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In recent years, students of animal ecology have turned their endeavours more and more toward the investigation of animal populations. Particularly to those interested in the problems of conservation, the necessity of having an accurate knowledge of the numbers of the animals with which they are dealing is becoming apparent. For this reason, methods of quantitative estimation have received increasing attention.

The efficient management and regulation of a commercial fishery to the end that the greatest production be secured without continually decreasing the numbers available for reproduction, can be evolved only after precise information is obtained as to the "catch" (the number taken by the fishery) and the "escapement" (the number surviving to perpetuate the species). The correct evaluation of the "escapement" is the most difficult task.

The proper exploitation of the Pacific coast salmon depends on a knowledge of the numbers of adults which spawn from year to year in the streams, rivers, and lakes into which they run. The following discussion is an attempt to evaluate one method which has been suggested as a means of arriving at an estimate of these spawners.

Previous attacks

Until the necessity of introducing more accurate checks on the size of spawning populations became so obvious, the common system which was followed consisted of careful surveys of all the easily accessible spawning areas. From these, rough ideas as to the concentration of fish could be obtained. By comparing the estimate of the numbers of fish in a certain year with that observed for the same locality during the previous "brood year", the relative increase or decrease in successive generations could sometimes be determined. Complications often arose when such a method was employed, in view of the difficulty of determining accurately the age of the spawners and thus the "brood" to which they should be assigned. Furthermore, although the results were required to be only sufficiently accurate for comparative purposes, such accuracy could not always be obtained, since considerable error was introduced if different persons made estimates either in the same or successive years.

"Counting fences" have recently been introduced in certain localities to arrive at the correct census for a particular area. These are so constructed that the counts may be made in one of two ways. In one the adults migrating upstream are guided through narrow openings where actual counts can be made by the observer. In the second, fish find their way through leads into pens from which they may be dipped, examined and enumerated. Unfortunately, conditions which permit the construction of such fences are not found in all spawning streams. In many cases, even though the engineering difficulties are surmountable, the financial expense of construction and operation is prohibitive.

It becomes necessary then, to develop an accurate and more widely applicable means of determining populations of spawning fish, which is not dependent upon personal acumen, and which is comparatively inexpensive to employ.

The Estimation of an Animal Population by Tagging

1. Its general principle:

One method of estimating the numbers in animal communities has been used by ecologists with varying degrees of success. Briefly, it consists of marking, branding, tagging, or banding a definite number of individuals and considering the ratio of the marked to the unmarked in subsequent recaptures as representative of the proportion which exists in the total population. This proportion will indicate the total numbers in the community. Such a method is naturally subject to the ordinary errors of sampling and must be applied with extreme caution, especially when the investigator is not intimately acquainted with the habits of the species.

2. Its practical application in estimating spawning salmon:

It has been suggested that if a known number of spawning salmon were tagged, the total population in the stream could be determined, if even a portion of the fish might be later discovered and enumerated. Such a system, if practical, would be most useful. Its successful prosecution would be independent of the observers' experience or prowess, and accurate information might be obtained easily and inexpensively.

The method of application is as follows: A number of fish moving into a spawning stream are captured and counted. They are then released bearing a brightly colored tag. At various times after their release, the accessible regions of the stream are explored, and the ratio of tagged to untagged individuals noted. The average percentage of tagged fish in the total number of fish observed is then employed to calculate the total population in the stream. Suppose two thousand fish in all are tagged, and that the surveys showed the tagged individuals made up twenty per cent of the fish observed. It would be concluded that there was a total population of ten thousand fish in the stream.

There are several variable factors which will have a bearing on the practicability of such an application. The number of fish tagged, the duration of the tagging program, the nature and frequency of the experimenter's observations, can be determined by his operation. Factors beyond his control are the character of the run, the distribution of the spawning fish, the length of time the fish remain alive in the stream, how long they can be observed after they die, and physical conditions such as the geography of the stream, and its variation in water height.

In the following pages an attempt will be made to study the interrelation of these variables and to investigate their possible effect on each other under the conditions which can be established by the methods of operation.

The analysis appears to resolve into a consideration of two types of conditions, that in which there is a constant proportion of tagged fish in the stream over the whole duration of the run, and that in which the tagged percentage varies during the run. The first is secured by a method of tagging which we are pleased to call "proportionate", the latter by "disproportionate tagging".

Proportionate Tagging

To ensure a constant proportion of tagged fish in a stream during the course of a run, a constant proportion of the migrants into the stream must bear tags. A possible, but difficult method of attaining this end, might be to introduce at the mouth of the stream a system of traps or nets which by the peculiarities of their operation took a definite percentage of the immigrants per day. Even if such a construction were possible, however, the tendency for a run to vary considerably from day to day might complicate the actual tagging operation. Unless the tagging could cope with the captures, the lag in releasing the marked individuals would effect a disproportionate distribution in the stream, and the advantage of this type of tagging would be lost.

Another method of proportionate tagging might be to sample the total population in a random manner before migration into the stream commenced. For instance, it might be desirable in connection with the operation of a counting fence at the outlet of a lake through which sockeye salmon pass, to determine the number of fish spawning in a stream tributary to that lake. If one out of every ten fish passing the fence were tagged, it might reasonably be expected that ten per cent of each day's migrants into the stream above the lake would bear tags, and as a result the same percentage would prevail in the stream for the duration of the run.

If the habits of the fish were such, that all the run entered the lake before any moved into the stream, and furthermore, if complete mixing occurred, so that there was no tendency for the fish which entered the lake first to migrate into the stream before the others, tagging of the necessary number could be performed at the fence at any time during the run.

Perhaps too, even if there were no fence in operation, a random sample might be taken by a seine at the time the salmon were preparing to enter the stream, but this of course would only be possible if the total population were schooled up together at one time.

The advantages of obtaining a constant proportion of tagged fish in the stream are obvious. One inspection would be sufficient to establish the percentage value. Since the proportion would be constant over the whole area, only a small portion of the stream would require a survey. Counts could be made either on the dead or the live fish, for the proportion would persist after death, and a freshet which might wash the bodies out of the stream or into deep holes, would have no effect on the percentage among the fish remaining.

Disproportionate Tagging

The conditions which will permit the type of tagging described above seldom are encountered. The investigator has yet to develop the type of trap or net which will take a constant proportion of migrants day after day throughout a spawning run, if it is set at the mouth of a creek into which they are entering. Though it is probable that certain types will operate so that the fish captured per day will reflect to some extent the entire migration that day, the percentage captured will not be constant over the duration of the run, and varying proportions of tagged fish will be liberated into the stream on successive days.

The theoretical run

To better illustrate the complications which may arise when disproportionate tagging is employed, the author has taken the liberty of setting up what might be termed a "theoretical run". It is commonly observed that spawning runs have a certain general character, which is modified in various directions and to various degrees depending on a number of interrelated factors. It is usual to find that a run commences with the appearance of a few individuals in the stream. The number of migrants per day increases to a peak and finally falls off to scattered fish that enter when it is nearing completion.

Since most spawning runs which the investigator will be called upon to study will have the common characteristic of a general rise in the daily migration over the first part of the run and a downward trend in the latter part of the run, the author feels that the most satisfactory description would be to liken it to the normal frequency curve $y = ke^{-bt^2}$, where y represents the number of fish per day entering at time t, reckoned from the peak of the run, and the constants k and b determined by both the total number of migrants and the duration of the run. If we evaluate the effect of the variables on a run of this type, we can determine the complications which arise purely from the upward and downward trend. Variations away from this general trend will introduce complications peculiar to each run. The actual results will differ somewhat from those which we shall describe, but only to the extent of the effect of those peculiar variations.

The run described in Table I has been developed from an equation similar to that above. The left-hand column (n) gives the consecutive days in which the number of fish (M_n) in the second column enter the stream. The total number which are in the stream at the end of the nth day are listed in the third column (P_n). A total of 10,000 fish enter in the space of thirty-seven days, half of them before noon on the 19th and half of them after this time. Figure I illustrates the character of such a run in graphical form.

The effect of tagging a constant daily number

The simplest type of disproportionate tagging is that in which a constant number of fish are tagged per day. For the purposes of this paper this will be used to illustrate the salient features of that system.

Let us first consider the conditions which would obtain if two thousand immigrants in our "theoretical run" are tagged as they enter the stream, 100 per day from the 10th to the 29th days inclusive. One hundred fish per day will make up varying percentages of each day's migration. These ($\%t_n$) are listed in the fifth column of Table I. The varying percentages which would result in the stream from day to day are set out in the last column ($\%T_n$). If these percentages could be determined by observation on the stream, their combination with the knowledge of the number of tags used to date would give the total migration into the stream up until that time.

The duration of tagging

The question of when the tagging should take place and how long it should continue will depend upon the information we desire. Should it be desirable to investigate the run's progress it would seem advisable for tagging to begin as soon as practicable. If the run is large and the method of capture is such that only a small number can be taken each day we should tag as long as possible to ensure a reasonable tagged percentage in the stream. The actual tagging manipulation is somewhat time-consuming and for a small crew to tag a large number of fish the whole duration of the run may be necessary.

To illustrate the relative effect of tagging during the first half of the run and tagging in the latter half, Table II has been set up. The fourth column shows the percentages to be found in the stream if 100 fish per day were tagged from the 10th to 19th days inclusive ($\%T_{nb}$), the fifth column the tagged percentages[1] if 1000 fish were tagged, 100 per day beginning on the 20th day ($\%T_{ne}$). These percentages are graphically illustrated in Figure 2.

The frequency of inspection

A consideration of how often the stream should be inspected and the tagged percentage determined will depend, of course, on what figure we are interested in obtaining. Should only an estimation of the total run be desired, we would expect that only a count at the completion of the run is required. In some cases, however, it may be the early part of the run which is most important. The number of fish which have entered a stream by a certain date may be required in instances where fishery boundaries are adjacent to the mouth and the investigator is interested in the minimum escapement at that time.

The distribution of spawning fish

No information regarding the way spawning adults distribute themselves along the length of a stream has been encountered in the literature which the author has investigated. It would seem that if the distribution be other than random a serious impediment to the successful application of the method might arise. Should the migrants which enter on one particular day proceed to a certain area, the population will not be mixed thoroughly and the tagged percentages will vary from place to place. A total count of all the tagged and untagged individuals which could be observed would not necessarily give

[1] The term "tagged percentage" will be defined as the percentage of tagged fish in the stream ($\%T_n = M_n/P_n \times 100$).

the actual percentage in the stream, unless all the population had been inspected, in which case the tagging is not necessary. The whole stream would have to be considered in each inspection and such is manifestly impossible. The closest approach would not have any advantage over an actual estimation of the population by counting all the visible fish.

For the efficient operation of this method, then, the distribution must be random, and mixing must occur very quickly after entrance.

The death of spawned fish

The method of discovering the tagged percentage is complicated by the death of the spawning fish. (For the sake of brevity, we shall denote the time in days which an adult fish spends alive in the stream as its stream life. A fish immigrating on the first day and dying on the eleventh day will be considered to have a stream life of ten days.)

It is recognized that there is considerable variation in the stream life of spawning fish from species to species and from stream to stream, but it is a common observation that fish spawn and die in many cases a considerable time before the actual spawning run of the whole school has been completed.

It would appear probable, then, that of a whole school of migrants, there would be at least a tendency for those which entered the stream first to spawn and die earlier than the last immigrants. The ramifications of such an actuality are very important. If a number of dead fish are lying on a bar it is a simple matter for the observer to examine them closely, and make an accurate count without difficulty. The complication arises, however, when it is realized, that though fifty fish spawning in a shallow riffle may be difficult to count accurately to the last fish, they are much more apparent than they would be after they died and some of them were swept down into a deep hole, or entangled in the intricacies of a log jam. There would be more tendency, then, to favour the live percentage[1] than the dead percentage[1], and the figure for the tagged percentage would be in error.

The peculiar conditions resulting from the death of spawned salmon are so important that the following pages will be given over to a more particular study of the effect of this phenomenon. The conditions which would arise if each fish died exactly the same time after immigration will be investigated. The influence of an average stream life will then be discussed. The effect of variations in the individual stream lives about this average will be pointed out. The result of a change in the length of the average stream life will be considered, and the effect that tagging at various times during the run will have on the resulting percentage of tagged fish in the stream will be shown.

The effect of an exact stream life

Let us first assume the admittedly artificial condition which would exist if each fish had a stream life of exactly ten days (not necessarily exactly 240 hours, but that it would die on the tenth day after it had entered the stream). If such a condition were to obtain, the live percentage would be made up of only the fish which had entered in the previous ten days, the dead percentage would reflect exactly the live percentage of ten days before. Table III and III A illustrate such a case, and Figure 3 shows graphically, the changing values of the tagged percentage $\%T_n$; the dead percentage $\%TD_n$ and the live percentage $\%TL_n$ as the run progresses.

[1]"live percentage" - the percentage of the live fish which bear tags.
"dead percentage" - the percentage of the dead fish which bear tags.

It is apparent after a glance at the character of the graphs, that the live percentage will give a comparatively close estimate of the tagged percentage during the first stages of the run, but that after the dead fish begin to appear in considerable numbers the use of the live percentage as an index of the tagged percentage will become more and more misleading. Conversely the dead percentage will be of use only to indicate the numbers which had migrated up to ten days before. It will only give a dependable estimate of the run when an insignificant number of fish are left alive in the stream. In order to determine the actual numbers in the stream at a time about half way through the run (and after the deaths begin to have a noticeable effect on the live percentage), it would be necessary to calculate both the live percentage and the dead percentage and to weight them according to the actual proportion of live to dead in the stream, an almost impossible task.

The effect of an average stream life

An objection naturally arises: granting all this difficulty which would arise if the fish died at a certain time after they entered, it would be absurd to suggest that they all would die exactly ten days after they came in. Even if all the fish <u>on the average</u> lived for just ten days, we would expect to find some dying sooner than this and others again remaining for a longer period. Will not this have a decided tendency to "balance up" the figures, and as a result ensure the percentage of tagged to untagged remaining fairly constant, or at least make the discrepancy insignificant?

The author has made an attempt to discover the damping effect that variations in stream life would have on the figures, and has established a formula which is an aid in studying this factor. In order not to confuse the reader unduly the mathematical development has been omitted from the main body of this discussion, and is submitted in the appendix.

We must needs set down, however, the assumptions which have been made to arrive at the number of fish which may be expected to die on any one day, when the variation is of the simplest type:

1. It is assumed that there is no significant tendency for the fish that enter the stream first to have an average lifetime longer or shorter than those which make up the latter part of the run; i.e. that the fish which enter on any one day will on the average have the same length of stream life as those entering on any other day, and that this average will be that of the total population.

2. It is assumed that the deviations from the mean value for the average stream life are distributed symmetrically about the mean and can be described as subject to the normal law of error, and that the standard deviation of the stream lives is the same for each day of the run[1].

The above assumptions are admittedly broad in character. There is a possibility that in natural conditions the average stream life of early migrants may differ significantly from that of those which enter the stream late in the run. The variation in the life of one day's migrants may be more or less than those of another day. It is quite conceivable too, that the variations may not be distributed symmetrically about the mean. The deviation may suggest a skewed curve rather than a normal curve of error. If such be the case, however, the picture becomes even more complicated; the factors which determine the changing percentages are more complex and only a "fortuitous combination

[1]The standard deviation of a group of variables is a convenient statistical expression which describes the manner in which the individual values differ from the mean, or average value. The greater the variation in the values the greater is the standard deviation.

of circumstances" would result in the curves becoming more simple rather than more intricate.

To sort out the relative effect of wide variation in the stream life, and of the effect of a longer or shorter stream life, on the percentages, it will be instructive to set up tables illustrating first the conditions which will result as the variation in the stream lives becomes greater.

Standard deviation of one day. Table IV gives the values of the expressions which we wish to compare when the following state of affairs exists:

Average stream life - 10 days

Standard deviation - 1 day

Migrants entering as in Table I

Tagging continuing from the 10th to 29th days, 100 fish per day

Total percentage tagged - 20

The values of D_n have been calculated by the use of the formula developed in the appendix, from which amounts the figures for $\%TD_n$ and $\%TL_n$ have been obtained. Table V is included to facilitate comparison of the three percentages, $\%T_n$, $\%TL_n$, and $\%TD_n$, (the percentage of the total migrants tagged, the percentage of tagged live fish in the stream, and the dead tagged percentage, respectively). The figures in brackets are those (from table III) which would have been found had the lifetime been exactly ten days.

It will be noted that for a standard deviation of this small amount, very little damping has occurred. It would still require much manipulation to evaluate the population except toward the end of the run.

Standard deviation of three days. Let us next consider the percentages which follow from the same average lifetime but with a standard deviation of 3 days. Table VI illustrates the percentages which would be found under the following conditions:

Average lifetime - 10 days

Standard deviation - 3 days

Migrants entering as in Table I.

Tagging continued from the 10th to 29th days, 100 fish per day

Total percentage tagged - 20

The graphs in figure 4 represent the percentages in Table VII. It is apparent at once that the curves are flattening out, but unfortunately, though the live fish in the stream during the first of the run, still show percentages similar to the actual tagged percentage, the dead percentage is losing its similarity to the "true curve" of ten days before. Furthermore the $\%TD_n$ curve, except when it crosses the other curves does not give the value we desire till about the fortieth day of the run - after all the migrants have entered the stream.

The effect of the length of stream life

To consider the effect the "life span" has on the percentages, we have reproduced the conditions which would appear if the following characteristics of the run held:

Average stream life - 15 days

Standard deviation - 3 days

Migrants entering as in Table I

Tagging continued from the 10th to 29th days, 100 fish per day

Total percentage tagged - 20

To better visualize the variation described by a standard deviation of 3, figure 5 shows in polygonal form the number of fish which die on various days after a migration of 500 fish on the 15th day, the average stream life being 15 days.

An examination of Table VII will demonstrate the percentages produced under the above conditions, which differ from those considered immediately before only in the average stream life. This table is graphically reproduced in figure 6. Note that due to this longer lifetime, the live percentage follows the true percentage even more closely. Its use will give an accurate estimation until the 23rd day of the run, and will be subject to a maximum of approximately 5% error until as late as the 33rd day. As before, the dead fish count will only be useful well after the run is over and the fish have died.

The effect of the duration of tagging

It might be interesting to consider what effect tagging at various times has on the figures we desire to obtain. Graphs are submitted in figures 7, 8 and 9, illustrating tagging at the beginning of the run (100 fish per day from the 10th to 19th days inclusive), in the latter part of the run (100 fish per day from the 20th to 29th days inclusive), and also at the peak of the run (500 fish on the 19th and 20th days).

Early tagging

Lifetime - 15 days

Standard deviation - 3 days

Migrants entering as in Table I

Tagging from 10th to 19th days inclusive -
100 fish per day.

Figure 7, is fairly well self-explanatory. It will be seen that the live fish count is of value until just after the peak of the run, the dead fish count cannot be used till the fish have all died.

Late tagging

Lifetime - 15 days

Standard deviation - 3 days

Migrants entering as in Table I

Tagging from 20th to 29th days inclusive -
100 fish per day.

Figure 8, which illustrates this condition, shows that the live fish count is accurate only for three days. At the completion of tagging there is a 30% error. The only count of value is again the dead fish count at the completion of the run.

"Peak" tagging

Tagging at the peak - 500 fish per day for two days. Here too, (see figure 9), the live fish count shows a considerable error -- 10% only five days after the completion of tagging. The dead fish count will be in error until after the fish have all died.

Summary

The conclusions that can be drawn from this rambling discussion are perhaps the following:

To use with any hope of accuracy such a method, we must have the conditions in which the fish have a long life in the stream compared with the duration of the run, in order to use the live count with reasonable accuracy. Variation in the life of the fish will not have a great tendency to prevent the discrepancy in the counts, and variation of any appreciable extent will negative the value of a dead fish count until the end of the run.

If the life span is short, but with considerable variation, the only count of value is the final dead fish estimation, but, it must be remembered that we cannot hope too optimistically that its value at the end of the run will give us a true estimate. It will be realized that we have assumed that all the dead fish remain in the stream, and that, if they are not all visible when the count is made, the individuals we see represent the percentage as it exists over the entire area. Consider, however, what would occur should a heavy freshet come during the run. Neglecting its effect on the actual migration of the live fish for the moment, it will result in all or most of the dead bodies being swept downstream, and if they are not discharged at the mouth of the creek, they will certainly have a tendency to drop into deep holes and thus be lost to sight. The count at the end of the run then will reflect only the percentages which existed among the dead fish after the freshet occurred, and only by coincidence would be expected to be that which is necessary to give a correct estimate.

The author admits that there is every likelihood of the events described in this "theoretical run" never occurring in natural conditions. What effect differences in the standard deviations of the lifetime of each days migrants will have on the counts, would be difficult to determine without a knowledge of what those differences are. The departure of an actual migration from the regular movement into the stream which we have stipulated will change the shape of the curve considerably. It is felt, however, that there is no definite reason why these irregular departures from the rigid conditions we have set up, should serve to eliminate the sources of error we have described. There is as great a possibility that these irregularities might accentuate rather than diminish them.

To a reader overcritical of the use of this system of estimating populations, the outlook for a facile method of enumeration appears rather dark and foreboding, but it is possible that if the physical conditions are such that tagging can be completed before the run begins, that is, so that the population is tagged randomly and that a constant proportion of the migrants as they run into the stream and subsequently die bear tags, there is a possibility of obtaining accurate data. Until such an operation be performed we must consider the method still in its experimental stage.

Appendix

The development of the formula for deaths under conditions of an average stream life

Let M_n be the number of migrants entering on the nth day,

d_n be the number of fish dying on the nth day,

a be the average lifetime of the fish in the stream,

s be the standard deviation of this average.

We shall first consider the distribution of the deaths of fish which enter the stream on the "nth" day. To simplify the calculations somewhat, we shall consider noon on the "n+a" day to be exactly "a" days after <u>all</u> these M_n fish entered.

It can be shown statistically that the proportion of these fish (this proportion to be represented by the notation k_m) that die on the day "n+a-m" is defined by the following expression,

$$K_m = \frac{1}{\sqrt{2\pi}\,s} \int_{m-.5}^{m+.5} e^{-x^2/2s^2}\,dx$$

where "m" is any positive integer and "z" the time in days reckoned from the mean time of the deaths, that is, from noon on the day "n+a".

It follows from the conditions we have set up that the same proportion (k_m), will die on the day "n+a+m".

Similarly, k_m will be the proportion of the fish which migrate on the "n+1" day (M_{n+1}), that die on the days "n+a+1-m" and "n+a+1+m".

Setting up the following table may assist in understanding the foregoing, and also lead to the development of the expression which will give the total number of fish which die on any one day. To simplify the illustration we shall assume that all the fish of a particular day's migration die within, say, sevem days of each other; in other words, that the standard deviation of the average lifetime is small enough that k_4 is insignificant.

Proportion of migrants dying

Day of death	M_{n-4}	M_{n-3}	M_{n-2}	M_{n-1}	M_n	M_{n+1}	M_{n+2}	M_{n+3}	M_{n+4}
n+a-4	k_0	k_1	k_2	k_3					
n+a-3	k_1	k_0	k_1	k_2	k_3				
n+a-2	k_2	k_1	k_0	k_1	k_2	k_3			
n+a-1	k_3	k_2	k_1	k_0	k_1	k_2	k_3		
n+a		k_3	k_2	k_1	k_0	k_1	k_2	k_3	
n+a+1			k_3	k_2	k_1	k_0	k_1	k_2	k_3
n+a+2				k_3	k_2	k_1	k_0	k_1	k_2
n+a+3					k_3	k_2	k_1	k_0	k_1
n+a+4						k_3	k_2	k_1	k_0

It follows at once from this table that the total number of fish which die on day "n+a" = $k_0M_n + k_1(M_{n+1} + M_{n-1}) + k_2(M_{n+2} + M_{n-2}) + k_3(M_{n+3} + M_{n-3})$ or $d_{n+a} = k_0M_n + \sum_{m=1}^{m=3} k_m (M_{n+m} + M_{n-m})$.

By deduction, then, the general equation for this number is:

$$d_n = k_0M_{n-a} + \sum_{m=1}^{m=4-1} k_m (M_{n-a+m} + M_{n-a-m}) \qquad (I)$$

where m represents the successive positive integers, and r the integer for which k_m becomes insignificant or the expression $(M_{n-a+m} + M_{n-a-m})$ is equivalent to zero.

The evaluation of the constants "k_m"

The definite integral $\frac{1}{\sqrt{2\pi}\, s}\int_{m-.5}^{m+.5} e^{-x^2/2s^2}\, dt$ which determines the constant k_m appears rather formidable at first glance. Fortunately, however, by the substitution of $z/s = x$, it may be transferred into the following form, which can be quickly evaluated by referring to a set of probability tables:

$$K_m = \frac{1}{2\pi}\int_{\frac{m-.5}{s}}^{\frac{m+.5}{s}} e^{-\frac{x^2}{2}}\, dx$$

As might be expected k_m depends only upon "s" -- the standard deviation of the average "stream life". The following table gives the values of the constants for four values of the standard deviation.

The evaluation of the constant k_m for successive values of m, and for the values of "s" noted at the top of each column -

m	k_m	k_m	k_m	k_m
	s = 1	s = 2	s = 3	s = 4
0	.3830	.1974	.1324	.0996
1	.2417	.1747	.1253	.0964
2	.0606	.1210	.1062	.0879
3	.0060	.0655	.0807	.0752
4	.0002	.0279	.0548	.0604
5		.0092	.0334	.0458
6		.0024	.0183	.0325
7		.0005	.0089	.0217
8		.0001	.0039	.0135
9			.0015	.0080
10			.0006	.0045
11			.0002	.0023
12				.0011
13				.0005
14				.0003
15				.0001

The use of the equation I for the evaluation of d_n will perhaps best be illustrated by considering a specific example.

To calculate the number of fish that die on the 32nd day after the start of the run, assuming that the average stream life is 15 days, with a standard deviation of 2.

Applying our equation and substituting

$n = 32$, $a = 15$, and the values for k_m as on the previous page,

we have

$$d_{32} = k_0 M_{17} + \sum_{m=1}^{m=8} k_m(M_{17+m} + M_{17-m})$$

$$= k_0 M_{17} + k_1(M_{18} + M_{16}) + k_2(M_{19} + M_{15}) + k_3(M_{20} + M_{14}) + k_4(M_{21} + M_{13}) + k_5(M_{22} + M_{12}) + k_6(M_{23} + M_{11}) + k_7(M_{24} + M_{10}) + k_8(M_{25} + M_9)$$

$$= .1974(737) + .1747(782 + 667) + .1210(798 + 579) + .0655(782 + 484) + .0279(737 + 388) + .0092(667 + 299) + .0024(579 + 222) + .0005(484 + 158) + .0001(388 + 108)$$

$$= 690.7318 \quad (691)$$

Under the conditions stipulated, 691 fish will be expected to die on the 32nd day of the run.

It will be observed that as m increases the values of k_m become very small. It is perhaps permissible to ignore these, or better still add their value to smallest constant which might be significant. In this case there would be little error in adding k_7 and k_8 to k_6, giving the latter constant a value of .0030 instead of .0024.

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TABLE I

A THEORETICAL SALMON MIGRATION AND THE EFFECT OF TAGGING A CONSTANT NUMBER OF THE TAGGED PERCENTAGE IN THE STREAM

100 tagged per day for 20 days, 2000 fish in all

Day	Migrants per day	Total in stream	Tagged per day	% Tagged per day	Tagged to date	% Tagged to date
n	M_n	P_n	t_n	$\%t_n$	T_n	$\%T_n$
1	1	1				
2	3	4				
3	5	9				
4	9	18				
5	16	34				
6	27	61				
7	45	106				
8	71	177				
9	108	285				
10	158	443	100	63.3	100	22.6
11	222	665	100	45.0	200	30.1
12	299	964	100	33.4	300	31.1
13	388	1352	100	25.8	400	29.6
14	484	1836	100	20.7	500	27.2
15	579	2415	100	17.3	600	24.8
16	667	3082	100	15.0	700	22.7
17	737	3819	100	13.6	800	20.9
18	782	4601	100	12.8	900	19.6
19	798	5399	100	12.5	1000	18.5
20	782	6181	100	12.8	1100	17.8
21	737	6918	100	13.6	1200	17.3
22	667	7585	100	15.0	1300	17.1
23	579	8164	100	17.3	1400	17.1
24	484	8648	100	20.7	1500	17.3
25	388	9036	100	25.8	1600	17.7
26	299	9335	100	33.4	1700	18.2
27	222	9557	100	45.0	1800	18.8
28	158	9715	100	63.3	1900	19.6
29	108	9823	100	92.6	2000	20.4
30	71	9894				20.2
31	45	9939				20.1
32	27	9966				20.1
33	16	9982				20.0
34	9	9991				20.0
35	5	9996				20.0
36	3	9999				20.0
37	1	10000				20.0

TABLE II

THE TAGGED PERCENTAGES RESULTING IN THE STREAM WHEN TAGGING IS CARRIED ON OVER THE WHOLE OF THE RUN, OVER THE BEGINNING OF THE RUN, AND OVER THE LATTER HALF OF THE RUN

Day	Total in stream P_n	Percentage tagged to date: Throughout the run $\%T_n$	The first half of the run $\%T_{nb}$	The latter half of the run $\%T_{ne}$
1	1	100 per day for 20 days	100 per day for 10 days	100 per day for 10 days
2	4			
3	9			
4	18			
5	34			
6	61			
7	106			
8	177			
9	285			
10	443	22.6	22.6	
11	665	30.1	30.1	
12	964	31.1	31.1	
13	1352	29.6	29.6	
14	1836	27.2	27.2	
15	2415	24.8	24.8	
16	3082	22.7	22.7	
17	3819	20.9	20.9	
18	4601	19.6	19.6	
19	5399	18.5	18.5	
20	6181	17.8	16.2	1.8
21	6918	17.3	14.5	2.9
22	7585	17.1	13.2	4.0
23	8164	17.1	12.2	4.9
24	8648	17.3	11.6	5.8
25	9036	17.7	11.1	6.6
26	9335	18.2	10.7	7.5
27	9557	18.8	10.4	8.4
28	9715	19.6	10.3	9.3
29	9823	20.4	10.2	10.2
30	9894	20.2	10.1	10.1
31	9939	20.1	10.1	10.1
32	9966	20.1	10.0	10.0
33	9982	20.0	10.0	10.0
34	9991	20.0	10.0	10.0
35	9996	20.0	10.0	10.0
36	9999	20.0	10.0	10.0
37	10000	20.0	10.0	10.0

TABLE III

THE EFFECT OF A CONSTANT "STREAM LIFE" OF TEN DAYS UPON THE PERCENTAGES

Day	Total in Stream P_n	Total dead to date D_n	Number alive L_n	Tagged dead TD_n	% Tagged dead $\%TD_n$	Tagged alive TL_n	% Tagged alive $\%TL_n$
1	1		1				
2	4		4				
3	9		9				
4	18		18				
5	34		34				
6	61		61				
7	106		106				
8	177		177				
9	285		285				
10	443		443			100	22.6
11	665	1	664			200	30.2
12	964	4	960			300	31.2
13	1352	9	1343			400	29.8
14	1836	18	1818			500	27.5
15	2415	34	2381			600	25.2
16	3082	61	3021			700	23.2
17	3819	106	3713			800	21.5
18	4601	177	4424			900	20.4
19	5399	285	5114			1000	19.5
20	6181	443	5738	100	22.6	1000	17.4
21	6918	665	6253	200	30.1	1000	16.0
22	7585	964	6621	300	31.1	1000	15.1
23	8164	1352	6812	400	29.6	1000	14.6
24	8648	1836	6812	500	27.2	1000	14.6
25	9036	2415	6621	600	24.8	1000	15.1
26	9335	3082	6253	700	22.7	1000	16.0
27	9557	3819	5738	800	20.9	1000	17.4
28	9715	4601	5114	900	19.5	1000	19.5
29	9823	5399	4424	1000	18.5	1000	22.6
30	9894	6181	3713	1100	17.8	900	24.2
31	9939	6918	3021	1200	17.3	800	26.5
32	9966	7585	2381	1300	17.1	700	29.4
33	9982	8164	1818	1400	17.1	600	33.0
34	9991	8648	1343	1500	17.3	500	37.2
35	9996	9036	960	1600	17.7	400	41.7
36	9999	9335	664	1700	18.2	300	45.2
37	10000	9557	443	1800	18.8	200	45.2
38		9715	285	1900	19.6	100	35.1
39		9823	177	2000	20.4		0.0
40		9894	106		20.2		
41		9939	61		20.1		
42		9966	34		20.1		
43		9982	18		20.0		
44		9991	9		20.0		
45		9996	4		20.0		
46		9999	1		20.0		
47		10000	0		20.0		

TABLE III A

A COMPARISON OF THE PERCENTAGE MIGRANTS TAGGED WITH THE PERCENTAGE LIVE TAGGED AND THE PERCENTAGE DEAD TAGGED (CONSTANT STREAM LIFE)

Day n	% Migrants Tagged to Date $\%T_n$	% Live Tagged $\%TL_n$	% DEAD Tagged $\%TD_n$
9			
10	22.6	22.6	
11	30.1	30.2	
12	31.1	31.2	
13	29.6	29.8	
14	27.2	27.5	
15	24.8	25.2	
16	22.7	23.2	
17	20.9	21.5	
18	19.6	20.4	
19	18.5	19.5	
20	17.8	17.4	22.6
21	17.3	16.0	30.1
22	17.1	15.1	31.1
23	17.1	14.6	29.6
24	17.3	14.6	27.2
25	17.7	15.1	24.8
26	18.2	16.0	22.7
27	18.8	17.4	20.9
28	19.6	19.5	19.6
29	20.4	22.6	18.5
30	20.2	24.2	17.8
31	20.1	26.5	17.3
32	20.1	29.4	17.1
33	20.0	33.0	17.1
34	20.0	37.2	17.3
35	20.0	41.7	17.7
36	20.0	45.2	18.2
37	20.0	45.2	18.8
38	20.0	35.1	19.6
39	20.0	0.0	20.4
40	20.0	0.0	20.2
41	20.0		20.1
42	20.0		20.1
43	20.0		20.0
44	20.0		20.0
45	20.0		20.0
46	20.0		20.0
47	20.0		20.0

TABLE IV

THE EFFECT OF AN AVERAGE STREAM LIFE OF 10 DAYS
- STANDARD DEVIATION OF 1 DAY

Day n	Migrants to date P_n	Total deaths to date D_n	Total tagged dead TD_n	% tagged dead $\%TD_n$	Live L_n	Tagged live TL_n	% tagged live $\%TL_n$
1	1				1		
2	4				4		
3	9				9		
4	18				18		
5	34				34		
6	61				61		
7	106				106		
8	177				177		
9	285				285		
10	443	1			442	100	22.6
11	665	2			663	200	30.2
12	964	5			959	300	31.3
13	1352	11			1341	400	29.8
14	1836	22			1814	500	27.6
15	2415	40			2375	600	25.2
16	3082	71			3011	700	23.2
17	3819	120	1	.83	3699	799	21.6
18	4601	197	8	4.07	4404	892	20.2
19	5399	312	39	12.5	5087	961	18.9
20	6181	477	108	22.6	5704	992	17.4
21	6918	706	201	28.2	6212	999	16.1
22	7585	1011	300	29.7	6574	1000	15.2
23	8164	1403	400	28.4	6761	1000	14.8
24	8648	1887	500	26.5	6761	1000	14.8
25	9036	2462	600	24.3	6574	1000	15.2
26	9335	3119	700	22.4	6216	1000	16.1
27	9557	3843	800	20.8	5714	1000	17.5
28	9715	4609	900	19.5	5106	1000	19.5
29	9823	5391	1000	18.5	4432	1000	22.6
30	9894	6157	1100	17.9	3737	900	24.1
31	9939	6881	1200	17.5	3058	800	26.2
32	9966	7538	1300	17.3	2428	700	28.8
33	9982	8113	1400	17.4	1869	600	32.1
34	9991	8597	1500	17.5	1394	500	36.9
35	9996	8989	1600	17.8	1007	400	39.9
36	9999	9294	1700	18.3	705	300	42.5
37	10000	9523	1799	18.9	477	201	42.2
38		9688	1892	19.6	312	108	34.6
39		9803	1961	19.9	197	39	19.8
40		9880	1992	20.2	120	8	6.6
41		9929	1999	20.2	71	1	1.4
42		9960	2000	20.0	40	0	0.0
43		9978		20.0	22		
44		9989		20.0	11		
45		9995		20.0	5		
46		9998		20.0	2		
47		9999		20.0	1		
48		10000		20.0	0		

TABLE V

THE PERCENTAGES RESULTING FROM AN AVERAGE STREAM LIFE OF TEN DAYS WITH A STANDARD DEVIATION OF 1

Day n	% Migrants Tagged $\%T_n$	Live Percentage $\%TL_n$		Dead Percentage $\%TD_n$	
9					
10	22.6	22.6	(22.6)		
11	30.1	30.2	(30.2)		
12	31.1	31.3	(31.2)		
13	29.6	29.8	(29.8)		
14	27.2	27.6	(27.5)		
15	24.8	25.2	(25.2)		
16	22.7	23.2	(23.2)		
17	20.9	21.6	(21.5)	.8	(0.0)
18	19.6	20.2	(20.4)	4.1	(0.0)
19	18.5	18.9	(19.5)	12.5	(0.0)
20	17.8	17.4	(17.4)	22.6	(22.6)
21	17.3	16.1	(16.0)	28.2	(30.1)
22	17.1	15.2	(15.1)	29.7	(31.1)
23	17.1	14.8	(14.6)	28.4	(29.6)
24	17.3	14.8	(14.6)	26.5	(27.2)
25	17.7	15.2	(15.1)	24.3	(24.8)
26	18.2	16.1	(16.0)	22.4	(22.7)
27	18.8	17.5	(17.4)	20.8	(20.9)
28	19.6	19.5	(19.5)	19.5	(19.6)
29	20.4	22.6	(22.6)	18.5	(18.5)
30	20.2	24.1	(24.2)	17.9	(17.8)
31	20.1	26.2	(26.5)	17.5	(17.3)
32	20.1	28.8	(29.4)	17.3	(17.1)
33	20.0	32.1	(33.0)	17.4	(17.1)
34	20.0	36.9	(37.2)	17.5	(17.3)
35	20.0	39.9	(41.7)	17.8	(17.7)
36	20.0	42.5	(45.2)	18.3	(18.2)
37	20.0	42.2	(45.2)	18.9	(18.8)
38	20.0	34.6	(35.1)	19.6	(19.6)
39	20.0	19.8	(0.0)	19.9	(20.4)
40	20.0	6.6	(0.0)	20.2	(20.2)
41	20.0	1.4	(0.0)	20.2	(20.1)
42	20.0	0.0	(0.0	20.0	(20.1)
43	20.0			20.0	(20.0)
44	20.0			20.0	(20.0)
45	20.0			20.0	(20.0)
46	20.0			20.0	(20.0)
47	20.0			20.0	(20.0)
48	20.0			20.0	(20.0)
49	20.0			20.0	(20.0)

TABLE VI

THE PERCENTAGES RESULTING FROM AN AVERAGE STREAM LIFE OF TEN DAYS WITH A STANDARD DEVIATION OF 3

Day	% Migrants Tagged $\%T_n$	Live Percentage $\%TL_n$	Dead Percentage $\%TD_n$
9			
10	22.6	22.9	
11	30.1	30.7	0.0
12	31.1	31.8	4.3
13	29.6	30.2	7.7
14	27.2	27.9	9.4
15	24.8	25.4	12.6
16	22.7	23.1	15.6
17	20.9	21.1	18.5
18	19.6	19.4	21.2
19	18.5	18.0	23.0
20	17.8	17.6	24.3
21	17.3	16.1	24.7
22	17.1	15.6	24.5
23	17.1	15.3	23.9
24	17.3	15.4	23.0
25	17.7	15.9	22.0
26	18.2	16.7	21.0
27	18.8	17.9	20.1
28	19.6	19.8	19.3
29	20.4	22.3	18.4
30	20.2	23.2	18.3
31	20.1	24.4	18.0
32	20.1	25.9	17.9
33	20.0	27.6	17.9
34	20.0	29.4	18.1
35	20.0	31.3	18.3
36	20.0	32.7	18.6
37	20.0	33.8	18.9
38	20.0	34.0	19.2
39	20.0	33.1	19.5
40	20.0	31.3	19.7
41	20.0	28.1	19.8
42	20.0	24.3	20.0
43	20.0	20.3	20.0
44	20.0	15.4	20.0
45	20.0	13.0	20.0
46	20.0	7.7	20.0
47	20.0	0.0	20.0
48	20.0		20.0
49	20.0		20.0
50	20.0		20.0
51	20.0		20.0

TABLE VII

THE PERCENTAGES RESULTING FROM AN AVERAGE STREAM LIFE OF FIFTEEN DAYS WITH A STANDARD DEVIATION OF 3

Day n	% Migrants Tagged $\%T_n$	Live Percentage $\%TL_n$	Dead Percentage $\%TD_n$
9			
10	22.6	22.6	
11	30.1	30.1	
12	31.1	31.2	
13	29.6	29.6	
14	27.2	27.3	
15	24.8	24.9	
16	22.7	22.8	0.0
17	20.9	21.0	4.3
18	19.6	19.7	7.7
19	18.5	18.6	9.4
20	17.8	17.9	12.6
21	17.3	17.4	15.6
22	17.1	17.1	18.5
23	17.1	17.1	21.2
24	17.3	17.0	23.0
25	17.7	17.1	24.3
26	18.2	17.4	24.7
27	18.8	17.9	24.5
28	19.6	18.6	23.9
29	20.4	19.6	23.0
30	20.2	19.5	22.0
31	20.1	19.7	21.0
32	20.1	20.1	20.1
33	20.0	20.7	19.3
34	20.0	21.5	18.4
35	20.0	22.6	18.3
36	20.0	24.0	18.0
37	20.0	25.6	17.9
38	20.0	27.4	17.9
39	20.0	29.3	18.1
40	20.0	31.2	18.3
41	20.0	32.8	18.6
42	20.0	33.8	18.9
43	20.0	34.0	19.2
44	20.0	33.1	19.5
45	20.0	31.3	19.7
46	20.0	28.1	19.8
47	20.0	24.3	20.0
48	20.0	20.3	20.0
49	20.0	15.4	20.0
50	20.0	13.0	20.0
51	20.0	7.7	20.0
52	20.0	0.0	20.0
53	20.0	0.0	20.0
54	20.0	0.0	20.0
55	20.0	0.0	20.0
56	20.0	0.0	20.0