

The Effect of Removal of Fixed Percentages of the Newborn on Size and Variability in Populations of *Daphnia pulex* (Forbes)

L. BASIL SLOBODKIN AND SUMNER RICHMAN

Department of Zoology, University of Michigan, Ann Arbor, Michigan

ABSTRACT

Populations of *Daphnia pulex* were maintained under laboratory conditions of constant food supply and temperature. Varying percentages of the newborn were removed from the populations at four-day intervals. Mean size of the residual populations decreased with increasing removal rate, while yield and yield per individual increased. Mean differences between the number of animals present at successive censuses after removal of the newborn decreased with removal rate while mean differences between successive yields increased. The sum of mean differences in residual population and yield was a constant, independent of removal rate. That is, total variability in the population-removal system was not changed by removal rate, although the variability was divided between yield and residual population. The ratio of yield variability to population variability was dependent on removal rate and on the fact that only newborn animals were removed, but was independent of food supply and temperature differences between populations. This ratio also may be independent of the physiological peculiarities of *Daphnia*. Median life expectancy of the survivors was increased 13–15 days when the removal rate was increased from 25% to 90% of the newborn. The median life expectancy with 90% removal was 32 to 36 days.

INTRODUCTION

While there have been many studies of population growth in the laboratory, until recently there have been no published laboratory experiments on exploitation or predation of populations in the laboratory. The present experiments were therefore started in March 1954 to determine experimentally the effect of removal of varying percentages of newborn animals from populations of *Daphnia pulex*. It was hoped that the effect of predation on these populations could be determined in the laboratory without the obscuring factor of environmental change.

Concurrently and independently two similar studies were being conducted, one by Nicholson (1954a) using *Lucilia cuprina* and one by Watt (1955) using *Tribolium confusum*. Due to the taxonomic and ecological disparities between the organisms used, these studies are complementary and will be compared in greater detail below.

The role of theoretical and experimental models in fishery exploitation theory

In the process of exploiting any non-domesticated population of organisms, man

assumes the role of a predator. He differs from a non-human predator in his ability to attempt to calculate his strategy of predation so as to maximize both his profit and the likelihood that the exploited resources will persist from year to year. These maximizations may be mutually incompatible in particular cases, but as a rule both are considered in designing an exploitation program. Extra-biological factors often influence exploitation procedure. These may include such things as the aesthetic or political opinions of the consuming public or mechanical problems of packing or transportation.

It is obvious therefore that no one exploitation theory can be considered universally applicable. It can be demanded, however, that any theory purporting to deal with the purely biological aspects of an exploitation situation must be powerful enough to account for at least the minimum of biological complexity that might be expected to arise in the natural world.

In particular, all exploited populations, to our knowledge, are composed of multicellular organisms. It is only recently that models which acknowledge the difference between individual animals of a population of metazoans have been constructed. The

work of Ricker (1954b), Beverton (1953), Slobodkin (1953b), and Watt (1955) are typical examples of these models.

Two of these models have been applied to laboratory or field data. Beverton has discussed the applicability of his model to the plaice fishery, and Dickie and McCracken (1955) have applied the same model to a flounder fishery. Ricker has applied his model to the data of Pratt (1943) on laboratory populations of *Daphnia magna*. While Beverton's model has been used for prediction, to date the predictions have not been tested. Ricker's analysis of Pratt's *Daphnia* data produced a graph of theoretical population size against time which was very similar to the actual observations. Both of these models make empirical assumptions which detract from their generality. Beverton assumes a constant recruitment of new stock and Ricker assumes that mortality is independent of population density after sexual maturity.

While the models of Slobodkin and Watt are almost completely general, they also involve such a large number of fitted constants as to be inapplicable to any real situation. What is required is a model or a set of generalities which combines the applicability of Beverton and Ricker with the flexibility of the other two.

This study has been undertaken in the hope that empirical conclusions derived from an extremely simplified system may facilitate formation of more satisfactory theories of exploitation, or at least be of help in determining the minimum level of complexity of even the simplest of exploitation systems.

Population dynamics of Daphnia

Daphnias are particularly convenient organisms for population studies. They are normally parthenogenetic, so that both genetic heterogeneity and complex sex behaviour are absent. Since they are aquatic filter feeders the geometric complexity of the culture vessels is minimized. The animals of a population interact with each other only through their effect on the food supply, thereby eliminating social complexity from the system.

Normal population growth in *Daphnia* has been examined in *Daphnia magna* (Pratt 1943), *D. pulicaria* (Frank 1952) and *D. obtusa* (Slobodkin 1954). The pattern derived from these studies has not been reexamined in the present experiments but there is no reason to doubt its applicability.

Briefly outlining the normal population pattern of *Daphnia*, mean population size is determined exclusively by the rate of feeding in any constant set of physical conditions. There is no evidence at all of any metabolites, or any other interaction between animals except competition for food (Slobodkin 1954). The feeding rate varies with the size of the individuals (Ryther 1954) as do the food requirements for survival. The growth rate of animals of any particular age depends on their food supply (Rodina 1946) and on their previous nutritional history (Slobodkin 1954). The same statements apply to the reproductive rate. Detailed quantitative interactions of age, growth, reproduction, previous history, and food supply have not yet been worked out.

Due to the differences between the individual animals in the population, oscillations in population size are found even in the most carefully controlled environments. Under certain conditions of temperature these oscillations eventually disappear and a population equilibrium occurs in which the total number of animals, reproductive rates, growth rates, and size-frequency distribution remain invariant with time (Pratt 1943, Slobodkin 1954).

Fluctuations occur in the present experiments, which may be either internal or determined by environmental changes. The cause of the fluctuations is irrelevant to the conclusions to be drawn.

Acknowledgements

Dr. John L. Brooks kindly identified the *Daphnia pulicaria*. Mr. Robert Paterson provided the original stock of *Chlamydomonas*.

Mrs. Shanti Latta Kanungo and Mr. Thomas Parker helped with the population counts.

The program was supported by research grants to the senior author from the Rackham Faculty Fund of the University of Michigan and from The Rockefeller Foundation.

TECHNIQUE

The procedure followed in these experiments was a modification of that reported by Slobodkin (1954).

Populations were started with from ten to thirty adult animals in 50 cc of conditioned water. The animals were counted, dead were removed, the water was changed, and the appropriate number of living animals was removed every fourth day. The populations were fed a measured amount of *Chlamydomonas Reinhardi* either every other day or every fourth day. At the time of counting the populations were divided into four arbitrary and subjective size categories: young, small adolescent, large adolescent, and adult. The number of eggs in the brood chamber of fertile females was counted.

Fixed percentages of the newborn animals were removed. In cases where the number of animals to be removed was fractional the next lowest whole number of animals was removed. The removal percentages listed are therefore maximum values, so that "not more than 25% removal" should be read for "25% removal" and similarly for the other removal rates.

The water used in these experiments was Ann Arbor tap water which was stored in a large concrete tank containing attached algae, clams, and several small fish. The water was aerated and lighted continuously.

The experimental containers were soft glass, wide-mouthed bottles of approximately 130 cc capacity and 6 cm outside diameter. Glassware was washed in the way indicated in Slobodkin (1954) with the added precaution of rinsing with de-mineralized distilled water.

The algae were raised on sterile agar plates. The algal medium is indicated in Table 2.

The algae were suspended in conditioned water and the concentration of the suspension was measured with a Klett photometer

TABLE 1. Dates of initiation and termination of experimental populations, and initial number of animals (adult females) in the populations

The populations of series H-15 have not been listed separately in the table. The populations of this series were maintained at 0%, 25%, 50%, 75%, and 90% fishing rates and were all initiated with 20 adult animals on June 29, 1954, and were terminated on March 31, 1955.

Series	Fishing rate	Date started	Initial size
L-19	0%	March 18, 1954	20
All terminated	25%	March 16, 1954	15
March 29, 1955,	33%	October 4, 1954	20
except 66% &	50%	January 12, 1955	30
33%	66%	October 4, 1954	20
	75%	July 20, 1954	20
	90%	March 14, 1954	20
H-19	0%	July 11, 1954	52
All terminated	25%	October 5, 1954	20
March 30, 1955	50%	September 11, 1954	30
	75%	July 11, 1954	20
	90%	July 11, 1954	20

TABLE 2. Nutrient agar for growing *Chlamydomonas*

*Beyerinck's solution	100 cc
Soil extract	50 cc
Distilled, demineralized water	850 cc
3 drops 1% aqueous FeCl ₃	
Agar	15 g
*Beyerinck's solution	
Distilled, demineralized water	1000 cc
NH ₄ NO ₃	0.5 g
K ₂ HPO ₄	0.2 g
MgSO ₄ ·7H ₂ O	0.2 g
CaCl ₂ ·2H ₂ O	0.1 g

using a red (no. 64) filter. An amount of this suspension sufficient to give a Klett reading of 5 in 50 cc of medium was added to the *Daphnia* populations at each feeding. For example, one cc of a suspension with an initial Klett reading of 250 would constitute one feeding.

All the populations were kept in dark incubators except during the actual counts.

There were three experimental series of populations. One, kept at 15°C and fed every other day will be referred to as H-15. One, kept at 19°C and fed every other day will be referred to as H-19.

One, kept at 19°C and fed every fourth day will be referred to as L-19.

In all three series populations were maintained at removal rates of 0, 25, 50, 75 and 90 per cent of the newborn. In series L-19, populations were also maintained at removal rates of 33 and 66 per cent of the newborn for brief periods.

The number of newborn animals in a population was computed by taking the sum of the living and dead animals found in the container at any particular count and subtracting from this the number of living animals returned to the container after the previous count.

The fishing procedure consisted of multiplying the number of newborn by the appropriate fishing rate, rounding off the product to the next lowest whole number and removing the appropriate number of animals at random from the newborn. The term "random" is used in a limited sense. For example, if twenty-five per cent of the newborn were to be removed from a particular population, the individual doing the counting placed three successive animals in the new culture vessel and discarded the fourth. The animals were taken in order of catching with a medicine dropper.

Fairly often the number of animals in the "young" size-category was not equal to the calculated number of newborn. If the number of young animals was in excess of the calculated number of newborn it was assumed that the growth rate of the newborn animals remaining after the previous census was so low as to prevent them from growing into the "small adolescent" size-category in the interval between counts. If the number of young animals was less than the number of newborn we assumed that the growth rate of the newborn animals produced since the last census had been sufficiently rapid to permit them to grow into the small adolescent size-category in the interval between their birth and their first census.

In the first case the number of animals removed from the young size-category was the number derived from the product of the fishing rate and the calculated number

of newborn. That is, in a twenty-five per cent fished population with four newborn animals, only one animal would be removed regardless of the number of young animals found.

In the second case the appropriate percentage would be removed from the young category and the remainder removed from the small adolescents. On rare occasions the calculated number of newborn exceeded the total number of young and small adolescents together, in which case large adolescent animals were also removed. In no case did an animal grow into the adult category between counts.

There are two sources of error in this procedure: 1. fractional animals were left to the population; 2. any animals that died and decomposed completely between counts would tend to increase the estimated number of newborn. These two sources of error counteract each other to some extent. The first is probably not of major importance. The second is probably not significant at the temperatures used. Newborn *Daphnia* show characteristic oil droplets which act as a check on the calculated number of newborn to some degree. In short, there is an unknown amount of error in the procedure, but the mutual consistency of the results indicates that this error is not appreciable.

The percentage of the animals which were to be removed from any population was fixed at the initiation of that population and was not changed during the life of the population.

The present experiments more closely simulate natural predation than commercial fishing since we removed newborn animals rather than adults. At the present stage of experimental analysis it seemed advisable to deal with a system that showed promise of being extremely simple. Further experiments, in which adult animals are removed, are now in progress.

EXPERIMENTAL RESULTS

Mean population size and yield

While temporal variation is of particular interest in these studies, it is simplest to

first analyze the values of yield and population size taken as averages over the entire history of the individual populations. These means are distorted by the fact that the initial population size was independent of the fishing rates but, as will be demonstrated below, the effect of initial population composition is insignificant after sufficient time has elapsed.

We will use the term "population size" or "size" to mean the number of animals present in the population after the completion of the counting and fishing procedure. The term "total standing crop" will be used to refer to the number of animals present in the experimental containers prior to fishing, following the usage of Watt (1955).

In all three experimental series, mean population size decreased with fishing intensity (Fig. 1). In general the decrease was non-linear. This is particularly well demonstrated in series H-15. The departures from a smooth non-linear decrease shown by series H-19 and L-15 are artifacts caused by premature termination of the experiments. In particular, the mean size of the 0% fished population of H-19 is excessively high as are the means of the 25% and 0% fished populations of L-19.

Average yield increased with fishing rate, with a consistent maximum at 90% fishing. The average yield over infinite time of a population fished at a rate of 100% is obviously zero, so that the yield at 100% fishing has been assigned a value of zero in all three series.

The yield from any population is the increase above the requirements for population maintenance, expressed either as growth or reproduction, multiplied by the total number of individuals in the population. Yield per individual was accordingly computed by dividing the mean yield of each population by mean population size. This is indicated in Figure 1. Since the major portion of the yield was in animals of uniform size, biomass yield and numerical yield are directly proportional. The yield per individual is a smooth, non-linearly increasing function of fishing rate in all three series.

Variability in total population size

In Figures 2, 3, and 4 are indicated total population size as a function of time in all three series. There is some fluctuation in size in every population. At the moment it is impossible to state precisely what proportion of the total variability is due to slight alterations from time to time in the environment. The degree of correlation between different populations would indicate some environmental variability. Comparison of these figures with other published graphs of *Daphnia* populations indicates that at least some of the fluctuation is due to the internal population adjustment mechanisms outlined in the introduction and discussed in detail elsewhere (Slobodkin 1954).

Size-frequency distribution, fishing rate, and stability

Stability characteristics have been partially defined for natural communities by MacArthur (1955). The interaction between stability and reproductive patterns in a restricted single species population model has been discussed by Ricker (1954a, b). Existence criteria for population equilibrium, implicitly containing necessary but not sufficient conditions for single species population stability, have been developed for a more general model by Slobodkin (1955). It is now possible to demonstrate an experimental correlation between population stability and size-frequency distribution.

In Figures 5, 6, and 7 the total number of animals in each of the four size-categories has been summed over the entire census period for each population.

In series H-15 (Fig. 7) all of the populations were maintained for an identical length of time so that the absolute heights of the histogram bars are comparable. It will be noted that in this series the number of animals in each category decreases with fishing intensity, demonstrating that the reduction of population size with fishing intensity is an actual reduction in biomass and not merely a decrease in numbers.

In all three series the relative number of

AVERAGE YIELD, SIZE AND
% INCREASE VS % FISHING

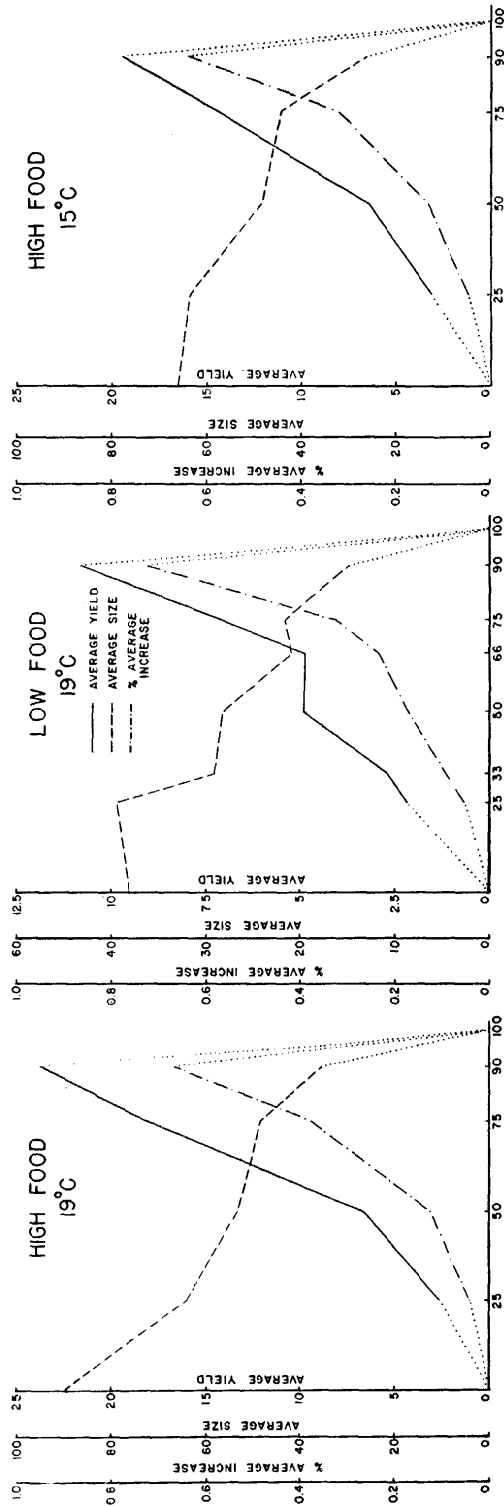


Fig. 1. Mean size of populations after fishing (—), mean yield per day (---), and yield per individual per day (· · ·) for the three series of experiments. The data for Series H-15 (far right) are probably more accurate than those of the other two series.

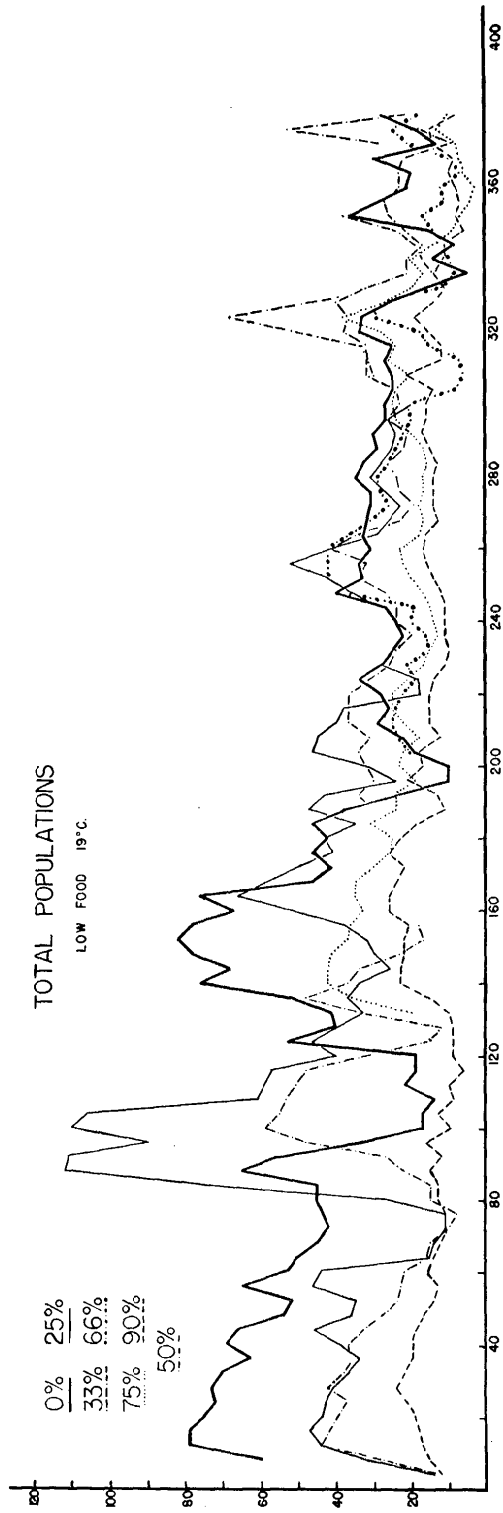


Fig. 2. Number of animals remaining in the populations after fishing (i.e. "population size") in the seven populations of series L-19, plotted against time in days.

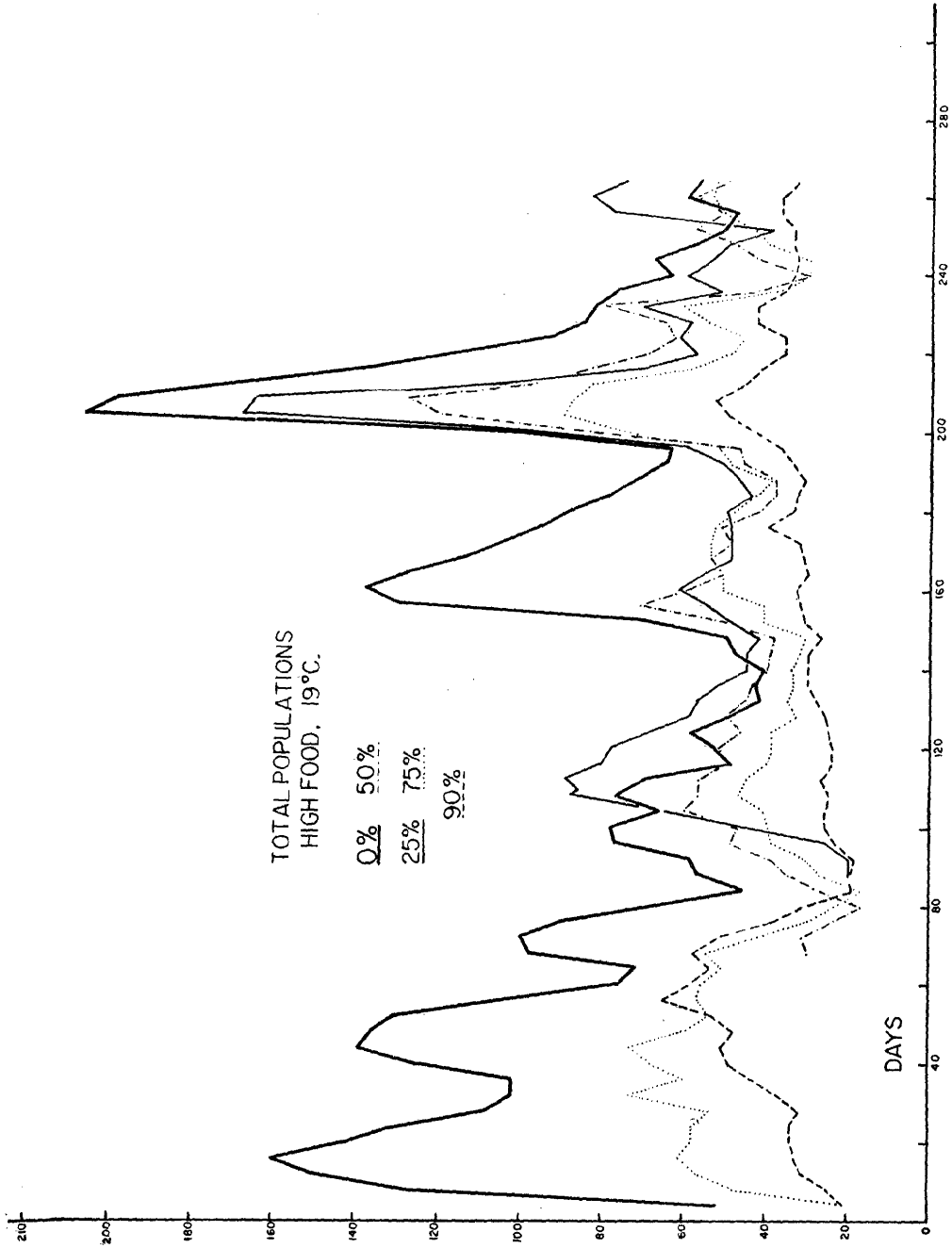


Fig. 3. Population size in the five populations of series H-19, plotted against time in days.

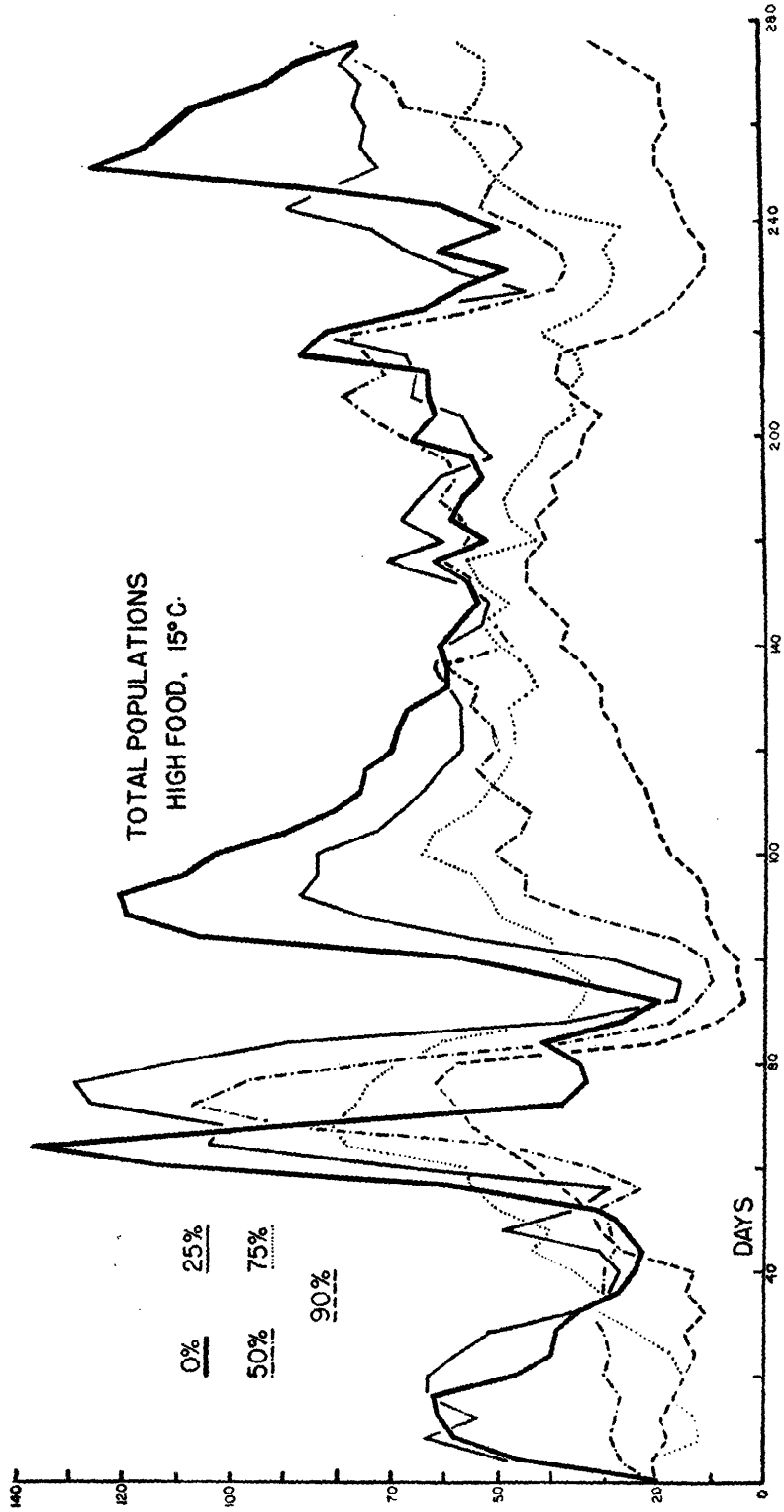


FIG. 4. Population size in the five populations of series H-15, plotted against time in days.

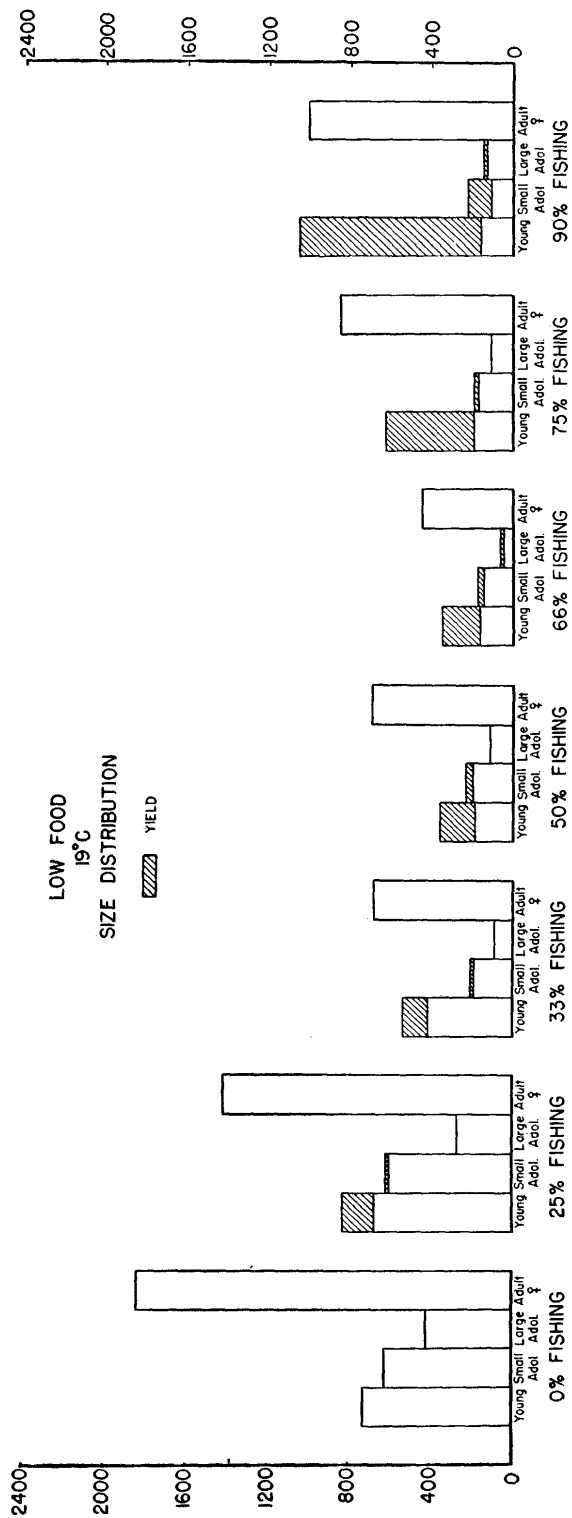


Fig. 5. Cumulative totals of the number of animals in each of the four size-categories during all censuses of series L-19. The cross-hatched portions of the bars represent the animals removed during fishing.

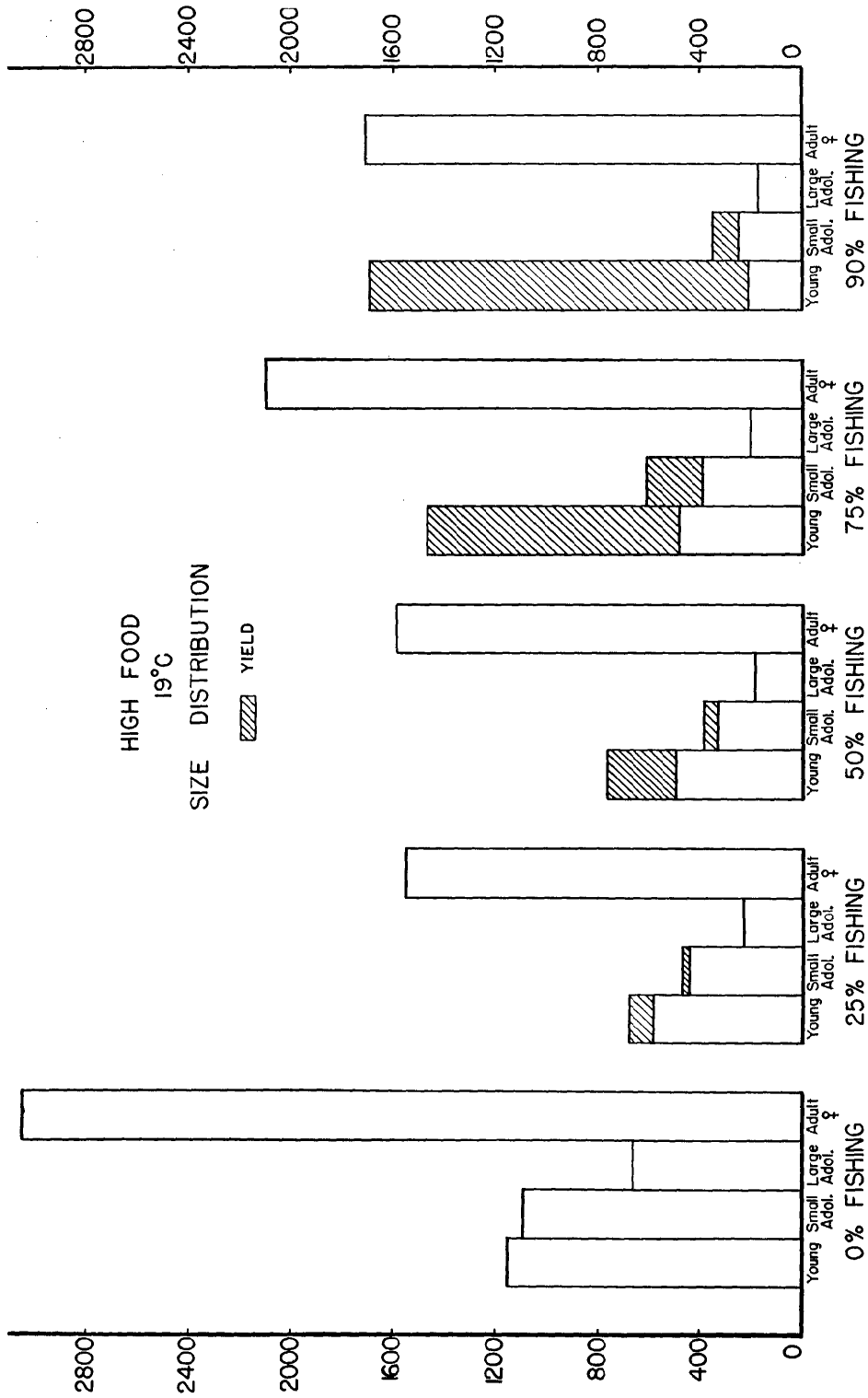


Fig. 6. Cumulative totals of the number of animals in each of the four size-categories during all censuses of series H-19. The cross-hatched portions of the bars represent the animals removed during fishing.

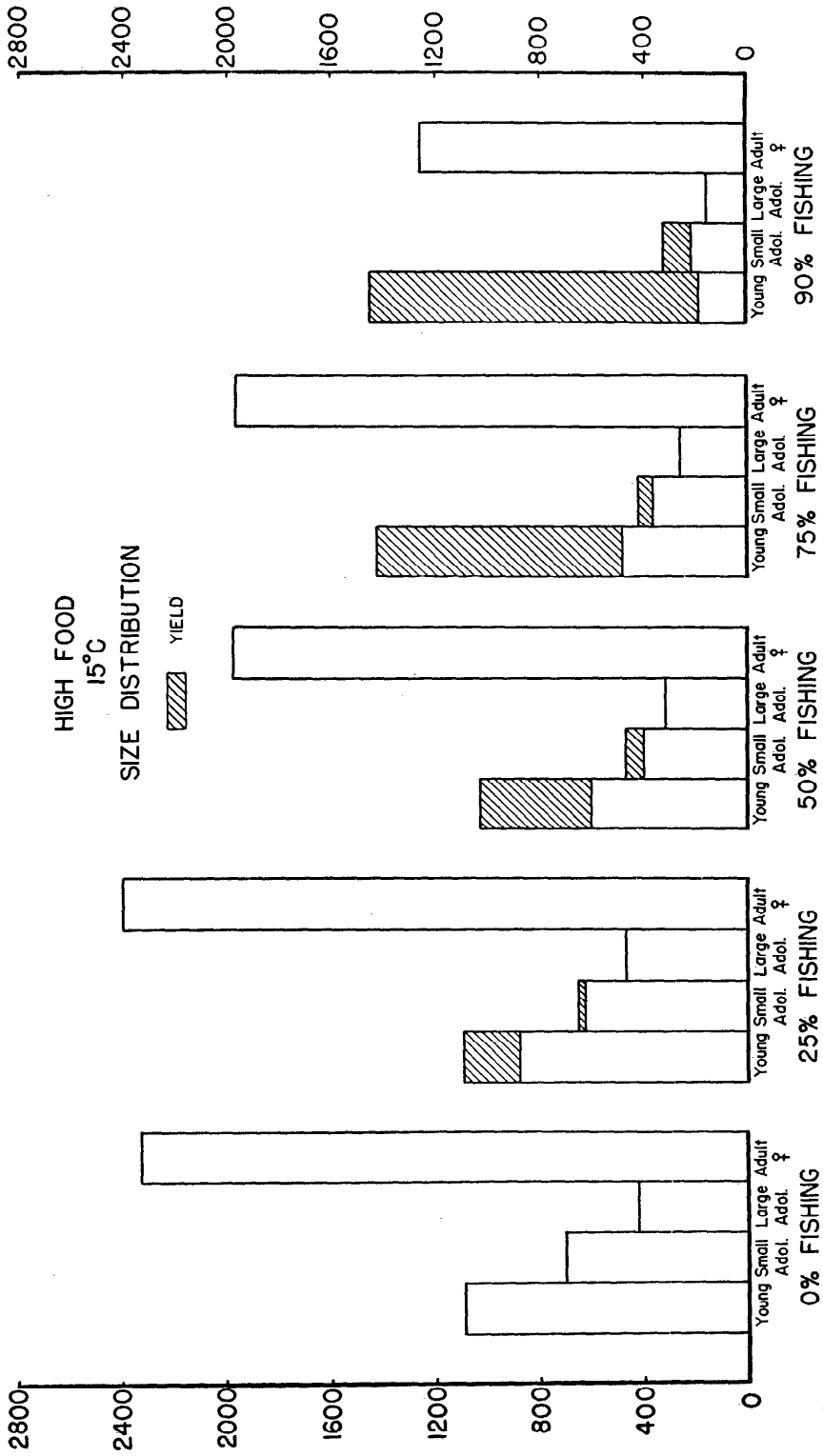


Fig. 7. Cumulative totals of the number of animals in each of the four size-categories during all censuses of series H-15. The number of censuses was identical in all the populations of this series. The cross-hatched portions of the bars represent the animals removed during fishing.

animals in the three smaller size-categories changes in a regular way with fishing intensity. With 0% fishing there is a preponderance of young animals and a minimum of large adolescent animals. It must be emphasized that these terms are size categories and not age categories. It is impossible to determine the age of individual animals in these populations once they are older than four days. As fishing intensity increases, the disparity between the number of animals in the three smaller size-categories decreases until at 90% fishing the number in these three categories is approximately equal.

It can be shown theoretically that given an animal with a rectangular survivorship curve (Deevey 1947), in which mortality affects primarily old individuals and is concentrated in a narrow age span, the relative number of animals in any size-category in an equilibrium population is inversely proportional to the first derivative of the growth curve of an individual in that size-category. That is, the faster the animals grow through any size range, the smaller the number of animals that will be found in that size range at population equilibrium. Incidentally, the number of animals in any two equal age-intervals of an equilibrium population with a rectangular survivorship curve is identical.

Pratt (1943) and Anderson and Jenkins (1942) have demonstrated that there is very little mortality prior to the adult stage in *Daphnia magna*, and Frank (1952) has repeated these observations for *Daphnia pulex* (not, however, the same strain as that used in these experiments). It seems safe to assume the mortality pattern of the present strain of *Daphnia pulex* to be similar to that found by these workers.

It has been shown by Anderson, Lumer, and Zupancic (1937) and Tonolli (1947) that the growth curve of an individual *Daphnia* consists of a decelerating increase approaching an upper asymptote, with a remarkable short accelerating phase at the young end.

It is to be expected, therefore, that the size distribution in equilibrium populations of *Daphnia pulex* should be approxi-

mately the same as that found in the 90% fished populations. Similar size distributions have been found in equilibrated populations of *Daphnia magna* (unpublished data of David Pratt) and *Daphnia obtusa* (Slobodkin 1954). The size-frequency distributions found at low fishing intensities are clearly incompatible with population equilibrium. We might expect that stability of the populations should be proportional to the fishing rate. This expectation can be confirmed intuitively by examining Figures 2, 3, and 4.

*Food consumption, fishing rate,
and stability*

Considering the *Daphnia* populations as simple feedback systems (Wiener 1948), the degree of instability is proportional to the time lag in the reactions of the populations to alterations of the environment. The greater the time lag between the moment an adjustment to environmental alteration is started by a population and the completion of that adjustment, the more unstable the population.

There are three major lag effects inherent in almost all metazoa. An animal born at one instant dies at some subsequent instant. An animal born at one instant begins to reproduce at some subsequent instant. An animal born at one instant will make a certain contribution to population density at that instant, and this contribution to population density may be expected to change as the animal grows older. The first two of these sources of instability are essentially immune to modification by fishing. The third can be completely eliminated by suitable exploitation.

If the total contribution to population density of a group of animals immediately after their birth is x , which is just sufficient to restore population density equilibrium, and the total contribution to population density by these animals at the age of maximum density contribution is $x + y$, then the portion of their density contribution which will contribute to population instability is y . Removal of $\frac{y}{x + y}$ of the

animals at birth will minimize this source of oscillation.

From the life table data of Pratt (1943), the weight-increase data of Edmondson (1955), the feeding rate observations of Ryther (1954), and the fact that *Daphnia* populations are limited solely by food supply (Slobodkin 1954), it is possible to estimate that the density contribution, i.e. the food consuming capacity, of a group of *Daphnia* at birth is from one-sixth to one-tenth the density contribution of the same group at maturity, assuming complete survival of the members of the group to maturity. The minimization of population fluctuations at 90% fishing rates, which has been found in these experiments, would be expected on the basis of this analysis.

It is of interest that fluctuations were not damped to the same degree by 90% fishing in the experiments of Nicholson (1954a). He was removing adult flies from populations of *Lucilia cuprina*. These flies had already made their chief contribution to population density.

It seems possible that the same arguments might apply to the exploitation of any density-dependent natural population. In general, if the minimum marketable size consists of a group of animals whose total contribution to population density is x , and the density contribution of the same group at maturity is $x + y$, removal of the animals at the rate of $\frac{y}{x + y}$ will minimize fluctuations from this source.

This assumes no inherent incompatibility between satisfying this condition and satisfying the equilibrium condition indicated above; that the relative number of animals in any size category of an equilibrium population is proportional to the inverse of the growth rate of an individual of that population at any particular size, multiplied by a correction term computed for each size as the product of the survival rates of all smaller size categories.

The partitioning of variability between yield and population size

While it is intuitively apparent that the heavily fished populations are less variable

in size than the less heavily fished populations (Figs. 2, 3, and 4), it seems desirable to quantify this variability in some way. Recent work and controversy have amply demonstrated the dangers of most of the methods used to search for "cycles", periodicities, or even variability in population data (Hewitt 1954). We have nevertheless attempted to get a measure of total variability by summing the differences between successive counts regardless of sign for each population.

Variability in this sense has been computed for both total standing crop and population size and, since the length of time of observation varied from population to population, the total variability has been divided by the number of censuses giving mean change per census for each population (Table 3).

The total standing crop variability represents the sum of the variability in population size and in yield. If the total variability of the population-yield system was being changed by fishing we would expect some significant relation between total standing crop variability and fishing rate. It can be seen from Figure 8 that there is no significant relation at all.

TABLE 3. Mean total standing crop, yield, population size, and variability in total standing crop and in population size

Population	Mean total standing crop	Mean population size	Mean yield per census	Variability in total standing crop	Variability in population size
H-19					
0%	90.833	90.833	0	14.892	14.892
25%	66.900	64.341	2.659	14.023	11.930
50%	66.449	59.898	6.551	13.714	9.020
75%	66.499	48.287	18.212	19.061	6.323
90%	59.272	35.530	23.742	17.108	3.369
H-15					
0%	66.072	66.072	0	11.809	11.809
25%	67.043	63.899	3.144	11.250	9.456
50%	55.115	48.666	6.449	10.544	6.926
75%	59.145	44.696	14.449	12.074	4.735
90%	45.782	26.289	19.493	14.265	3.691
L-19					
0%	38.032	38.032	0	6.731	6.731
25%	42.053	39.893	2.160	10.000	8.351
33%	31.751	29.063	2.688	9.583	6.521
50%	36.026	30.821	5.205	10.615	6.256
66%	25.773	20.909	4.864	7.222	4.022
75%	28.667	21.635	7.032	9.159	3.143
90%	25.663	14.874	10.789	10.347	2.295

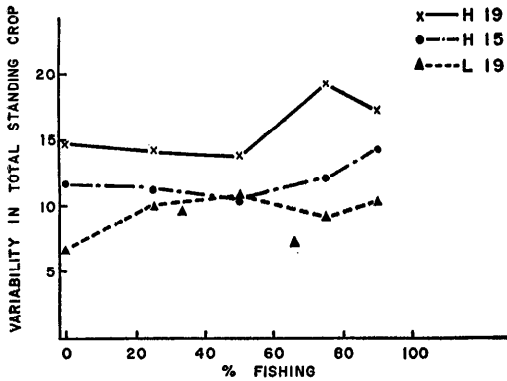


Fig. 8. Variability in total standing crop as a function of fishing rate. Variability is defined as the sum of the absolute differences between successive counts of total standing crop, divided by the number of censuses. The values at 33% and 66% removal are probably aberrant. There is no significant relation between total standing-crop variability and fishing rate.

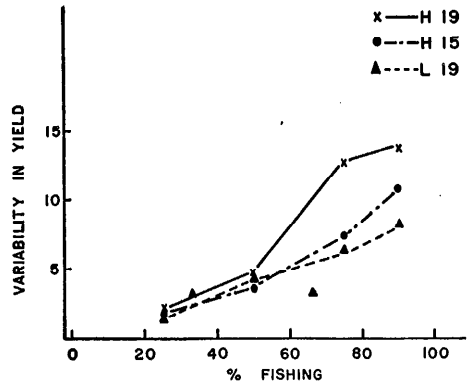


Fig. 10. Variability in yield, measured as the difference between total standing-crop variability and population-size variability, as a function of fishing rate. There is a significant increase of yield variability with fishing rate.

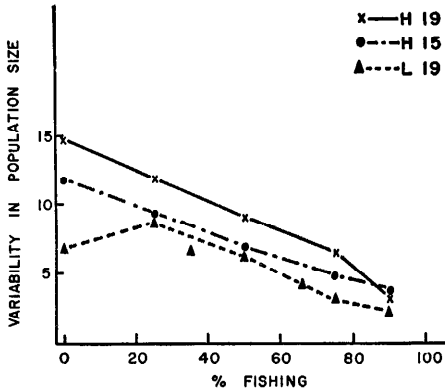


Fig. 9. Variability in population size as a function of fishing rate. Variability is defined as the sum of absolute differences between successive counts of population size (i.e. animals remaining after fishing) divided by the number of censuses. There is a significant decrease of population-size variability with increased fishing.

The decrease of population size variability shown in Figures 2, 3, and 4 is more clearly demonstrated in Figure 9 where variability in population size is plotted against fishing rate.

Variability in yield can be computed as the difference between total standing-crop variability and population-size variability. Yield variability has been plotted against fishing intensity in Figure 10, demonstrating the increase of yield variability with fishing intensity.

We conclude that fishing simply divides a fixed amount of total variability into two portions, one being assigned to the yield and the other to the population size. It is now necessary to find out what properties of the system determine the relative amounts of variability in the two components.

If we replace the fishing rate by $\frac{1-p}{p}$, where p is the percentage removal, and plot this against the ratio of yield variability to population variability, an equilateral hyperbola is produced (Fig. 11). The total range of calculated values for the coordinates of the focus of the hyperbola, computed as a, a , where

$$a = \sqrt{2 \frac{(1-p)}{p} \frac{\text{yield variability}}{\text{population variability}}}$$

is 0.630 to 1.384 with a mean of 1.002 (Table 4). On a double log plot, Figure 11 is a straight line with slope of -1 . The 5% confidence-limits of the slope are 0.86 and 1.18, by the Kendall sum method (Tukey 1950). This confirms the hyperbolic pattern of Figure 11.

Due to the close similarity between the three experimental series we can conclude that in *Daphnia pulex* the apportioning of total variability between yield and the residual population is independent of temperature and food supply.

This result is not particularly surprising, but it is surprising to find that the relation

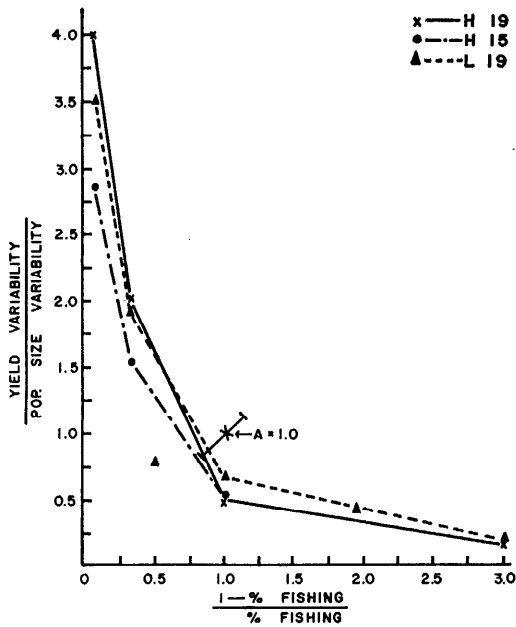


FIG. 11. The ratio of yield variability to population-size variability plotted against $\frac{1 - \text{fishing rate}}{\text{fishing rate}}$. The focus of this hyperbola is indicated by X at the point $A = 1, 1$. The total range of calculated values for the focus (with the exception of the data from population L-19 33%) is indicated by the diagonal line through X.

can be expressed by a simple hyperbola of unit focus. If the shape of Figure 11 were free to vary from species to species it would seem highly unlikely that the first species examined experimentally would be describable by such simple constants. We are tempted to conclude tentatively that the relation shown in Figure 11 is independent of the precise physiology of *Daphnia pulicaria*, and that it either would be found in all other species examined or that all species are divisible into a fairly small number of classes, for which the shape of the relation would vary from class to class but would be constant within each class. Implications of this conclusion are examined in the discussion.

We have already suggested that removal of newborn animals will probably have a greater tendency to lower population variability than would removal of older animals. If this suggestion is valid, then the shape of Figure 11 will depend on the

TABLE 4. Calculated values of a for the hyperbolic relation shown in Figure 11

$$x = \frac{\text{variability in yield}}{\text{variability in population size}}$$

$$y = \frac{1 - \text{fishing rate}}{\text{fishing rate}}; \quad a = \sqrt{2xy}$$

focus is at point a, a .

Population	x	xy	a
H-19 25%	0.175	0.525	1.025
50%	0.520	0.520	1.020
75%	2.015	0.665	1.153
90%	4.078	0.449	0.948
H-15 25%	0.190	0.570	1.068
50%	0.522	0.522	1.022
75%	1.550	0.512	1.012
90%	2.865	0.315	0.794
L-19 25%	0.198	0.594	1.090
33%	0.470	0.940	1.371*
50%	0.697	0.697	1.176
66%	0.796	0.398	0.892*
75%	1.914	0.632	1.124
90%	3.509	0.386	0.873

(* These values are from populations which had not yet reached stable mean size estimates and are probably not as trustworthy as the other values.)

fishing method. This conclusion is now being tested experimentally.

A hyperbola could be derived by assuming that variability in population size is proportional to population size. If our decrease of population variability were simply a reflection of decreased population size it would have as a consequence that variability per animal would itself be independent of population size. It is found however, by a graphical corner test (Bliss and Calhoun 1954: 197), that there is a significant increase of variability per animal (P less than .05) with increasing population size (Fig. 12). This confirms our previous analysis and specifically denies the contention that our observed reduction of variability with increased fishing was merely an effect of reducing total population size.

Life expectancy as a function of fishing intensity

If our argument on the relation between stability and size-frequency is valid, we

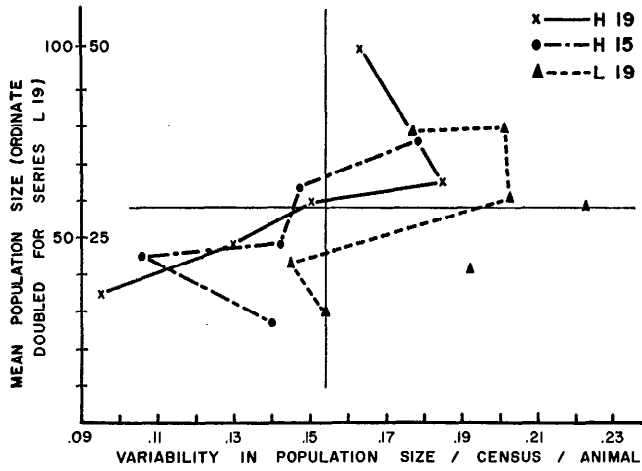


FIG. 12. The relation between mean population size and variability in population size per animal per census, demonstrating that the reduction of population-size variability at high fishing intensities was not simply due to a decreased population size. Horizontal and vertical lines have been drawn through the median points.

SURVIVORSHIP CURVES OF DAPHNIA PULICARIA
(AFTER FRANK 1952)

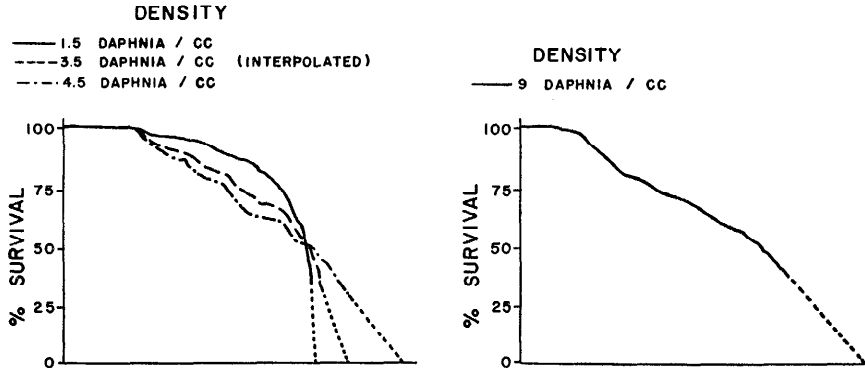


FIG. 13. Survivorship curves for *Daphnia pulicaria*, adapted from Frank (1952). The terminal portions of each curve are extrapolations. The survivorship curve for population density 3.5 has been interpolated.

should be able to demonstrate that the shape of the *Daphnia pulicaria* survivorship curve does not vary excessively with changes in population density. We can estimate the shape change by determining the ratio between mean and median life expectancies at the various population levels. Median life expectancy can be calculated from our data, while mean life expectancy can be determined by combining our data with the survivorship data of Frank (1952).

Knowing the mean size of a population

which is neither increasing nor decreasing without bounds and knowing the mean rate at which the animals of that population are being replaced, it is possible to determine the median life expectancy of animals in that population, assuming that the replacement rate is effectively constant with time. The computation is a simple iterative process in which the replacement rate is computed as the quotient of mean number of animals entering the population per unit time divided by mean population size. This replacement percentage is then

multiplied by an arbitrarily chosen number (100 for the sake of simplicity). The resultant product is then subtracted from the original number, the difference is again multiplied by the replacement rate, and the subtraction is repeated. The number of times that this process must be repeated in order to reduce the original number to one-half its original magnitude is equal, in time units used, to the time required for one-half of the animals to be replaced, or simply to the median life expectancy.

Mean population size could be immediately computed from existing data. Replacement rates for the fished population were computed by assuming that the number of surviving newborn was equal to $\left(\frac{1-p}{p}\right)$ times the mean yield, where p is the percentage fishing.

No computation of median life expectancy was made for the unfished populations since not so great care was exercised in recovering all of the dead animals at censusing, making computation of the mean number of newborn less satisfactory than in the fished populations.

Calculated median life expectancies for all of the fished populations are listed in Table 5. It is clear that the median life expectancies of the animals that survive fishing in the highly fished populations are greater than those of the less highly fished populations, although the data do not permit more precise analysis of the

relation between fishing and median life expectancy. The relation would be expected on the basis of previous analyses which indicate that life expectancy is increased by increasing the food supply per animal (Slobodkin 1954).

Mean life expectancy, the average age of animals at the time of their death, can only be computed when the shape of the survivorship curve is known (Devevy 1947). We have not conducted experiments to determine survivorship curves. Frank (1952) has published survivorship curves for *Daphnia pulicaria* maintained under constant "density" conditions. His experiments were discontinued before the last animals had died. It is still possible, nevertheless, to use his data to make some estimate of the relation between median and mean life expectancy in these experiments.

Since Frank's data are presented in terms of "density" it is first necessary to translate his density values into terms which are meaningful in the present context. Frank states that mean population size under conditions of constant feeding was equal to 8 animals per cc. Since we know that population size in unfished populations is directly proportional to food supply, we can assume that the physiological condition of animals in an unfished population is essentially the same as that in a group of *Daphnia* living under a density of 8 in Frank's terminology. We can further assume that as population size is reduced by fishing in these experiments the equivalent "density" will be proportionately reduced.

As will be explained below, there is some reason to believe that the estimates for mean size of the 25% fished populations are somewhat more authoritative than those for the unfished populations. Also, as shown in Figure 1 the difference in mean size to be expected between unfished and 25% fished populations in these experiments is small. We have therefore considered that Frank's density of 8 was equivalent to the mean density in 25% fished populations in these experiments.

The ratios of the mean size of the 90%

TABLE 5. Median and mean life expectancy

Population	% replacement per census	Median life expectancy, in days	Approx. mean life expectancy
L-19	25%	13.05	19.8
	50%	16.89	15.0
	75%	10.83	24.2
	90%	8.06	33.0
H-19	25%	12.40	21.0
	50%	9.14	29.0
	75%	8.03	33.2
	90%	7.43	36.0
H-15	25%	14.76	17.4
	50%	13.25	19.6
	75%	10.78	24.4
	90%	8.24	32.2

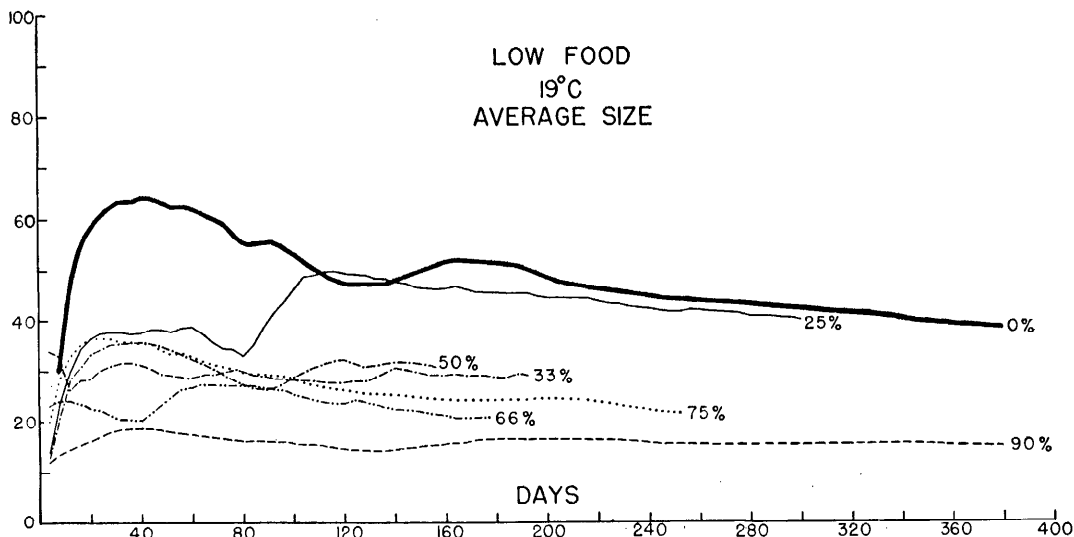


FIG. 14. Cumulative mean population size as a function of time in series L-19. Note the departure from a stable estimate of the mean in the populations fished at rates of 33%, 50%, and 66%.

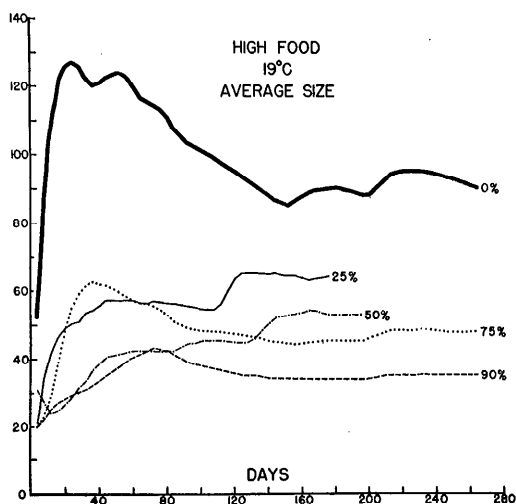


FIG. 15. Cumulative mean population size as a function of time in series H-19. Note that the estimate of mean population size in the unfished control was excessively high at the termination of the experiment.

fished populations of series H-19, H-15, and L-19 to the 25% fished mean population size are 1.805, 2.430, and 2.685 respectively. The average ratio is 2.31. Assuming the density equivalent of a 25% fished population to be 8, the mean density equivalent of a 90% fished population is 3.45.

Frank's experiments on survival were run at densities ranging from 9 to 1.5. No experiments were conducted at densities of 8 or 3.45. Frank's data were presented in units of median life expectancy. Considering the median life expectancy of population H-19 25% to be 21 days and graphically determining the mortality per day from Frank's published data for a density of 9, we can consider the mean life expectancy of population H-19 25% to be 17.8 days. Similarly, mean life expectancy acquired for the population H-19 90% (by graphically interpolating between Frank's survivorship curves at densities of 1.5 and 4.5 and extrapolating the terminal portions to zero survivors) is 34.6.

The weaknesses of the procedure are obvious. We nevertheless feel that the median life expectancy of *Daphnia pulex* populations is from 1.18 to 1.06 times the mean life expectancy. The overall effect on the shape of the survivorship curve of increasing population density was not very great over the density range considered.

The significance of mean values

Throughout our previous discussion we have been referring to mean values of various sorts derived from all of the data available about individual populations.

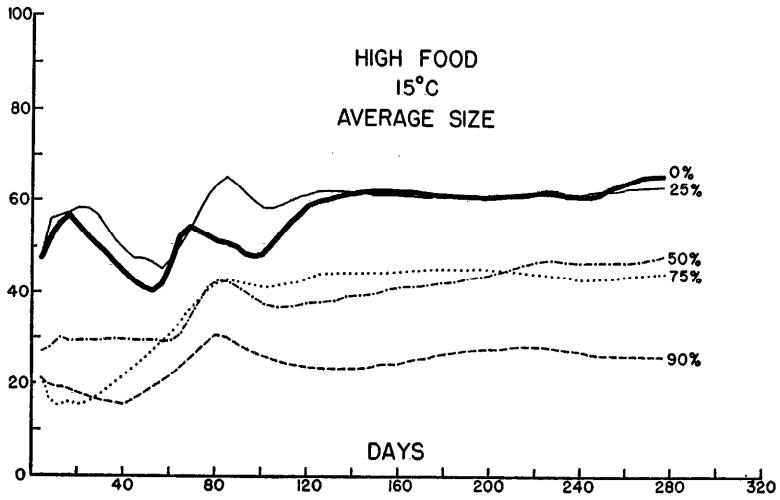


FIG. 16. Cumulative mean population size as a function of time in series H-15.

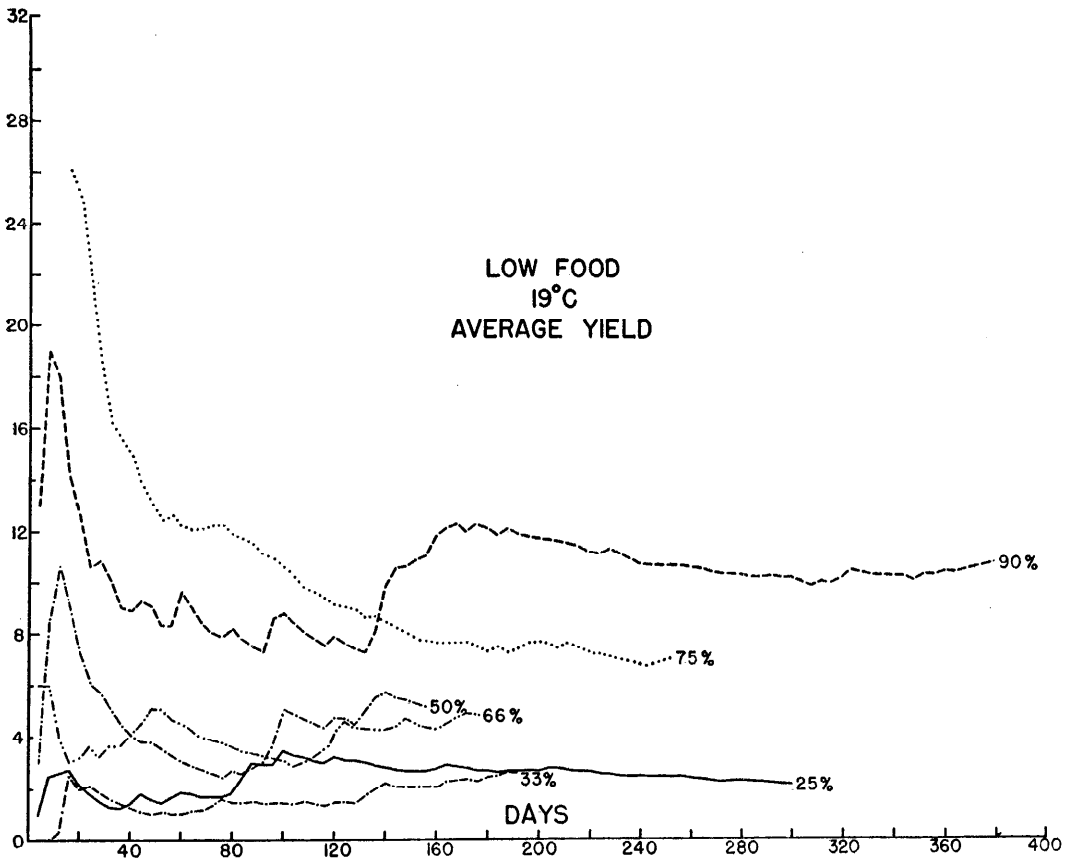


FIG. 17. Cumulative mean yield as a function of time in series L-19.

Since our populations are auto-correlated time series, the significance of these mean values cannot be determined by normal statistical techniques, which depend on the

independence of successive estimates of the mean.

We must, nevertheless, have some objective criterion for determining the relative degree of confidence that can be placed in these means, or in general there must be some criterion for determining when all of the available information has been extracted from a given experimental population. If we consider any system which is fluctuating within certain bounds, the estimate of the mean state of that system over a given time interval will also tend to fluctuate. The shorter the period over which the mean is estimated the less reliance can be placed in it, and obviously the mean estimated over an effectively infinite length of time will not be altered by subsequent observations of the system. That is, if, for example, we plot the cumulative mean size for a population (for the time interval prior to any particular time) against time we will find the graph of the cumulative mean will fluctuate greatly at first, and then as time goes on, new observations will make relatively less difference to our estimate of the cumulative mean, and the graph of cumulative mean size against time will approximate a straight horizontal line. When this stage is reached, we can confidently discontinue the experi-

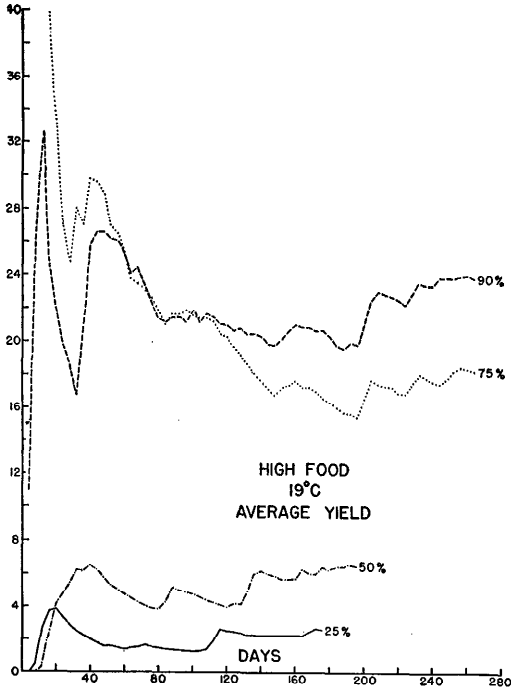


FIG. 18. Cumulative mean yield as a function of time in series H-19.

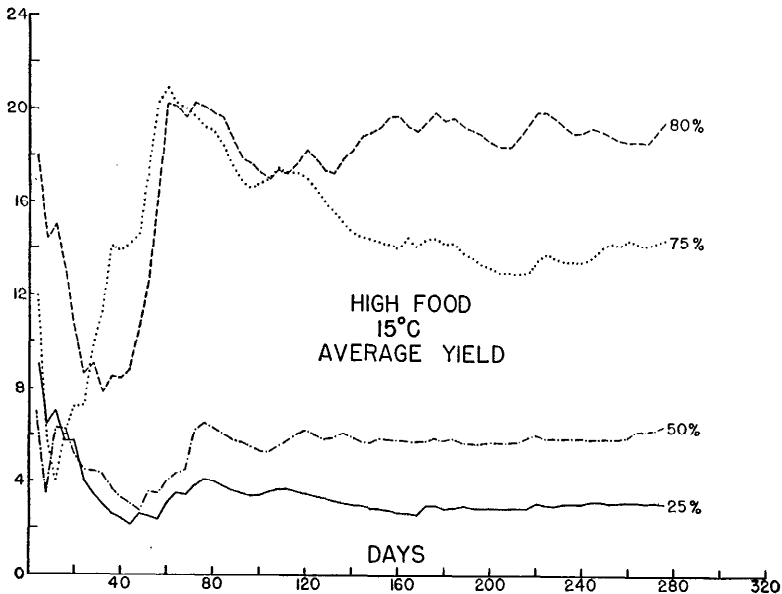


FIG. 19. Cumulative mean yield as a function of time in series H-15.

ments, on the assumption that all interesting information has already been acquired.

In Figures 14 to 16 cumulative mean population size has been plotted against time for all three experimental series. In general the terminal portions of these graphs are straight horizontal lines. In series H-19 the unfished population is not yet stabilized nor is the unfished population in series H-15, although the inadequacy of the size estimate is probably less in this case. There is an increasing trend of the estimate of the mean in series H-15 at 50% fishing and decreasing trends are apparent in series L-19 at 0 and 25% fishing. The estimates of the mean for the 33%, 50% and 66% fishing levels of series L-19 are weaker than the others.

In Figures 17 to 19 cumulative mean yields have been plotted against time for the three series. In general, yield estimates are more likely to be in error than population-size estimates but the error is probably not great enough to seriously distort the relation presented in Figure 1.

DISCUSSION

Many of the results of this investigation may be considered as suggestive but cannot, at the present time, be integrated into any general theory. Among these are the interaction between yield and fishing, population size and fishing, and the life expectancy effects. Some of the results, particularly the interactions between fishing and stability, are probably of more immediate theoretical significance. It should be borne in mind throughout that very few experimental exploitation studies have been attempted, so that comparative data are generally lacking.

Population size and yield

In the present experiments, yield per residual individual, increased in a non-linear way with fishing intensity while population size decreased non-linearly. It is apparent from elementary geometrical considerations that the product of two curves, one of which is increasing non-linearly and the other decreasing non-linearly, can be either a unimodal or bi-

modal curve, depending on the precise shape of the original curves. If the type of relation between fishing intensity, population size, and increase per individual found in our experiments is at all general, then bimodal yield versus fishing intensity relations may prove to be fairly common. The low-fishing-rate maximum in the yield versus fishing intensity relation would be due to a large number of animals, each increasing at a relatively low rate. The high-fishing-rate maximum would represent a small number of animals each reproducing or growing at a very rapid rate. The intermediate trough would be due to a fishing intensity which has lowered the population size enough to reduce the total yield, but not enough to permit compensatory increase in yield per individual. The precise pattern will depend on the mechanism of density interaction in the species involved.

Stability in populations and communities

Given any set of varying environmental factors, such as light, temperature, or the chemical composition of the air or water that surrounds the animals, different species will fluctuate to different degrees in population size. A two-day drought might destroy certain populations of insects completely but have no noticeable effect on a population of elephants in the same region. We will use the term "intrinsic variability" to refer to the relative degree of responsiveness of populations of different species to environmental variation. A species with a high intrinsic variability will show more fluctuation than a species with a low intrinsic variability when they are both subjected to identical environmental conditions.

The "actual variability" will be taken to mean the observable fluctuations in population size in a particular environment and is considered to equal the product of the intrinsic variability and the fluctuations of relevant environmental factors (including interaction with other species in the community). It seems intuitively clear that the overall actual variability that will be

found in a community of many species (defined in the sense of MacArthur 1955), will be some combination of the actual variabilities of the component species.

MacArthur (1955) has shown that the formal properties of the food web of a community will determine its intrinsic stability in part. In particular he has shown that, with a constant number of species in a community, the intrinsic stability of the community increases with the number of links in the food web. It is therefore clear that if we are going to determine the actual variability of a community as a combination of the variabilities of the component species we must take account of the food web and cannot simply sum the actual variabilities of the component species.

We have demonstrated that in our fishing experiments the total actual variability present in the population-predation system is unchanged by fishing rate. This means that the actual variability removed from the residual population in the form of yield variability is quantitatively transferred to the environmental variability (i.e. food supply) of the predator. A predator is, therefore, not only subjected to the variability of the physical environment, which will also affect its prey, but also to the actual yield variability inherent in the process of predation. We can therefore consider that the predators should either fluctuate to a greater degree than their prey or that the intrinsic variability of predators is in general less than that of animals lower in the food chain.

As a matter of fact, predatory species show relatively less actual variability than their prey. Therefore we conclude that the intrinsic variability of predatory species is relatively low.

This low intrinsic variability can be assigned to several causes. In general predators are larger and longer-lived than their prey. These properties tend to prevent small scale spatial and temporal irregularities from seriously influencing the predator populations.

Predators in general have a lower reproductive rate than their prey. Variability is decreased by this reduction in reproduc-

tive rate, presumably according to the pattern shown in Figure 11.

We can tentatively conclude that actual variability in a natural community is transmitted through the food chain in much the same way as energy. Each species in the community is offered a certain amount of environmental variability, either from the physical or biological environment. This variability may be amplified or reduced by that species as a function of its own intrinsic variability. Certain general observations on predators, which indicate that they have a low intrinsic variability, presumably associated with low thermodynamic efficiency in energy conversion (MacArthur 1955, Slobodkin 1953a) would seem to indicate a selective significance for community stability during the course of evolution, or equivalently a selective significance for population stability which has been of greatest effect on predator species. If predators, by and large, have lower intrinsic variability than their prey it becomes of interest to discover, if possible, the evolutionary conditions required for the development of low intrinsic variability. That is, is it conceivable that low variability as such might have a selective advantage? An animal characterized by low actual variability in population growth will have a lower rate of growth, lower reproductive rate, and lower thermodynamic efficiency in the conversion of food into protoplasm (Smith 1954). The interesting problem is how could an animal of this sort have a selective advantage over a more rapidly reproducing, more efficient animal of the same species. Lack (1954) has discussed the problem of the development of relatively low reproductive rates in populations of birds and small mammals and presents evidence which indicates that the survival of animals from large litters or broods is significantly lower than that of animals from smaller litters or brood. In effect, the large litters were too large to receive the amount of parental care per animal which would admit of optimal survival. He further notes that the clutch size of birds increases with latitude. He attributes this to the increased hours of daylight, permitting more time for

hunting of food by the parental birds. This viewpoint has been criticized by other authors (Skutch 1949) on the grounds that parental birds do not seem to exert undue effort in the care of their young and probably could care for a larger clutch if their activities were more clearly focused on care of the young. Ignoring this kind of objection and assuming that litter or clutch size is actually hereditary to some degree, which is supported by evidence from domestic animals presented by Lack (1954), Lack's argument is superficially a good one.

It can, however, be considered to be part of a broader argument, which for the moment rests on fairly speculative grounds, but nevertheless can be stated in some detail. The basic problem faced by Lack is the apparent inconsistency between the general tenets of modern evolutionary theory, which would predict that an animal with a high reproductive rate would have a selective advantage over a member of the same population with a lower reproductive rate, all other conditions being equal, and the observed reduction of reproductive rates during the course of evolution in certain species. Arguments to the effect that territoriality, parental care, courtship behaviour, etc. arose through evolution for the "good of the species" are justly condemned by Lack and most other modern investigators as vitalistic, orthogenetic, and generally out of line with the modern philosophical approach to biological problems. Several arguments have nevertheless been presented on sound theoretical and experimental grounds which permit the development of a non-vitalistic approach to the problem of group selection. These examples will be discussed in order of generality, and the relevance of the present studies to them will then be introduced.

Slobodkin (1953b) developed a hypothetical model in which a species was assumed to exist as a series of semi-isolated populations. Each one of these populations was assumed to be highly unstable, with a very high reproductive rate. It was further assumed that in the course of time each one of the semi-isolated populations would have become extinct, due to excessive population

fluctuation, were it not for the arrival of migrants from the other semi-isolated populations which either recolonized the localities suitable for the species or damped the fluctuations to some degree. If a mutant which has a lower reproductive rate (hence higher population stability) should arise, it would be eliminated by natural selection in favor of the more efficient and less stable form. However, if the rate of migration between populations should now decrease, due to the development of barriers of some sort, the pattern of selective advantage would shift in favor of the less efficient, more stable form which was capable of persisting in one place without the arrival of new migrants. The conditions for the development of low reproductive rates, high complexity, low efficiency, and high population stability would be extreme isolation between colonies of the same species. Furthermore, unstable populations would be expected to have mechanisms for rapid migration, or a resting stage to permit temporal redistribution, or both. (These mechanisms are discussed further in Slobodkin 1954.) This basic argument permits further discussion of the evolution of population stabilizing factors without the omnipresent trap of vitalism.

On the basis of a simple mathematical analysis of the form of density dependence in various groups of species, Slobodkin (1953a) showed that a "social" species, defined as a species in which the density term in the population equation must be computed as a second or higher order function of the number of animals present, will come to equilibrium at a lower population size than a non-social species, and that the equilibrium value would be less dependent on alterations in the environment than it would be in a non-social species, all other factors being equal.

This is essentially a simplified form of the argument developed by Smith (1954). Smith noted that over any long period of time the average increase of any population is approximately zero. Nevertheless, the "intrinsic rate of natural increase" (Andrewartha and Birch 1954) differs widely from species to species. Smith considers that the

average "harshness" in some sense of the environment is proportional to the intrinsic rate of natural increase. That is, a species with a high intrinsic rate of natural increase is more often faced with the problem of rapidly taking advantage of an ecological opportunity than a species with a low intrinsic rate of natural increase. In our notation this would be a species with a high actual and intrinsic variability. Conversely, in the present experiments removal of the newborn has lowered the effective rate of increase and correspondingly reduced actual variability.

Furthermore, behavioral complexity in a species, including such things as intelligence and alertness, clearly require energy. Energy so utilized is no longer available for growth or reproduction. Reduction of the intrinsic rate of natural increase is compensated for by further development of other aspects of the animals, all of which tend toward higher population stability. In this connection it should be recorded that many of the more bizarre forms of animal behavior and the extremes of slow development and low reproductive rate are found in isolated island populations (for examples see Richdale 1952, Murphy 1936, Marshall 1954, Hutchinson 1954b, etc.).

Nicholson (1954a), discussing his experimental studies of predation in *Lucilia cuprina* says: "That the genetical compositions of populations of the same species do often vary considerably from place to place is now well known; but natural selection (which governs these compositions) could not possibly produce and preserve the precise adjustment [between populations and their environment . . .]. To do so, it would often be required to operate in reverse by selectively destroying any abnormally potent individuals which appeared; for the preservation of these at the expense of the previously normal individuals by the characteristic process of selection would lead to progressive and indefinite population growth, in the absence of some other mechanism with a compensatory influence." In other words, the population control mechanism itself is subject to natural selection.

All of these ideas are essentially equivalent

to that of Lack if the stipulation is made that natural selection tends to favor the individuals with the greatest number of ultimate descendants, not simply the greatest number of offspring. The validity of this statement is tautological.

If it be conceded that reduction of reproductive rate increases population stability, then we can consider that Figure 11 indicates the rate at which this increase of stability occurs. The animals which we removed from the population can be interpreted as never having been born, from the standpoint of the remaining animals, although the energy used in their production is not available for further growth. In the case of the *Daphnia* populations, it has simply been lost, but in actual cases of evolutionary reduction of reproductive rates this energy would presumably be available for further behavioral or morphological complexity.

The interaction between environmental and population stability

It has been noted that the seasonal appearance of insects is correlated with the seasonal breeding of the birds that will utilize them as food. When the insects are late, the breeding season of the birds is late, etc. (Lack 1954). This suggests a possible interpretation of some of the data found in the present experiments. We have previously discussed the fact that the feeding capacity of *Daphnia pulex* increases approximately sevenfold from birth to maturity. In nature, *Daphnia* tend to be seasonally distributed, with the first young being born in the spring shortly before the initial vernal plankton bloom. In fact, it is not unreasonable to consider that the algal food supply available in a pond increases approximately tenfold between the time the first large group of *Daphnia* are born and the time at which they reach their adult feeding capacity. That is, the increase in feeding capacity with age, which tends to produce instability in the laboratory, will probably not produce a corresponding instability in nature since the natural environment may be expected to expand proportionately.

It becomes of extreme interest to discover whether this relation between the expected

variability in the natural environment and the inherent variability of the population size is at all general. Data are not abundant but certain examples are available. Members of the genus *Chydorus* are small bottom feeding cladocerans that produce no more than two eggs at a time. These eggs are very large relative to the size of the adults. If we assume that the *Chydorus* are limited by food supply in the same way as daphnias, then we must consider that the lag effect involved in their increased feeding capacity as they grow larger is of the order of one to two. It might also be expected that the seasonal variation in food supply at a mud-water interface would not be so extreme as that found in the open water. *Daphnia magna* is a common, very large daphnid found in extremely small temporary ponds, where very great food supply variability would be expected. The young of *Daphnia magna* are much smaller in relation to the adults than they are in *Daphnia pulex*. Accurate figures for the size of the newborn are not available for enough species to carry this discussion much further. It is presented as a possibility at the present time. The same relationship might explain in part the latitudinal differences in brood size found by Lack and would also explain the increase in clutch size of the European robin, *Erithacus rubecula*, and other birds found when passing from regions of oceanic climate to the central continental mass (Lack 1954), in terms of the greater seasonal variation to be expected in a continental climate as opposed to an oceanic climate.

A critical case for this hypothesis which has not yet been analyzed would involve a species in which there is either no parental care for the young, as in reptiles, or in which parental care is not confined to the natural parents, as in 'rafting' of ducklings. If these should prove to have the same latitudinal variation in clutch size as has been found in species with parental care, then Lack's hypothesis as stated must be considered incomplete.

Relation between the experiments of Nicholson and Watt and the present studies

Nicholson's studies (1954a, b) consisted of maintaining *Lucilia cuprina* in situations in

which either the larvae or the adults were limited in food supply, and in situations in which oviposition by the adults was made more difficult by interposing a screen between the adults and the oviposition sites. In the normal population growth of *Lucilia*, extreme population fluctuations occur. These are due to the fact that a very small number of females is capable of laying enough eggs to thoroughly saturate the larval food supply. The larvae completely exhaust the food supply and then an overwhelming majority of them die. As the number of adult animals is decreased by fishing, with imposed destruction of as much as 99% of the emerging adult flies, the number of eggs laid is reduced sufficiently to greatly enhance the survival of the larvae, producing a compensatory increase in the pupal population. Situations in which the larval food was available in excess but in which the amount of protein food available to the adults was limiting were also highly resilient to the destruction of adults on emergence. Population oscillations were extreme in all but the situation in which 99% of the emerging adults were destroyed and larval food was limiting. In an experiment in which larval food was limiting and adult protein was also restricted, population fluctuations were damped without any imposed mortality. While the ecological differences between *Lucilia* and *Daphnia* make direct comparisons difficult, several of the differences between the experimental results are significant, in particular the extreme fishing intensity required to damp fluctuations in Nicholson's experiments. In a situation in which the population is limited by larval food supply, an emerging adult has already made its most significant contribution to population density at the time of removal, and its removal would not be expected to dampen population fluctuations. It seems likely that the elimination of population fluctuations at 99% removal is due to the extreme reduction in the reproductive potential of the population and has nothing to do with density time-lags dependent on growth rates. That is, sufficiently high destruction of the adults can alter the relative survival pattern so as to make

equilibrium possible. The relation between survival patterns, reproductive patterns, and the possibility of population equilibrium is discussed in Slobodkin (1955).

The interaction between yield and fishing intensity in Nicholson's study is almost identical with that reported in the present experiments, presumably because the main factor in the determination of yield was reproductive rate per individual rather than number of reproducing individuals in both studies.

The experiments of Watt (1955) were done on flour beetles and were designed in a somewhat more complex pattern than either Nicholson's studies or ours. Varying percentages of the larvae and adults were removed simultaneously at thirty-day intervals. In addition, experiments were conducted in which all the adults, all the pupae, and half the large larvae were removed at thirty-day intervals, the exploitation rate being calculated *a posteriori*. Each fishing level was replicated many times and the results are presented as averages of the replicates, making analysis of individual population variability impossible. The data are presented in the form of total standing crop only. So far as Watt's complex design admits of brief summarization, the rate at which animals entered any stage, i.e. adults, pupae, or larvae, was directly and simply a function of exploitation rate. Total variability was measured as distance between maximum and minimum productivity and total standing crop for thirty-day intervals. Measured in this way the variability of adult productivity increased with fishing intensity, but no other variabilities seemed to alter significantly with fishing rate. No tests of significance were applied to these relations by Watt, who has subjected his data to a detailed analysis using multidimensional matrices and has constructed a mathematical model using thirty-six parameters.

We must conclude that due to differences in experimental material and experimental design, translation and interpretation of the results of any one of the three experimental studies so far available in terms of any of the others is not particularly rewarding. The simple fact that all three situations demonstrate homeostasis in the

response of populations to exploitation can be stated, but probably could have been stated *a priori*. It should also be emphasized that all three experiments contradict the simple exploitation models which have been based on the logistic curve, for the same reason that any experimental population of metazoa cannot be reconciled with the predictions of the logistic curve; that is, age structure and the variation of physiology with age are of overwhelming importance in the growth of populations of metazoa.

The experiments of Nicholson and Watt do not contradict the conclusions which have been drawn from the present experiments, but since the presentation of data in the three studies is not strictly comparable, they cannot be considered to confirm them either.

If this much variability and complexity can occur in the only three experimental exploitation studies which have as yet been completed, we must conclude that development of specific deterministic or stochastic models is premature. We can hope that future experiments will suggest new approaches and generalizations, but for the moment a general theory of exploitation seems further away than it did before the experiments were started. This in itself is probably a valuable conclusion to establish.

CONCLUSIONS

Removal of newborn animals at varying rates from populations of *Daphnia pulex* tends to reduce the size of the residual populations, but not in direct proportion to either the number or percentage of the newborn animals that have been removed. This lack of direct proportionality can be accounted for in terms of a shift in the age structure of the residual population, an increase in the growth rate and reproductive rate of those that survive the fishing procedure, and in their longevity. These effects can be adequately explained in terms of what is known of the dependence of *Daphnia* populations on the food supply per individual and the fact that removal of newborn individuals increases the available food supply for the animals that remain. Maximum yield occurred when approximately 90% of the newborn animals were removed.

As the removal rate increased, the absolute stability of the residual populations increased as did the stability per animal. The increased stability of the residual populations was precisely compensated for by increased variation in the yield from census to census. The variability of the total standing crop was unaltered by fishing.

The ratio of yield variability to population-size variability plotted against the percentage of the newborn that were not removed divided by the percentage of the newborn that were removed, produced an equilateral hyperbola with focus at the point 1,1. The simplicity of this relation makes us suspect that it is not confined to *Daphnia pulex* alone.

Two general conclusions that are indicated but not unequivocally demonstrated by the present study are that the observed low variability of populations of predators can be fitted into a general scheme of community stability patterns and that it seems very likely that the positive feedbacks in any population are adjusted to the expected variability in the environment of that population in nature, so that a highly variable system in the laboratory may not depart from equilibrium with the environment in nature.

Comparing these studies with other published experimental work on fishing laboratory populations, it was found that differences in the published results to date only emphasize the diversity to be expected in an exploitation system and accentuate the need for further experimentation as a prerequisite for general theory development.

REFERENCES

- ANDERSON, B., AND J. C. JENKINS. 1942. A time study of events in the life span of *Daphnia magna*. *Biol. Bull.*, **83**: 260-272.
- ANDERSON, B., H. LUMER, AND L. J. ZUPANCIC. 1937. Growth and variability in *Daphnia*. *Biol. Bull.*, **68**: 444-463.
- ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. *The Distribution and Abundance of Animals*. Chicago, Univ. of Chicago Press. vii + 782 pp.
- BEVERTON, R. J. H. 1953. Some observations on the principles of fishery regulation. *J. Cons. Expl. Mer.*, **19**: 56-68.
- BLISS, C. I., AND D. W. CALHOUN. 1954. An Outline of Biometry. New Haven, Yale Cooperative Corporation. 272 pp.
- DEEVEY, E. S. 1947. Life tables for natural populations of animals. *Quart. Rev. Biol.*, **4**: 283-314.
- DICKIE, L. M., AND F. D. MCCracken. 1955. Isoleth diagrams to predict equilibrium yields of a small flounder fishery. *J. Fish. Res. Bd. Canada*, **12**: 187-209.
- EDMONDSON, W. T. 1955. Seasonal life history of *Daphnia* in an arctic lake. *Ecology*, **36**: 439-455.
- FRANK, P. W. 1952. A laboratory study of intraspecies and interspecies competition in *Daphnia pulex* (Forbes) and *Simocephalus vetulus* (O. F. Müller). *Physiol. Zool.*, **25**: 178-204.
- HEWITT, O. H., ed. 1954. Symposium on cycles in animal populations. *J. Wildl. Mgt.*, **18**: 1-112.
- HUTCHINSON, G. E. 1954a. Notes on oscillatory populations. *J. Wildl. Mgt.*, **18**: 107-109.
- . 1954b. Marginalia. *Am. Sci.*, **42**: 300-308.
- LACK, D. 1954. *The Natural Regulation of Animal Numbers*. London, Oxford Press. viii + 343 pp.
- MACARTHUR, R. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology*, **36**: 533-536.
- MARSHALL, A. J. 1954. Bower birds. *Biol. Rev. Cambridge Phil. Soc.*, **29**: 1-45.
- MURPHY, R. C. 1936. *Oceanic Birds of South America*. New York, American Museum of Natural History. 1245 pp.
- NICHOLSON, A. J. 1954a. Compensatory reactions of populations to stresses and their evolutionary significance. *Australian J. Zool.*, **2**: 1-8.
- . 1954b. An outline of the dynamics of animal populations. *Australian J. Zool.*, **2**: 9-65.
- PRATT, D. M. 1943. Analysis of population development in *Daphnia* at different temperatures. *Biol. Bull.*, **85**: 116-140.
- RICHDALE, L. E. 1952. Post-egg period in albatrosses. *Biol. Monographs (Dunedin, N. Z.)*, **4**: 1-166.
- RICKER, W. E. 1954a. Effects of compensatory mortality on populations. *J. Wildl. Mgt.*, **18**: 45-51.
- . 1954b. Stock and recruitment. *J. Fish. Res. Bd. Canada*, **11**: 559-623.
- RODINA, A. G. 1946. Experiments on the feeding habits of *Daphnia magna*. *Zool. Zhur.*, **25**: 237-244 (In Russian).
- RYTHER, J. H. 1954. Inhibitory effects of phytoplankton upon the feeding of *Daphnia magna* with reference to growth, reproduction and survival. *Ecology*, **35**: 522-533.
- SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis*, **91**: 430-455.

- SLOBODKIN, L. B. 1953a. On social single species populations. *Ecology*, **34**: 430-434.
- . 1953b. An algebra of population growth. *Ecology*, **34**: 513-519.
- . 1954. Population dynamics in *Daphnia obtusa* Kurz. *Ecol. Mongr.*, **24**: 69-88.
- . 1955. Conditions for population equilibrium. *Ecology*, **36**: 530-533.
- SMITH, F. E. 1954. Quantitative aspects of population growth. In: *Dynamics of Growth Processes*. Princeton Univ. Press. pp. 277-294.
- TONOLLI, V. 1947. Il ritmo cardiaco della *Daphnia pulex* de Geer. *Mem., Ist. Ital. di Idrobiol.*, **3**: 415-429.
- TUKEY, JOHN W. 1950. The Kendall sum. Seminar in statistics given at Yale University, February, 1950. (multilithed).
- WATT, K. E. F. 1955. Studies on population productivity. Three approaches to the optimum yield problem in populations of *Tribolium confusum*. *Ecol. Monogr.*, **25**: 269-290.
- WIENER, N. 1948. *Cybernetics*. New York, John Wiley. 194 pp.