SOME ASPECTS OF ENVIRONMENTAL VARIABILITY IN RELATION TO STOCK RECRUITMENT SYSTEMS by

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## ABSTRACT

For a variety of stock-recruit systems in which environmental variability is simulated by random normal deviates used as multipliers or divisors, Ricker (1958) and Larkin and Ricker (1964) demonstrated the benefits of complete`stabilization of escapement as opposed to removal of a fixed proportion of the stock each year. Part I is primarily concerned with the response of these same systems to a pattern of stochastic modification which is more regular in form, a pattern such as might be imagined to result from longterm trends in environmental conditions. In addition, some mathematical properties of these systems are discussed.

Part II considers the stock-recruit relationship from a more reductionist or mechanistic point of view. Evidence for differential utilization of spawning areas is presented and spawner distributions in three different environments are compared. These results are discussed in terms of their relevance to existing stock-recruit theory. Also, observations on egg retention and social facilitation are presented.

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## GENERAL INTRODUCTION

The establishment of levels of exploitation consistent with optimal utilization of stocks of commercially important species remains as a primary focus of contemporary fisheries biology. This problem of maximum sustained yield is, in essence, a problem of population ecology, and it is not surprising therefore that fisheries and population theory have followed similar, though distinguishable, courses of evolution. Aside from the fact that fisheries biology is concerned with fishes, it is best characterized by its pragmatic, if perhaps inelegant, nature. Thus, many management programs are largely concerned with the collection of catch and escapement statistics which, when added to previous records, should provide some insight into optimal levels of escapement. Given enough of this type of information, one has a reasonable expectation of successful management, provided that the variation in recruitment of a stock of a given size is not excessive. Unfortunately, the stock-recruit data which is now available indicates that this variation is considerable and therefore historical approaches can only meet with limited success. Thus, the development of better management programs would seem dependent on the incorporation of recruitment variation into management theory and a corresponding analysis of the sources of this variation.

Ricker (1958) showed the initial interest in this problem, and developed a conceptual framework and numerical model which simulated the behaviour of stock-recruit systems when exposed to randomly-fluctuating environments. The basic model was derived earlier (1954) from a consideration of the effects
of predation and cannibalism on numbers, the result of which was the wellknown stock-recruit or reproduction curves. Larkin and Ricker (1964) confirmed earlier conclusions concerning the behavior of the se systems by the use of computer techniques.

The reproduction curve is dome-shaped which, in theory, results from an increase in the number of predators to degree such that the absolute number of prey survivors is decreased. Though one may justifiably object to predation as the controlling mechanism for some specific situations, the dome-shaped curve seems to be a reasonable fit for many fisheries (e.g, Garrod, 1966), and may be taken as one general form of parent-progeny relationships given density dependent mechanisms of regulation.

The bedraggled debate of density dependent versus density independent mortality which occupied much of the ecologists' time, never became a critical problem in fisheries biology. It was clear from the outset that weather and climate played an important role in influencing production of most stocks. Consequently, the addition of stochastic variation to a system which was basically density dependent in form, was not considered as an outrageous distortion of reality.

At this level of investigation one further attribute of the system was in need of study, namely, the effects of long term trends in density independent mortality factors. Many environmental variables; e.g., current patterns, temperatures, etc., seem to follow a more regular pattern of variation than a random model would suggest. Thus, it was of interest to determine if the addition of the se long term phenomena would markedly affect previous con-
clusions concerning the gross behavior of these systems. This discussion comprises Part I of the following thesis.

While the above discussions provide a useful framework for the formulation of general management policy, their yalue is limited for specific situations. One cannot, for example, determine the carrying capacity of a given stream and consequently a stock unit cannot be defined. Thus, a different level of investigation is required and a preliminary study consistent with this approach is described in Part II, which discusses some aspects of the spawning behavior of sockeye salmon, Oncorhynchus nerka.

At the specific level one must investigate those aspects of the population and environment relevant to the definition of carrying capacity. One need ask, for example, which areas of a stream are suitable for spawning, whether qualitative differences exist in the areas which are utilized, which factors influence nearest neighbor distances, and others.

The particular problem investigated in Part II is, in reality, pertinent to both levels of investigation. At the general level it considers the effect of environmental variability operating in a density dependent manner while, at the specific level it presents evidence for the mechanism of site selection and the ability of spawners to distinguish habitats of different quality.

[^0]The Basic Systems

The curves used in the present simulations are identical to those described by Ricker (1958). Curves A, B and C are members of the exponential family $\quad Z_{t}=w e^{a}(1-w)$ where

$$
\begin{aligned}
& \mathrm{Z}_{\mathrm{t}}=\text { production in year } \mathrm{t} \\
& \mathrm{w}=\text { spawning stock size }
\end{aligned}
$$

"a" is a parameter determining maximum production and, consequently, the shape of the reproduction curve. For curves $A, B$ and $C$ the parameter "a" assumes a value of $1.000,2.000$, and 2.678 respectively (Fig. 1).

Curve A describes the situation where maximum production occurs at the equilibrium position $w=1.000=Z_{\max }$. Displacements to the left of equilibrium ( $\mathrm{w}<1.0$ ) result in a "climbing" of the a scending limb of the curve. Displacements to the right of equilibrium ( $w>1.0$ ) result in an immediate compensation, the stock being depressed to a level below equilibrium density to which it gradually returns.

Curve B. In this case the maximum production is associated with a stock den sity of approximately one-third that of equilibrium density. Comparing Curve $B$ with $A$, production per spawner at any given stock density is greater in Curve $B$ for $0<w<1$, and smaller for

> All values are expressed in stock units, where one stock unit is the number of individuals associated with the unexploited equilibrium position.


Figure 1. Stock recruitment curves A, B, C of Ricker (1958) in which $z=$ we $^{\mathrm{a}(\mathrm{l}-\mathrm{w})}$ for $\mathrm{a}=1.000,2.000$, and 2.678 respectively.
$w>$. Arbitrary displacement from equilibrium results in the production of a damped oscillation of abundance which returns the stock to the equilibrium position.

Curve $C$ is a more extreme version of $B$ in that production rates are greater and compensation is more severe. The system is unstable in the sense that displacements from the equilibrium position result in the production of permanent oscillations and there is no tendency for the stock to return to the equilibrium of $w=1$.

Curves F, G and H (Fig. 2) each belong to a different family of curves. Curve $H$ represents the converted Beverton-Holt relationship as described in Ricker (1958), while Curves $F$ and $G$ are contrived equations representative of the remaining types of stock-recruit systems.

Curve F is characterized by an ascending limb which conforms to Curve $B$ for $0<Z<1$, coupled with an asymptotic part which maintains the stock at the equilibrium density for all other values of. w.

Curve $G$ may be considered as a representative of systems influenced by depensatory mortality factors, i.e., factors which are proportionately more severe at lower stock densities. The curve is identical to $A$ except for $w<0.4$, in which case production is calculated by $Z=w e^{.433 w}$.


Figure 2. Stock recruitment curves F, G, H of Ricker (1958). See text for explanation.

Simulation Procedure

The procedure of simulation was as described by Larkin and Ricker (1964) with modifications for the long-term effects. Representing long-term fluctuations by a sin wave, each generation the value was assessed of

$$
Q=P \underline{\sin }\left[\frac{m}{\ell} \cdot 2 \pi\right]
$$

where $m$ is the year in a cycle and $\ell$ is the cycle length. Thus, for the second year of a six-year cycle $Q$ is the sin of $\frac{2}{6}(2 \pi)$. This is scales by the multiplier, $P$, to define amplitude, augmented by one, and used as a multiplier or divisor depending on sign.

Depending upon what is envisaged, there are various ways in which the sin function might be coupled with random normal deviates in the simulation of long-term fluctuations with superimposed random fluctuations. In addition to using either effect separately, two alternatives were provided for combined effects:
(1) Sin plus random - the value of $R$ was added to the value of a random normal deviate, after each was scaled to a desired order of magnitude. Then the absolute value was augmented by one and, depending on the sign, used as a multiplier or divisor. This representation might be appropriate for a situation in which both effects were visualized as occurring in the same environment.
(2) Sin times random - the value of $R$ was scaled; augmented by one, used as a multiplier or divisor, then was followed by a random normal deviate used in the same way. This type of simulation might be taken to represent the situation in which the effects were occurring in different environments -- say, for example, long-termeffects in the sea; short-term random effects in freshwater.

Algebraically, the sin wave modified system may be written

$$
\begin{aligned}
Z_{t} & =\left[w_{t} e^{a\left(1-w_{t}\right)}\left(1+P \underline{\sin }\left(\frac{m_{t} 2 \pi}{\ell}\right)\right)\right] ; m=1, \ldots \frac{\ell}{2} ; \sin \left(\frac{m_{t} 2 \pi}{\ell}\right) \geq 0 \\
& =\left[w_{t} e^{a\left(1-w_{t}\right)}\left(\frac{1}{1+P \left\lvert\, \frac{\sin \frac{m_{t} 2 \pi}{\ell}}{\ell}\right.}\right)\right] ; \quad m=\frac{\ell}{2}, \ldots l ; \sin \left(\frac{m_{t} 2 \pi}{\ell}\right) \leq 0
\end{aligned}
$$

where $Z_{t}=$ production in year $t$
$\mathrm{w}_{\mathrm{t}}=$ spawning stock size in year t
$m=y e a r$ in sequence of cycle (i.e., $m$ varies from 1 to 6 in each 6-year cycle)
$\ell \quad=$ length of cycle in years
$\mathrm{P}=$ scaling factor

For a fixed rate of fishing

$$
\begin{aligned}
& C_{t}=F Z_{t} \\
& w_{t+1}=(1-F) Z_{t}
\end{aligned}
$$

where $C_{t}=$ catch in year $t$

$$
F=\text { fixed rate of fishing }
$$

For complete stabilization of escapement:

$$
\begin{array}{rlrl}
C_{t} & =Z_{t}-w_{\text {II }} & & Z_{t}>w_{\text {II }} \\
& =0 & & Z_{t}<w_{m} \\
Z_{t+1} & =w_{m} e^{a\left(l-w_{m}\right)} & & \\
Z_{t}-w_{m}>0
\end{array}
$$

where $\mathrm{w}_{\mathrm{m}}=$ escapement associated with maximum equilibrium catch (m.e.c.)

The computer simulations conducted were all run for 200 simulated years for all combinations of:
(1) four long-term cycle lengths: 6, 11, 12, 24 years.
(2) Six stock recruit curves: A, B, C, F, G, H.
(3) Two levels of random effects.
(4) Two levels of long-term effects.
(5) Three patterns of fishing: fixed percentage, partial and complete stabilization of escapement (Ricker 1958).
(6) Three patterns of environmental effects: sin effects only, sin plus random, sin times random.

## Deterministic Sin Effects

In the simulations using the sin wave modifier and a fixed percentage fishery, the catch pattern was initially one of erratic changes in abundance. Within a few generations a repeatable pattern of catch and escapement was evident, the values oscillating in phase with the sin modifier but at lower amplitudes. (The initial period of instability was a result of starting the simulations with the stock at its equilibrium density ( $w=1$ ). Two levels of amplitude ( $P=.5, P=2.0$ ) were used in conjunction with four cycle lengths and the resulting mean catch and escapement values for two hundred simulated years are summarized in Table II, which can be compared with the simple deterministic case (Table I).

For curves A, B and C, the tabulated escapement values differ only slightly from the deterministic values associated with maximum equilibrium catch (m.e.c.)* The differences are attributable to the initial period of instability and the fixed 200 year period of simulation which did not always end on year completing a cycle.

For curve $F$, the mean catch is slightly less than the deterministic model and curve G goes to extinction under conditions of fixed percentage

[^1]TABLE I. Mean catch and escapement in deterministic models of six stock-recruit relationships.

| CURVE | CATCH | ESCAPEMENT |
| :---: | :---: | :---: |
| A | 0.330 | 0.433 |
| B | 0.935 | 0.361 |
| C | 1.656 | 0.314 |
| F | 0.760 | 0.210 |
| G | 0.330 | 0.433 |
| H | 0.520 | 0.240 |

TABLE II. Mean catch and escapement in 200 year simulations of fixed percentage exploitation for each of six reproductive curve systems, with long-term environmental fluctuations, represented by sin modifiers, at cycle lengths of 6, 11,12 and 24 years, and at two levels of amplitude. See text for explanation.

| CYCLE |  | 6 years |  | 11 years |  | 12 years |  | 24 years |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Curve | Level | Catch | Escap. | Catch | Escap. | Catch | Escap. | Catch | Escap. |
| A | 1 | . 333 | . 436 | . 333 | . 436 | . 336 | . 440 | . 340 | . 445 |
|  | 2 | . 338 | . 442 | . 338 | . 442 | . 346 | . 453 | . 358 | . 469 |
| B | 1. | . 937 | . 360 | . 936 | . 360 | . 940 | . 362 | . 949 | . 365 |
|  | 2 | . 948 | . 365 | . 945 | . 364 | . 956 | . 368 | . 981 | . 377 |
| C | 1 | 1.657 | . 313 | 1.656 | . 313 | 1.660 | . 314 | 1.676 | . 316 |
|  | 2 | 1.673 | . 316 | 1.673 | . 316 | 1.684 | . 318 | 1.723 | . 325 |
| F | 1 | . 739 | . 204 | . 728 | . 201 | . 731 | . 202 | . 724 | . 200 |
|  | 2 | . 746 | . 206 | .711. | . 197 | . 742 | . 205 | . 750 | . 208 |
| G* | 1 | . 013 | . 018 | . 019 | . 024 | . 020 | . 026 | . 037 | . 049 |
|  | 2 | . 014 | . 099 | . 026 | . 034 | . 028 | . 037 | . 057 | . 075 |
| H | 1 | . 543 | . 250 | . 550 | . 254 | . 553 | . 255 | . 562 | . 259 |
|  | 2 | . 686 | . 317 | . 752 | . 347 | . 766 | . 354 | . 823 | . 380 |

[^2]exploitation. Curve $H$ is the only system which responds favorably to the combination of sin modification and fixed percentage exploitation. Curve $H$ is similar to $A$ in that maximum production is associated with a stock size much larger than the stock size which provides maximum catch, but differs in that there is no compensation at the higher stock densities. Since the catch is proportional to production in the fixed percentage fishery, gains are to be expected.

Table III summarizes the results of simulations using the same amplitude and cycle length modifications but with a stabilized fishery. Comparing the se results with Table $I$, it is apparent that a stabilized fishery results in an increased yield in all cases.

The Effect of Cycle Length and Amplitude Modifications

In the previous section it was shown that the mean catches for curves $A, B$ and $C$ are unchanged with the combination of sin modification and fixed percentage exploitation. Nevertheless, the pattern of the catch responds to both changes in cycle length and amplitude.

Figure 3 compares, for curve C, the pattern of a 12-year cycle with that of a 24-year cycle, while Figure 4 shows the effect of varying the amplitude of the sin modifier. For the fixed percentage exploitation, variation in cycle length has almost no effect on the standard deviation of catch ( $\sigma_{c}$ ), and serves only to increase the length of the series of


Figure 3. Catch in deterministic simulation of a fixed percentage fishery on curve C systems with 12 - and 24 -year $\sin$ wave cycles for amplitude scaling factor $P=2.0$.

TABLE III. Mean catch and escapement in 200 year simulations of a fishery with completely stabilized escapement for each of six reproductive curve systems, when long-term environmental fluctuations are represented by sin modifiers, at cycle lengths of 6, 11, 12 and 24 years and at two levels of amplitude. See text for explanation.

| CY CLE |  | 6 years |  | 11 years |  | 12 years |  | 24 years |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Curve | Level | Catch | Escap. | Catch | Escap. | Catch | Escap. | Catch | Escap. |
| A | $1$ | . 368 | . 433 | . 367 | . 433 | $.369$ | . 433 | . 375 | . 433 |
|  | 2 | . 624 | . 370 | . 643 | . 351 | $.649$ | . 348 | . 686 | . 330 |
| B | 1 | . 994 | . 361 | . 994 | . 361 | . 996 | . 361 | 1.007 | . 361 |
|  | 2 | 1.422 | . 361 | 1.436 | . 361 | 1.442 | . 361 | 1.482 | . 361 |
| C | 1 | 1.744 | . 314 | 1.744 | :314 | 1.748 | . 314 | 1.765 | . 314 |
|  | 2 | 2.392 | . 314 | 2. 414 | . 314 | 2.424 | . 314 | 2.487 | . 314 |
| F | 1 | . 837 | . 210 | . 837 | . 210 | . 839 | . 210 | . 847 | . 210 |
|  | 2 | 1.169 | . 210 | 1.179 | . 210 | 1.184 | . 210 | 1.214 | . 210 |
| G | 1 | . 368 | . 433 | . 367 | . 433 | . 369 | . 433 | . 375 | . 433 |
|  | 2 | . 394 | . 322 | . 312 | . 250 | . 311 | . 243 | . 236 | . 174 |
| H | 1 | . 557 | . 240 | . 556 | . 240 | . 558 | . 240 | . 564 | . 240 |
|  | 2 | . 811 | . 240 | . 817 | . 240 | . 821 | . 240 | . 843 | . 240 |



Figure 4. Catch in deterministic simulation of a fixed percentage fishery on a curve C system with 12 -year sin cycle for amplitude scaling factor at two levels, $P=0.5$ and $\mathrm{P}=2.0$.
good and poor catches. As might be expected, $\sigma_{c}$ responds to amplitude modifications, increasing as the amplitude becomes larger.

For the stabilized fishery two slightly different catch patterns were evident. - In the systems which had a relatively high production per spawner at low stock densities (Curves $B$ and $C$ ), the production never dropped below $w_{\mathbb{m}}$ and consequently the stocks always reproduced at an optimal rate (Fig. 5). In the less responsive systems (Curves A and G) the catch pattern is typically a series of relatively good catches followed by a series of zero catches, the length of the series increasing as a function of the amplitude of the modifiers.

Stochastic Modifications

The deterministic sin modifications described above were stochastisized by either additive or multiplicative superimposition of random normal deviates. Algebraically, the modifications ( $R$ ) may be represented as:

## Additive Effects

$$
\begin{aligned}
R & =(1+Q+R N D) & & \text { for } Q+R N D>0 \\
& =\left(\frac{1}{1+Q+R N D}\right) & & \text { for } Q+R N D<0
\end{aligned}
$$



Figure 5. Catch in deterministic simulation of a completely stabilized fishery on curve $A$ and curve $B$ systems with a 12 -year sin cycle and amplitude scaling factor $P=2.0$.

Multiplicative Effects

$$
\begin{array}{ll}
=(1+Q)(1+R N D) & \text { for } Q>0, \text { RND }>0 \\
=(1+Q)\left(\frac{1}{1+R N D}\right) & \text { for } Q>0, \quad \text { RND }<0 \\
=\left(\frac{1}{1+Q}\right)(1+R N D) & \text { for } Q<0, \quad \text { RND }<0 \\
=\left(\frac{1}{1+Q}\right)\left(\frac{1}{1+R N D}\right) & \text { for } Q<0, \quad R N D<0
\end{array}
$$

where $Q=$ scaled sin modifier
RND $=$ scaled random modifier

In general, the addition of the stochastic modifiers serves only to accentuate the basic patterns described for the deterministic sin effects, the frequency of zero catches becoming greater for the stabilized fishery, and $\sigma_{0}$ becoming larger for fixed percentage exploitation. The catches for the stabilized fishery are larger as a function of $\sigma_{c}$ while no changes are observed for fixed percentage exploitation.

The Nature of the Modifications

From the preceding results three general conclusions pertaining to curves $A, B$ and $C$ are evident.
(1) For a stabilized fishery, an increase in yield over the deterministic maximum is apparent for all sy stems subjected to stochastic modifications, and this increase is commensurate with the variance of the modifiers.
(2) The addition of stochastic modifiers to a system undergoing fixed percentage exploitation has no effect on the mean catch, its value remaining the same as the deterministic maximum.
(3) The pattern of modification (i.e., sinoidal, random, etc.) is unimportant relative to the variance of the modifications.

The increased yields for the stabilized fishery can, in a sense, be attributed to the technique of stochastic modification. Augmenting by one the absolute value of the random variate and subsequently using it as a multiplier or divisor, has the effect of multiplying production by an average modifier which is greater than 1 . Algebraically, if $X$ is a symmetrically distributed variable with mean 0 , the frequency of a particular positive variate $X_{1}$ is the same as the frequency of the corresponding negative value. The appropriate modifiers would be $1+X_{1}$ for the former and $\frac{1}{1+\left|X_{1}\right|}$ for the latter.

It is easily demonstrated that the mean of a pair of the se modifiers is greater than l, from which it follows that the mean of a series of the se modifiers $(\bar{R})$ is also.greater than l. For example, if $X_{1}=+1$, the corresponding multiplier $=2$, and for $X_{1}=-1$, the appropriate multiplier $=\frac{1}{2}$. Furthermore, since $(1+X)+\left(\frac{1}{1+|X|}\right)$ is 2
an increasing function of $X$, and since increasing the standard deviation $\left(\sigma_{x}\right)$ results in the more frequent occurrence of large values, it follows that the mean modifier $\overline{\mathrm{R}}$ will also increase as a function of $\sigma_{\mathrm{x}}$

Thus, for a stabilized fishery

$$
\bar{c}=\left[w_{m} e^{a\left(l-w_{m}\right)}\right] \bar{R}-w_{m} \quad \text { for } Z_{t} \geq w_{m}
$$

where $\overline{\mathrm{C}}=$ mean catch
$\mathrm{w}_{\mathrm{m}}=$ escapement associated with m.e.c.
$\bar{C}$, then, is a linear increasing function of $\bar{R}$.

The case of the fixed percentage fishery is somewhat less straightforward. For curves $A, B$ and $C$, average production per spawner is higher than the deterministic case, for the same reason given in the preceding paragraph. However, the mean catch is virtually identical to the deterministic maximum.

The sufficient conditions necessary for this result are demonstrable algebraically. For a fixed percentage fishery

$$
c_{t}=\left[w_{t} e^{a\left(l-w_{t}\right)}\right][R][F]
$$

where $c_{t}$ catch in generation $t$, $w_{t}$ spawning stock in generation $t, R$ stochastic modifier, and $F$ exploitation rate appropriate for m.e.c. ( (1- $\left.e^{-a\left(l-w_{m}\right)}\right)$. Substituting the expression for $F$ we have

$$
c_{t}=\left[w_{t} e^{a\left(1-w_{t}\right)}-w_{t} e^{a\left(w_{m}-w_{t}\right)}\right][R] .
$$

Harvesting at the equilibrium rate implies that $\bar{w}_{t}=w_{m}$. Substituting $w_{m}$ for $w_{t}$ in the expression for catch, the expected catch in a time period becomes

$$
c_{t}=R_{t} w_{m} e^{a\left(1-w_{m}\right)}-R_{t} w_{m}
$$

Because $R_{t} w_{m}$ is the escapement, the expected catch in period $(t+1)$ is

$$
c_{t+1}=R_{t+1} R_{t} w_{a} e^{a\left(1-R_{t} w_{m}\right)}-R_{t+1} w_{m}
$$

and in $(t+2)$ is

$$
c_{t+2}=R_{t+2} R_{t+1} R_{t} w_{n} e^{a\left(l-R_{t+1} R_{t} w_{a}\right)}-R_{t+2^{w_{m}}}
$$

The successive product of $R_{t+i}(i=1, n)$ is $l$, and ignoring the value of the last modifier $R_{t=n^{\prime}}$ it is apparent that

$$
\bar{c}=w_{m} e^{a\left(l-w_{\mathrm{n}}\right)}-w_{\mathrm{m}}
$$

which is the deterministic maximum.

Biologically, the mathematics imply that the production from any given number of spawners exposed to a varying environment will, on average, be larger than if conditions were constant at mean value. In the stabilized fishery this gain in production is reflected by increased yields, whereas in the fixed percentage fishery any gain is eliminated by the subsequent compensatory response.

Because the standard deviation of catch $\left(\sigma_{c}\right)$ and mean catch ( $\bar{c}$ ) are both increasing functions of $\bar{R}, \bar{c}$ and $\sigma_{c}$ are correlated. This relationship provides a means of determining, in the absence of information concerning the exact shape of a reproduction curve, whether a particular escapement is appropriate for m.e.c. By expressing $\bar{c}$ in stock units for a series of escapements of approximately the same size, it may be assumed that variations in the resultant catch may be attributed to environmental factors acting independently of the density of
the stock. Since $\sigma_{c}$ and $\bar{c}$ are unique for a given optimal escapement and curve type, (Fig. 6), it is possible to obtain a deterministic value of "a" associated with the particular $\bar{c}$ and $\sigma_{c}$ considered. Having an estimate of "a", solving for $w_{m}$ the expression

$$
-a w_{m} e^{-a\left(1-w_{m}\right)}+e^{a\left(1-w_{m}\right)}-1=0
$$

and comparing this value to the actual escapement, provides the check. If they are identical, it may be concluded that m.e.c. is being obtained. Harvesting at levels other than m.e.c. results in a decrease of $\bar{c}$ which will cause the theoretical and actual escapement values to differ.

## Discussion

The superimposition of simulated long-term environmental effects on stock recruit systems does not alter the general conclusions of Ricker (1958). Environmental variability, whether of a random or regular nature, results in benefits from complete stabilization of escapement and, the greater the . variability, the greater the benefits. Benefits in yield are obtained from the combination of stochastic variability with completely stabilized escapements, the size of the benefit being an increasing function of the variance of the modifiers.

This conclusion in large part hinges on the validity of the assumptions implicit in the procedure of simulating environmental effects by using multipliers or divisors of production. It might be more reasonable to suppose that a stock at high density would be more susceptible to harmful environmental effects (such as low water levels for salmon). In such a situation the scaling


Figure 6. Relationship between mean catch ( $\bar{c}$ ) and standard deviation of catch ( $\sigma_{c}$ ) in completely stabilized fisheries for 200 year simulations for curves $A, B$, and $C$ for which environmental effects at various levels were simulated by scaled random normal deviates used in the method of Ricker (1958).
factor for environmental effects might be made larger at higher densities. A great many techniques might be contrived to approximate whatever was envisaged. However, there is relatively little information on the mechanisms by which environmental factors influence production at various stock levels. It is also not known that the values of relevant environmental variables are distributed in the special pattern of Ricker's system (it is to be noted that the distribution of random normal deviates augmented by one as multipliers and divisors is not $\log$ normal). Further understanding of stock recruit systems, as influenced by environmental fluctuations, probably depends primarily on more detailed knowledge of the mechanisms by which environmental factors influence production at various stock sizes.

## PART II

```
Introduction
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In a series of papers concerned with the techniques of harvesting commercial stocks subjected to various forms and levels of environmental variability, Ricker (1958), Larkin and Ricker (1964) and Tautz, Larkin and Ricker (1969) have demonstrated mathematically the gains in yield associated with maintaining a constant escapement. Tautz, et al., showed that the method used to introduce stochastic variability had the effect of increasing average production per spawner. This, combined with the lack of severe compensatory mortality (because stocks were not allowed to reach high density conditions) resulted in the increased yields observed in simulation studies. Thus, for a given deterministic relationship, the increase in yield was found to be some increasing function of the variance of the stochastic modifications.

These conclusions are necessarily the product of a model in which specific assumptions have been made with respect to the representation of density dependent processes and the external stochastic variability associated with them. Because they are of some importance in the development of management policy, it is useful to consider whether they are general for mechanisms. other than those envisaged by Ricker in his development of the model.

Data which have recently been collected for the Skeena River sockeye suggest that highest recruitment rates are associated with intermediate levels
of escapement (I.S. Todd, pers.comm.). Thus, the dome-shaped reproduction curve would seem to be a better average relationship for salmon than the asymptotic form suggested by Beverton and Holt.

In the existing model, however, the meaning of the deterministic relationship is not explicitly stated. It is generally assumed that the curve(s) represent the relationship of stock to recruitment in the absence of environmental variability, and this in turn provides the basis for the concepts of "equilibrium density" and "stock unit." However, by assuming that stocks are buffered against detrimental environmental change, the average recruitment curve in the stochastic version is different from the deterministic form (Fig. 7), with the result that average equilibrium density (i.e., the intersection of the recruitment curve and the replacement line) is greater than one stock unit. In other words, although the deterministic curve may describe the behavior of a stock recruitment system for a particular set of environmental conditions, (i.e., average conditions) it does not necessarily follow that the same curve will be evident when the environment is allowed to vary about that average condition.

Another feature of the existing model which may require modification, is the complete separation of density dependent and density independent mortality. At present, the degree of compensatory mortality is assumed to be only a function of the difference between the stock size and equilibrium density, a constant. In other words, the term $e^{a(l-w)}$ in Ricker (1958), Larkin and Ricker (1964) and Tautz, et al., (1969), is independent of any


Figure 7. Stock recruitment curve A and average curve when the system is exposed to stochastic variation $A^{\prime}$.
variable environmental influence, and consequently no provision would seem to be made for environmental changes to operate in a density dependent manner. Thus, the system now envisaged is one in which the carrying capacity is considered to be a random variable; that is, equilibrium density changes from year to year and the compensatory response of the stock is in relation to that particular condition rather than to an average value.

Since, for most commercially important species, compensation is assumed to occur in the reproductive and early stages of the life history, it was felt that the above condition could be best demonstrated by examining the mechanisms associated with spawning and survival of fry. This, then, would allow one to hypothesize the nature of the curve relating survival of fry (production) to stock size, and by an understanding of the relevant mechanisms, to suggest the nature of the variability about that curve. Furthermore, a stock recruit curve would be suggested from this relationship, if one assumes that the number of recruits is some constant proportion of the number of fry, i.e., that the density dependent effects are confined to a life history stage for which the carrying capacity of the associated environment is small, relative to the lake and oceanic life history stages. This is, to some degree, er roneous and it would be surprising indeed if recruitment was found to be a constant proportion of the number of fry produced. However, for some situations (e.g., Skeena River) it serves as a reasonable approximation. Even if it were shown that limitation was a property of the lake and/or ocean environments, the above relationship would remain as an important management tool since fry production must still be determined so as to optimize the number of individuals
entering the limiting life history stage.

Specifically, then, the purpose of this paper is: (l) to describe some of the behavioral mechanisms operating during spawning; (2) to develop the concept of preferred and marginal habitats for spawning fish; and (3) to consider how this mechanism would influence the existing stock-recruit model.

Site Selection and Extrapensatory Mortality

During spawning aggressive behavior is maximal, there is obvious competition for space, and the eggs, when deposited in the gravel, are sensitive to environmental change. Flooding, erosion, and drying up of certain areas often result in severe egg mortality (Neave, 1953) and, consequently, the mechanisms responsible for the pattern of nest location are of considerable interest.

It is evident that with respect to a given source of mortality, certain areas of the stream constitute marginal habitates; e.g., shallower areas are more susceptible to drying up than deeper ones. It is also possible that under different sets of circumstances shallower areas may be considered as optimal habitats and deeper areas marginal. Thus, over a large number of generations, the probabilities of survival associated with physically different areas of the stream may be similar to one another, and therefore the mortality rate associated with various environmental changes may be density independent in the manner described by Ricker (1958). This is not the only way that the conditions of the Ricker formulation are fulfilled, however, since it is possible
that certain areas of the stream are consistently better than others, yet the adult spawners may not have the capacity to differentiate between these areas. This, too, would result in a situation where mortality rate was, on the average, independent of the density of the stock. Therefore, given either of the se two situations, one might anticipate that the distribution of eggs would be random with respect to any measurable physical variable, since there would be no selective pressure which would influence the choice of a site. An alternative hypothesis would be one which would predict that the "optimal" areas of a stream would be colonized initially and marginal areas would only be used in the event of high stock densities. This would suggest that the order of colonization would correspond to some measurable physical variable. Therefore, field studies were conducted in an attempt to determine which patterns characterized the behavior of natural populations.

The Study Areas

## I Four Mile Creek

The first study was conducted at Four-Mile Creek, an inlet stream of the Babine Lake system, which has been described in detail by Hanson (1964). A series of pools along the length of the creek (depths of up to 1.5 metres) serve as resting areas for the fish during their migration upstream. These are interspersed with shallower areas suitable for spawning. A waterfall 1.8 km upstream from the lake confines the run to the lower area of the stream and, under conditions of low discharge, migration is further restricted at 550 m upstream from the lake due to a trifurcation in the creek and resulting shallownes
of the flow. The creek is heavily shaded throughout its length and contains a good representation of the range of conditions in which sockeye are likely to spawn.

The run in Four-Mile Creek appears to be a distinct stock in the sense that it is clearly separated in both space and time from other segments of the Babine run. It is one of the earliest runs to arrive and averages 2300 individuals per year (Hanson, 1964).

## Methods

The 550 m section of the creek below the trifurcation was enclosed using two broom stick fences, the lower fence being equipped with a $V$ trap and a holding facility to aid in counting, measuring and tagging the salmon. This particular area was chosen because most of the good spawning grounds are found below the trifurcation and, if the run were small, it could easily be observed. It was also desirable because a natural barrier to migration periodically occurs at the trifurcation. The conditions, however, were not ideal since it was necessary to have enough individuals in the study area to ensure colonization of the marginal areas, yet not severely damage production by overcrowding the spawners. This proved to be a difficult situation since neither the total size of the run, nor the temporal distribution, could be estimated in advance. The run was larger than anticipated and, consequently, the upper fence had to be removed periodically when large numbers of spawners accumulated at this location.

Within the lower section ten fairly uniform areas, which differed from one another, were selected for intensive observation (Fig. 8). Each area was approximately 7 m in length and was divided into 1 m strips across the width of the stream; e.g., if the stream were 5 m wide, five $1 \times 7 \mathrm{~m} \cdot \mathrm{grids}$ would be formed. The contours, depths and gradients were determined using ordinary surveying techniques and velocities were taken using a Gurley flow meter. The velocities were measured a standard distance from the bottom $(10 \mathrm{~cm})$ in order to determine the range of velocities a spawner would be subjected to, rather than determining the average velocity of the stream section. For each of the $1 \times 7 \mathrm{~m}$ sections, nine measurements of depth and velocity were made, three measurements across the top of the section, three across the middle, and three across the bottom. Gravel samples in each of the sections were also taken using a core sampler and analyzed using the volumetric technique described by McNeil (1964). Samples could not be obtained in all areas since the grade was too coarse, but photographs of all grids were taken with the aid of a plexiglass-bottomed box and a wide angle lens. Staff gauges were installed in each of the ten sections and an additional staff gauge was set up as indicated in Figure 8, which served as a standard metering site.

These measurements were taken in the three-week period prior to the onset of the run, the velocities being taken last (July 22-23). It is therefore necessary to assume that the relative differences in depth and velocity remained constant during the spawning period, which is probably not quite true for all of the cases considered. However, this method was more desirable than the alternative of making daily measurements during the spawning period


Figure 8. Four Mile Creek showing location of grids A-J and the metering site. (*).
as daily disturbances would probably influence the normal pattern of colonization and egg survival.

Each day during the spawning run all of the fish trapped during the previous 24 -hour period were counted and a representative sample of the female spawners was tagged, measured and checked for state of maturity. The latter procedure involved gently squeezing the belly of the females and, if eggs were expelled, the fishes were considered to be mature. Prior to this, each day, the spawners in each of the grids were counted and their position recorded on maps of the areas. This, each day's escapement was given a 15-20 hour period to distribute in the stream without being disturbed by observations or by new fish entering the stream.

## Results

Physical characteristics of the sections.

The depths, velocities, and an index of substrate permeability for each of the ten sections described previously, are presented in Table IV. The permeability index is expresssed as a percentage of the core sample passing through a 1.19 mm seive. This was slightly different from the technique described by McNeil (1964) in that his calculations are expressed as a percentage passing through a 0.883 mm seive. Thus, these calculations probably underestimate actual permeability, but even ignoring this discrepancy, almost all of the areas would be classified as medium to high in permeability (coefficient of permeability associated with 10 per cent of fine material is

TABLE IV. Physical characteristics of grids A-J with permeability mindex expressed as per cent of sample passing through a 1.19 mm sieve.

| Grid | $\begin{aligned} & \text { Depth }(\mathrm{cm}) \\ & \text { (max) } \end{aligned}$ | Permeability Index (\%) \# samples max min |  |  | Velocity (cfs) $\max \quad \min$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| A | 43.5 | (15) | 17.5 | 3.0 | 3.20 | .63 |
| B | 69 | ( 6) | 0 | 0 | 4.16 | . 91 |
| C | 43 | ( 9) | 13.6 | . 02 | 3.73 | . 50 |
| D | 39 | ( 6) | 9.7 | 1.4 | 3.36 | 1.37 |
| E | 47 | ( 9) | 9.0 | 1.8 | 5.68 | 1.37 |
| F | 37 | ( 6) | 10.9 | 1.4 | 3.36 | 1.04 |
| G | 41 |  |  |  | 3.89 | . 59 |
| H | 48 |  |  |  | 2.93 | . 08 |
| I | 32 |  |  |  | 4.07 | 1.49 |
| J | 37 |  |  |  | 3.58 | . 78 |

approximately $200 \mathrm{~cm} / \mathrm{min}$ ) ( McNeil and Ahnell, 1964). These samples were taken shortly after freshet conditions and therefore represent maximum "natural" permeability. Areas of lower permeability were undoubtedly present in the stream along the sides and in very shallow areas, but these were not used as spawning sites.

It was also evident that the spawning material was not a homogeneous mixture of the gravel sizes; i.e., the beds were stratified, with the finer material being present in greater concentrations at lower depths.

The spawning run.

The run commenced on 29 July and a few fish were still entering the stream when the fence program was terminated on 15 August 1968. Because of two breaks in the fence, the numbers for August 3 and 4 are estimates, but even allowing for large errors (in these estimates) it was apparent that the run had a distinctly bimodal distribution (Fig. 9).

Each day the number of females on each of the $1 \times 7 \mathrm{~m}$ grids was counted and the mean number of sightings per day (over a period of 23 days) was calculated. These values were then used as the dependent variable in a multiple regression analysis, i.e., mean number of sightings in each grid was regressed against the estimated depth and velocity of that grid. The independent variables, depth and velocity, were not correlated ( $\mathrm{r}=.01$ ) and produced a significant regression ( $\mathrm{p}=.0 \mathrm{l}$ ) on the mean number of sightings (Fig. 10).


Figure 9. Temporal distribution of spawning run and a relative measure of changes in discharge.


Figure 10. Regression lines fitted to mean number of sightings per grid plotted against the depth and velocity of the grid.

The fit, though significant, still leaves over half of the variability unexplained $\left(r^{2}=.36\right)$, and the analysis confounds two effects, time of occupancy and density; e.g., a section with four fish present for one day would receive the same weight as a section with one fish present over a period of four days. In order to separate the se effects, individual grids were examined to determine whether the preferred areas were also the first colonized. Figure ll shows, for section $A$, (which is wide and contains a large range of depths) mean depth of the spawners for any given day plotted against day and also percentage of maximum density ( 17 females). It can be seen that the deep areas were colonized initially and, as the density increased, shallower areas were utilized as evidenced by a smaller mean depth.

Stream migratory behavior.

The previous conclusions are further confounded by the migratory behavior of spawning salmon upon entering the stream. The best spawning gravel is situated in the lower section of the stream, but the typical pattern of migration seemed to be one in which the fish moved past these lower areas until they were unable to migrate further. In the study area the barrier was the upper fence, but those fish which were allowed to move past the fence continued their migration upstream to natural barriers. No quantitative data were collected on this aspect of their behavior, but days on which large numbers of fish were counted passing through the lower fence, large schools of adults were subsequently observed at the upper barrier. Thus, it would


Figure 11. Mean depth of the redds in grid A plotted against per cent of maximum spawner density (18 redds).
seem that most of the fish moved upstream to the fence and later travelled downstream to select a site. This behavior would have some effect on the technique used for measuring desirability since the probability of physically identical areas being colonized is a function of the relative position of the sites and the number of spawners already present in the stream. Thus, significant differences might be detected solely as a function of the position in the stream of different areas of depth and velocity, without any behavioral mechanism of selection operating. However, were this to be the case, one would expect some ordering of selection from the top of the stream to the bottom. No such position effects are revealed by the data--fish were observed in all of the sections (i.e., A, B. C) on the second day of the run and later fish tended to fill in the remaining sites. It is suggested, therefore, that the physical differences between areas were sufficiently great as to obscure any effects of position.

## Egg retention.

On the basis of the preceding observations, it may be concluded that certain combinations of depth and velocity are subject to more intensive use by spawning fish, and that these aspects of the environment are of greater importance than the relative positions of the areas in the stream. This may be interpreted as evidence for the site selection and, consequently, optimal and marginal habitats. However, site selection per se, does not account for the descending limb of the reproduction curve; i.e., at high densities total production is less than at lower densities. Thus, in order to conform to the
empirical curve, it is necessary to hypothesize an interference component such that deposition success and/or survival rate of the eggs is reduced to a large degree at high density. Survival of eggs already deposited in the gravel could be affected by superimposition or by mechanical disturbances resulting from spawners in close proximity, whereas deposition success could be influenced by fish not being able to obtain territories and also frequently interrupted spawning behavior.

It was felt that the degree of egg retention might reflect deposition success and/or the inability to obtain a territory and so dead females for which the date of entry, state of maturity on entering, and duration of stay, were known were examined for retained eggs. A total of 231 spawners was collected throughout the run, but no clear relationship of egg retention to date of entry, duration of stay, or state of maturity, was revealed, ( $2 \%$ retained over 2000 eggs; $10 \%$ retained over 500). However, large numbers of dead eggs were observed in pools below areas of intensive spawning, indicating that superimposition was of relatively common occurrence in these areas.

II Pinkut and Weaver Creeks

The Four-Mile Creek study may be considered as an example of the colonization behavior of stocks at high densities in a fairly heterogenous environment. For the purpose of comparison, two other situations were observed which provided information for conditions of: (1) low stock density,
medium environmental heterogeneity (Pinkut Creek); and (2) low stock density, uniform environment (Weaver Creek spawning channel). Pinkut Creek is an inlet of the Babine system and is situated eleven miles west of Four-Mile Creek. The major spawning area is much larger than any found in Four-Mile and the creek, being fed from a lake, is less subject to rapid changes in discharge. The creek is fairly uniform along the length of the spawning area and, in this sense, it is less diverse, although a greater range of depth and substrate type than was observed at Four-Mile Creek was apparent in cross section. The run at Pinkut is often bimodal with an early peak occurring in mid-August and a later peak occurring in September (Department of Fisheries, Canada).

Two grids were placed across the width of the creek (as in Four-Mile), one near the upstream end of the area, the other 40-50m downstream. Depths and velocities were recorded and daily counts of individual fish in each of the areas were again made. The early peak, however, was very small with a large percentage of this early run spawning in the area around the upstream grid. Daily counts for this grid are presented in Figure 12, and it was apparent that a relatively wide range of depth and velocity ( $17.3 \mathrm{~cm}-36.8 \mathrm{~cm}$ depth, $0.8--2.3 \mathrm{ft} / \mathrm{sec}$ velocity) was utilized, even though areas of depth and velocity similar to the most preferred area, were readily available in locations further downstream. Although this observation may be construed as being contrary to the situation described for Four-Mile Creek, it is worth noting that the spawning activity was still confined to a small range of the


Figure 12. Daily number of fish plotted against a cross section of the upper grid at Pinkut Creek.
depths and velocities available.

The fact that the upstream grid was used exclusively tends to reinforce the idea that the process of site selection does not begin immediately after the samon enter the stream. Thus, only after they reach some state of physiological maturity do they appear to begin searching and, at this point, two explanations are plausible for their subsequent behaviour:

1) that the process of site selection is influenced only by the presence or absence of certain environmental cues and that the range of optimal cues is related to the total range available in the stream;
2) that the presence of other individuals in a spawning area tends to take precedence over small relative differences in the environmental stimuli (i.e., social facilitation).

Thus, in order to obtain more information on the role of social facilitation, further observations were made on the sockeye in Weaver Creek (Lower Mainland, British Columbia). Because the major part of this run is diverted into a large spawning channel, an opportunity was available for the examination of colonization behavior in a completely uniform environment. Since the channel was designed so as to provide "good" spawning conditions, in terms of depth, velocity, and substrate type, the previous speculations concerning the initiation of spawning behavior in relation to the presence of appropriate physical and social stimuli could be tested in a more rigorous manner. This information was obtained for a small number of females (42) by capturing fish as they entered the fishway, dividing the fish into two groups, tagging the members of each group with Petersen discs, releasing one of the groups into the channel,
and holding the other group in pens near the fishway. When members of the released group were all seen to be defending territories, the penned fish were allowed to enter the spawning channel and comparison of the distribution of groups was made.

As was anticipated, all of the individuals which were released immediately into the spawning channel migrated upstream as far as possible and virtually all of the spawning activity was confined to the upper five legs of the 26 legs in the channel. Because the fish in the pens should be at the same average state of maturity as those released, it was felt that, if the only factors involved in the initiation of spawning activity were appropriate physiological state and environmental cues, penned fish, when released, would occupy areas in lower legs of the spawning area. This did not occur and, without exception, these fish moved upstream to the areas of intensive activity. Thus, the speculations concerning the behavior of unripe fish and the role of social facilitation would seem to be substantiated.

The element of circularity involved in defining behavioral responses without having an independent measure of physiological state is recognized and the same criticism may be made for the definition of optimal and marginal habitats. However, in the absence of long term studies of mean survival and variance of survival for areas which provide detectably different stimuli for the spawner, the site selection would seem to be sufficiently plausible as to warrant consideration in the development of stock recruit theory.

## IMPLICATIONS OF THE STUDIES

Within the context of the original intention of the study, namely, that of establishing the mechanisms of density dependent mortality in the stream environment and their relation to random environmental variability, the following observations are of importance:

1) the rate of colonization of spawning areas in a stream is related to the depths and velocities of water in those areas for conditions of high spawner density;
2) that the site selection process does not immediately commence on entering the stream--rather, some physiological state of maturity would seem to be necessary to initiate spawning activity;
3) social facilitation is likely to be of some consequence in the selection of a site;
4) that fish spawning early in the run are susceptible to having their nests destroyed by the activity of later arrivals;
5) egg retention does not serve as a good indicator of deposition succes, and the number of eggs retained does not relate to time of entry, state of maturity (at least for the crude measure of maturity used here) or time of residence.

Before dealing with the se observations in a specific manner, it will be useful to examine one way in which the existing model may be modified so as to include the effect of density dependent mortality due to random environmental changes. The model, as described by Ricker (1958), Larkin and Ricker (1964),

Tautz, et al., (1969), is of the form

$$
z=w^{e} a(l-w)[R]
$$

where $R$ is a scaled random environmental variable, the value of which is selected at random and subsequently scaled for use as a multiplier or divisor in the manner of Ricker (1958). This variable is density independent in that the proportional effect of the modifier is the same, irrespective of the size of the stock, $w, R$ is distributed over the range ( 0 to $\infty$ ) with a mean greater than 1 as a function of the variance (Tautz, et al., 1969).

In this system, the degree of compensatory mortality is only a function of the term $\mathrm{e}^{\mathrm{a}(\mathrm{l}-\mathrm{w})}$, i.e., the difference between size of stock and equilibrium density or carrying capacity. Therefore, if the changes in the environment are to act on or change the carrying capacity, it seems reasonable to suggest that the stochastic variable (RND) be added or subtracted to the 1 in the exponent, that is, $a\left(1 \pm \frac{R N D}{a}-w\right)$ where the RND is normally distributed with mean 0 and variance $\sigma^{2}$. This formulation would allow for a stock of a given size to show different degrees of response, depending upon the difference between the size of the stock and the carrying capacity of the environment for that particular year. The complete formulation may then be written as

$$
Z=w e^{a\left(1 \pm \frac{R N D}{a}-w\right)}
$$

However, while this may at first seem to be more appealing, it is only trivially different from the existing model. This is apparent if the equation is re-written
as

$$
Z=w e^{a(l-w)}\left[e^{(R N D)}\right]
$$

where the bracketed expression is a log-normal distribution. This distribution has similar properties of asymmetry to the distribution of $[R]$ but has the slight advantage of being soluble analytically for a mean, viz:

$$
\begin{aligned}
& \text { RND }=\frac{1}{\sqrt{2 \pi \sigma}} \\
& E\left(e^{R N D}\right)=e^{-\sigma^{2} / 2 \sigma^{2}}
\end{aligned}
$$



It can be seen that the expected value of the modifier is an increasing function of the variance, specifically, $e^{\sigma^{2} / 2}$, and also that equilibrium density is obtained for $w=1+\sigma^{2} / 2$, since $Z=w e^{a\left(1+\sigma^{2} / 2-w\right)}$ substituting the expectation) reduces to $Z=w$ for $w=1+\sigma^{2} / 2$.

Viewed in this way, the difficulty in defining a stock unit and equilibrium density becomes apparent, since one stock unit cannot be related to average or expected carrying capacity, given multiplicative systems of stochastic variation. One might envisage different ways in which the parameter $a$ and the variance of the environment could be altered to circumvent this difficulty, but a model which is more reductionist in form could perhaps more easily overcome this difficulty.

Although a model of the reductionist type is beyond the scope of this paper, it is useful to consider the way in which the field observations described previously, may be of some consequence in the construction of such a model,
and also to indicate how the phenomenon of site selection violates the assumptions of the Ricker formulation.

A simplified example of such a system would be a stream in which the mortality of eggs and alevins is due solely to normally distributed random changes in water level during the time for which the eggs are in the gravel. In this situation, deep areas of the stream would be associated consistently with high survival rates, and shallow areas would be more "sensitive" to changes in discharge. Thus, the process of site selection would allow for deeper areas to be colonized initially and shallower areas to be used only under conditions of high density. For a given minimum discharge, the number of sites destroyed would be a density dependent phenomenon. This is distinct from Ricker's formulation in that, in the Ricker model, the number of sites destroyed would be some constant proportion of the total number of sites. In this system a wide range of stream levels may be completely equivalent in terms of their effect on a small number of well placed nests, a feature which is not a property of the existing model. This manner of argument suggests the use of threshold phenomenon as opposed to continuous functions in the description of some density dependent processes, and a more reductionist model would be better suited to this approach.

In such a model, a stream may be considered as a matrix of sites and each site (over a period of years) is associated with a different probability density function of survival rate, with a different mean and possibly a different variance. The site selection process enables the spawners to detect these
areas of high probability survival. Furthermore, in the same way as one may associate different probabilities of survival to different locations in the stream, one may also consider this matrix of elements to change as some function of time, and there are many ways in which this temporal variation may be envisaged as being important. For example, early fish entering the stream are more likely to obtain better areas for spawning, but, at the same time, the eggs are more susceptible to being disturbed by superimposition, particularly if the site selection process is very accurate. Also, the accuracy of the site selection process is a variable which should be considered and is also density dependent since, at low densities, the effect of making an "error" in the selection of a site is relatively important in terms of influencing total production, while at higher densities these errors are "corrected" by the "filling in" of later spawners.

Several other "compromise" situations may be envisaged as being important for describing "optimal" escapements into different stream environments, and these considerations can only be viewed in proper perspective by the use of a theoretical system which is more specific than present models.

## CON CLUSIONS

The preceding paper has presented circumstantial evidence for the process of site selection and social facilitation in the spawning behavior of sockeye salmon. The existence of preferred and marginal habitats and the ability of the spawners to differentiate between these types of areas, suggest that Ricker's formulation of stock and recruitment is not a general description of
this phenomenon. Although the shape of the curve is substantiated by field data; the assumptions concerning the variance about the curve are probably not correct for situations in which site selection is operating in conjunction with random environmental changes. The exact nature of the variance is a property of the situation in question, and is probably defined by the relative abundance of marginal and optimal habitats, the degree of temporal variability in arrival of the spawners, the accuracy of the selection process, and, the absolute size of the spawning run, among others.

A general model incorporating the se variables is now being considered, but for specific management situations it is important to bear in mind that optimal escapements must be related not only to total escapement and total spawning area available, but also to the degree of temporal variation in arrival times and spatial heterogeneity.

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[^0]:    ${ }^{1}$ Part I has been published as "Some effects of simulated long-term environmental fluctuations on maximum sustained yield', in the J.Fish.Res.Bd. Canada, 26:2715-2726.

[^1]:    * The deterministic values of m.e.c. in Table I are determined by setting the first derivative of $w_{t} e^{\left(a-w_{t}\right)}-w_{t}$ equal to zero and solving for $w$.

[^2]:    * Curve G goes to extinction in a few generations under conditions of fixed percentage exploitation.

