plants in laboratory stream communities are that prey density appears to be some relatively simple function of the biomass of the predator and its principle competitors and that the growth rate of the predator is some relatively simple function of the density of its prey. This is true both within and between systems. These relationships and the production-biomass relations they define are functions of the basic productive capacity of the ecosystem. Whenever such relations exist equilibria between the density of consumers and the density of their food organisms must develop.

There is considerable evidence that such relationships exist in natural ecosystems. Data of Allen (1951) suggest a relationship existed between the density of food organisms in the benthos and the growth rate of trout, and data of Horton (1961) indicate a similar relationship between benthos density and total food consumption by brown trout (Warren and Davis, 1967). Johnson (1961) has shown, as mentioned earlier, that in a series of seven basins in the Babine and Nilkitkwa Lake system in British Columbia, the mean weight of

juvenile sockeye salmon in mid-October exhibits a high positive correlation with the mean dry weight of zooplankton per cubic meter from mid-June to mid-October, the period of the year when nearly all of the growth of the zero age group occurs. The dry weight of zooplankton during this period exhibited a high negative correlation with the late August density of the fish in numbers. Brocksen, Davis, and Warren (1969), using data from studies conducted in large lake systems by Krogus and Krokhin (1948); Johnson (1961); and Ruggles (1965), illustrated rather dramatically the effect of increasing juvenile sockeye salmon biomass on the production of this species in systems having greatly different capacities to produce food organisms. From these same data, I have also suggested that the growth rate that sockeye salmon can maintain at a given plankton density is more a characteristic of this salmon than of the particular ecosystem. This suggestion is reinforced by data from the laboratory streams studies of trout (Figure 12) and sculpins (Figure 13).

The idea that equilibria are established in nature is further reinforced by an examination of the results of two other studies. The production values for juvenile sockeye salmon in the Babine-Nilkitkwa lake systems all fall on the ascending or left hand side of the production-biomass curve (Brocksen, Davis, and Warren, 1964). McIntyre (unpublished data) has found this to be true also for populations of cutthroat trout stocked in a small woodland stream and allowed

to emigrate from the stream sections under study. Thus, there may be some tendency for the biomasses of consumers to increase to the point at which maximum production occurs in systems, but not to increase further. Such density-dependent equilibria may operate through food, space, or other groups of factors.

Under Results and Interpretation, I referred to the possibility of space being a limiting factor in some of the experiments in which trout were stocked in the laboratory streams. During the spring 1968 experiment (Table 2), observations were made of the feeding activity, locations, and general behavior of individual trout. The results of this experiment indicate that, because of the filamentous character of the algae in one of the streams, the number of feeding locations available to the trout were reduced. The trout in this stream had the lowest production level of the six streams, even though food density was greatest in this stream. This limit of space per individual, coupled with the increased cover available for insects, generally reduced the amount of food actually available per fish. In addition, the increase in agonistic behavior of the fish probably reduced the efficiency with which the available food was utilized by the fish, due to increased respiratory costs. Brocksen, Davis, and Warren (1969) point out in their analyses of juvenile sockeye salmon production in three lakes with differing capacities to produce food organisms that space may have been the limiting factor in the lake with the greatest

basic productivity.

I have been successful in demonstrating that density-dependent relationships do exist at all levels of the simplified communities which developed in the laboratory streams, and I have cited corroborative evidence that such relationships exist in nature. Those who have been concerned with the culture of fish in ponds have long known that increasing the biogenic base often results in increasing production of the fish stocked in the ponds. Nelson (1958) has shown the growth rates of juvenile sockeye salmon in an oligotrophic lake to be increased by the addition of organic nitrogen and phosphorous. And Warren et al. (1964) found the production of cutthroat trout in a small experimental stream to be increased by addition of sucrose and organic nitrogen and phosphorous. Smith (1968) found such increases in the growth rates and yield of brook trout (Salvelinus fontinalis) as a result of fertilizing small lakes in New Brunswick, Canada. However, the factors intermediate between basic nutrient resources and the production of fish have not usually been elucidated. This is not surprising, when we consider the complexity of the processes leading from basic nutrients to fish production. But where natural equilibria lead to definable relations between the density and growth rates of consumers and their food organisms, we appear to have an exceedingly simple and powerful analytical tool.

In an earlier paper (Brocksen, Davis, and Warren, 1968)

possible ways were suggested of modeling the production of a species of interest by using functions of the densities of the species of interest, its competitors, and its prey. The separation of the relationships involved in the production of a predator of interest has facilitated the identification of the kinds of changes in the predator, its competitors and its prey that determine the function that its production is of its biomass. The concepts developed in this thesis regarding the effects different biogenic bases have on the production of a species in different ecosystems identify another set of factors that must be considered in defining the relations between the biomass and production of a consumer. It may one day be possible to relate by means of relatively simple functions the energy utilization and production of carnivores and herbivores to the physical and chemical factors determining the basic productive capacities of ecosystems. This, indeed, is one of the primary objectives of the study of trophic relations. These studies suggest not only the possibility of this but also an analytical system for its accomplishment.

I am suggesting, then, that even for complex ecosystems it may be possible to relate rigorously the growth and production of particular species not only to their direct energy resources but also to the factors leading to these resources. To do this would not require extensive and individual studies of all of the species in an ecosystem. Where equilibrium relationships exist between consumer growth

rates and between consumer and food densities, only density measurements, not production measurements, of the food are necessary.

Then, if food densities are found to be relatively simple functions of the biogenic base of an ecosystem, we approach very near an explanation of the capacity of that system to support a particular consumer. Such relationships probably will not lead to the perhaps unattainable goal of complete accounting of energy transfer in complex ecosystems. But to the extent the approach can be exploited, sound information on important biological relations should be obtained. And it provides a framework for investigating most of the important questions concerning ecosystems when the human and material resources for extensive study are available.

If the information on the competitive interactions of a consumer of interest and on intermediate links in the food chain of an ecosystem became available through intensive studies, the expenditure of considerable effort in the manipulation of trophic processes would be warranted when the consumer is a human resource. Control of competing species might be found to be economically justifiable, and, were utilization of competing species to be found possible, there would be added economic incentive beyond that of maximizing the production of the consumer of primary interest. Ultimately, there always remains the possibility of increasing the productive base of an ecosystem through addition of nutrients. This, of course, is being done

in aquiculture in fresh waters, and extention of this practice to larger bodies of fresh and marine waters is promising even if perhaps more remote.

The fact that density-dependent relationships do exist in nature has been well documented and I have discussed their utility in studying ecosystems of varying complexity. However, great interest will remain in systems where such density-dependent relationships, superficially at least, do not appear. It is entirely possible, for example, that such relationships would not be apparent in highly eutrophic systems. In attempting to elucidate density-dependence in such situations, it is not inconceivable that investigators would be forced to look for the reasons such density-dependence was lacking; and in so doing they could discover phenomena that could further aid in the evaluation of trophic processes. As described by Chamberlin (1897), the method of multiple working hypotheses should preclude a premature explanation passing "first into a tentative theory, then into an adopted theory, and lastly into a ruling theory." Chamberlin believed that his method could lead to the explanation of phenomena too complex to be explained by a single hypothesis, and it is through this method that ecologists should continue to attempt to increase their body of knowledge.

Lindeman (1942) contributed much breadth to trophic perspectives. Those who have followed him have contributed little substance

to the broad picture he sketched. As he emphasized, our studies and discussions of trophic relations must conceptually encompass ecosystems, for only in this context can we come to understand the persistence and production of populations. A holism, however, that does not give due attention to its parts is intellectually sterile. Studies of trophic relations must advance knowledge of the feeding, bioenergetics, and growth of individual organisms, must increase our knowledge of the trophic pathways leading to products of interest, and must enlarge our understanding of the competitive interactions that are so important in the production of a particular species and the structure of communities, before these studies can contribute much to man's knowledge or management of the trophic processes of the earth.

BIBLIOGRAPHY

- Allen, K. R. 1951. The Horokiwi Stream. Wellington. 231 p.
(New Zealand. Dept. of Fisheries. Bulletin no. 10)
- Averett, R. C. 1969. Influence of temperature on energy and material utilization by juvenile coho salmon. Ph.D. thesis. Corvallis, Oregon State University. 74 numb. leaves.
- Backiel, T. and E. D. LeCren. 1967. Some density relationships for fish population parameters. In: The biological basis of freshwater fish production, ed. by S. D. Gerking. Oxford, Blackwell. 261-293.
- Brocksen, R. W. 1966. Influence of competition on the food consumption and production of animals in laboratory stream communities. Master's thesis. Corvallis, Oregon State University. 82 numb. leaves.
- Brocksen, R. W., G. E. Davis and C. E. Warren. 1968. Competition, food consumption, and production of sculpins and trout in laboratory stream communities. Journal of Wildlife Management 32:51-75.
- _____. 1969. The analyses of trophic processes on the basis of density-dependent functions. In: A symposium on marine food chains, ed. by J. S. Steele. Berkeley, University of California. (In press)
- Chamberlin, T. C. 1897. The method of multiple working hypotheses. Journal of Geology 5:837-848.
- Darwin, C. R. 1859. The origin of species by means of natural selection or the preservation of favored races in the struggle of life. London, Murray. 619 p.
- Davis, G. E. and C. E. Warren. 1965. Trophic relations of a sculpin in laboratory stream communities. Journal of Wildlife Management 29:846-871.
- Horton, P. A. 1961. The bionomics of brown trout in a Dartmoor Stream. Journal of Animal Ecology 30:311-338.

- Howard, L. O. and W. F. Fiske. 1911. The importation into the United States of the parasites of the Gypsy moth and the Brown-tail moth. Washington, D. C. 312 p. (U. S. Dept. of Agriculture. Bulletin no. 91)
- Hutchinson, G. E. 1963. The prospect before us. In: Limnology in North America, ed. by D. G. Frey. Madison, University of Wisconsin. p. 683-690.
- Ivlev, V. S. 1945. The biological productivity of waters. Montreal. 35 p. (Fisheries Research Board of Canada. Translation Series no. 394. Translated from Uspekhi Sovremennoi Biologii 19:98-120)
- _____. 1947. Effect of density of planting on the growth of carp, tr. by G. E. Davis. Biulletin BOIP, Otdelenie Biologii 52(1):29-38. (Reprint)
- _____. 1961a. Experimental ecology of the feeding of fishes. New Haven, Yale University. 302 p.
- _____. 1961b. On the utilization of food by plankton-eating fishes. Montreal. 16 p. (Fisheries Research Board of Canada. Translation Series no. 447. Translated from Trudy Sevastopol'skoi Biologicheskoi Stantsii 14:188-201)
- Johnson, W. E. 1961. Aspects of the ecology of a pelagic, zoo-plankton-eating fish. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 14: 727-731.
- Krogus, F. V. and E. M. Krokhin. 1948. On the production of young sockeye salmon (Onchorhynchus nerka Walbaum). Montreal. 31 p. (Fisheries Research Board of Canada. Translation Series no. 109. Translated from Izvestiia Tikhookeanskovo Nauchno-Issledovatel'skogo Instituta Rybnovo Khoziaistva; Okeanografi 28:3-27)
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 24:399-418.
- McIntire, C. D. 1966. Some effects of current velocity on periphyton communities in laboratory streams. Hydrobiologia 27:559-570.

- McIntire, C. D. 1968. Structural characteristics of benthic algal communities in laboratory streams. *Ecology* 49:520-537.
- McIntyre, J. D. 1968. Unpublished research on production of trout and salmon in a small woodland stream. Corvallis, Oregon State University, Dept. of Fisheries and Wildlife.
- Malthus, T. B. 1798. First essay on population. London, McMillan. 396 p.
- Nelson, P. R. 1958. Relationship between rate of photosynthesis and growth of juvenile red salmon. *Science* 128:205-206.
- Nicholson, A. J. 1933. The balance of nature in animal populations. *Journal of Animal Ecology* 2:132-178.
- Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecological Monographs* 27:55-112.
- Ruggles, C. P. 1965. Juvenile sockeye studies in Owikeno Lake, British Columbia. *Canadian Fish Culturist* 36:3-21.
- Smith, H. S. 1935. The role of biotic factors in the determination of population densities. *Journal of Economic Entomology* 28: 873-898.
- Smith, M. W. 1968. Fertilization and predator control to increase growth rate and yield of trout in a natural lake. *Journal of the Fisheries Research Board of Canada* 25:2011-2036.
- Verhulst, P. F. 1838. Notice sur la loi que la population suit dans son accroissement. *Correspondance Mathematique et Physique* 10:113-121.
- Walter, E. 1934. Grundlagen fur algemeinen fischerie-liechen. Produktionslehre. *Handbuch fur Binnen-fischerie Mittle Europa* 4:480-662.
- Warren, C. E. and G. E. Davis. 1967. Laboratory studies on the feeding, bioenergetics, and growth of fish. In: *The biological basis of freshwater fish production*, ed. by S. D. Gerking. Oxford, Blackwell. p. 175-214.
- Warren, C. E. et al. 1964. Trout production in an experimental stream enriched with sucrose. *Journal of Wildlife Management* 28:617-660.

Wolny, P. 1962. The influence of increasing the density of stocked fish populations on the growth and survival of carp fry. Rocznik Nauk Rolniczych 81-B, 2:171-178.