THE FOOD TURNOVER OF A BLUEGILL POPULATION[1]

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Introduction

The growth rate of populations of aquatic organisms has become a dominating topic of limnological research, constituting the production problem. The trophic-level concept of Lindeman (1942) cut through the maze of data on aquatic food relations and pointed out the possibility that the quantitative aspect of production could be attacked by considering the energy content of the organisms and the energy flow from one trophic level to another. Lindeman's ideas have been justifiably criticized by Ivlev (1945), but, despite certain inadequacies, remain a significant contribution. The concept of production is still undergoing an evolution and is now in the process of refinement. Macfayden (1948) has traced the development of this concept and of closely associated ideas. Clarke (1946) considerably sharpened the working definitions of production rate, standing crop, and yield; as a result, terminology is becoming more stabilized.

The writer is particularly interested in fish production, feeling that investigation of this part of the aquatic ecosystem will contribute significantly to the general problem. The intrinsic biological interest of fishes and their considerable economic value are incentives to a more complete understanding of this part of the production process. Ricker (1946) accelerated the study of fish production by reviewing past achievements in this field and by pointing out areas for profitable research. The present work on the food turnover by a fish population was stimulated by Ricker's analysis of the subject.

The supply of food is one of the major, basic factors controlling the density and production of fishes. To understand more clearly the relationship between the fish population and its food supply, the efficiency of food conversion by sunfishes of various ages has been investigated in the laboratory. Experimental feeding of longear sunfish (*Lepomis megalotis*) and green sunfish (*Lepomis cyanellus*) was begun in 1950, and the results of these experiments have recently been published (Gerking 1952). The experiments have been continued, using the bluegill (*Lepomis macrochirus*) because it is widely distributed in the United States and because its population characteristics are more completely known than are those of other species in our region.

For our purposes, growth is defined as the synthesis of new protoplasm. Since the synthesis of protein is the most characteristic feature of growth, protein accumulation is used as the index of the efficiency of the growth process. There are objections against using other possible indices, such as wet weight, dry weight, weight of organic matter, fat, and carbohydrate. Wet weight has the obvious disadvantage that water content varies considerably under different conditions of nutrition. Dry weight and weight of organic matter (dry weight minus ash weight) are not true reflections of growth because the quantity of fat varies tremendously. Under experimental conditions fat has been found to vary between 3 and 33 per cent of the dry weight. The variability is almost as great under natural conditions. Bluegills from a northern Indiana lake have been sampled at all seasons for two years and the fat content has varied from 8 to 33 per cent of the dry weight. Neither is true growth reflected by the caloric content of the body as measured by a bomb calorimeter. The variability in the quantity of fat is again the complicating factor, especially since fat has the greatest caloric value of the three principal organic materials. Other aquatic organisms may or may not be as variable as fish in this respect, but the difficulty should be appreciated when estimating "energy flow" through a food chain. The accumulation of fat by fish is no indication of the actual amount of material being synthesized in the growth process. Fat is generally deposited in practically the same molecular arrangement as it occurs in the food (Lovern 1951). Carbohydrate is not stored in the animal body to any appreciable extent and cannot be used to indicate growth.

Protein turnover will be defined as the amount of protein that is required by a population for growth, for the metabolic expenditure of energy, and for the replacement of proteins broken down during the normal course of living. Protein turnover is thus synonymous with the amount which is absorbed by the intestinal tract except that it describes the various uses which are made of the protein within the body. To illustrate the

[1] Contribution No. 532 from the Department of Zoology, Indiana University.

computation of protein turnover, the vital statistics of the bluegill population of Gordy Lake, Indiana, will be used. Estimates of the abundance and mortality rates of this population have been completed (Gerking 1953), and its growth rate has been investigated more thoroughly since that time. The variables of abundance, growth, mortality and efficiency of protein utilization for growth will be combined to procure an estimate of protein turnover by the population.

Population Estimates

The bluegill population of Gordy Lake was estimated by Petersen and by Schnabel methods, using the fishermen's catch to determine the ratio of marked to unmarked fish in the lake. The population estimates presented here are based on the same data as in the previous study, but they have been reassembled. A rigorous examination of the estimates was made in the earlier paper and will not be repeated here. All estimates apply to the month of June.

A fair number of age II fish were caught in cylindrical wire traps, and it was possible to estimate their abundance by the Schnabel method, using only trap-caught fish. The traps sampled age II bluegills ranging in size from 90 to 115 mm. There is no information about a group of age II fish smaller than 90 mm. An estimate of 5300 will be referred to as "age II," although it represents only a part of that age-group.

Age III and age IV numbered about 8850. A considerable size overlap between the age-groups prevented separate estimates of abundance. The total number was apportioned between the two ages by using the relative frequency of each age in a large sample of the fishermen's catch. Of 798 fish assigned to the two ages by scale reading, 446 were age III and 352 were age IV. The population assigned to age III thus becomes 4950, and that of age IV is 3900. Not quite all of the age III fish were vulnerable to capture at the time sampling began. The sample is slightly biased in favor of the age IV fish, but this method of apportioning the population estimate seems to be as accurate as possible under the circumstances.

There was an estimated 1315 fish of ages V to VIII. The catch sample included 58 age V, 16 age VI, 4 age VII, and 1 age VIII. The population of this group was distributed according to the proportion of each age in the catch as follows: 965 age V, 266 age VI, 67 age VII and 16 age VIII.

Mortality Rates

The total annual mortality rate was estimated to be 72.5 per cent by comparing the number of individuals of successive ages in the catch (Fig. 1). This is somewhat lower than the annual mortality rate estimated in the earlier paper, and it is apparently a more accurate interpretation of the data. Age III fish were almost completely vulnerable to fishing when the samples were taken, and they have been included in the computation.

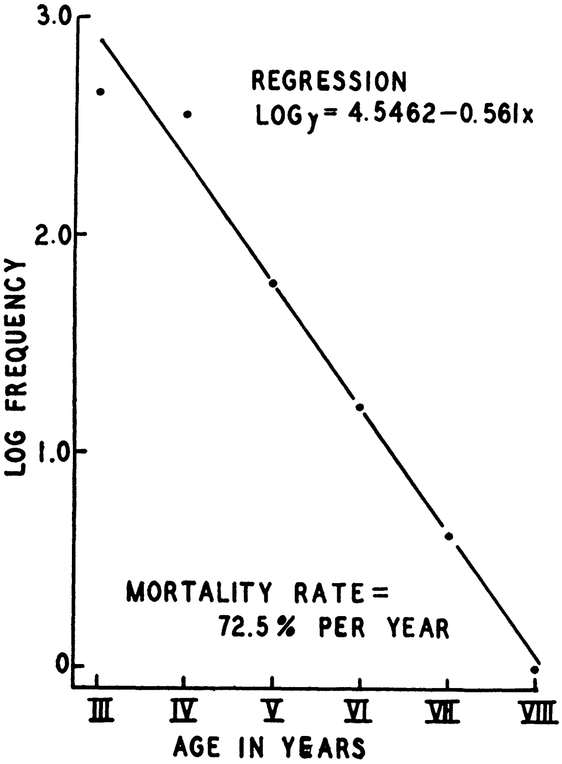

Fig. 1. Total annual mortality rate of the bluegill population of Gordy Lake, Indiana, calculated from the relative frequency of each age in the catch.

Age IV was a strong year-class in the population in 1950. These factors influence the estimation of mortality rate, but the regression agrees with the constant mortality rate affecting ages V to VIII.

The rate of exploitation, *i.e.* the annual expectation of death from fishing, was determined by recaptures from a known number of marked fish in the lake. The vulnerable population was removed at a rate of 32.2 per cent from June 2 to September 4. The winter and late fall fishing, although not observed, was known to be small. The yearly rate of exploitation was estimated to be only slightly above the summer rate, or about 35 per cent. The annual expectation of natural death is $72.5 - 35.0 = 37.5$ per cent.

In calculations which follow it is desirable to express these mortality rates as instantaneous rates, following the methods developed by Ricker (1944). Conversion to instantaneous rates is the only practical method so far devised to combine growth and mortality rates. The definitions of certain symbols are repeated here.

a = total annual mortality rate
i = total instantaneous mortality rate
μ = rate of exploitation (annual expectation of death from fishing)
υ = annual expectation of natural death
p = instantaneous mortality rate from fishing
q = instantaneous mortality rate from natural causes

The determination of instantaneous rates from the empirical data becomes:

(1) where $a = 0.725$, $i = 1.29$

(2) since $\frac{i}{a} = \frac{p}{\mu}$, then $p = \frac{1.29 \times 0.350}{0.725} = 0.623$

(3) since $\frac{i}{a} = \frac{q}{\upsilon}$, then $q = \frac{1.29 \times 0.375}{0.725} = 0.667$

By definition, $a = \mu + \upsilon$, and $i = p + q$. The instantaneous total mortality rate was taken from Ricker's (1948) tables.

Age and Growth

Age and growth of the Gordy Lake bluegills have been analyzed by standard methods, employing scale reading for age determinations. The scales were unusually well marked, and the age assessment was relatively simple. The radius of the anterior field of the scale and the distance from the focus to each annulus were measured. The fork length of the fish at the time of capture is essentially proportional to the anterior radius of the scale, with the intercept of the x and y axes at 20 mm. (Ricker 1942). The length of individual fish at each annulus was calculated as follows:

$$\text{Fork length of fish at time of annulus formation} = 20 + \frac{(\text{scale radius at year x})\ (\text{fork length} - 20)}{\text{total scale radius}}$$

The fork lengths were converted to weights from a length-weight graph, and the average weight of the fish at each age was computed. The maximum age in our sample was age VIII. The weight at age IX was extrapolated in order to estimate the growth of the fish during the last year of life.

The instantaneous rate of growth in terms of weight, k, is a useful statistic for relating growth and mortality. The k values were found by plotting age and the logarithms (base 10) of the weight at each age (Fig. 2). Free-hand tangents to the resulting curve were drawn midway between successive ages. The slope of each tangent was converted to natural logarithms by multiplying by 2.30. This method is the same as that employed by Ricker (1945) for a somewhat different purpose.

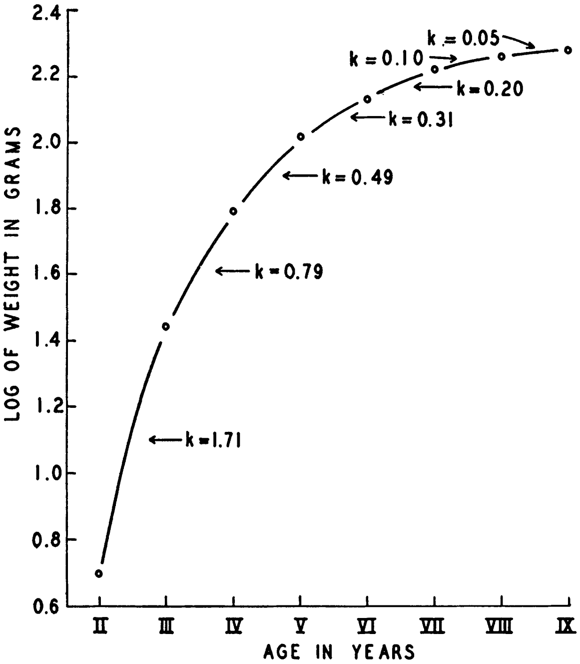

Fig. 2. Method of computing instantaneous rate of growth, k, for the bluegill population of Gordy Lake, Indiana. See text for further explanation.

Protein Utilization

The efficiency of protein utilization for growth by bluegills of various ages was determined by feeding the fish a weighed amount of meal worms (*Tenebrio mollitor* larvae) each day for 50 days. Meal worms were selected as food because they simulate the insect larvae which compose a large share of the bluegill diet in nature. Protein nitrogen was estimated in the food and feces by the Kjeldahl method. The amount of protein retained during feeding was found by measuring the dry weight and nitrogen content of fish at the beginning and end of the experiment. A group of sample fish represented the experimental group at the start of feeding. The efficiency of protein utilization for growth was calculated by relating the amount of protein nitrogen retained to the amount of protein nitrogen absorbed. The efficiency of protein utilization decreases as the fish increase in size (Fig. 3). A semi-logarithmic transformation of the data seems most appropriate, and the regression has been calculated in this way.

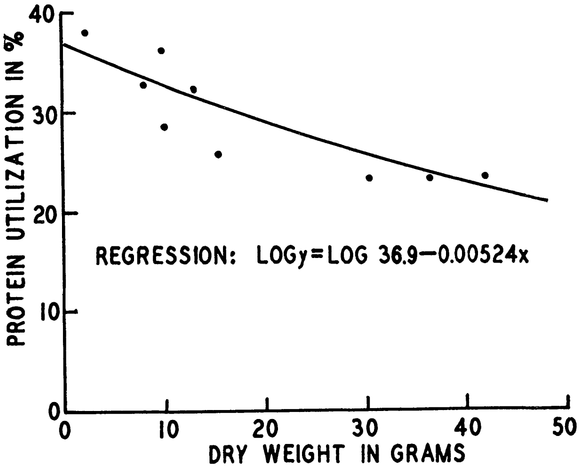

Fig. 3. The relationship between the dry weight of bluegills and the utilization of protein for growth. The fish were fed meal worms in 50-day aquarium experiments.

The amount of protein required for growth by individual fish having the characteristics of Gordy Lake bluegills can be estimated (Table I) by utilizing the age-growth data and the efficiencies of protein utilization as related to the size of the fish. The wet weight of the fish at each age was converted to dry weight by assuming that the dry substance makes up 27.8 per cent of the wet weight. This percentage was derived by averaging many dry weight measurements of bluegills taken from several sources during the past three years. The protein content, 61.25 per cent of the dry weight, is based on the same observations. The efficiency of protein utilization was calculated

Table I. *Estimate of the protein turnover by individual fish of the Gordy Lake bluegill population. Weight at each age was calculated from age-growth determinations.*

Age	Weight	Dry weight*	Protein**	Protein gain	Efficiency of protein utilization	Amount of protein required for growth
	g.	g.	g.	g.	%	g.
II....	5	1.4	0.86			
				3.92	35	11.21
III....	28	7.8	4.78			
				5.76	32	18.03
IV....	62	17.2	10.54			
				7.35	28	26.24
V....	105	29.2	17.89			
				5.26	25	21.04
VI....	136	37.8	23.15			
				5.45	22	24.80
VII....	168	46.7	28.60			
				2.58	21	12.28
VIII....	183	50.9	31.18			
				1.53	20	7.65
IX....	192	53.4	32.71			

*Dry weight assumed to be 27.8 per cent of wet weight.
**Protein assumed to be 61.25 per cent of dry weight.

for each age from the regression equation of Figure 3. For example, the average dry weight of age II fish in their third year of life is about 3.6 g. (0.278 × average weight of age II fish from Figure 2, 13.0 g.). The efficiency of protein utilization is calculated as follows:

$$\log y = \log 36.9 - 0.00524 \times 3.6 = 1.5484,$$
$$y = 35.4 \text{ per cent}$$

Variability is associated with each column of the table, and estimates of reasonable accuracy have been chosen.

The data can also be construed as representing the amount of protein turnover by an individual fish from age II to age IX, or 121.25 g. Estimates made for fish of age 0 and age I increase this amount by 2.5 g. A total of 123.8 g. of protein would, therefore, be required to produce a fish containing 32.7 g. of protein, an average efficiency of 26 per cent. This average efficiency is an overestimate because the amount of "replacement protein" has not been included in the computations. The determination of replacement protein requires separate laboratory analysis which has yet to be done.

Replacement protein may be a significant quantity. It is required at all times, and it probably varies with temperature. Growth does not occur in the winter among bluegills, although they feed in cold weather (Moffett and Hunt 1945). The protein consumed during the winter would be used only for energy expenditure and replacement.

No correction for unabsorbed protein has been made. In our experiments only 2 per cent of the protein nitrogen fed to the fish was found in the feces and a part of this can undoubtedly be accounted for by the "metabolic nitrogen," *i.e.* nitrogen derived from digestive juices and epithelial cells abraded from the alimentary canal. For practical purposes, the protein consumed by the fish is equivalent to that absorbed.

Food Turnover by the Population

The four estimates of growth, mortality, abundance and protein utilization can now be combined to provide a measure of the protein turnover by the population (Table II). It will be convenient to obtain a value for the average population during the summer, and Ricker (1944, 1945) has provided the mathematical treatment necessary for this computation. The following relationships are of primary interest:

(4) $k - i = g$, where g is the net instantaneous rate of increase in weight of an age-group.

(5) $e^g - 1 =$ the fractional net increase in weight of an age-group.

(6) $\frac{e^g - 1}{g} \times$ initial weight of an age group $=$ the average weight of an increasing age-group.

The weight of the population at the beginning of the summer is found by multiplying the abundance of each age-group by the average weight of the individuals of that group as determined from the age-growth data. The average number in each age-group during the summer is estimated by dividing its average weight by the mean weight of the individuals of that group. The mean weight of the individuals in each age-group was read from Figure 2 at a point mid-way between successive ages. The protein turnover by a single individual in each age-group (Table I) is multiplied by its average population to provide an estimate of the protein turnover for that age-group. The total protein turnover for the whole population during its season of growth is found by summing the protein required by all age-groups.

One of the notable features of the Gordy Lake population is that none of the age-groups from III to VIII shows a net increase under the observed conditions of growth and total mortality. Growth is not adequate to compensate for the rate of mortality. On the other hand, growth exceeds mortality among age II fish, primarily because less than half of them became vulnerable to fishing. The instantaneous rate of total mortality of age II fish, 0.54, was based on the rate of exploitation of these fish (4.5 per cent) and the rate of natural mortality corresponding to older fish.

Our method of calculation shows that 156.8 kg. of protein are required by the population during the summer growth period. The source of this protein is, of course, the various organisms which comprise the food of the bluegill, and it is worthwhile to attempt to estimate the total weight of organisms which this amount of protein represents. For this purpose, the excellent data of Geng (1925) are available. He analyzed various aquatic organisms for water, protein, chitin, fat, carbohydrate, and ash. The average protein content of 24 different organisms listed by Geng was 9.59 per cent of the live weight. (Geng's tabulation of "raw protein" rather than "true protein" has been used because the data are more extensive, and the small difference between the two is unimportant in the estimations which are made.) The approximate weight of organisms consumed by the population is $\frac{1}{0.0959} \times 156.8 = 1635.0$ kg. (3597 pounds). The area of Gordy Lake is 11.5 hectares, and on a relative basis the bluegill population consumed some 142 kilograms of organisms per hectare (126 pounds per acre).

Catch and Natural Mortality

The rate of exploitation and expectation of natural death are known for the Gordy Lake population and the estimates of deaths from these sources will be presented since they offer partial confirmation of the previous computation. The estimated catch can be secured by multiplying the average weight of each age-group by the instantaneous mortality rate from fishing (p), which applies to the appropriate age-group, and summing the entries (Table III). A total of 233.2 kg. (513.0 lbs.) make up the catch as estimated

Table II. *Estimate of the protein turnover by the Gordy Lake bluegill population in 1950.*

Age	k	i	g	e^g-1	Beginning of summer			$\frac{g-1}{g}$	Average during summer			Protein turnover by each individual *g.*	Protein turnover by population *kg.*
					Population	Individual weight *g.*	Population weight *kg.*		Population weight *kg.*	Individual weight *g.*	Population		
II	....	....	......	....	5300	5	26.5						
	1.71	0.54	+1.17	+2.222	....	..	....	1.899	50.3	14	3590	11.21	40.2
III.....	....	....	......	....	4950	28	138.6						
	0.77	1.29	−0.52	−0.406	....	..	....	0.781	108.2	42	2580	18.03	46.5
IV	....	....	......	....	3900	62	241.8						
	0.49	1.29	−0.80	−0.551	....	..	....	0.689	166.6	80	2080	26.24	54.6
V.....	....	....	......	....	965	105	101.3						
	0.31	1.29	−0.98	−0.625	....	..	....	0.638	64.6	120	538	21.04	11.3
VI.....	....	....	......	....	266	136	36.2						
	0.20	1.29	−1.09	−0.664	....	..	....	0.609	22.0	153	144	24.80	3.6
VII.....	....	....	......	....	67	168	11.3						
	0.10	1.29	−1.19	−0.696	....	..	....	0.585	6.6	176	38	12.28	0.5
VIII.....	....	....	......	....	16	183	2.9						
	0.05	1.29	−1.24	−0.711	....	..	....	0.573	1.7	188	9	7.65	0.1
IX.....	....	....	......	....	....	192							
					15,464	....	558.6	....	420.0	....	8979	....	156.8

by this method. The actual catch was 267.7 kilograms (589.6 pounds) of bluegills, based on an intensive creel census. Our estimate is 12.9 per cent lower than the observed amount. On a relative basis the estimated catch was 20.2 kilograms per hectare (18.0 pounds per acre) and the actual total was 23.2 kilograms per hectare (20.7 pounds per acre), a difference of 3.0 kg. per hectare.

TABLE III. *Estimation of the total catch and the weight of fish which died from natural causes in the Gordy Lake bluegill population.*

Age	Average Population Weight *kg.*	Instantaneous rate of fishing mortality *p*	Catch Weight *kg.*	Instantaneous rate of natural mortality *q*	Died from Natural Causes *kg.*
II					
	50.3	.058	2.9	.481	24.2
III					
	108.2	.623	67.4	.667	72.2
IV					
	166.6	.623	103.8	.667	111.1
V					
	64.6	.623	40.2	.667	43.1
VI					
	22.0	.623	13.7	.667	14.7
VII					
	6.6	.623	4.1	.667	4.4
VIII					
	1.7	.623	1.1	.667	1.1
IX					
Total	....	....	233.2	....	270.8

Since there is no method of checking the food turnover by the population, such good agreement in a part of the over-all computation is gratifying. The discrepancy between the estimated catch and actual catch may be accounted for by the fact that average weights for individual age-groups were back-calculated to the time of annulus formation in May, while the population estimates were made in June. The growth which occurred during this month has not been considered, and the average population weight should be somewhat higher than is shown in Tables II and III. This error could be corrected by further refinement, but it would be of doubtful significance in this case.

The weight of fish which died from natural causes can be computed similarly to that just described, by substituting q, the instantaneous rate of mortality from natural causes, for p. The fish which died in the lake during 1950 were 270.8 kg. or 595.8 pounds.

Appraisal of Possible Sources of Error

Sampling errors. All the basic data used in the calculations of population size, growth, and mortality are subject to sampling error (Ricker 1948; Hile 1941). Apparently these errors have been kept at a minium in the present estimates, but they should not be overlooked.

Timing of growth and mortality. It has been assumed that growth and mortality coincide in time. This assumption needs to be examined critically because it has an important bearing on the dynamics of fish populations. Methods are available for treating population data when the timing of growth and mortality is established.

Application of laboratory data to the field situation. The application of the laboratory experiments on protein utilization to the natural situation deserves to be examined carefully. Obviously, the measurements of growth efficiency can be made with more precision in the laboratory than in the field. The laboratory methods used are common in agricultural nutrition work (Maynard 1951), although they have never before been applied to fishes. The technical difficulties of working with an aquatic animal have been largely overcome but certain refinements are still to be desired.

The genetic influence on the growth efficiency of fishes has not been appraised critically. Different races of fish may respond differently to the same food, since there are indications that the utilization of protein for growth is genetically variable. Recently, Prather (1951) accomplished an improvement in the efficiency of food conversion in the largemouth bass, *Micropterus salmoides,* by selective breeding. In trout culture it is common practice to select fast-growing races for hatchery breeding, and the growth of domestic animals has been greatly improved by selective breeding programs. In our experiments the bluegills used in the laboratory were from Yellowwood Lake, near Bloomington, Indiana—not from Gordy Lake. A genetic difference between these races in the ability to utilize protein for growth would alter the estimate of the food turnover.

The laboratory experiments were performed in summer at room temperature (average = 25.9° C.) which is higher than lake temperatures generally encountered at the same time of year. Food intake is affected by temperature (Markus 1932), but the effect of temperature upon the *rate* at which food is utilized for growth remains a most important subject for future investigation. By analogy, the efficiency of protein utilization is not expected to vary much with temperature on the basis of Terroine and Wurmser's (1922) work on *Aspergillus niger.* They observed that the coefficient of utilization of glucose $\left(\frac{\text{weight increase of mycelium}}{\text{glucose consumed}}\right)$

was the same over a temperature range of 22-38° C.

As far as the food is concerned, meal worms probably resemble the natural food of the bluegill as well as can be done in the laboratory. Live food is likely to contain sufficient vitamins and other growth factors, although aquatic organisms may be better or worse than meal worms in this respect.

High rates of feeding were employed in the laboratory. The experimental fish were fed at the rate of approximately 3 per cent of their body weight per day. This is very close to the maximum food intake under the conditions of our experiments. The amount of protein used for growth depends in part upon the intake of protein above the amount needed for energy requirements. The efficiencies reported here, based on near-maximum food consumption, therefore represent nearly maximum efficiencies. Whether bluegills in nature eat such large quantities of food is not known, but some indirect evidence indicates that they do. A comparison of the linear growth increments of the laboratory bluegills and those from Gordy Lake (Fig. 4) shows that both groups were growing at about the same rate. Consequently, the rate of food consumption must have been approximately the same in the two groups.

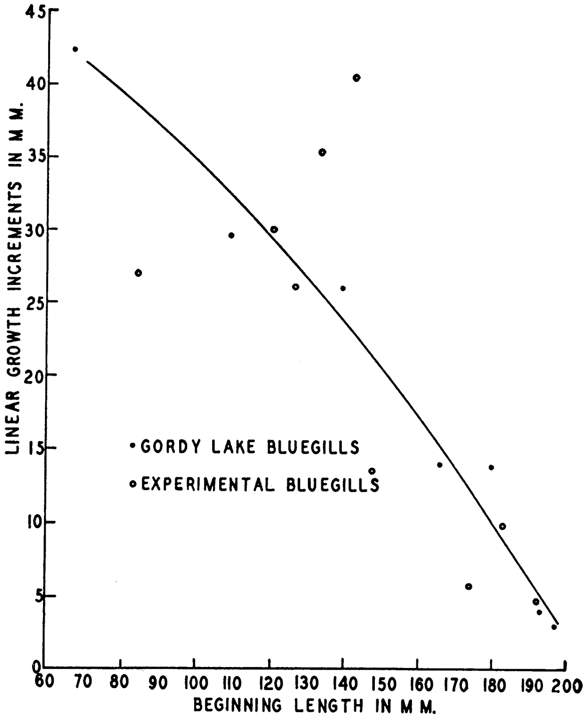

Fig. 4. The relation between linear growth increment and the size of fish at the beginning of a growth period. Data for Gordy Lake bluegills were taken directly from age-growth analyses, and the freehand regression is based on this information. The growing season lasts about 150 days in nature. Growth increments of fish in 50-day feeding experiments have been multiplied by 3 to approximate the total growth which might have been achieved in a natural growing season.

Discussion

The selection of food by the bluegill has received considerable attention. Ball (1948) demonstrated that insects are the most important food organisms found in the diet and that the aquatic forms are derived almost entirely from the littoral zone. About 50 per cent of the diet was composed of plants, zooplankton and terrestrial insects. Parks' (1949) analysis of the bluegill diet showed that 24 per cent of the food included the latter food items. Vascular aquatic plants were found to be an important constituent of the diet in both studies, and Ball showed that plant consumption varied inversely with the amount of invertebrates in the lake. McCormick (1940) also presented evidence that bluegills eat considerable quantities of higher aquatic plants (49 per cent), and other studies have confirmed this fact still further. Plants are not consumed incidentally in the process of capturing animal food. Ball wrote, "In the great majority of cases when the stomach contained *Najas,* there was no other food present, and the individual leaves were nearly of the same length, as if they had been cropped off intentionally. . . ." It remains to be learned whether aquatic plants contribute significantly to the protein requirement of the bluegill. About 2-20 per cent of the food comes from terrestrial sources.

Regardless of its source, about 157 kilograms of protein which were consumed by the bluegills must have originated in the lake or entered from the outside. This represents the turnover of protein by the population, not the total available supply. The total protein turnover by the bluegill population can be partitioned as follows (Table IV): 47.9 kilograms were used for growth and about 108.9 kilograms were used to contribute to the metabolic expenditure of energy. Replacement protein has not been included for reasons mentioned above. The nitrogenous excretory products resulting from protein catabolism are soluble in water and become available for use by other organisms in the aquatic nitrogen balance. These products are for the most part simple molecules (Smith 1929) and can be utilized quickly. Our own analyses have shown that ammonia makes up about 60 per cent of the total nitrogen excreted by bluegills.

The protein incorporated into the bodies of the bluegills themselves can also be partitioned.

TABLE IV. *Partition of protein and protein nitrogen consumed by the bluegills of Gordy Lake, Indiana, into various segments of the aquatic nitrogen cycle. Values apply to the bluegill population from age II to age VIII.*

Item	Partition	Protein *kg.*	Protein lbs.	Protein nitrogen* *kg.*	Protein nitrogen* lbs.
1	Consumed	156.8	345.0	24.3	53.5
2	Used for growth	47.9	105.4	7.4	16.3
3	Used for metabolism	108.9	239.6	16.8	37.0
4	In fish which died from natural causes	46.0	101.2	7.2	15.8
5	In catch	39.6	87.8	6.3	13.4
6	In average standing crop	71.4	157.1	11.2	24.6

Explanation of above items:
1. From Table II.
2. Summation of items in column 5, Table I, times average population of each age-group, Table II.
3. Item 1 minus item 2.
4. From Table III, converted to protein by multiplying by 17 per cent.
5. Same as preceding statement.
6. From Table II, converted to protein as above.

*Protein × 0.16=protein nitrogen.

Angling removed 39.6 kilograms which represents a permanent loss to the lake. The 46.0 kilograms of protein in the fish which died from natural causes can be utilized directly by scavengers, and the products of bacterial decomposition can be used by other organisms. A small quantity of this protein may be removed from the lake by predators such as fish-eating birds and mammals.

From this point of view, our information contributes to the quantitative relationships in the nitrogen balance of the aquatic environment. Exploitation by man plus a small unknown amount removed by birds, etc. represents the only significant loss of nitrogen from the biomass. Bluegills were by far the dominant species in the Gordy Lake catch and the protein nitrogen loss from this source was only 6.3 kilograms or 0.55 kilograms per hectare. Rain, run off, inorganic wind-blown material, and leaf-fall could probably replace this loss. It has been gradually realized from other studies that nitrogen is not the limiting factor in aquatic productivity, and these data are in keeping with that opinion.

Recruitment has not been taken into consideration in the computation. The young fish, which were not sampled, are growing rapidly and adding to the total protein of the population. The potential recruitment required to maintain the average standing crop is indicated by the partition of Table IV. Natural deaths accounted for 46.0 kg. of protein and 39.6 kg. were removed by fishing, a total of 85.6 kg. At the same time, 47.9 kg. of protein were added to the population in growth. The net decrease in the population is therefore $85.6 - 47.9 = 37.7$ kg. of protein, which is about one-half the average standing crop (71.4 kg.). In order to maintain the standing crop, 33.7 kg. of protein must be added to the population by growth, principally by the younger age-groups.

The objective of quantitative studies of the food chain is to establish some measure of the "ecotrophic coefficient" (Ivlev 1945), which is defined as the fraction of the production of a food organism which is actually consumed. Ivlev stressed the importance of individual species of food organisms. Our calculation of the food turnover has not been so specific, but it is a step toward the accomplishment of the same general purpose. The efficiency of productivity will be more completely understood when the relationship between the food turnover and the total food supply is known.

SUMMARY

The food turnover of the bluegill (*Lepomis macrochirus*) population of Gordy Lake, Indiana was estimated by emphasizing the role of protein in the nutrition of fishes. Protein turnover is defined as the amount of protein that is required by a population for growth, for the metabolic expenditure of energy, and for the replacement of proteins broken down during the normal course of living. The efficiency of protein utilization for growth was determined by experiments on bluegills in the laboratory. Field studies provided information about the vital statistics of the Gordy Lake population. The protein turnover was computed by combining measurements of protein utilization, growth, mortality and the population of bluegills in the lake.

It was estimated that about 156.8 kg. of protein were consumed by the bluegill population in 1950. About 47.9 kg. of protein were added to the population in growth, and the remainder (108.9 kg.) was used for the metabolic expenditure of energy. No estimate of replacement protein could be made. The total amount of food organisms which was represented by the protein turnover was computed from an average percentage of protein in the living weight of various aquatic animals (9.59 per cent). On this basis the total amount of food organisms consumed by the bluegill population was 1635.0 kg. or 142 kg. per hectare (126 pounds per acre).

A contribution to the aquatic nitrogen cycle was made by partitioning the protein in the average standing crop of bluegills into various segments Natural deaths accounted for 46.0 kg. of protein, and 39.6 kg. were removed from the lake by fishing. Since 47.9 kg. of protein were added to the population by growth, the net decrease in

population protein was $(46.0 + 39.6) - 47.9 = 37.7$ kg. of protein. Recruitment must make up for this net decrease in order to maintain the average standing crop of 71.4 kg. of protein. Under the observed conditions of mortality and growth, recruitment must replace about one-half the average standing crop per year.

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A STUDY OF SOME OF THE FACTORS AFFECTING THE NATURAL REGENERATION OF TAMARACK (*LARIX LARICINA*) IN MINNESOTA[1]

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Introduction

Sound management of any renewable natural resource upon which man is dependent for his well-being involves sustained yield. Land economically suited to the production of some particular commodity, be it trees, grass, wildlife, water or recreation, must be maintained in a continuously productive condition if it is to assist in maintaining high standards of living among the inhabitants of the region. Whenever the commodity is a biological product, a vulnerable point in the sustained yield cycle is that point separating one generation from the succeeding generation. As early as 1908, Henry Graves wrote, "The study of natural reproduction consitutes one of the most important lines of research of the American forester." If reproduction cannot be attained satisfactorily by natural means, some artificial, and frequently costly, method must be resorted to if

[1] Published as Scientific Journal Series Paper No. 2841 of the Minnesota Agricultural Experiment Station.

[2] The writer wishes to acknowledge his gratitude to Dr. Henry L. Hansen of the School of Forestry, and to Dr. Donald B. Lawrence of the Department of Botany at the University of Minnesota, both of whom provided advice and constructive criticism throughout the period of investigation. Sincere appreciation is expressed to