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A conceptual model for managing fisheries to maintain reproductive fitness is proposed. Reproductive fitness is defined genetically as the contribution of an individual in a breeding population to the next generation. The reproductive fitness of a stock is described by a probability distribution (W) with a corresponding mean ($\bar{W}$) and variance (V_w). In applying the stock concept to fisheries management, the goal is to maintain the stock as a self perpetuating system. This requires that the stock maintain the W (with a sufficiently broad V_w around $\bar{W}$) to allow it to perpetuate in the face of fishing and natural mortality in a changing environment. If W is the probability distribution of fitness at breeding seasons when stock abundance was acceptable to management, then it should remain constant in subsequent breeding seasons (V'_w), thus W = W'.

Examples of functional relationships for the conceptual model are presented. These equations, derived from existing principles of population biology and population genetics, express the variance effective number ($N_{e(v)}$) of a stock as a function of population size in successive breeding seasons, age stucture, the variance of successful gametes (V_k, estimating V_W) and immigration.

Application of the model to stock management is accomplished by equating the value of $N_{e(v)}$ to $N'_{e(v)}$. The inputs for the functional relationships can be estimated or measured directly from life history information or population variables monitored in fishery management. They do not require estimation of classical genetic properties of populations such as gene frequencies and percentage homozygosity. The output is the number of reproducing adults required in a given breeding season to insure the maintenance of stock fitness. Features and limitations of the functional relationships for stock management are discussed.

The sensitivities of $N_{e(v)}$, V_k and V_k/kbar (estimating $V_W/\bar{W}$) to changes in input variables are reported. The descending order of importance for the inputs controlling the value of $N_{e(v)}$ is: (1) population size; (2) the probability distribution of age specific fitness; (3) age structure; (4) immigration. Interactions among the inputs preclude a ranking applicable to all cases when there are simultaneous changes in two or more variables. The results are discussed in terms of the data required for rational stock management.

The generalized genetic fitness model is applied to the management of Pacific salmon fisheries. Adjustment of the functional relationships to accomodate the different life histories of different Pacific salmon species is demonstrated for fictitious chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon stocks.

A Genetic Fitness Model for Fisheries Management

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

A GENETIC FITNESS MODEL FOR FISHERIES MANAGEMENT

INTRODUCTION

Perhaps no questions in contemporary fishery science have stimulated more debate than those that relate to the long term genetic implications of fishery management and exploitation. In his eloquent review of the subject as it related to the management of Pacific salmon fisheries, Larkin (1981) noted that "It is rather surprising that there is currently no explicit working hypothesis of population genetics in the salmon management kit box". The lack of a conceptual framework for studying the genetic implications of stock management is not unique to salmon but is a general concern in fisheries science and, indeed, to the entire fields of natural resource management and gene conservation.

In attempting to develop an appropriate conceptual framework, Dr. Lannan and I speculated that this task could be accomplished by drawing on the existing principles of population genetics and population biology. We are prepared to propose a conceptual framework that represents a synthesis rather than the development of new theory.

A conceptual framework must address the definition of the management unit and the properties of the unit to be managed. A conceptual framework presently exists for the former but not the latter.

What is the Unit of Management?

We cannot improve upon the concept of stocks as a management unit. The definition proposed by Larkin (1970) seems entirely adequate as a basis for most management situations. As he perceived it, a stock is "a population of organisms which, sharing a common environment and participating in a common gene pool, is sufficiently discrete to warrant consideration as a self perpetuating system which can be managed".

Stocks can be described by a variety of criteria consistent with Larkin's definition. Stocks were initially described in terms of spatial and temporal distributions. More recently stocks have been described in terms of biochemical, immunological, behavioral or morphometric phenotypes.

Virtually all contemporary approaches to natural resource management are directed toward a common goal: perpetuation of the resource. This consideration is implicit in the stock concept and necessitates that management insures an adequate number of reproducing adults in breeding populations. In recent years, there has been a proliferation of quantitative methods intended to estimate escapements required to provide a sustained harvest based upon this principle. Functions that describe the relationship between surplus production and stock biomass (Schaefer 1954) or between spawners and recruits (Ricker 1954) are examples of contemporary efforts to apply the principles of population biology to fisheries management. However, none of these quantitative models allow the assessment of genetic changes caused by management and exploitation. This is a serious limitation because even if the model predictions result in adequate escapement and subsequent recruitment in the next generation, one cannot exclude the possibility that the stock experiences a net reduction in diversity of genetic information that limits its opportunities for adaptation in a dynamic environment.

What Genetic Property of Stocks Should be Managed?

If fitness is the genetic property related to the perpetuation of a breeding population, then maintaining fitness must be the goal of fisheries management. Fitness is defined genetically as the contribution of an individual in a breeding population to the next generation. Mean fitness (symbolized by $\bar{W}$) is defined as the average fitness of a population. It is important to recognize that both populations and individuals comprising populations exhibit fitness. Recognizing that the fitness of individuals within a fish population is highly variable, we can conceptualize a probability distribution of fitness (W) for an entire stock with a corresponding mean ($\bar{W}$) and variance (V_w). Williams (1977) noted that fitness variability must be substantial and that only a few genotypes make an effective contribution to the next generation in populations of high-fecundity animals, for example, many fishes. It is also important to recognize that fitness has dimensions in time, i.e., the dimensions of fitness are offspring per unit time, and that the instantaneous probability distribution of fitness strictly applies only to the specific sequence of environmental circumstances the population has encountered. The probability distribution may be substantially altered through changes in W or V_W if the stock encounters substantial environmental change. This idea is implicit in the description of "sisyphean" fitness by Williams (1977):

> "an individual in the top end of the fitness distribution has achieved its near maximum of fitness by an only momentarily effective combination of genetics and individual history. The necessarily low heritability of such fitness would probably drop that same genotype into the range of mediocrity in the next generation."

We realized that _a priori_ knowledge of specific gene frequencies isn't particularly useful in the assessment of a managed population's fitness or in the management of its genetic health because: 1) the sequence of environmental circumstances to be encountered through the life history of the stock cannot be predicted before the fact and 2) we do not know the relationship between specific gene frequencies and fitness. Also, it is unlikely that electrophoretically observed loci are the major determinants of fitness because these loci are restricted to structural genes which represent a small proportion of the entire genome (Falconer 1981). Additionally, phenotypic values of fitness can only be predicted within broad ranges, even in cases where individual genotypes are known, because of pleiotropic and other interactive effects.

Fitness is a quantitative trait with little additive genetic variance, high heterosis and substantial inbreeding depression (Falconer 1981, Gjedrem 1983, Kincaid 1983, Kirpichnikov 1981). Thus, 1) the fitness of progeny cannot be predicted from knowledge of the fitness of their parents, and 2) any genotype may result in a variety of phenotypes, each with a different fitness (Birnbaum 1972, Lewontin 1982). Also, the greater the variance of fitness in a mating population, the more opportunity there is for heterosis in the progeny. In the context of probability theory, fitness is a phenomenon that has uncertainty associated with it where the uncertainty is caused by variability due to the inconsistency of natural phenomena or to sources of variation that elude control. If the phenomenon exhibits some degree of regularity, then its variation can be described by a probability model (Hillier and Lieberman 1974). Therefore, we can model fitness as a random variable with a continuous probability distribution for a large number of individuals in the stock.

The long-term survival of a stock is more dependent on the maintenance of an adequate degree of the variance of fitness around the mean than simply on the value of mean fitness because the stock must be able to adapt to changing environmental conditions. Therefore, we conclude that the genetic objective of fisheries management is: maintaining the probability distribution of fitness to allow a stock to perpetuate in the face of fishing and natural mortality in an uncertain environment. Figure I.1.a illustrates a number of possible probability distributions of fitness for individuals of the same age in a given stock. Individual fitness is expressed in terms of the number of successful progeny per parent where successful means survival to the reproductive stage. We can generate a graph for fitness as a function of age by integrating values for $\bar{W}$ and V_w (taken from a given curve in Fig. I.1.a) over all ages (Fig. I.1.b). Then, we can restate the genetic objective as maintaining the variance (shaded area) around the entire curve in Figure I.1.b.

The contemporary literature of life history theory contains numerous references to the importance of maintaining V_w in natural populations. Real (1980) proposed that natural selection maximizes a function containing terms for both V_w and $\bar{W}$. Also, he emphasized that natural variation (thus V_w) is the cornerstone of Darwinian selection. Another example is the suggestion of an "adaptive coin-flipping" principle by Kaplan and Cooper (1984). Using a decision theory analysis, they argued that the highly variable reproductive characters (e.g., clutch size, egg size) observed in cold-blooded vertebrates were adaptations to unpredictable environments. Their discussion can be extended to V_w because reproductive characters are major components of fitness. Conrad (1983) stated that the variability of biological matter is the *sine qua non* for the ability of organisms to cope with the uncertainty of the environment.

THE CONCEPTUAL MODEL

Given this background, we are prepared to propose a conceptual model and a set of illustrative functional relationships for fisheries management that intend to insure the long term reproductive fitness of stocks. The model is an extension of the stock concept, and includes the following features:

- It is a generalized fisheries management model that can be applied to any species because it provides for appropriate consideration of life history patterns, reproductive strategies, and the like.
- The inputs for the functional relationships, including stock abundance, age structure, immigration and the variance of successful gametes per parent (an estimate of V_w), are phenotypic variables that can be estimated or measured directly.
- The model output is the number of reproducing adults required in a given breeding season to insure the maintenance of the probability distribution of fitness for the particular life history of the stock.
- The functional relationships of the model can stand alone or can be linked to other predictive models of population dynamics.
- The model is applicable to single or mixed stock fisheries and permits substantial management flexibility in assessing the genetic status of stocks relative to management goals. Thus it is equally applicable to managing the harvest of surplus production on the one hand, and to stock rehabilitation on the other.

Let W equal the probability distribution of fitness (with a characteristic $\bar{W}$ and V_w) in past breeding seasons and W' equal the probability distribution of fitness in the breeding seasons of management concern. Assuming that W is at a value consistent with management goals, conservative management dictates that it should remain constant in subsequent breeding seasons, thus:

$$W = W'. \qquad (1)$$

The functional relationships W = f(population variables) and W' = f(population variables') can be substituted into equation (1), and the equation rearranged to solve for any one population variable, assuming numerical values for the remaining variables are available.

Fig. I.1.a and I.b.

a: Possible probability distributions for fitness (the number of successful progeny/parent) for one reproductive age class in a stock.

b: Fitness (number of successful progeny/parent) as a function of age for all reproductive ages in a stock.

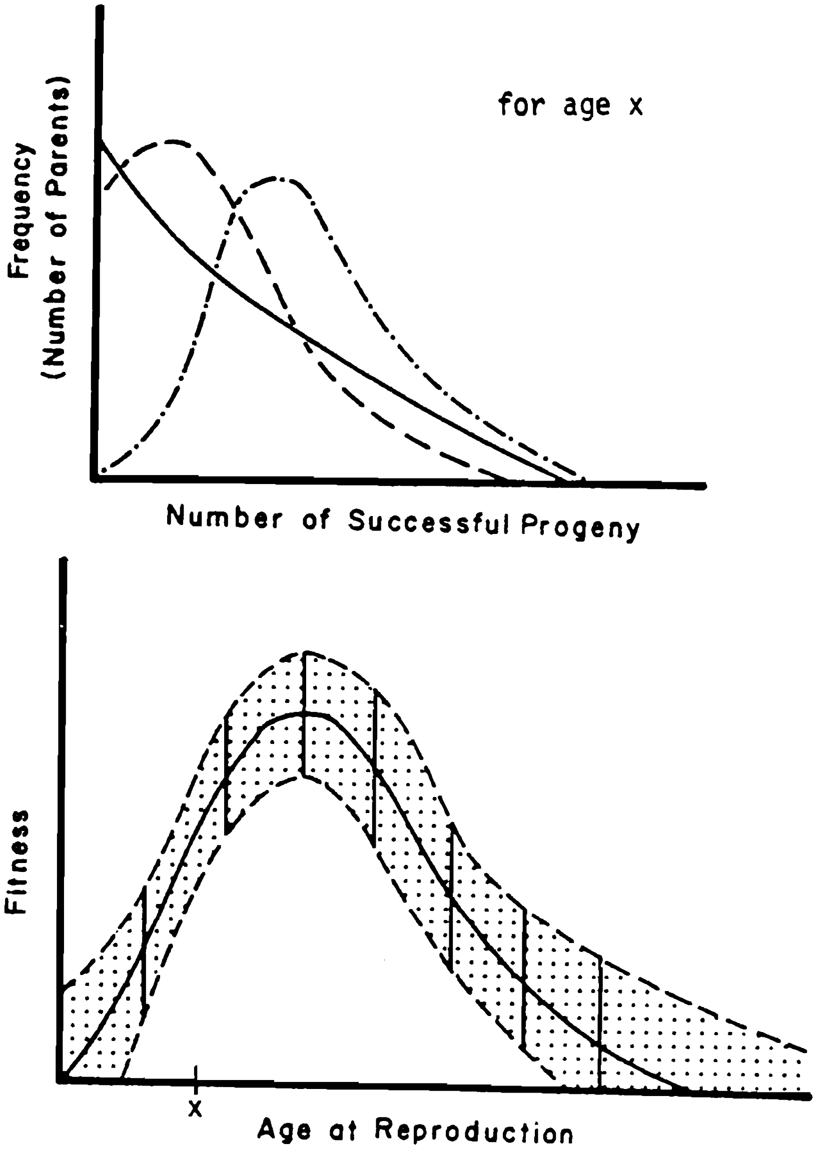

Fig. I.1.a and I.b

DESCRIPTION OF FUNCTIONAL RELATIONSHIPS FOR A GENETIC FITNESS MODEL FOR FISHERIES MANAGEMENT

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ABSTRACT

An example of functional relationships for a genetic fitness model for fisheries management is presented. The expressions were derived from the variance effective number for a reproducing population and include variables for population size in successive breeding seasons, age structure, the variance of successful gametes (an estimate of the variance of fitness) and immigration rate.

The management objective of maintaining the probability distribution of fitness in a stock is met by: (1) identifying reference breeding seasons when stock abundance was consistent with management desires and (2) equating the variance effective number ($N_{e(v)}$) for the reference seasons to the variance effective number ($N'_{e(v)}$) for the stock in present time. The required inputs can be estimated or measured directly from life history information or population variables routinely monitored in fishery management. Determination of genetic properties of the stock such as gene frequencies, homozygosity, and the like are not required. The output is the number of reproducing adults required in a given breeding season to insure the maintenance of the probability distribution of stock fitness.

Application of the model to stock management is discussed in the context of both features and limitations of the functional relationships.

INTRODUCTION

We have developed a conceptual genetic fitness model for fisheries management. The model treats stock fitness as a random variable described by a continuous probability distribution when there is a large number of individuals in the stock. The model defines the genetic goal of fisheries management to be maintaining the probability distribution of fitness to allow the stock to perpetuate in the face of fishing and natural mortality in an unpredictable environment. This is achieved by equating the probability distribution of fitness, W, at a time when stock abundance was acceptable for management desires to W' in the breeding seasons of immediate management concern. A characteristic mean ($\bar{W}$, $\bar{W}'$) and variance (V_w,V'_w) is associated with each probability distribution.

This paper describes the translation of the conceptual model into quantitative terms. The functional relationships are based on a synthesis of contemporary principles of population genetics and biology. They represent a second approximation of functional relationships consistent with the objectives of stock management. Owing to problems with the incorporation of age structure, the first approximations (Kapuscinski and Lannan 1984) have been revised into the present forms. These functional relationships are presented as one example of quantitative expressions for the conceptual model. It is anticipated that new derivations will result in the conceptual model becoming more comprehensive with time.

POPULATION VARIABLES INFLUENCING STOCK FITNESS

Let us assume that the stock under consideration is not likely to undergo any significant evolutionary change during the period in which management is applied. Then, the quantitative expressions for the model must address three principal mechanisms that can effect substantial changes in the diversity of genetic information in a stock in one to several generations. These include changes in population size, immigration into the stock and the presence or absence of age structure in the reproductive stock.

FUNCTIONAL RELATIONSHIPS

The functional relationships for the model are based on the concept of a variance effective number. Relating any genetic property of a population to actual population numbers is complicated because not all individuals in a population, not even all sexually mature individuals, necessarily become parents (Falconer 1981). The concept of effective population size was introduced by Wright (1931) to reduce the complicated breeding structure of real populations to the mathematically equivalent and simpler case of an idealized population. According to theory, two related processes, inbreeding and random drift, contribute to an average increase in homozygosity within a population of finite size. Thus two definitions (Kimura and Crow 1963) of the effective population number, N_e, must be considered:

1. the inbreeding effective number, $N_{e(f)}$, is the size of an idealized population that has the same rate of inbreeding as the observed population, and
2. the variance effective number, $N_{e(v)}$, is the size of an idealized population that has the same amount of random gene frequency drift as the observed population.

The two effective numbers are equivalent for populations that remain constant in size over time, and are approximately equal for populations whose periods of increase and decline tend to negate one another over time (Crow and Kimura 1970). However, for small populations that are in decline, especially those that are in danger of extinction, gene frequency drift results in greater homozygosity than does inbreeding (James Crow, personal communication). Thus, although one can derive a functional relationship using either $N_{e(f)}$ or $N_{e(v)}$, conservative management seems to favor the latter. The variance effective number offers the additional advantage of incorporating the probability of increasing homozygosity, thus eliminating the requirement of estimating homozygosity in managed populations.

An equation for $N_{e(v)}$ can be derived that incorporates population size, immigration, age structure and the variance of fitness. Let us define genetic risk as the probability of a reduction in the adaptibility of a stock to its habitat due to a reduction in genetic variation. The final expression for $N_{e(v)}$ will be a measure of genetic risk. It will not be equivalent to the $N_{e(v)}$ presented in the literature of population genetics (Crow and Kimura 1970).

Recognizing that $N_{e(v)}$ is an abstraction, the reason for including it in the quantitative expressions is to permit the unification of the principal mechanisms affecting stock fitness. Then we can use the functional relationship $N_{e(v)}$ = f(population variables) for the conceptual model if we note that the probability distribution of fitness is a function of $N_{e(v)}$.

The equation for $N_{e(v)}$ will be used to satisfy the following management objective. If $N_{e(v)}$ is calculated for a stock during a breeding interval when stock abundance satisfied management goals, then conservative management dictates maintaining this value of $N_{e(v)}$ in subsequent breeding seasons, thus:

$$N_{e(v)} = N'_{e(v)} \qquad (1)$$

where the prime notation distinguishes the breeding seasons in present time from the reference breeding seasons. Functional relationships for $N_{e(v)}$ and $N'_{e(v)}$ can be substituted into equation (1), and the equation rearranged to solve for any one population variable, assuming numerical values for the remaining variables are available.

Population Size. Because $N_{e(v)}$ is the size of an idealized population, the simplifying properties of an idealized population must be considered in the present derivation. Thus we consider an observed population with the following properties:

1. Mating is at random,
2. the sexes are separate but the numbers of each sex need not be equal,
3. self-fertilization does not occur,
4. migration into the population does not occur,
5. parents reproduce at only one age (generations are discrete),
6. the population is composed of diploid individuals,
7. the number of offspring per parent contributed to the next generation can vary.

The variance effective number for this population is

$$N_{e(v)} = \frac{N_{t-1}\bar{k}}{1 + \frac{V_k}{\bar{k}}} \qquad (2)$$

where: N_{t-1}= the number of breeding individuals in breeding season t-1, $\bar{k}$ (kbar) and V_k are, respectively, the mean and variance of successful gametes (i.e. gametes which survive to become parents in the next generation) contributed per parent (Kimura and Crow 1963; Crow and Kimura 1970). The variance effective number can be weighted for differential contributions of male and female parents by calculating N_e^* for females, N_e^{**} for males and combining them according to the formula of Kimura and Crow (1963)

$$N_{e(v)} = \frac{4\,N_e^{*}\,N_e^{**}}{N_e^{*} + N_e^{**}} \qquad (2a)$$

Because kbar and V_k express a relationship between parents in generations t-1 and t, kbar is proportional to $\bar{W}$ on the one hand and V_k is proportional to V_w on the other. We propose to use V_k in place of V_w without solving the proportion in the present discussion because we will ultimately equate $N_{e(v)} = f(V_k)$ to $N'_{e(v)} = f(V'_k)$ as suggested in equation (1). Similarly, kbar becomes a convenient term to retain because it can be estimated as

$$\bar{k} = \frac{2N_t}{N_{t-1}} \qquad (3)$$

(Crow and Kimura 1970), a form which may be calculated from estimates of population abundance at t and t-1.

Because equation (2) applies to the observed population described above, it does not apply to cases where migration or age structure occur. The next step in our synthesis must therefore address migration and age structure.

<u>Migration</u>. Migration reduces the probability of random drift among

subpopulations. The simplest model for migration, the Island Model (Wright 1951), assumes that the immigrants into a subpopulation are a random sample of the entire population. Thus the migrants have a gene frequency equal to that for the whole population.

The Island Model can be applied to the present case by assuming the stock to be a subpopulation. Let M be the fraction of the stock (subpopulation) replaced by migrants in a generation. The probability that neither of two genes uniting in a zygote has been exchanged for a migrant gene is $(1-M)^2$. Because random drift of gene frequencies (and the corresponding loss of genetic variation) within stocks decreases as migration increases among them, inclusion of migration into equation (2) should result in an increase in $N_{e(v)}$ when M increases. The appropriate expression for $N_{e(v)}$ under these conditions is:

$$N_{e(v)} = \frac{N_{t-1}\,\bar{k}}{1 + \frac{V_k}{\bar{k}}(1-M)^2} \qquad (4)$$

based on the equation presented by Crow and Kimura (1970) for the rate of inbreeding as a function of M and $N_{e(v)}$.

The assumptions of the Island Model can be relaxed to correct for migration between subpopulations that are related due to exchange of genetic information in previous generations (Crow and Kimura 1970). If r is the correlation of gene frequencies between immigrants and the receiving subpopulations, M(1-r) is substituted for M in equation (4).

Age Structure. When individuals reproduce at two or more ages, a population may be composed of individuals representing two or more cohorts in a given calendar period. In a management sense, this period must include the interval during which fishing mortality and reproduction occurs. We find it useful to define a breeding season as an interval of management concern and to consider all cohorts represented during that interval in the calculations of N_{t-1}, kbar and V_k in equation (4).

Incorporation of age structure into equation (4) requires estimating the abundance of parents $N_{x,t-1}$, in each cohort, where x is the age at reproduction. Then the abundance of all parents at t-1 in equation (4), is

$$N_{t-1} = \sum_x N_{x,t-1} \tag{5}$$

Likewise, the contribution of each cohort to the average number of successful gametes must be considered. The appropriate expression is the weighted sum

$$\bar{k} = \frac{\sum_x \bar{k}_x N_{x,\ t-1}}{N_{t-1}} \tag{6}$$

where $\bar{k}_x$ is the average number of succcessful gametes produced by parents of age x.

Alternatively, $\bar{k}$ can be estimated as

$$\bar{k} = \frac{2\sum_n N_{x+n,\ t+n}}{N_{t-1}} \tag{7}$$

a form that may be calculated from estimates of population abundance at breeding season t-1 and $\sum_n$ t+n where the range of values for n is determined by the reproductive life history of a given stock. For example, if there is annual breeding and the progeny produced by parents at t-1 are sexually mature at ages 1 - 5, then the range of n is 0 - 4.

Finally, the variance of successful gametes can incorporate age structure by computing a weighted sum of the variances of each cohort. This requires a few intermediate steps based on statistical concepts.

If $\sigma^2_{k,x}$ is the true variance of k for all fish of age x and $s^2_{k,x}$ is the variance of k for fish of age x within a given stock, then $s^2_{k,x}$ for one stock is a sample of $\sigma^2_{k,x}$, the true variance for all stocks of the species:

$$\sigma^2_x = S^2_{\substack{\text{within}\\ \text{stocks}}} + S^2_{\substack{\text{among}\\ \text{stocks}}} \tag{8}$$

and

$$S^2_x < \sigma^2_x$$

The definition of $N_{e(v)}$ implies that it is a measure of the sampling bias in the transmission of genes from one generation to the next caused by the finite size of a stock. Thus, it is appropriate to make $s^2_{k,x}$ dependent on the sample or stock size. This requires removing the Gaussian correction from the variance formula and is accomplished by

$$s^2_{k,\,x} = \frac{\sigma^2_{k,\,x}\,(N_x - 1)}{N_x} \tag{9}$$

where N_x refers to breeding season t-1.

If it is assumed that $s^2_{k,x}$ at one age (x) is independent of $s^2_{k,y}$ at any other age (y) present in the reproductive stock, then

$$COV_{k,xy} = 0 \tag{10}$$

for all paired combinations of ages. Then, the contribution of each cohort to V_k is considered by computing the weighted sum

$$V_k = \frac{\sum_x S^2_{k,x} N_{x,t-1}}{\sum_x N_{x,t-1}} = \frac{\sum_x S^2_{k,x} N_{x,t-1}}{N_{t-1}} \tag{11}$$

When expression (10) is unacceptable, the summation in the numerator of expression (11) must include the appropriate covariances.

Substitution of expressions (5), (6) or (7), and (11) for N_{t-1}, kbar and V_k, respectively, into equation (4) provides a functional relationship between $N_{e(v)}$ and population size, the mean and variance of stock fitness, age structure and migration. The solution of equation (4) requires the following data from fisheries surveys:

- Estimates of stock abundance at $\sum_n$ t+n and t-1,
- the proportion of reproducing adults at $\sum_n$ t+n and t-1,
- the number of migrants into the stock in breeding season t-1,
- the age composition of reproducing adults at $_n$ t+n and t-1, and
- estimates of age specific variance of successful gametes ($s^2_{k,x}$) at t-1.

While the first four items can be estimated from data monitored in fisheries management, measurement of $s^2_{k,x}$ may require carefully designed field sampling of marked progeny (e.g., with coded wire tags) over $\sum_n$ t+n breeding seasons. An alternative method of estimating $s^2_{k,x}$ requires knowledge of the probability distribution of k and estimates of kbar$_x$ at each age x (Fig. I.1a). For some probability distributions (e.g., Poisson, gamma, exponential and binomial distributions), the variance can be expressed as a function of the mean. If the probability distribution of k at age x fits this condition, then

$$s^2_{k,x} = f(\mathrm{kbar}_x) \qquad (12)$$

However, estimation of kbar$_x$ still may require sampling of marked progeny.

APPLICATION OF THE MODEL TO STOCK MANAGEMENT

Equation (4) (containing substitutions from equations 5, 7, and 11 for age structure) is of a form which can be substituted into equation (1). Thus the conceptual model can now be applied to real management situations for stocks with migration and age structure. This application would typically involve the following stepwise process:

1. The historical records for a stock of concern would be surveyed, and successive breeding seasons, t-1 and $\sum_n t+n$, would be selected from an era when the stock would be considered to have N_e consistent with the management goal. The terms N_{t-1} (equation 5), $\sum_n N_{x+n,t+n}$, M and V_k (equation 11) would be compiled for the selected interval.

2. The immediate management objective is to determine the number of breeding individuals required in the present (or next) breeding season to insure the maintenance of N_e, thus the maintenance of W. This is done by evaluating population abundance, age structure, and migration in the generation interval of immediate concern. These data would provide numerical values for N'_{t-1}, M', and V'_k, where the prime notation is intended to distinguish these properties in present time from the corresponding terms for the reference generations. The variable for which we will ultimately solve is $\sum_n N_{x+n,t+n}$.

3. Consistent with equation (1), we now equate N_e for the reference generation to N'_e for the present generation, giving

$$\frac{N_{t-1}\,\bar{k}}{1+\frac{V_k}{\bar{k}}(1-M)^2} = \frac{N'_{t-1}\bar{k}'}{1+\frac{V'_k}{\bar{k}'}(1-M')^2} \tag{13}$$

Substituting $2\sum_n N_{x+n,t+n}/N_{t-1}$ for kbar and $2\sum_n N'_{x+n,t+n}$ for $\bar{k}'$ (equation 7) and rearranging terms, we arrive at

$$\sum_n N'_{x+n,\ t+n} = \frac{\sum_n N_{x+n,\ t+n}\left[1+\left(\frac{N'_{t-1}\ V'_k}{2\sum_n N'_{x+n,\ t+n}}\right)\left(1-M'\right)^2\right]}{1+\left(\frac{N_{t-1}\ V_k}{2\sum_n N_{x+n,\ t+n}}\right)\left(1-M\right)^2} \tag{14}$$

Equation (14) would be appropriate for species with age structure. A similar stepwise process would be employed for species with discrete generations, however the expression $\sum_n N_{x+n,t+n}$ reduces to N_t in this case.

DISCUSSION

The expressions presented in the previous section are composed of the conceptual model (W = W'), and an example of functional relationships for application of the model (represented by equations 1 through 4). In developing the latter, we have relied heavily upon the contributions of Kimura and Crow (1963) and Crow and Kimura (1970). It should be noted that other workers (for example see Choy and Weir 1978, Emigh and Pollak 1979, Felsenstein 1971, Hill 1979, Nei and Imaizumi 1966, Robertson 1961) have contributed alternate derivations for effective population numbers which also would be suitable as functional relationships in application of the conceptual model.

We have elected to use the equations of Kimura and Crow in the present discussion for a number of reasons. Because they have appeared in the literature for some 20 years, they are familiar to the community of population biologists. In spite of their simplifying assumptions, they provide substantial flexibility in adapting the model to the life history patterns of the species of concern. Most importantly, they offer the advantage of enabling one to deal quantitatively with population fitness using only estimates of population variables routinely recorded or capable of being recorded in fisheries survey work, thus avoiding the necessity of making direct estimates of other genetic properties of populations.

We regard the latter point to be of paramount importance. Whereas classical population genetics focuses upon the genetic structure of populations, natural resource management is more concerned with the phenotypic expression of the genetic information in a variable and unpredictable environment. Therefore, although the frequencies of various alleles in populations may be useful in identifying stocks as management units, such information is not particularly helpful when it comes to making decisions about how the stocks should be managed. In attempting to relate gene frequencies to stock management, it is necessary to assume that the gene frequencies are correlated with reproductive fitness irrespective of whether the frequencies are determined from electrophoretic evaluation of protein polymorphisms, meristic traits or any other methodology. The validity of this assumption is tenuous at best, for in addition to the technical questions associated with the methods of analysis, it is further assumed that the observed phenotypic variability in a limited number of structural genes reflects the variance of population fitness. If this assumption is valid, then (1) the loci observed are the major ones determining fitness, and (2) the loci act independently in their contribution to fitness. The likelihood that a structural gene with these properties exists is at best extremely remote.

In preceding sections we have made reference to idealized populations on the one hand and observed populations on the other. A clarification of the differences would be appropriate at this point. As noted earlier, Wright (1931) introduced the concept of an idealized population to simplify the properties of populations resulting from complicated breeding structure. Implicit in the concept of an idealized population are the following assumptions:

1. mating is at random, including a random amount of self-fertilization,
2. generations are discrete, i.e., there is only one reproductive age,
3. the number of breeding individuals is the same in each generation,
4. migration is excluded,
5. there is no selection,
6. mutation is disregarded.

Certain of these assumptions may be unacceptable when applying the principles of population genetics to management situations depending upon the life history pattern of the species under consideration. It is useful to start with the assumptions of an idealized population in deriving functional relationships for management models. Then the derivations can be modified to correct for untenable assumptions until the list is consistent with the properties of an observed population. In the present case, we commenced our derivation using an equation that retained assumptions 2, 4, and 6 and modified assumption 1 so as to exclude self fertilization. We then systematically addressed the remaining assumptions by appropriate changes to the functional relationship. This approach provided the means for developing consistency between functional relationships and the life history patterns of the species concerned.

Having devoted considerable attention to what the model can do, it seems appropriate at this point to recognize its limitations. Although the model provides a means for maintaining the probability distribution of fitness by maintaining the corresponding value for the variance effective number, it does not provide inference about the evolutionary mechanisms acting on population fitness. There is an inherent danger in placing an absolute numerical value on the variance effective number in the reference generations without giving careful consideration to the life history pattern and environment of the species of concern. The possiblity still exists to inadvertently modify population structure unless careful attention is paid to biological detail.

To expand on this point by illustrative example, consider a stock of marine fish composed of individuals representing a large number of age classes. If fishing selectively extracts the older age classes (presumably the larger fish), the average age of reproduction is reduced. If there is a genetic component to the age class structure this is tantamount to reducing the generation interval, which has the effect of increasing average fitness but reducing the variance of fitness. It would be useful to partition age structure into genetic and non-genetic components of variance, but in the absence of such information conservative management would dictate that we should attempt to harvest the stock such that the distribution of age classes in the catch is the same as in the stock at large.

Practicable application of the quantitative model to stock management is constrained by the estimations of $s^2_{k,x}$ values in equation (11) for the calculations of V_k and V'_k in equation (14). If the estimations of $s^2_{k,x}$ values require field sampling, there may be considerable cost and time delay involved in the application of equation (14) to the management of a given stock. The magnitude of this problem will be influenced by the life history of the species. Another constraint is the determination of appropriate reference breeding seasons for the estimation of population variables in equation (14). Data gaps in the historical record may preclude computation of the necessary variables for some stocks. Even when the data are available, equation (14) assumes that a stock's habitat in the reference breeding season is similar to the habitat in the season of management concern. Stock management via the sole application of equation (14) may be inappropriate when this assumption is unacceptable.

Data constraints may be circumvented by developing indirect estimates of the population variables required for equation (14). A simple example is the calculation of $s^2_{k,x}$ from estimates of age specific fecundity and survival by

$$s^2_{k,x} = f(\text{kbar}_x) = f[(\text{fecundity}_x)(\text{survival}_x]$$

where fecundity could be estimated as a function of length or weight at age (Pitcher and Hart 1982). However, indirect estimates will contribute error to the output of equation (14) and will increase the uncertainty involved in the application of equation (14) to stock management. Consideration must be given to such uncertainty if conservative management is desired.

There is an inherent danger in extending the generalizations of any simplistic quantitative model to management purposes. In the present case the model at least intends to address the long term perpetuation of the resource, and if it is found to be in error it is likely to err in favor of conservatism. In this sense we feel the model represents a modest improvement of the tools available for the application of the stock concept to fisheries management.

SENSITIVITY ANALYSIS OF FUNCTIONAL RELATIONSHIPS FOR A GENETIC FITNESS MODEL FOR FISHERIES MANAGEMENT

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ABSTRACT

This report describes the sensitivities of outputs from functional relationships for a genetic fitness model for fisheries management. The variance effective number ($N_{e(v)}$) is the principal output required for applying the genetic objective of maintaining the probability distribution of fitness (W) to allow the stock to perpetuate in the face of fishing and natural mortality in an unpredictable environment. The analysis included investigating the sensitivities of $N_{e(v)}$, V_k and V_k/kbar (where k, the number of successful gametes per parent, estimates individual fitness) to changes in the following inputs: population size, age structure (number of ages, age distribution, age specific mean fitnesses and variances of fitness), immigration rate and the probability distribution of age specific fitness (k_x).

The descending order of importance for the inputs controlling the value of $N_{e(v)}$ is: (1) population size; (2) the probability distribution of k_x; (3) age structure; (4) immigration. However, interactions among the inputs preclude a ranking applicable to all cases when there are simultaneous changes in two or more input variables. The results are discussed in the context of conservative stock management. The minimum data requirements for rational management are concluded to be estimates of the type of probability distribution for age specific fitness, age composition of the reproductive stock, age specific differences in the mean and variance of fitness, and population size.

INTRODUCTION

This paper describes the sensitivity analysis of functional relationships used in a genetic fitness model for fisheries management (Kapuscinski and Lannan 1984a). The response of a stock's variance effective number ($N_{e(v)}$) to changes in input variables was studied because application of the model to stock management involves maintaining the variance effective number in present time ($N'_{e(v)}$) at the level calculated for reference seasons in the past ($N_{e(v)}$). The analysis included changes in population size (in successive breeding seasons), age structure, immigration rate and the variance of fitness. Also, different probability distributions of fitness were examined because, for some distributions, the variance of fitness can be estimated from the mean.

Five possible probability distributions of fitness were considered. In all cases, k_x, the probability distribution of successful gametes at age x was used as an estimate of the probability distribution of fitness. A high frequency of low individual fitness ($0 \leq k_x \leq 1$) and a low frequency of very high values of individual fitness are expected in most commercial fish stocks, especially in the dynamic marine environment and in the face of large exploitation rates. Average fitness (kbar) for a stock is expected to be low because a kbar of 1 is associated with a rapidly declining stock ($N_t = 0.5N_{t-1}$), a kbar of 4 is associated with a rapidly growing stock ($N_t = 2N_{t-1}$) and a kbar of 2 is associated with a stable stock size ($N_t = N_{t-1}$). These conditions for the values of fitness are met by the following asymmetrical probability distributions of k_x: Poisson, negative exponential, gamma when β is small and binomial when n is much larger than the mean (kbar_x) (see appendix A for explanation of parameters). A contrasting set of conditions for a commercial stock would include a low frequency or even zero frequency of small individual fitness ($0 \leq k \leq 1$) and an increased frequency of large individual fitness. These conditions would apply to a stock experiencing very favorable environmental conditions for a number of breeding seasons in the wild or to a cultured stock. The following symmetrical (or nearly symmetrical) distributions satisfy these conditions: normal, gamma when β is large and binomial when n and the mean (kbar_x) are small.

METHODS

Sensitivity analysis of the functional relationships for the fitness model was conducted to study the response of output variables to changes in one or more inputs.

Functional Relationships

Functional relationships derived from principles of population biology and population genetics were described by Kapuscinski and Lannan (1984a). They relate the variance effective number, $N_{e(v)}$, for a reproductive stock to population size, the mean and variance of successful gametes (estimates of $\bar{W}$ and V_w), age structure and migration. The following equations were used in the sensitivity analysis:

$$N_{e(v)} = \frac{N_{t-1}\ \bar{k}}{1 + \frac{V_k}{\bar{k}}(1-M)^2} \qquad (1)$$

where:

$$N_{t-1} = \sum_x N_{x,t-1} \qquad (2)$$

$$\bar{k} = \frac{2\sum_n N_{x+n,\ t+n}}{N_{t-1}} \qquad (3)$$

$k_x = f(\bar{k})$ such that

$$\bar{k} = \frac{\sum_x \bar{k}_x N_{x,\ t-1}}{N_{t-1}} \qquad (4)$$

$$\sigma^2_{k,x} = f(\bar{k}_x) \qquad (5)$$

$$s^2_{k,\ x} = \frac{\sigma^2_{k,\ x}\ (N_x\ -1)}{N_x} \qquad (6)$$

and

$$V_k = \frac{\sum_x S^2_{k,x} N_{x,t-1}}{\sum_x N_{x,t-1}} = \frac{\sum_x S^2_{k,x} N_{x,t-1}}{N_{t-1}} \qquad (7)$$

Definitions for the terms in equations (1) to (7) are (Kapuscinski and Lannan 1984a):

x = the age of parents;

N_{t-1} = the number of parents in breeding season t-1 where $N_{x,t-1}$ represents the parents of age x;

$\bar{k}$ and V_k = the mean and variance of successful gametes (k) contributed per parent;

M = the fraction of the stock replaced by migrants in breeding season t-1;

$\sigma^2_{k,x}$ = the true variance of k for all fish of age x;

$\bar{k}_x$ and $s^2_{k,x}$ = the mean and variance of k for fish of age x within one stock.

Sensitivity analysis was conducted with a Pascal program (appendix B) developed from these equations and run on an Apple IIe computer. The program inputs included values for:

1. the range of ages (first x - last x),
2. $N_{x,t-1}$ for each x,
3. $\sum_n N_{x+n,t+n}$,
4. M,
5. the pattern of increase in $kbar_x$ as x increases, where the choices are linear or positive exponential and
6. the probability distribution of k within a given age class (x).

The choices for the probability distribution of k were (Hillier and Lieberman 1974):

1. Poisson where $\sigma^2_{k,x} = kbar_x$,
2. negative exponential where $\sigma^2_{k,x} = (kbar_x)^2$,
3. gamma where $\sigma^2_{k,x} = kbar_x \beta$ and an input value for β was required,
4. binomial where $\sigma^2_{k,x} = kbar_x(1-\frac{kbar_x}{n_x})$ and an input value for n_x was required or
5. normal where $\sigma^2_{k,x}$ cannot be estimated from $kbar_x$, thus an input value for $\sigma^2_{k,x}$ was required.

The derivations of the variance formulae and the ranges of input values (based on biologically meaningful values) are given in appendix A. The program outputs were:

1. N_{t-1} and kbar (equations 2 and 3) for an entire stock,
2. kbar_x, $\sigma^2_{k,x}$ and $s^2_{k,x}$ for each x (equations 4 - 6),
3. V_k (equation 7) for an entire stock and
4. $N_{e(v)}$ (equation 1) for an entire stock.

Sensitivity Tests

The sensitivity of $N_{e(v)}$ to changes in one or several variables at a time was studied. In some cases, the sensitivity of V_k or V_k/kbar was examined at the same time. Unless stated otherwise in the results, the range of ages (x) was 2 - 5, the numbers at each age corresponded to an intermediate age distribution (Table III.1), N_{t-1} was 1000, M was 0.1 and there was a linear increase in kbar_x as x increased. The numbers at each age for the cases where there was a predominantly young or a predominantly old age distribution and for the cases where the range of ages was 1 - 10 are given in Table III.1. A Poisson probability distribution of k, an intermediate age distribution and a constant kbar (kbar = 1) characterized the cases where M was varied.

The sensitivity of $N_{e(v)}$ to changes in program inputs was examined in a management context by defining the critical value of $N_{e(v)}$ to be the value required to maintain stock abundance at the replacement level, where kbar = 2. Thus, for conservative management, the critical $N_{e(v)}$ and $N'_{e(v)}$ are the smallest acceptable values for the genetic objective defined by Kapuscinski and Lannan (1984a):

$$N_{e(v)} = N'_{e(v)} \tag{8}$$

RESULTS

The results of the sensitivity analysis are presented graphically in Figures III.1 through III.13.

Response of Age Specific Fitness to Input Variables

Because the variables $kbar_x$ and $s^2_{k,x}$ were program outputs, their values at each age (x) were different for different ranges of x, different values of $N_{x,t-1}$ and kbar or for different patterns of increase in $kbar_x$ as x increased. Different inputs for x, $N_{x,t-1}$, kbar, or the pattern of increase in $kbar_x$ yield different curves with different values for each $kbar_x$ and $s^2_{k,x}$ associated with them. Thus, biological interpretation of all the sensitivity analysis results must be done in the following manner. Different curves on a figure represent either different stocks or the same stock at different breeding intervals. For example, if 1000 parents consisting of ages 1 - 10 are compared to 1000 parents consisting of ages 2 - 5, then:

a) $N_{e(v)}$ for ages 1 - 10 and $N_{e(v)}$ for ages 2 - 5 represent two stocks or

b) $N_{e(v)}$ for ages 1 - 10 represents one stock and $N_{e(v)}$ for ages 2 - 5 represents the same stock at another breeding season. In the latter case, a change in the stock's age structure resulted in a corresponding change in $kbar_x$ and $s^2_{k,x}$ values for each x. In evolutionary terms, the changes in $kbar_x$ and $s^2_{k,x}$ could result from changes in either the genetic or the environmental component of the phenotypic values (Falconer 1981).

Sensitivity of $N_{e(v)}$ and V_k/kbar to the Probability Distribution of k

There is interaction between the function $N_{e(v)}$ = f(kbar) and the probability distribution of k for distributions where the variance can be estimated from the mean (Fig.III.1). There is a linear increase in $N_{e(v)}$, reflecting a linear increase in V_k, as kbar increases for the Poisson, binomial and gamma distributions. There is little change in $N_{e(v)}$ as kbar increases for the negative exponential distribution because the quadratic increase of V_k in the denominator counteracts the linear increase of kbar in the numerator of equation (1) (refer to variance formula in methods). The gamma distribution is the most general distribution, yielding a family of straight lines for different values of β. Values for $N_{e(v)}$ for the gamma and Poisson distributions are identical when $\beta = 1$.

Values for $N_{e(v)}$ for the gamma and negative exponential distributions are identical when β = kbar.

The binomial distribution generates a family of straight lines for different values of n (Fig. III.2.) where n is the largest possible value for fecundity (refer to Appendix A). The lines approach the Poisson line (Fig. III.1) for intermediate values of n (e.g., n = 20 - 200) and are identical to the Poisson line for large n (e.g., n = 2000). The binomial lines differ significantly from the Poisson line only when n is very small (n = 2 - 8) because, then, V_k for a given kbar is much smaller in the binomial than in the Poisson distribution. Whereas $V_k = f(\sigma^2\text{kbar})$ is approximately equal to kbar for the Poisson distribution, $V_k = f(\sigma^2,\text{kbar},n)$ decreases when n decreases and kbar is held constant for the binomial distribution (refer to variance formulae in methods).

The probability distribution of k affects the critical value of $N_{e(v)}$ (Fig. III.1 and III.2). The critical value of $N_{e(v)}$ increases as β increases in the gamma distribution and as maximum fecundity (n) decreases in the binomial distribution. The critical value of $N_{e(v)}$ for the Poisson distribution is always greater than it is for the negative exponential distribution.

Results for other portions of the sensitivity analysis are restricted to the Poisson and negative exponential distributions because they show the greatest difference between their slopes for $N_{e(v)} = f(\text{kbar})$.

There is a linear increase in $N_{e(v)}$ as kbar increases for a normal distribution of k where the variance cannot be estimated from the mean (Fig. III.3). Also a family of straight lines is generated for different values of V_k/kbar. When V_k/kbar is 0.498 the line (slope = 712.57) approaches the Poisson line (slope = 553.48) in Figure III.1 for which V_k/kbar is 0.996. This suggests that the value of V_k associated with a given kbar in a stock with a normal distribution of k can be approximately one-half of the V_k in a stock with a Poisson distribution. Also the critical value of $N_{e(v)}$ increases as V_k/kbar decreases in the normal distribution. Thus the rational development of genetic objectives for stock management requires knowledge of the probability distribution of k in conjunction with estimates of V_k (Kapuscinski and Lannan 1984a).

There is interaction between the function V_k/kbar = f(kbar) and the distribution of k (Fig. III.4). The ratio V_k/kbar is constant as kbar increases for the following distributions: poisson, binomial (when n is small), gamma (when β is held constant) and normal (when V_k is allowed to increase as kbar increases). There is a linear increase in V_k/kbar as kbar increases for the negative exponential and gamma distributions (when β = kbar). V_k/kbar decreases to an asymptote as kbar increases for a normal distribution when σ^2_x is held constant for each x. The probability distribution of k affects the value of V_k/kbar associated with the critical value of $N_{e(v)}$ (i.e., where kbar = 2). A larger value of V_k/kbar is required for asymmetrical distributions (Poisson, negative exponential, gamma and binomial when n is large) than is required for symmetrical distributions (normal and binomial when n is small and the probability of yielding a successful gamete from each egg is 0.5).

Sensitivity of V_k to Age Specific Fitness

The probability distribution of k determines the general sensitivity of V_k to kbar (Fig. III.5): there is a slight linear increase in V_k as kbar increases (slope = 0.996) for a Poisson distribution and a quadratic increase in V_k as kbar increases for a negative exponential distribution. However, there is interaction between the pattern of increase in kbar_x with increasing x and the probability distribution of k. While there is little difference between the Poisson curves for a linear and an exponential increase in kbar_x, the elevation of the negative exponential curve is much greater for an exponential increase in kbar_x than it is for a linear increase in kbar_x. The value of V_k associated with the critical value of $N_{e(v)}$ is always greater for a negative exponential distribution of k than for a Poisson distribution of k. In addition, V_k associated with the critical value of $N_{e(v)}$ is greatest when there are a negative exponential distribution of k and an exponential increase in kbar_x with increasing x.

Sensitivity of $N_{e(v)}$ to Age Specific Fitness and the Number of Reproductive Ages

The variance effective number as a function of kbar is the same for different numbers of ages and different patterns of increase in kbar_x with increasing x when there is a Poisson probability distribution of k (Fig. III.6). This result applies only to the case where $kbar_x$ values (for a given kbar) are allowed to vary as the number of ages varies and N_{t-1} is held constant. Under natural conditions, $kbar_x$ values may remain constant, at least over the short term, when the age structure of a stock changes. Also, a change in age structure probably would result in a corresponding change in the total number of parents (N_{t-1}) and kbar. Thus the slope of the straight line shown in Figure III.6 would change.

The variance effective number as a function of kbar differs for different numbers of ages and patterns of increase in $kbar_x$ with increasing x when there is a negative exponential probability distribution of k (Fig. III.7). For a given pattern of increase in $kbar_x$, the elevation of the curve and the critical value of $N_{e(v)}$ decreases as the number of ages increases because V_k increases. For a given number of ages, the critical value of $N_{e(v)}$ is much smaller when the increase in $kbar_x$ is exponential than when it is linear. There is interaction between the number of ages and the pattern of increase in $kbar_x$: the difference in elevation between the curves for ages 2 - 5 and ages 1 - 10 is greater when the increase in $kbar_x$ is exponential than when it is linear. These results apply only to the case where $kbar_x$ values are allowed to vary. If $kbar_x$ values remain constant and N_{t-1} and kbar values change when age structure changes in a natural stock, then the differences among elevations of the curves may be greater than the differences shown in Figure III.7.

Sensitivity of V_k and $N_{e(v)}$ to Age Distribution, Age Specific Fitness and the Pattern of Increase in $kbar_x$ for a Constant Number of Ages

The functions V_k = f(kbar) and $N_{e(v)}$ = f(kbar) are the same for different age distributions and different patterns of increase in $kbar_x$ with increasing x when there is a Poisson probability distribution of k (Fig. III.8a and III.8b). Also, these functions are the same for different age distributions and a linear increase in $kbar_x$ when there is a negative exponential probability distribution of k (Fig. III.9a and III.9b). However, the functions are different for different age distributions and an exponential increase in $kbar_x$ when there is a negative exponential probability distribution of k (Fig. III.10a and III.10b). The elevation of the curve for V_k (Fig. III.10a) increases and the elevation of the curve for $N_{e(v)}$ decreases as the proportion of young fish increases (going from a predominantly old to a predominantly young age distribution). This result is due to concurrent increases in $kbar_x$ and $s^2_{k,x}$ at each age (x) and for each kbar (Table III.2a). There are similar but less dramatic increases in these variables for the data presented in Figures III.8a, III.8b, III.9a and III.9b (Table III.2b).

Sensitivity of $N_{e(v)}$ to the Immigration Rate

The variance effective number as a function of M when kbar and V_k are held constant is described by a curve with one inflection

(Fig. III.11): for lower values of M, there is a linear increase in $N_{e(v)}$ as M increases; the rate of increase in $N_{e(v)}$ is smaller (above the inflection) at higher values of M; $N_{e(v)}$ is equal to the total number of successful gametes ($2\Sigma_n N_{x+n,t+n}$) at M = 1.0. This function is identical for different numbers of ages, probability distributions of k (Poisson or negative exponential) and patterns of increase in $kbar_x$ with increasing x because age specific fitnesses ($kbar_x$, $s^2_{k,x}$) were allowed to vary. If age specific fitnesses remain constant in a natural stock, the elevation of the curve in Figure III.11 will change when the age structure changes. If the value of $N_{e(v)}$ calculated for a given stock under a given set of conditions for the other variables is below the critical value, then it can be raised by an increase in M.

The variance effective number as a function of M is different for different values of N_{t-1} when kbar and V_k are held constant (Fig. III.12). The elevation of the curve and the rate of increase (below the inflection) increases as N_{t-1} increases.

The variance effective number as a function of M is different for different values of kbar when N_{t-1} is held constant (Fig. III.13). The elevation of the curve and the rate of increase (below the inflection) increases as kbar increases.

DISCUSSION

Population size (N_{t-1}, N_t and thus kbar) is the principal input controlling the value of $N_{e(v)}$. The descending order of importance of the other variables is: (1) the probability distribution of k_x because it determines the range of $s^2_{k,x}$ values for each $kbar_x$ and thus the range of V_k for a given kbar; (2) age structure (number of ages, age distribution, $kbar_x$, $s^2_{k,x}$) with the differences among $kbar_x$ and $s^2_{k,x}$ values being most important; (3) migration. However, interactions among these variables preclude a ranking applicable to all cases when there are simultaneous changes in two or more variables.

The probability distribution of k_x reflects the outcome of all the events experienced by individuals of a stock during their life history. A characteristic distribution, a characteristic set of distributions (where each member of the set represents one stock) or different sets at different times for the species are possibilities that cannot be excluded given the present paucity of empirical information. The model behaves quite differently with asymmetrical probability distributions than it does with symmetrical or nearly symmetrical distributions. Questions about the probability distribution of k_x of particular interest to management include:

1. can the variance be estimated from the mean,
2. is there a constant or variable value for V_k/kbar of a stock when the variance cannot be estimated from the mean, and

3. is an unimodal probability distribution appropriate for a given age within a stock?

When there is an affirmative response to the first question, V_k can be increased only by increasing kbar. This requires increasing the escapement ($\sum_n N_{x+n,t+n}$) at t+n breeding seasons for a given escapement (N_{t-1}) at t-1. Recognizing that the present functional relationships of the genetic fitness model provide a simplistic picture of the genetic diversity of a stock, the maintenance of a probability distribution of fitness (estimated by V_k and kbar), apart from any consideration for the value of $N_{e(v)}$, may be the most important management objective for insuring the long term adaptibility of a stock to a dynamic habitat. For the second question, conservative stock management would benefit from knowledge about (a) the response of V_k/kbar values to alternative management strategies (e.g., different exploitation rates) and (b) a possible optimal range of V_k/kbar values based on environmental uncertainty and exploitation rates for a given stock. When there is a negative response to the third question, application of an unimodal distribution to the functional relationships (as done in this paper) may underestimate the impact of changes in age structure on V_k, kbar and $N_{e(v)}$. Evidence for a pronounced bimodal frequency distribution of larval survivals (i.e., one component of fitness) in Pacific oysters, Crassostrea gigas, suggests that bimodal or even multimodal distributions of k_x are possible (Lannan 1980).

The direction and magnitude of differences among kbar_x and

$s^2_{k,x}$ values (i.e., age specific fitnesses) as age (x) increases affect the sensitivity of V_k and $N_{e(v)}$ to changes in age structure. An increase in these variables with increasing age is consistent with the evidence for increasing fecundity averages and variability with age in fishes (Beacham 1982, Pitcher and Hart 1982, Williams 1977). But their direction of change warrants determination in managed stocks because fertility is only one component of fitness. Williams (1977) suggested that an increase in fitness variation with age follows from principles operative in the evolution of senescence. The magnitude of age specific differences in fitness will influence the impact of selective harvesting of certain ages (usually of the older, larger fish) on the value of $N_{e(v)}$. In this study, only one set of parameter values (i.e., slope and intercept) for linear and exponential increases in $kbar_x$ with age was used to simulate age specific differences in fitness. Thus, the simulated sensitivity of $N_{e(v)}$ to age structure may overestimate or underestimate the sensitivity for a given natural stock. This suggests a need for parameter estimation in managed stocks.

Also, stock management must address temporal changes in $kbar_x$ and $s^2_{k,x}$ values for each age (x). The sensitivity of $N_{e(v)}$ to age structure is different for the case where these values change (Fig. III.5 - III.12) than it is for the case where these values remain constant (Fig. IV.1 and IV.3) as N_x and kbar values change. Under natural conditions, $kbar_x$ and $s^2_{k,x}$ values may be constant over the short term while they may vary over the long term. In any case, the sensitivity of $N_{e(v)}$ to temporal changes in these variables will be the same whether the changes are due to the genetic or environmental components of phenotypic values.

An increase in kbar_x and $s^2_{k,x}$ for each age was observed in this study as the age distribution shifted from predominantly old to predominantly young fish (Table III.2). This leads one to speculate that similar increases in these variables over time could allow a stock to maintain a small critical value of $N_{e(v)}$ when there is continual selective harvesting of older fish. This would counteract the tendency for the overexploitation of older fish to raise the critical value of $N_{e(v)}$ (refer to results for Fig. III.10). Noting that the numerator of equation (1) can be simplified to $2\sum_n N_{x+n,t+n}$, the following suggestion can be made: smaller critical values of $N_{e(v)}$ increase the probability of stock persistence in the face of large exploitation rates because they require smaller escapements ($\sum_n N_{x+n,t+n}$) over t+n seasons than larger $N_{e(v)}$ values require. These speculations may explain, at least in part, the decreases in average size, average age and total abundance observed for Pacific salmon stocks that still persist, although at levels far below historical abundances, after many generations of heavy exploitation (Ricker 1981).

The variance effective number is relatively insensitive to changes in the immigration rate when parent stock size (N_{t-1}) is small and the stock is declining in abundance (kbar < 2). Furthermore, $N_{e(v)}$ is quite insensitive at the low values of M (M < 0.1) required to maintain genetically distinct stocks (Allendorf 1983, Falconer 1981).

For example, typical straying rates for Pacific salmon are believed to be well below 10%. Quinn (1984) reported rates of 0.6 - 1.5% for sockeye salmon. But he also discussed the influence of environmental factors (e.g., stability of the spawning stream) and life history pattern (e.g., the presence or lack of reproductive age variation) on the balance between straying and homing in Pacific salmon species. The simple incorporation of migration (M) into these functional relationships cannot address the full impact of migration on the maintenance of V_w in a stock.

Management must address the interaction of input variables on the sensitivity of $N_{e(v)}$. The minimum data requirements for developing a rational management plan for a given stock are: estimates of the type of probability distribution of k_x, age composition (N_x for each x), age specific differences in $kbar_x$ and $s^2_{k,x}$ and population size (N_{t-1} and ${}_n N_{x,t+n}$). Without all these estimates, the inherent dangers in applying simplistic functional relationships for $N_{e(v)}$ to the genetic objective of maintaining $\dot{W}$ will escalate (Kapuscinski and Lannan 1984a).

Fig. III.1. The variance effective number, N_e, as a function of the average number of successful gametes (kbar) and the probability distribution of successful gametes when the variance of the distribution is a function of the mean.

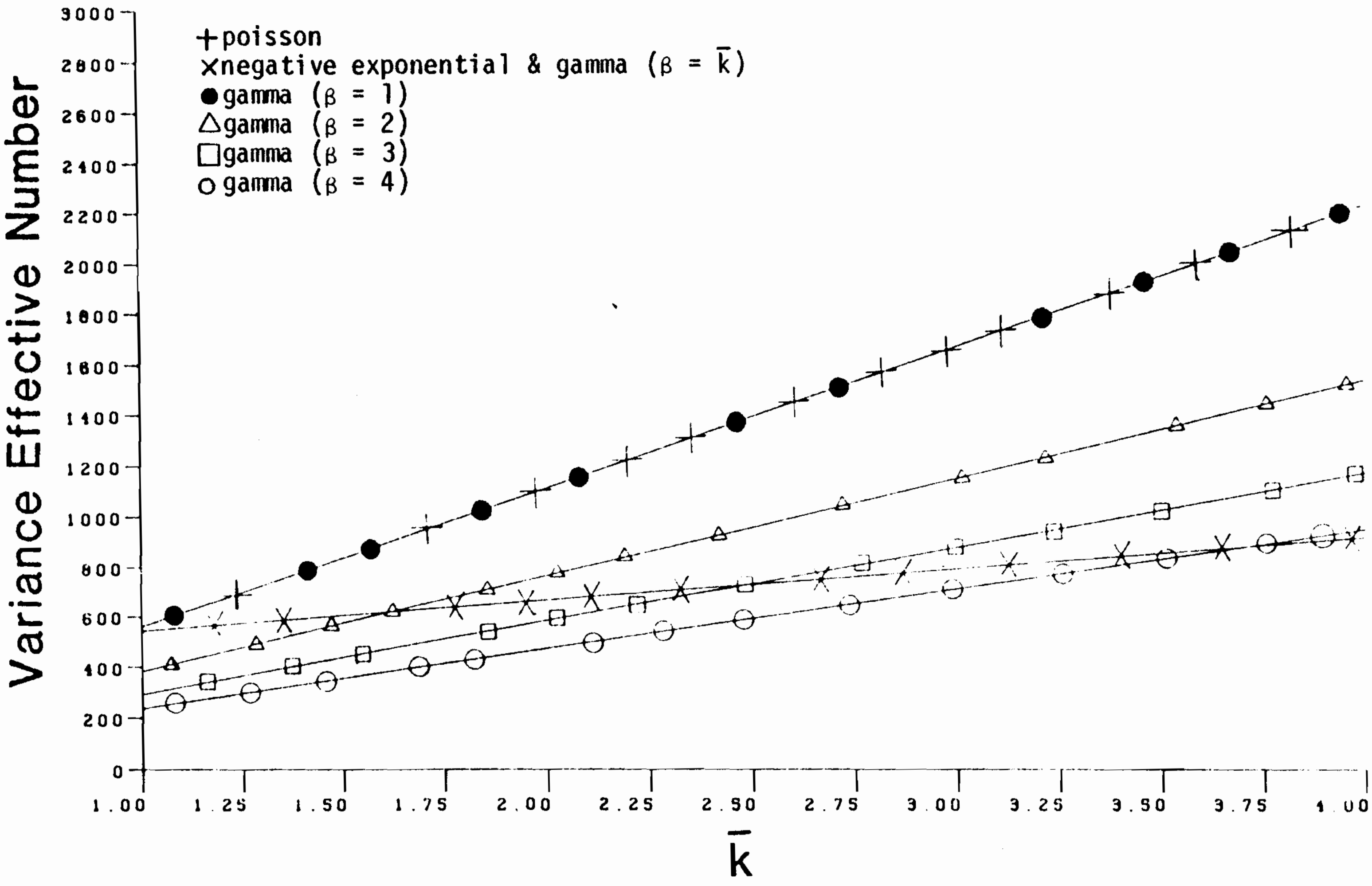

Variance Effective Number
3000
2800
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
1.00
1.25
1.50
1.75
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00
$\bar{k}$
+ poisson
× negative exponential & gamma ($\beta = \bar{k}$)
● gamma (β = 1)
△ gamma (β = 2)
□ gamma (β = 3)
○ gamma (β = 4)

Fig. III.1

Fig. III.2. The variance effective number, N_e, as a function of the average number of successful gametes (kbar) and the parameter n when successful gametes are binomially distributed.

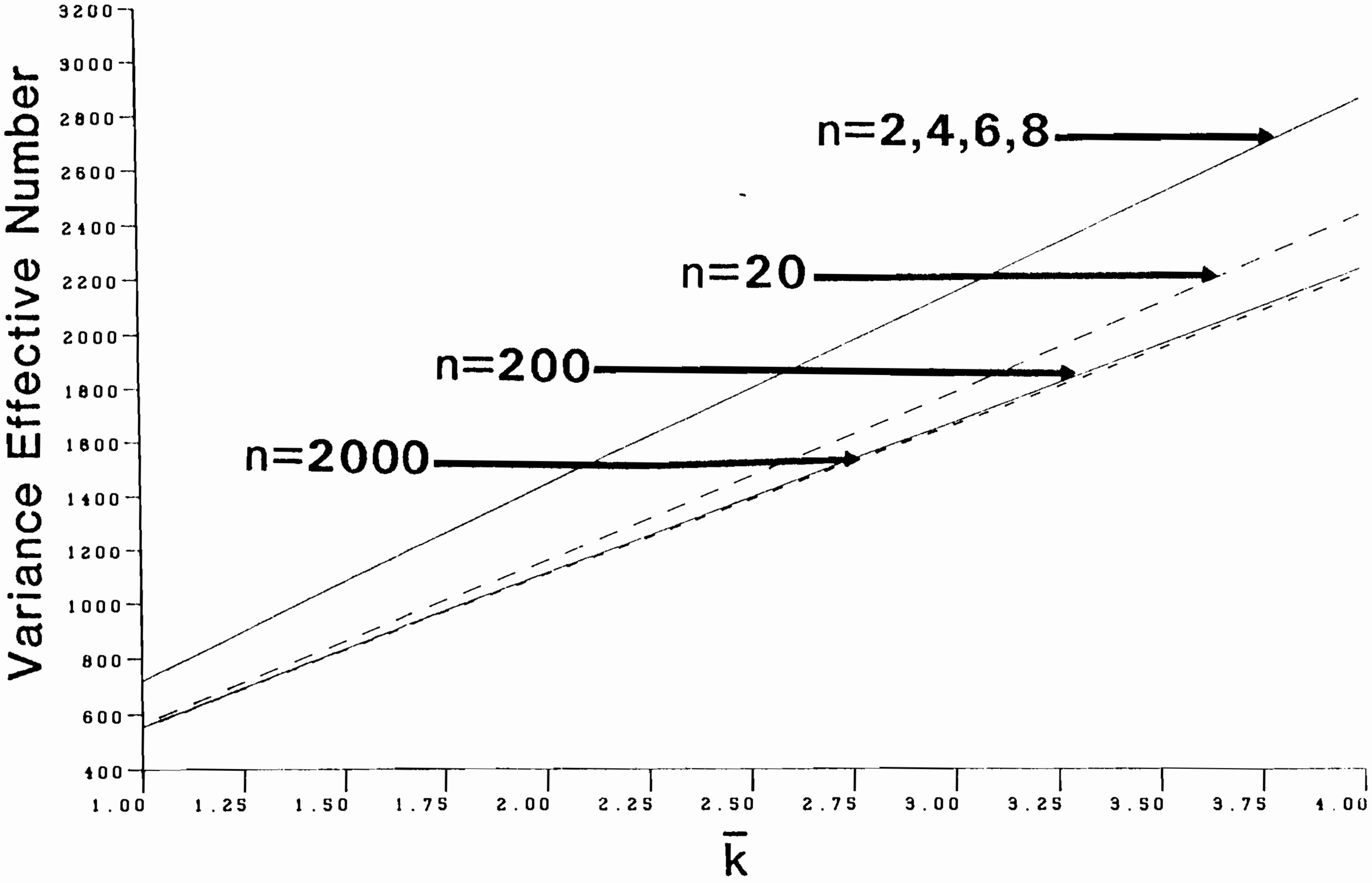
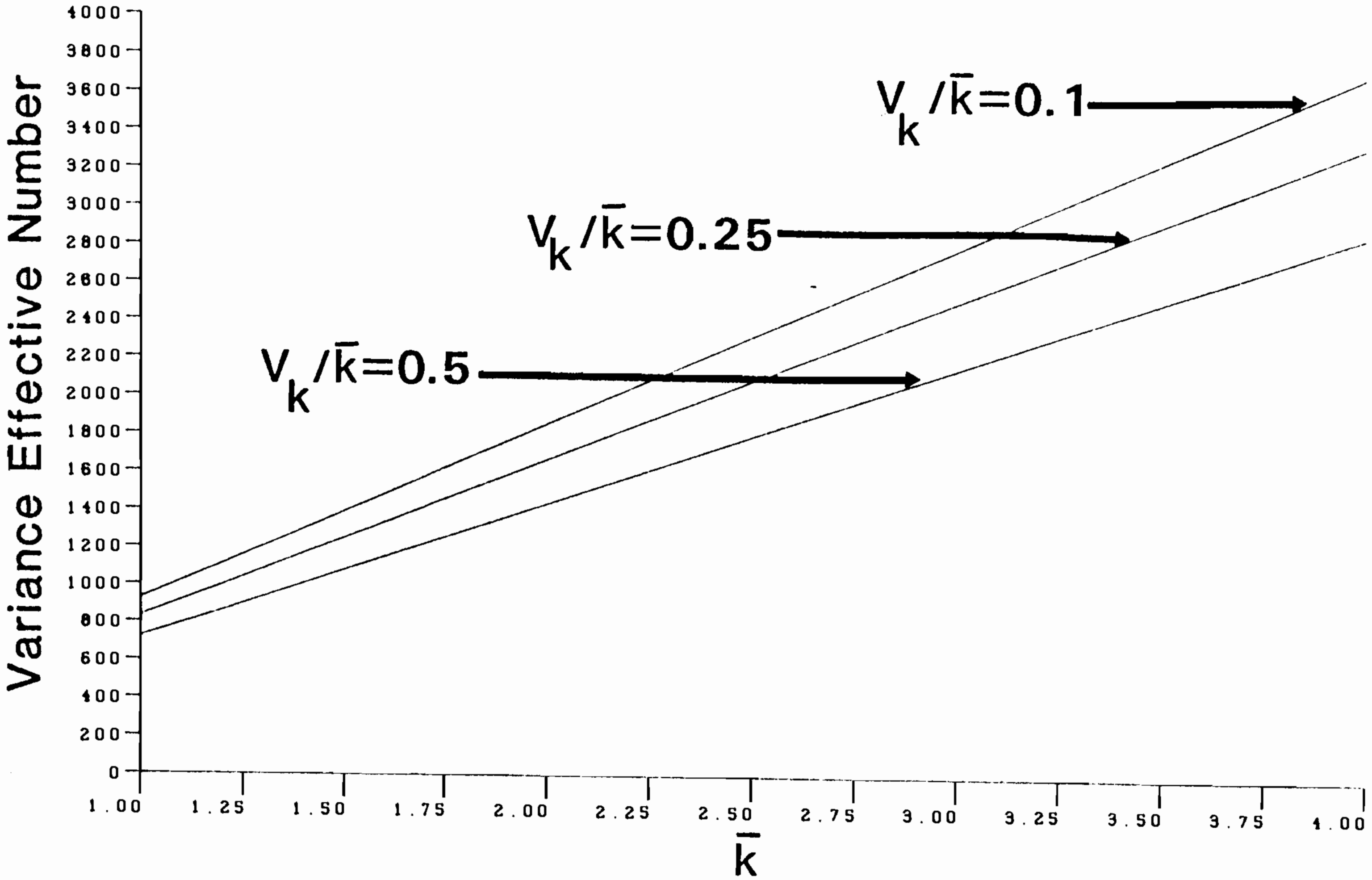

Variance Effective Number
3200
3000
2800
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
1.00
1.25
1.50
1.75
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00
$\bar{k}$
n=2,4,6,8
n=20
n=200
n=2000

Fig. III.2

Fig. III.3. The variance effective number, N_e, as a function of the average number of successful gametes (kbar) and the ratio V_k/kbar when successful gametes are normally distributed.



Variance Effective Number
4000
3800
3600
3400
3200
3000
2800
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
1.00
1.25
1.50
1.75
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00
$\bar{k}$
$V_k/\bar{k}=0.1$
$V_k/\bar{k}=0.25$
$V_k/\bar{k}=0.5$

Fig. III.3

Fig. III.4. The ratio V_k/kbar as a function of the average number of successful gametes (kbar) and the probability distribution of successful gametes.

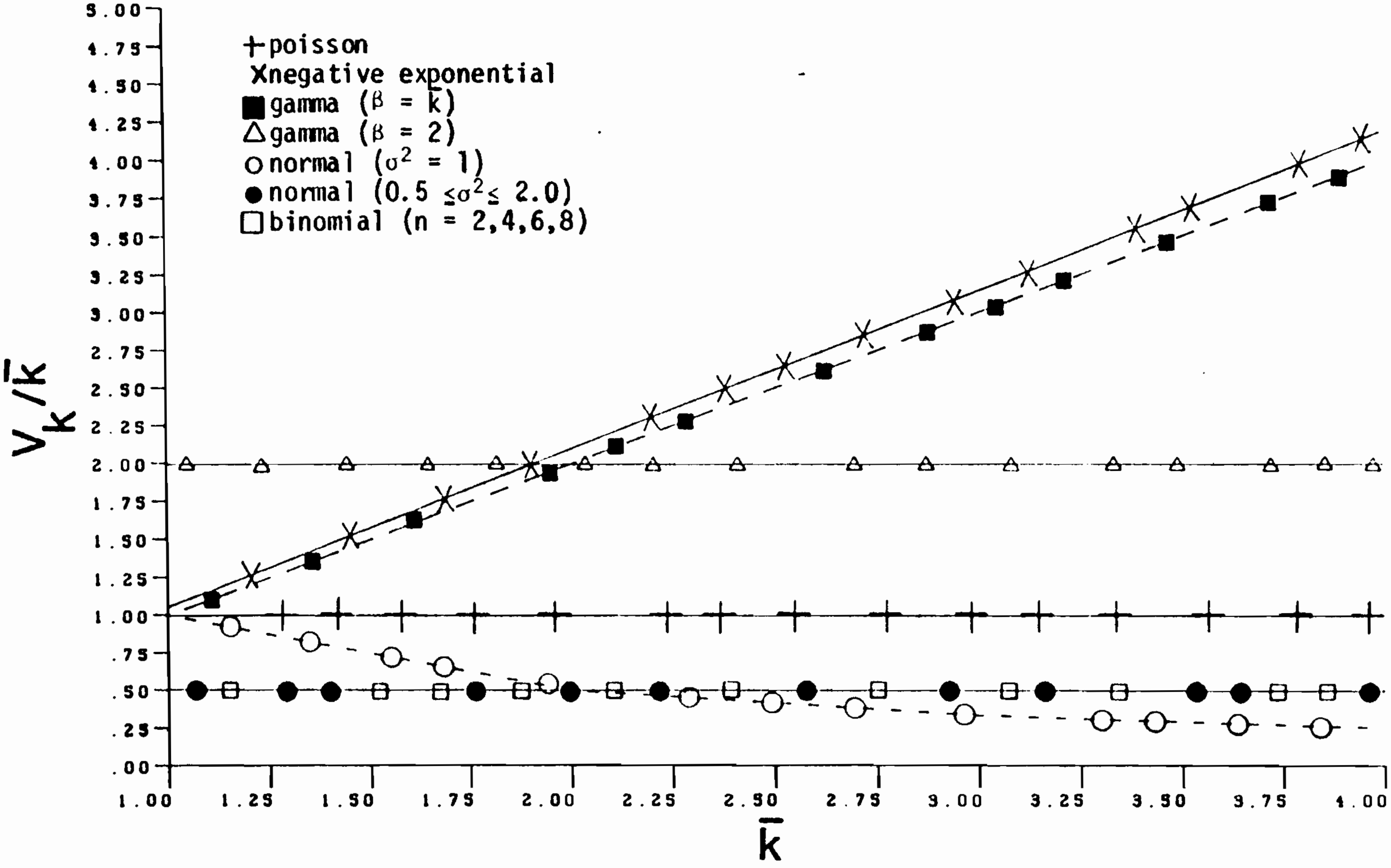

+poisson
Xnegative exponential
■gamma (β = k̄)
△gamma (β = 2)
○normal (σ^2 = 1)
●normal (0.5 ≤σ^2≤ 2.0)
□binomial (n = 2,4,6,8)
$V_k/\bar{k}$
5.00
4.75
4.50
4.25
4.00
3.75
3.50
3.25
3.00
2.75
2.50
2.25
2.00
1.75
1.50
1.25
1.00
.75
.50
.25
.00
1.00
1.25
1.50
1.75
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00
$\bar{k}$

Fig. III.4

Fig. III.5. The variance of successful gametes, V_k, as a function of the average number of successful gametes (kbar) and the pattern of age specific differences in kbar (kbar_x).

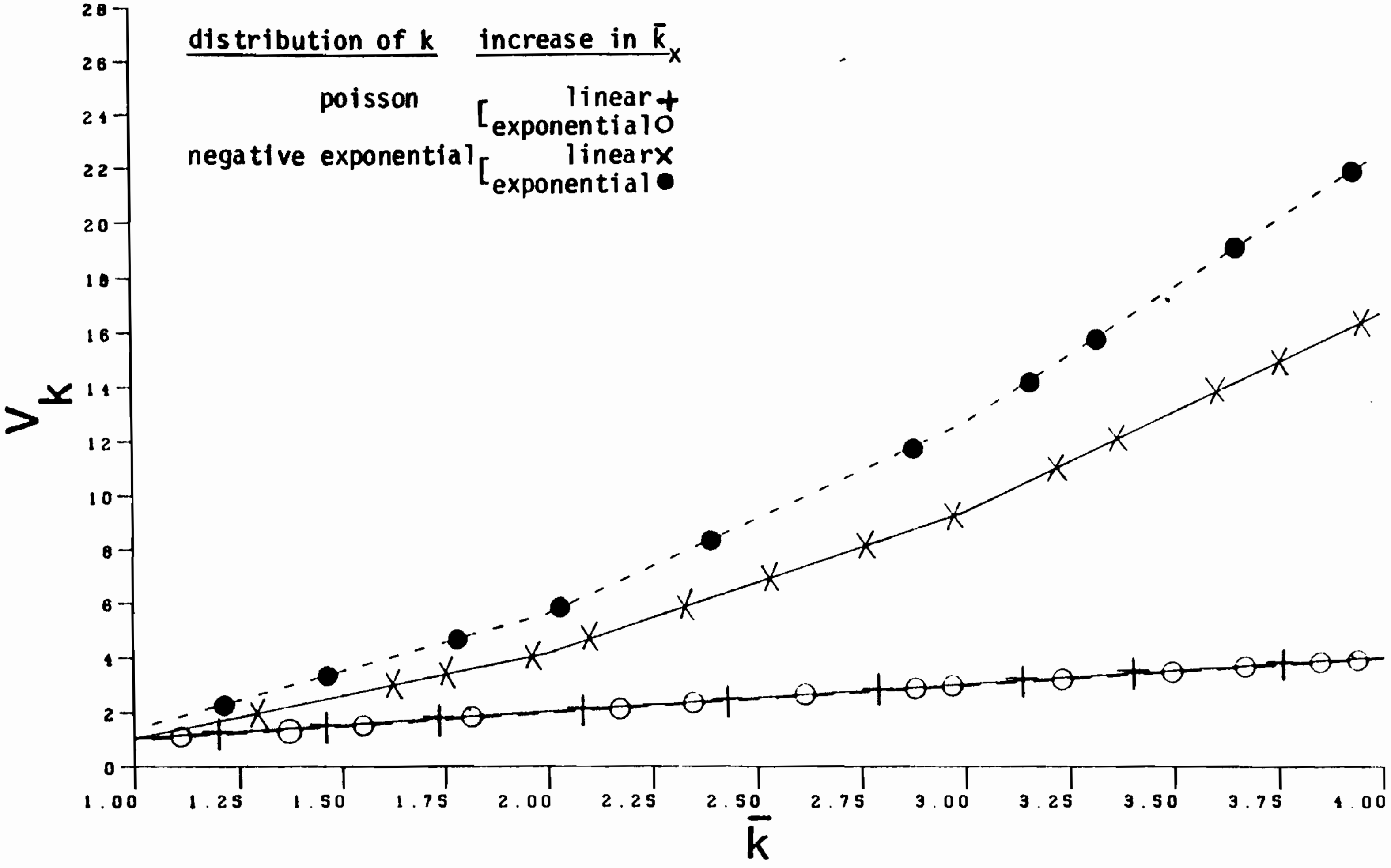

distribution of k
increase in $\bar{k}_x$
poisson
linear +
exponential ○
negative exponential
linear ×
exponential ●
V_k
$\bar{k}$
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
1.00
1.25
1.50
1.75
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00

Fig. III.5

Fig. III.6. The variance effective number, N_e, as a function of the average number of successful gametes (kbar), the pattern of age specific differences in kbar ($kbar_x$) and the number of reproductive ages when there is a Poisson distribution of successful gametes.

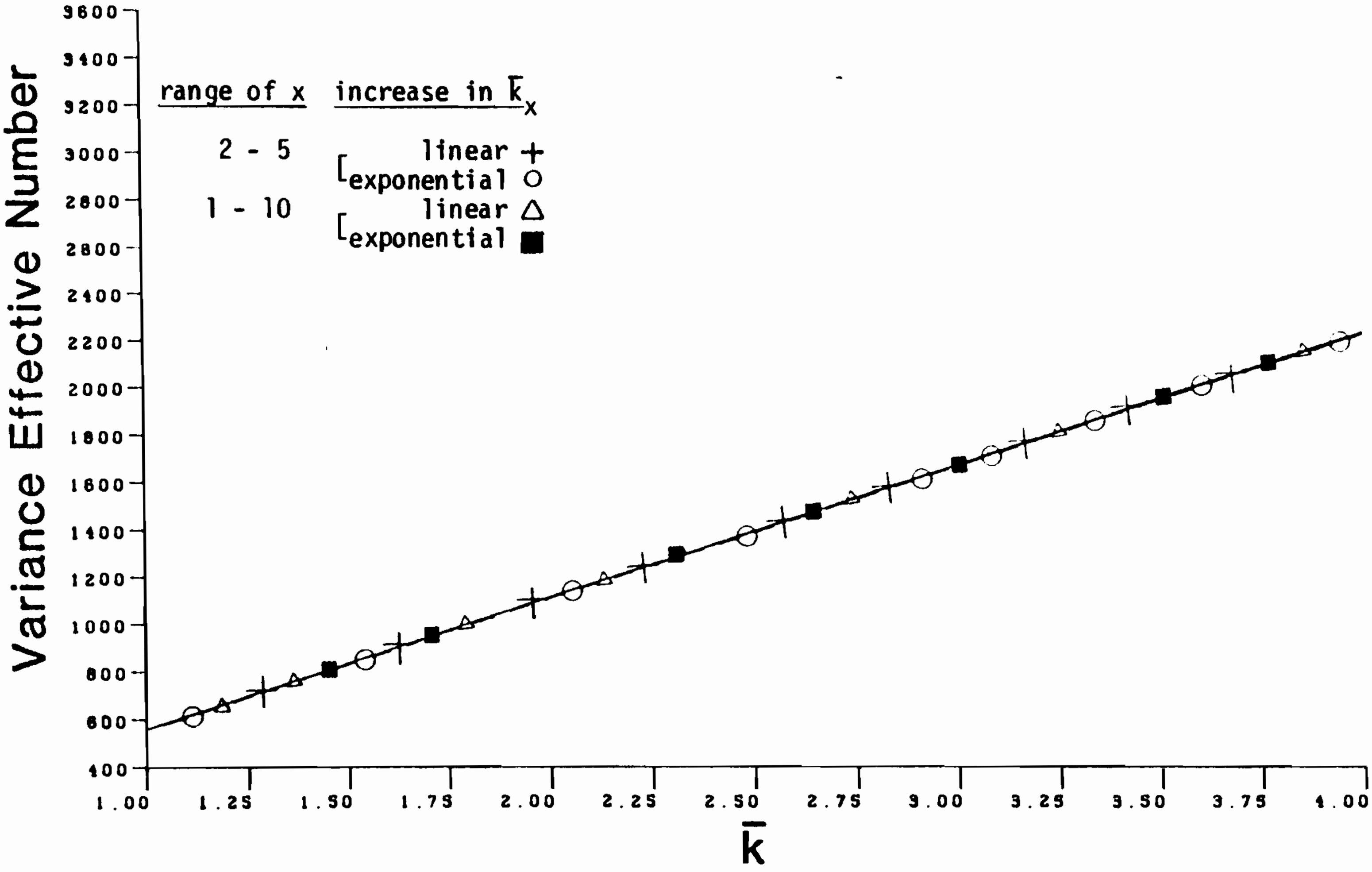

Variance Effective Number
3600
3400
3200
3000
2800
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
1.00
1.25
1.50
1.75
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00
$\bar{k}$
range of x
increase in $\bar{k}_x$
2 - 5
linear +
exponential ○
1 - 10
linear △
exponential ■

Fig. III.6

Fig. III.7. The variance effective number, N_e, as a function of the average number of successful gametes (kbar), the pattern of age specific differences in kbar ($kbar_x$) and the number of reproductive ages when there is a negative exponential distribution of successful gametes.

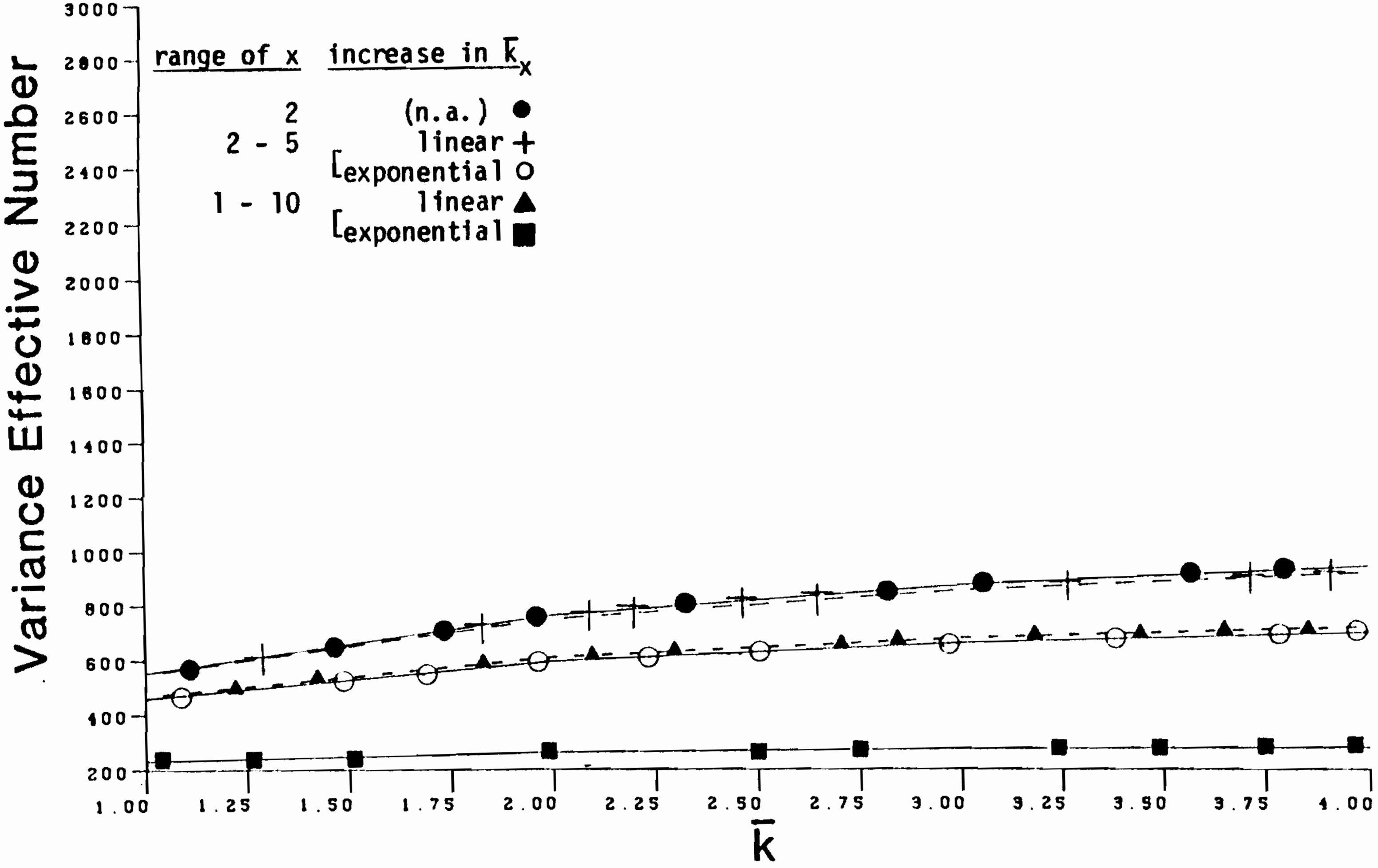

Variance Effective Number
3000
2800
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
1.00
1.25
1.50
1.75
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00
$\bar{k}$
range of x
increase in $\bar{k}_x$
2
(n.a.) ●
2 - 5
linear +
exponential ○
1 - 10
linear ▲
exponential ■

Fig. III.7

Fig. III.8.a and III.8.b. The variance of successful gametes, V_k, (a) and the variance effective number, N_e, (b) as a function of the average number of successful gametes (kbar), age distribution and the pattern of age specific differences in kbar ($kbar_x$) when there is a Poisson distribution of successful gametes.

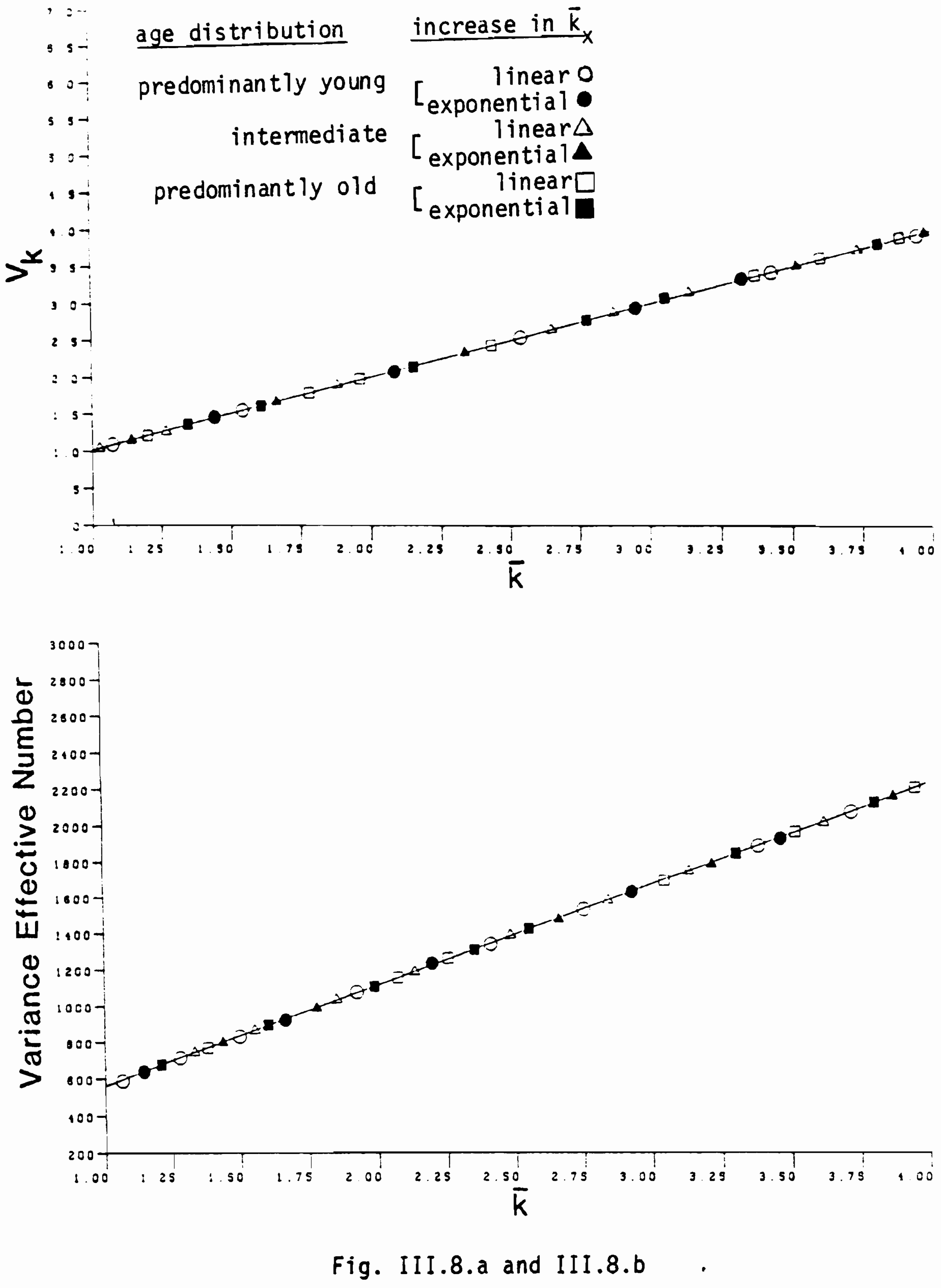


Fig. III.8.a and III.8.b

Fig. III.9.a and III.9.b. The variance of successful gametes, V_k, (a) and the variance effective number, N_e, (b) as a function of the average number of successful gametes (kbar), and the distribution of ages when there is a negative exponential distribution of successful gametes and the pattern of age specific differences in kbar ($kbar_x$) is linear.

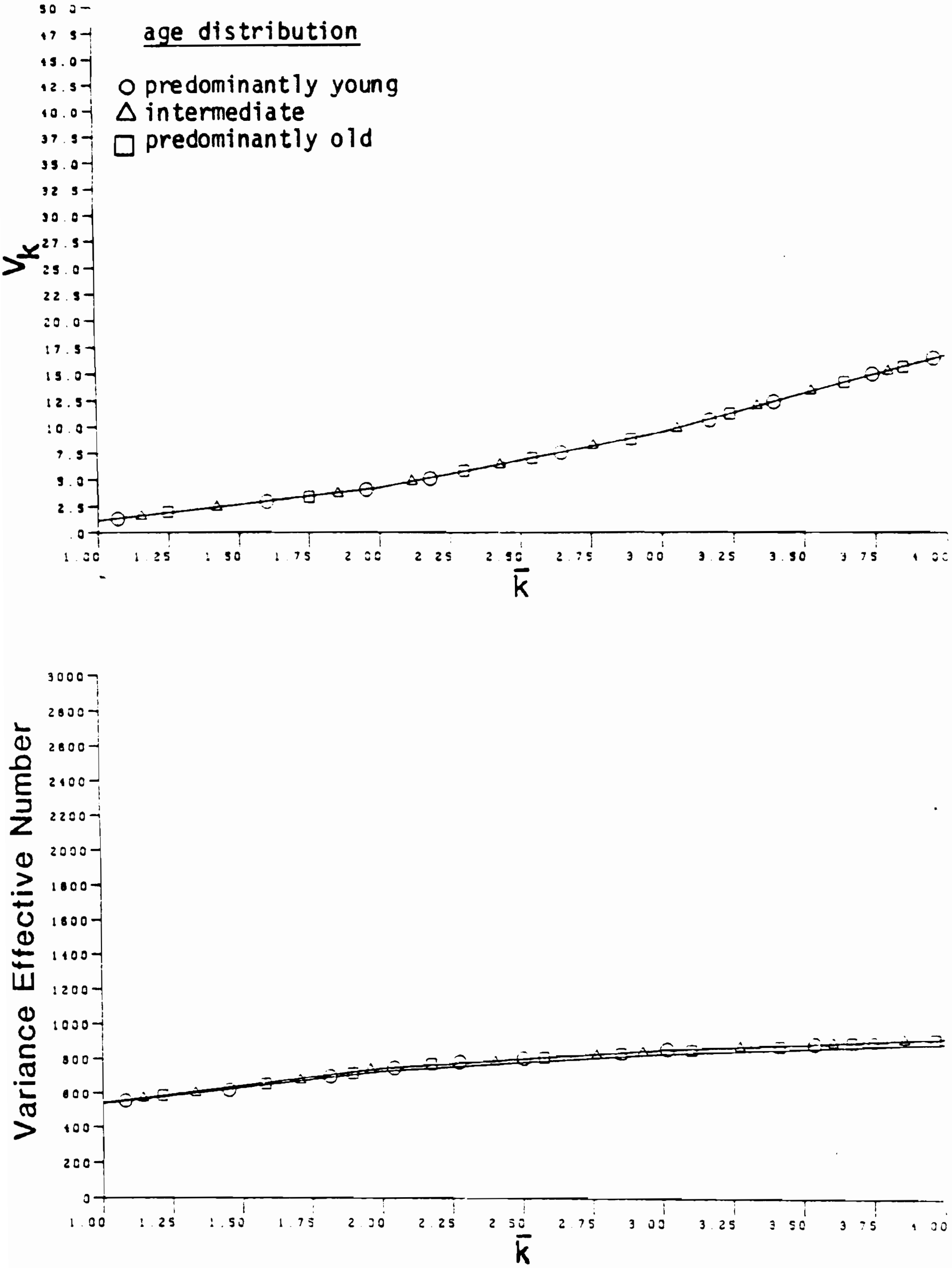


Fig. III.9.a and III.9.b

Fig. III.10.a. and III.10.b. The variance of successful gametes, V_k, (a) and the variance effective number, N_e, (b) as a function of the average number of successful gametes (kbar) and the distribution of ages when there is a negative exponential distribution of successful gametes and the pattern of age specific differences in kbar ($kbar_x$) is exponential.

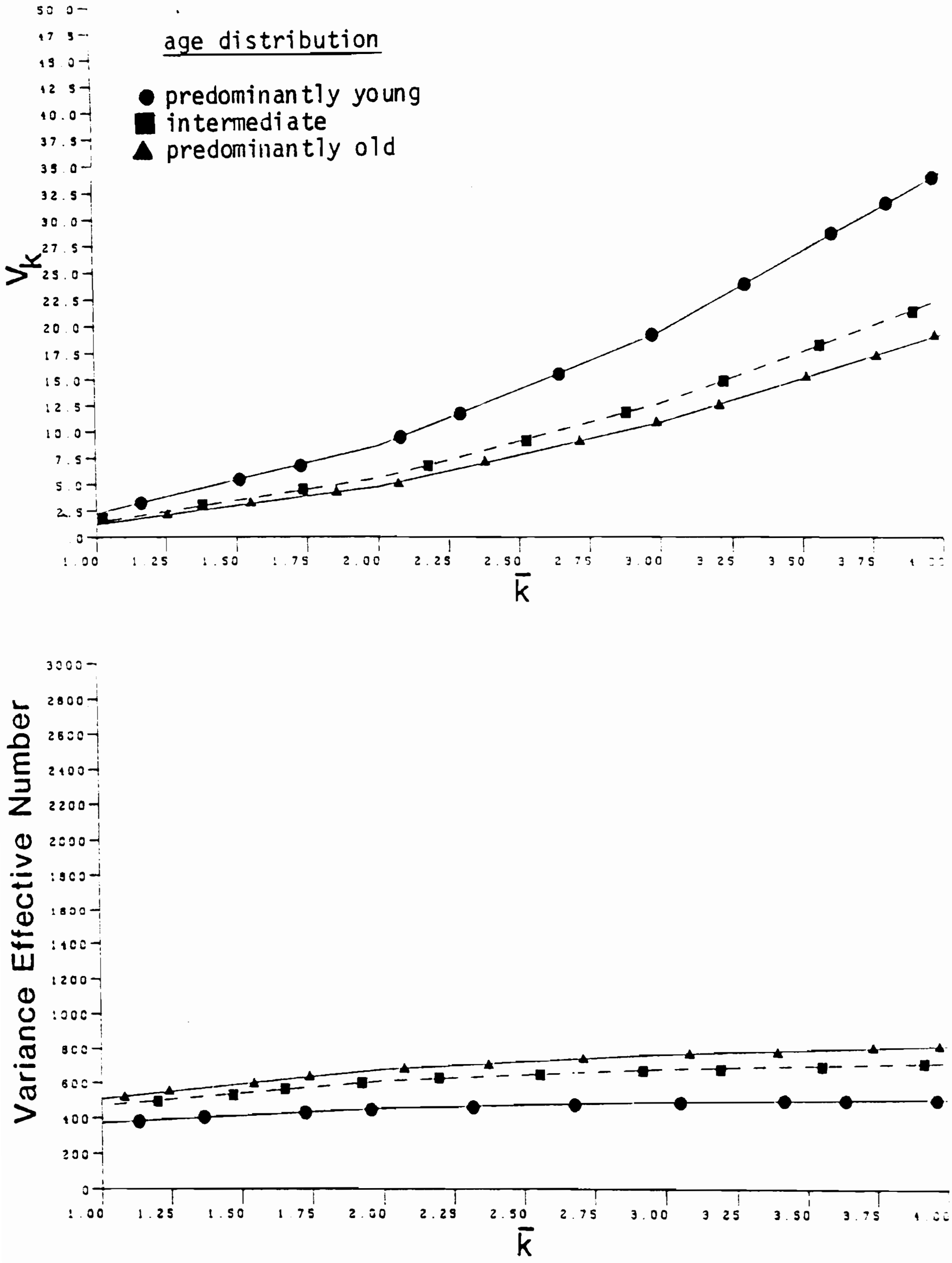


Fig. III.10.a and III.10.b

Fig. III.11. The variance effective number, N_e, as a function of immigration rate (M) when the average and variance of successful gametes (kbar and V_k) are held constant.

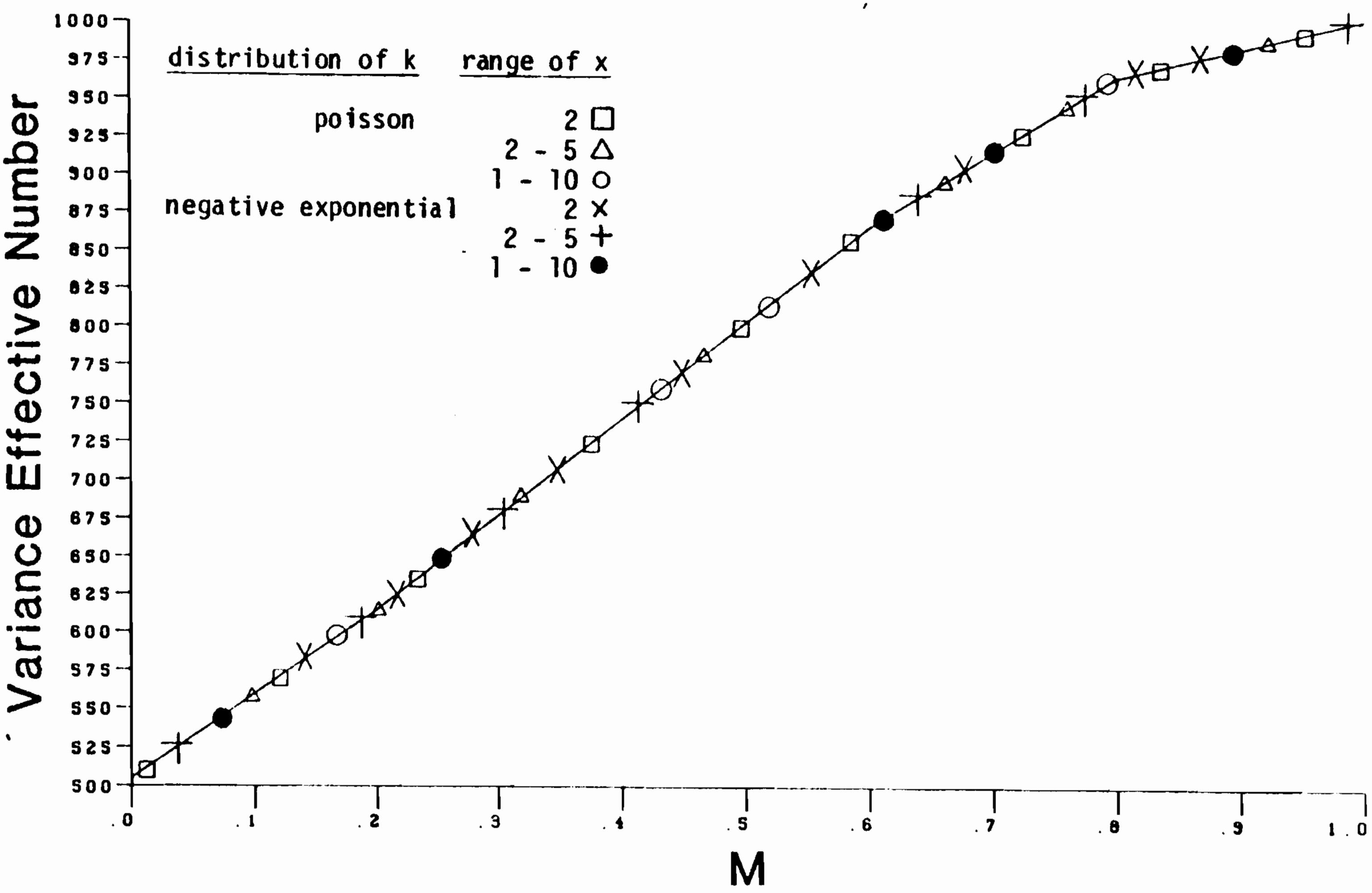

distribution of k
range of x
poisson
2
2 - 5
1 - 10
negative exponential
2
2 - 5
1 - 10
Variance Effective Number
1000
975
950
925
900
875
850
825
800
775
750
725
700
675
650
625
600
575
550
525
500
.0
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
M

Fig. III.11

Fig. III.12. The variance effective number, N_e, as a function of immigration rate (M) and number of parents (N_{t-1}) when the average and variance of successful gametes (kbar and V_k) are held constant.

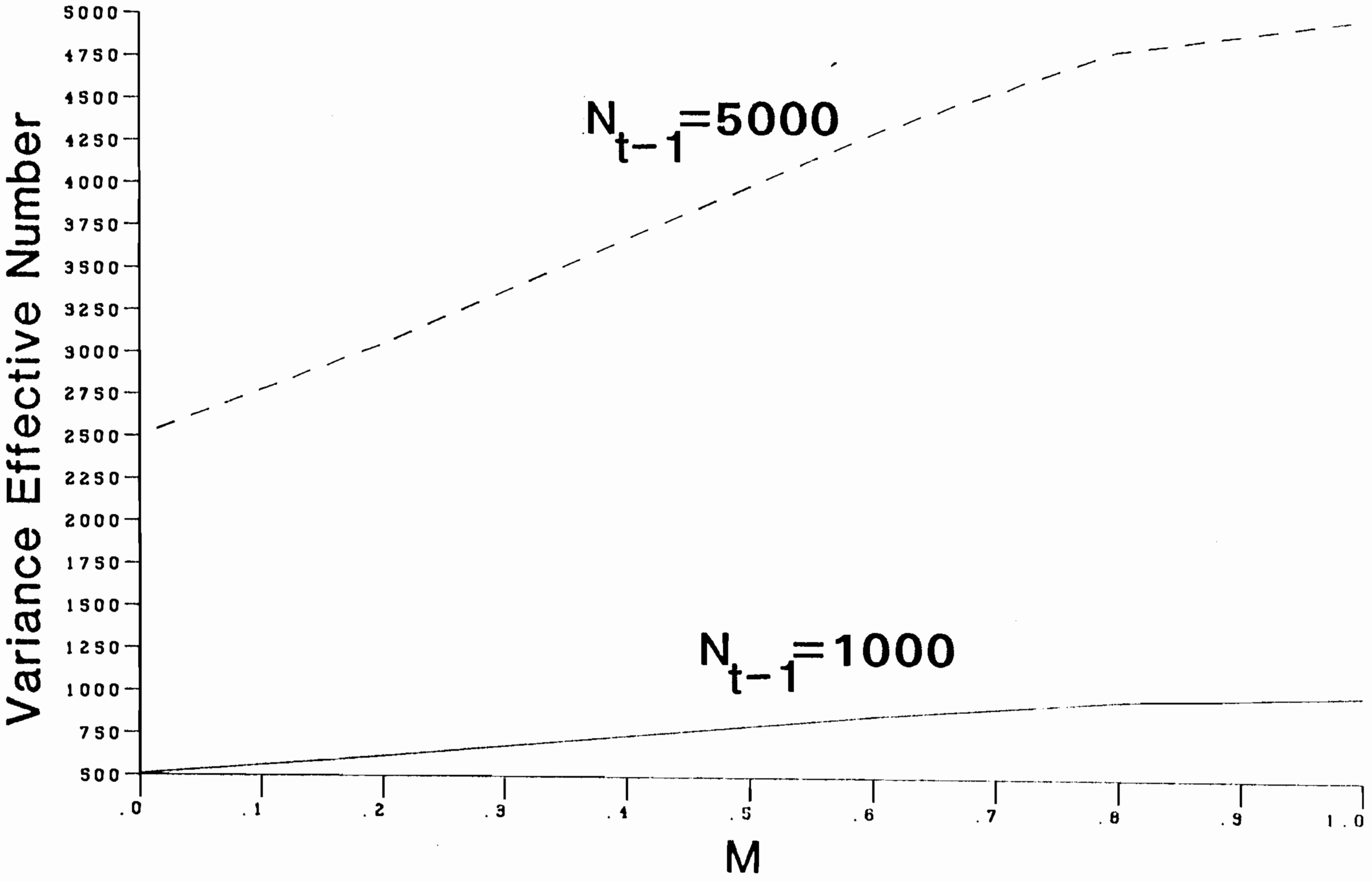

Variance Effective Number
5000
4750
4500
4250
4000
3750
3500
3250
3000
2750
2500
2250
2000
1750
1500
1250
1000
750
500
.0
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
M
N_{t-1}=5000
N_{t-1}=1000

Fig. III.12

Fig. III.13. The variance effective number, N_e, as a function of immigration rate (M) and the average number of successful gametes (kbar) when the number of parents (N_{t-1}) is held constant.

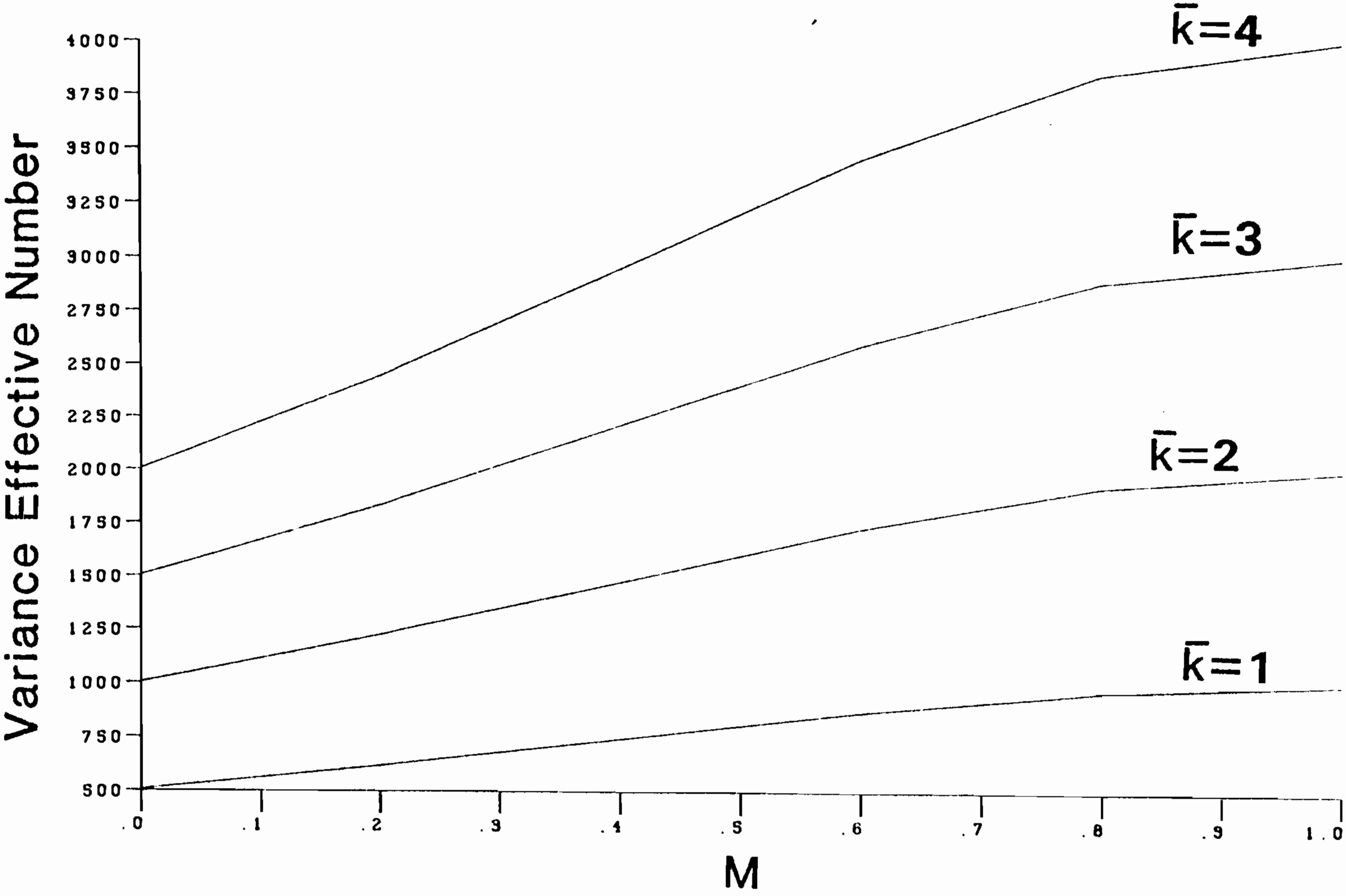

k̄=4
k̄=3
k̄=2
k̄=1
Variance Effective Number
4000
3750
3500
3250
3000
2750
2500
2250
2000
1750
1500
1250
1000
750
500
.0
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
M

Fig. III.13

Table III.1. The number of parents ($N_{x,t-1}$) of each age (x) at breeding season t-1 with the total number of parents held constant ($N_{t-1} = 1000$).

	Age of Parents at t-1									
Age Distribution	1	2	3	4	5	6	7	8	9	10
Predominantly Young		500	350	100	50					
Intermediate		50	500	350	100					
Predominantly Old		50	100	350	500					
Predominantly Young	256	192	142	115	90	64	51	36	28	26

Table III.2.a and III.2.b. Examples of values for kbar_x and $s^2_{k,x}$ (in parentheses) values for a negative exponential probability distribution of k (a) and a Poisson probability distribution of k (b) with the total number of parents and kbar held constant (N_{t-1} = 1000, kbar = 2).

	Age of Parents at t-1			
Age Distribution	2	3	4	5
a. exponential increase in kbar_x as x increases				
Predominantly Old	0.18 (0.03)	0.61 (0.38)	1.45 (2.12)	2.84 (8.07)
Intermediate	0.33 (0.11)	1.11 (1.22)	2.62 (6.88)	5.12 (26.24)
Predominantly Young	0.61 (0.38)	2.07 (4.28)	4.90 (24.05)	9.58 (91.75)
b. linear increase in kbar_x as x increases				
Predominantly Old	0.93 (0.91)	1.40 (1.38)	1.86 (1.86)	2.33 (2.32)
Intermediate	1.14 (1.12)	1.71 (1.71)	2.29 (2.28)	2.86 (2.83)
Predominantly Young	1.48 (1.48)	2.22 (2.22)	2.96 (2.93)	3.70 (3.63)

APPLICATION OF FUNCTIONAL RELATIONSHIPS FOR A GENETIC FITNESS MODEL FOR MANAGING PACIFIC SALMON FISHERIES

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and

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Oregon State University

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ABSTRACT

This report describes examples of functional relationships for a genetic fitness model for the management of Pacific salmon fisheries to maintain the long term reproductive fitness of breeding populations. We have concluded the genetic objective to be maintaining the probability distribution of fitness and, thus, the variance effective number, to allow the stock to perpetuate in the face of fishing and natural mortality in an unpredictable environment. Functional relationships for the variance effective number, derived by synthesis of the literature of population biology and population genetics, are briefly reviewed. These expressions relate the variance effective number to the number of spawners, age structure, the variance of fitness, and immigration. The inputs for the functional relationships are population variables that do not require estimation of classical genetic properties of populations such as gene frequencies and percentage homozygosity.

Adjustment of the model to accomodate the different life histories of the several species of Pacific salmon is demonstrated by application of the functional relationships to fictitious chum (Oncorhynchus keta) and pink (O. gorbuscha) salmon stocks. The

demonstration includes estimating changes in the variance effective number resulting from pre-selected escapement levels and the escapement required to maintain the variance effective number constant.

INTRODUCTION

We have developed a conceptual framework and illustrative functional relationships for a genetic fitness model for fisheries management. The functional relationships express the variance effective number of a stock as a function of population size, the variance of successful gametes, immigration and age structure (Kapuscinski and Lannan 1984a). The model is applicable to managing the genetic health of salmonid reproductive populations. The purpose of this paper is to illustrate the functional relationships of the model with fictitious salmon stocks.

To satisfy the management goal of maintaining a stock as a self perpetuating system over the long term, we have concluded the genetic objective to be maintaining the probability distribution of fitness to allow the stock to perpetuate in the face of fishing and natural mortality in an unpredictable environment. Although many fisheries biologists, for example Hynes et al. (1981) and Krueger et al. (1981), recommend maximizing the genetic variation of exploited stocks, we suggest that optimizing the variance of fitness may be more appropriate.

The genetic objective can be met by considering the model's variance effective number to be a measure of genetic risk (Kapuscinski and Lannan 1984a). If $N_{e(v)}$ is the variance effective number for a stock during a generation interval when stock abundance satisfied management goals, then conservative management dictates that $N_{e(v)}$ should remain constant in subsequent breeding seasons, thus:

$$N_{e(v)} = N'_{e(v)} \qquad (1)$$

where the prime notation denotes the breeding seasons in present time. Expressions for $N_{e(v)}$ and $N'_{e(v)}$ as a function of population size, the variance of fitness, immigration and age structure can be substituted into equation (1), and the equation rearranged to solve for any one population variable, assuming numerical values for the remaining variables are available (Kapuscinski and Lannan 1984a).

METHODS

Functional Relationships of the Model

In this paper, the functional relationships apply to a stock with the following properties:

1. Mating is at random.
2. The sexes are separate but the numbers of each sex need not be equal.
3. Self-fertilization does not occur.
4. Migration into the population may occur.
5. The population is composed of diploid individuals.

6. The number of successful gametes per parent contributed to the next generation can vary.
7. For each reproductive age, the frequency distribution of successful gametes per parent is described by a Poisson distribution (σ^2_k = kbar).
8. There is a linear increase in the average number of successful gametes per parent (kbar$_x$) as age increases.
9. There are no sex specific differences in the frequency distribution of successful gametes per parent.

The expression for $N_{e(v)}$ for this stock is

$$N_{e(v)} = \frac{N_{t-1}\,\bar{k}}{1 + \frac{V_k}{\bar{k}}(1-M)^2} \qquad (2)$$

where: N_{t-1} is the number of parents at breeding season t-1, M is the fraction of the stock replaced by migrants in a breeding season, and kbar and V_k are, respectively, the mean and variance of successful gametes (i.e., gametes that survive to become parents in the next generation) contributed per parent (Kapuscinski and Lannan 1984a).

The model can be applied to a salmonid species with two or more age classes in the mating population (for example chum salmon, (Oncorhynchus keta) by substitution of the following equations into expression (2) (Kapuscinski and Lannan 1984a, b):

$$N_{t-1} = \sum_x N_{x,t-1} \qquad (3)$$

$$\bar{k} = \frac{\sum_x \bar{k}_x N_{x,\, t-1}}{N_{t-1}} \qquad (4)$$

$$V_k = \frac{\sum_x S^2_{k,x} N_{x,t-1}}{\sum_x N_{x,t-1}} = \frac{\sum_x S^2_{k,x} N_{x,t-1}}{N_{t-1}} \qquad (5)$$

where x is the age at reproduction. The age specific variances in equation (5) are for Poisson distributions, thus:

$$s^2_{k,\, x} = \frac{\sigma^2_{k,\, x} (N_x - 1)}{N_x} \qquad (6)$$

and

$$\sigma^2_{k,\,x} = \bar{k}_x \qquad (7)$$

The model can be applied to a salmonid species with no age class structure (e.g., pink salmon O. gorbuscha) by substitution of the following equations into expression (2) (Kapuscinski and Lannan 1984a, b):

$$\bar{k} = \frac{2N_t}{N_{t-1}} \qquad (8)$$

where t-1 and t refer to breeding seasons for either an odd year or an even year stock,

$$V_k = \frac{\sigma^2_k\,(N_{t-1} - 1)}{N_{t-1}} \qquad (9)$$

and $\sigma^2_k = \bar{k}$ (10)

Application of the Model

The relationship between the dependent variable N_e, and the other population variables in equation (2) is demonstrated with data for fictitious chum and pink salmon populations. The variance effective number was computed while different combinations of variables were held constant. Chum salmon, which typically have four reproductive classes, and pink salmon, which have only one reproductive age class, were used to compare the behavior of a stock with age structure to that of one without age structure. The $kbar_x$ values for the chum stock were held constant in all the calculations. Unless otherwise specified in the results, the reproductive ages and the age distribution in the chum stock were: age 2 (5%), age 3 (50%), age 4 (35%) and age 5 (10%). Also, the chum and pink stocks were declining in abundance ($kbar \leq 1$). The values used to simulate three possible abundance trends in a pink salmon stock (Fig. IV.4) are given in Table IV.1.

RESULTS

Comparisons between the chum and pink stocks are presented in figures IV.1 through IV.4, showing $N_{e(v)}$ as a function of other input variables.

$N_{e(v)}$ as a Function of N_{t-1} for Constant $kbar_x$

There is a linear increase in $N_{e(v)}$ as N_{t-1} increases when the immigration rate (M) is held constant (Fig. IV.1). The pink and chum stocks behave identically when kbar (i.e., $kbar_2$) in the pink stock is equal to kbar weighted for all ages ($kbar_2$, $kbar_3$, $kbar_4$, $kbar_5$) in the chum stock. This result will occur in nature only if $kbar_2$ for pink salmon is greater than $kbar_2$ for chum salmon. A loss of reproductive ages in the chum stock results in a decrease in kbar and V_k. This leads to an increase in the escapement (N_{t-1}) required to maintain a given value of $N_{e(v)}$. For example, if $N_{e(v)}$ for the reference generation is 200 and if the management goal is to maintain this value, then the required N_{t-1} is 450 for a chum stock consisting of ages 2 and 3 versus 350 for a chum stock consisting of ages 2 - 5.

There is a linear increase in $N_{e(v)}$ as N_{t-1} increases when age class structure and M are held constant for different values of V_k and kbar (Fig. IV. 2). The pink and chum stocks behave identically when kbar (i.e., $kbar_2$) in the pink stock is equal to kbar weighted for all ages in the chum stock. The escapement of (N_{t-1}) required to maintain a given value of $N_{e(v)}$ decreases as V_k and kbar increase.

There is a linear increase in $N_{e(v)}$ as N_{t-1} increases for different age class structures and values of M (Fig. IV. 3). The pink and chum stocks behave identically for the same value of M when kbar in the pink stock is equal to kbar weighted for all ages in the chum stock. The escapement (N_{t-1}) required to maintain a given value of $N_{e(v)}$ decreases as M increases for a given age class structure.

In the chum stock, an increase in M counteracts the reduction in V_k caused by the loss of reproductive ages. The elevation and V_k

value of the curve for ages 2 and 3 are lower than are the elevation and V_k value of the curve for ages 2 - 5 when M is held constant (M = 0). Thus, N_{t-1} required to maintain a given $N_{e(v)}$ is greater for ages 2 and 3 than it is for ages 2 - 5. Although V_k remains constant, the elevation of the curve for ages 2 and 3 increases when M increases to 0.4. Then, N_{t-1} required to maintain a given $N_{e(v)}$ is smaller for ages 2 and 3 and M = 0.4 than it is for ages 2 - 5 and M = 0. If some mechanism other than a change in age class structure reduces V_k in a pink or chum stock, an increase in M will counteract the impact on $N_{e(v)}$.

$N_{e(v)}$ as a Function of the Trend in Stock Abundance.

The value of $N_{e(v)}$ at breeding season t-1 is different for stocks experiencing different trends in abundance when N_{t-1} (i.e., N at generation 3) is held constant (Fig. IV.4). At generation 3, $N_{e(v)}$ is much smaller for a pink stock declining in abundance than it is for a pink stock increasing in abundance. A 40% increase in M in the declining stock increases the value of $N_{e(v)}$, although it still is much smaller than $N_{e(v)}$ for the increasing stock. Thus, it may be difficult or even impossible to attain a given level of $N_{e(v)}$ (determined by management objectives) when a stock is experiencing a rapid decline in abundance. The escapement required to maintain a given value of $N_{e(v)}$ will have to be much greater in a declining stock than in an increasing stock.

DISCUSSION

The functional relationships for the fitness model are tools for examining the possible impacts of exploitation and management on the genetic health of salmon stocks. For example, they can determine the direction of change in $N_{e(v)}$ resulting from a change in the migration rate (Fig. IV.3) due to straying or resulting from a change in age class structure (Fig.IV.1) due to selective harvesting of the older age classes (i.e., the larger fish). Also they provide a quantitative method for making allocation decisions consistent with the goal of maintaining the variance effective number at an adequate level. The escapement (N_t) required to maintain N_e constant can be computed when the age class structure, the migration rate and the abundance of spawners at t-1 and the variance of successful gametes are known (Fig. IV.3). Fishery statistics on stock abundance over successive years can be used to make conservative escapement allocations (Fig.IV.4).

The functional relationships of the model for age structured salmon stocks assume a Poisson distribution for k at a given age, a constant value for each $kbar_x$ (when other stock variables change) and a linear increase in $kbar_x$. The present lack of appropriate data suggests a need to test these assumptions under field conditions. Because Pacific salmon usually experience high rates of mortality particularly during juvenile migrations into coastal waters, it is reasonable to assume a very high frequency of $k = 0$ (i.e., a large value for the y intercept), an average value (kbar) between 1 and 4 and a very low frequency of large values of k. These conditions can be met by a Poisson distribution, a negative exponential distribution or even a bimodal or multi-modal curve described by a polynomial function. A constant value for each $kbar_x$ is a simplifying assumption that ignores complicating factors, for example, density dependence. Evidence for increases in the fecundity of lake whitefish (Coregonus clupeaformis), lake trout (Salvelinus namaycush), and some British Columbia coho (Oncorhynchus kisutch) stocks after heavy exploitation suggests that fecundity is influenced by stock abundance in these fishes (Beacham 1982). Because fecundity is a major component of fitness (k = fecundity x survival), $kbar_x$ values may also change as stock abundance changes. The assumption of a linear increase in $kbar_x$ is based upon the linear increase in fecundity as age increases in Pacific salmon. This results from a linear relationship between fecundity and length where length increases as age increases (Beacham 1982). However, a linear increase in $kbar_x$ also requires that the average survival of gametes per parent ($lbar_x$) at each age is constant or nearly so.

Contradictory opinions in salmon management have been voiced on how to maintain the genetic health of exploited stocks because a unifying definition of the genetic objective of management has been lacking. Our model's goal of maintaining the probability distribution of fitness provides a rational approach to considering the implications of three contemporary scenarios for exploited salmon stocks:

1. Overfishing of the reproductive individuals of the less productive stocks in a multistock fishery could dramatically increase random genetic drift and inbreeding in these stocks and thus accelerate their decline in abundance,
2. Directional selection by the fishery for one trait (e.g., size, timing of reproduction) could cause either indirect selection for correlated traits or a response to selection, either of which may have a negative impact on survival and yield, and
3. Enhancement activities employing the transplantation of natural stocks or the introduction of hatchery stocks could decrease the abundance of both the native and introduced fish due to swamping of the gene pool by the less well adapted genotypes of the introduced fish.

While the results of reproductive overfishing presented in the first scenario are predicted by population genetics theory, they have not been documented with real or fictitious data. Using computer simulation, Ricker (1973) only went far enough to show that mixtures of stocks of unequal productivity, when harvested together, produce smaller recruitments than single stocks of the same original size and having the same optimum rate of exploitation. The equations for the fitness model can go one step further by simulating relative changes in V_k and corresponding changes in $N_{e(v)}$ of each stock in a mixed stock fishery.

The second scenario is supported by reports of long term declines in average age and size of harvested fish (Silliman 1975, Moav et al. 1978, Ricker 1981). Several controversial methods of counteracting this problem have been suggested. The use of enhancement practices, especially hatcheries, to offset selective effects of the fishery (Larkin 1981) is discouraged by the proponents of scenario three. The periodic reversal of the direction of fishing selectivity would be a management nightmare. Finally, the inevitable selectivity of all fishing methods could be exploited by intentionally selecting fish to achieve maximum or optimum sustainable yield (Larkin 1981). An initial assessment of the response of the variance of fitness and the variance effective number in a stock subjected to any of these methods can be made using the functional relationships of the fitness model. For example, alternative means of counteracting selective removal of older fish can be explored using information like that presented in Figure IV.1 for different age structures.

The third scenario is confounded by a prevalent belief that native fish are always genetically superior to transplanted fish. It is argued that (1) native fish stocks have evolved specific gene complexes highly adapted to their locality and (2) that they have more genetic variability than hatchery or transplanted stocks. Restated in terms of fitness, this argument implies that (1) average fitness is high and the variance of fitness is low in native stocks relative to hatchery and transplanted stocks and contradictorily, (2) the variance of fitness is high in native stocks relative to hatchery or transplanted stocks. The first claim implies that natural selection has reduced V_w in native stocks enough to remove most nonadaptive genes. Also, it ignores the random or unpredictable phenotypic expression (especially in an unpredictable environment) of genes influencing fitness. However, heterosis for yield in wild x domestic trout planted in the wild has been reported by Flick and Webster (1981) and Fraser (1981).

The second claim for the genetic superiority of native stocks implies that only hatchery and transplanted stocks have been exposed to random drift (which reduces V_w) due to the use of a small number of founder individuals. Yet the same mechanism applies to any natural salmon stock that evolved from small numbers of parents, i.e., that went through a bottleneck in abundance. Depleted natural stocks are timely candidates for reduced V_w caused by bottlenecks.

Within the conceptual framework of our fitness model, the transplantation of natural stocks and the introduction of hatchery stocks are ways of increasing M and thus increasing $N_{e(v)}$ for any value of V_k. Numerical outputs from the model can help in deciding whether or not $N_{e(v)}$ is sufficiently depressed in a particular stock to warrant application of these enhancement practices. Caution must be exercised in this decision making process because some biological matters related to stock transplantations, such as the possible introduction of foreign pathogens into the recipient stock, are beyond the scope of the model but must not be ignored.

Although there is an inherent danger in extending the generalizations of any simplistic quantitative model to salmon management problems, conservative management should favor the present form of the fitness model because it aims for long term perpetuation of the resource. We offer this model as a first attempt at providing an "explicit working hypothesis of population genetics" (Larkin 1981) to aid in the making of biological and social decisions in salmon management.

Fig. IV.1. The variance effective number, N_e, as a function of the number of parents (N_{t-1}) at breeding season t-1 and age class structure (for constant values of age specific average number of successful gametes, $kbar_x$) when immigration is held constant ($M = 0.2$).

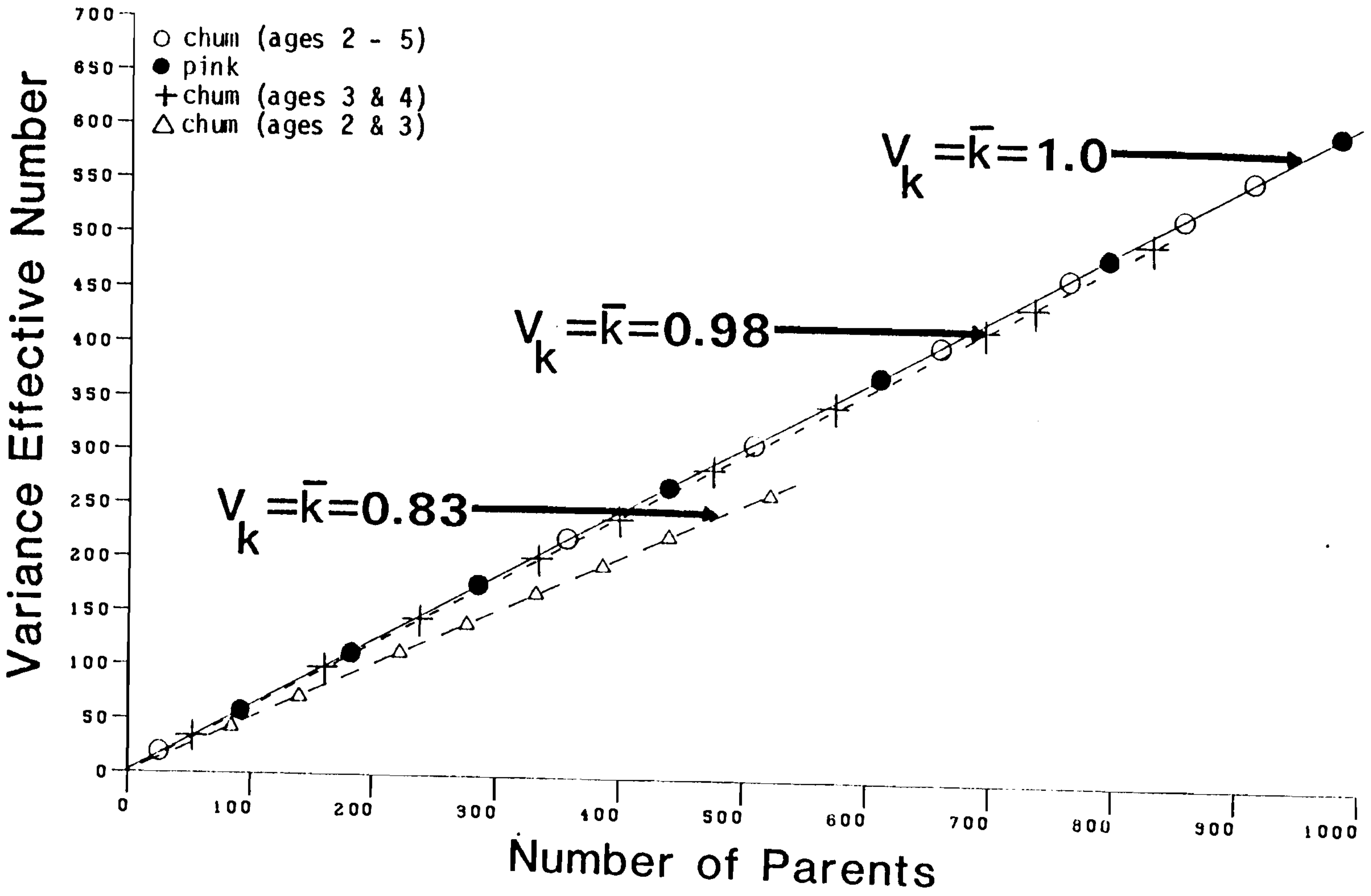

Variance Effective Number
700
650
600
550
500
450
400
350
300
250
200
150
100
50
0
○ chum (ages 2 - 5)
● pink
+ chum (ages 3 & 4)
△ chum (ages 2 & 3)
$V_k = \bar{k} = 1.0$
$V_k = \bar{k} = 0.98$
$V_k = \bar{k} = 0.83$
0
100
200
300
400
500
600
700
800
900
1000
Number of Parents

Fig. IV.1

Fig. IV.2. The variance effective number, N_e, as a function of the number of parents (N_{t-1}) at breeding season t-1 and the variance of successful gametes (V_k) when age class structure and immigration are held constant ($M = 0.2$)

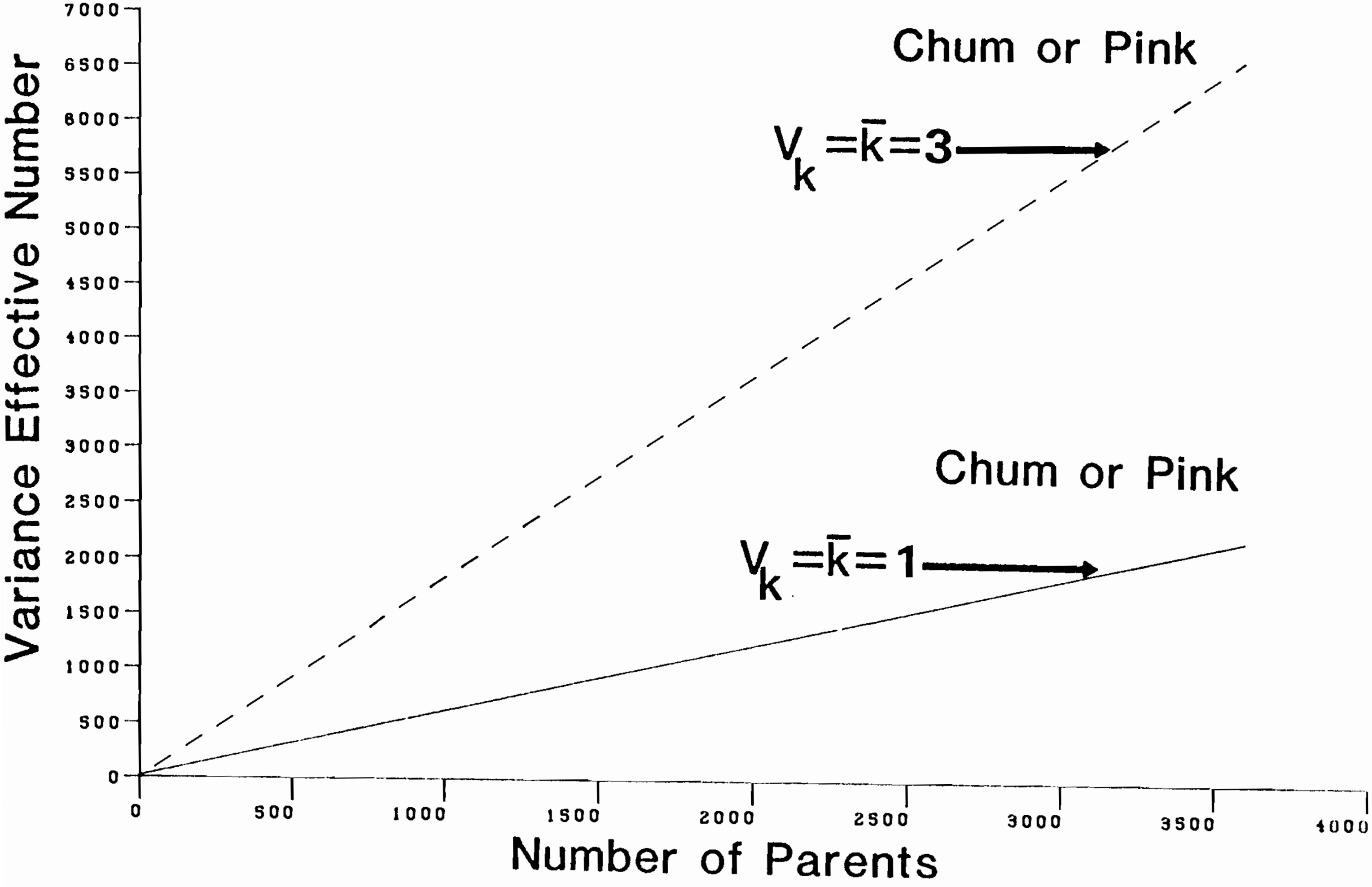
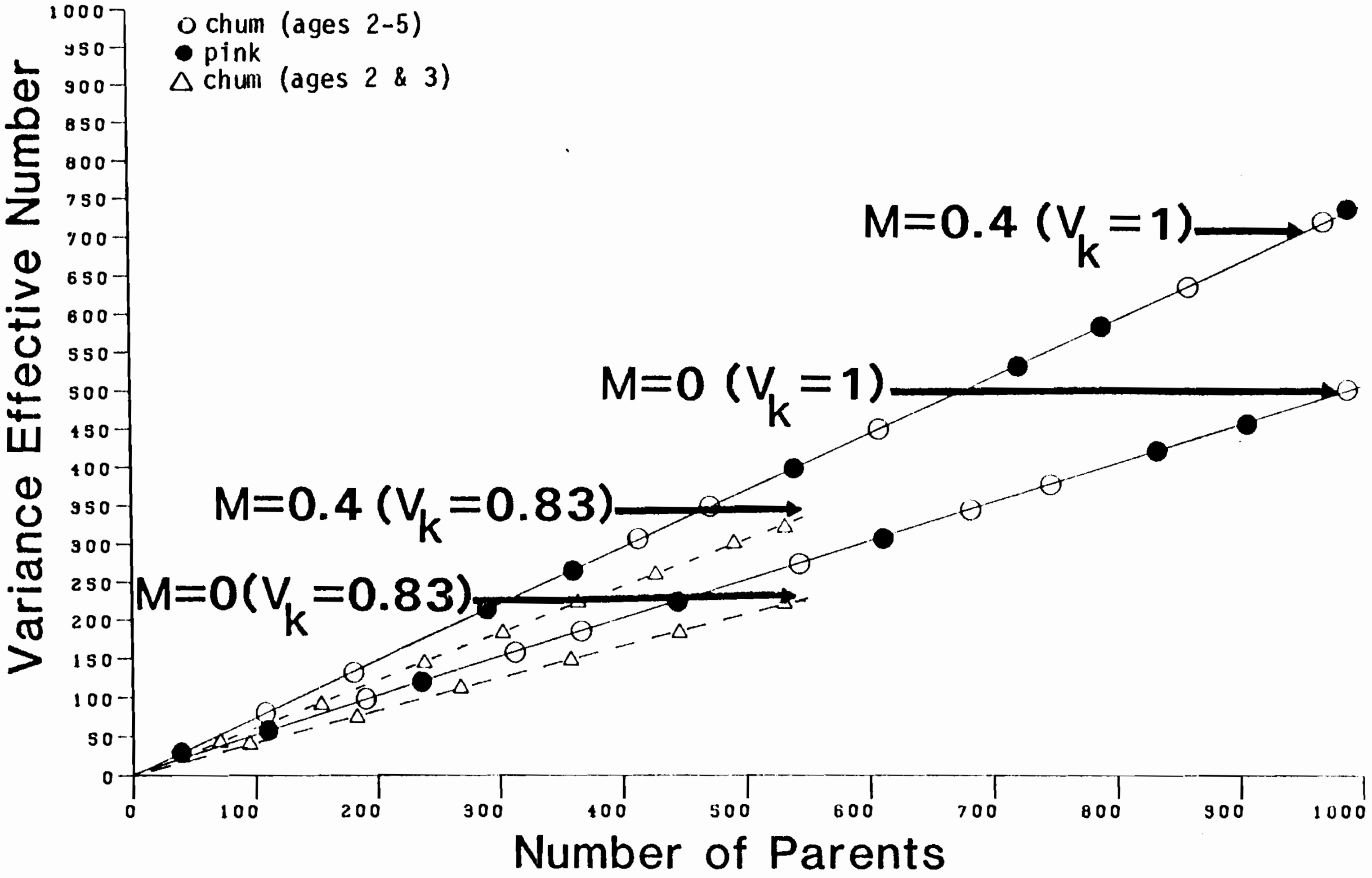

Chum or Pink
$V_k = \bar{k} = 3$
Chum or Pink
$V_k = \bar{k} = 1$
Variance Effective Number
7000
6500
6000
5500
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
Number of Parents
0
500
1000
1500
2000
2500
3000
3500
4000

Fig. IV.2

Fig. IV.3. The variance effective number, N_e, as a function of the number of parents (N_{t-1}) at breeding season t-1, migration and different age structures (with constant values of age specific average number of successful gametes, $kbar_x$).



o chum (ages 2-5)
● pink
△ chum (ages 2 & 3)
Variance Effective Number
1000
950
900
850
800
750
700
650
600
550
500
450
400
350
300
250
200
150
100
50
0
0
100
200
300
400
500
600
700
800
900
1000
Number of Parents
M=0.4 (V_k=1)
M=0 (V_k=1)
M=0.4 (V_k=0.83)
M=0(V_k=0.83)

Fig. IV.3

Fig. IV.4. The variance effective number, N_e, as a function of time, the trend in stock abundance and migration rate when the number of pink salmon spawners at breeding season t-1 is held constant (N_{t-1} = 1000).

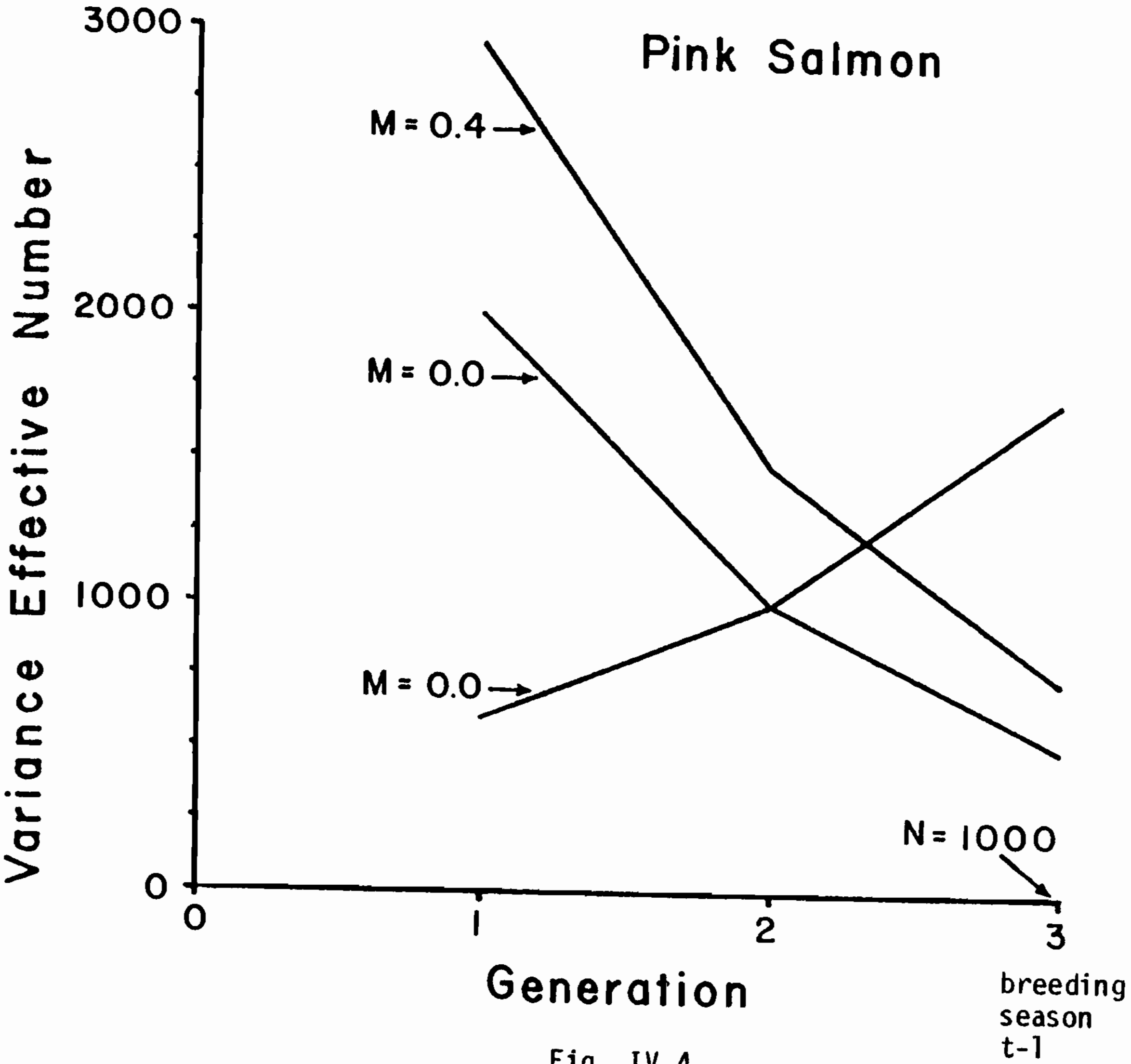

Pink Salmon
Variance Effective Number
3000
2000
1000
0
Generation
0
1
2
3
M = 0.4
M = 0.0
M = 0.0
N = 1000
breeding
season
t-1

Fig. IV.4

Table IV.1. Number of pink salmon spawners for three generations ($g = 3$). Data correspond to curves in Fig. IV.4.

Abundance trend	N_1	N_2	$N_3 = N_{t-1}$
Declining	5,000	2,000	1,000
Increasing	200	600	1,000

CONCLUSION

A generalized fisheries management model, which intends to maintain a stock's probability distribution of fitness (W), has been presented. If W (with a characteristic $\bar{W}$ and V_w) is the probability distribution of fitness at breeding seasons when stock abundance met management goals, and if W' is the stock's probability distribution of fitness in present time, then the objective of the conceptual model is expressed as

$$W = W'. \qquad (1)$$

An example of functional relationships for W = f(population variables) was developed from existing principles of population biology and population genetics. These express the variance effective number ($N_{e(v)}$) of a stock as a function of population size, the mean and variance of successful gametes (estimates of $\bar{W}$ and V_w), age structure and immigration. Thus,

$$W = f[N_{e(v)} = f(\text{population variables})] \qquad (2)$$

and

$$W' = f[N'_{e(v)} = f(\text{population variables}')] \qquad (3)$$

The appropriate application of the functional relationships to the conceptual model involves substitution of expressions (2) and (3) into expression (1).

Assumptions of the Functional Relationships

The present forms of the functional relationships (equations 2 and 3) provide a working hypothesis of genetic objectives consistent with the goal of perpetuation of the resource. However, caution is urged in their application to the development of any genetic stock management owing to certain assumptions and unknowns. The principal assumption is that the relationships among the population variables in the classical formula for $N_{e(v)}$ (Crow and Kimura 1970) are appropriate for the translation of the conceptual model into quantitative terms. Although this formula was selected after careful consideration of other quantitative expressions of population genetics (Kapuscinski and Lannan 1984a), it may be possible to develop more relevant relationships (among the various population variables) from first principles. In any case, we can expect that additional research will make the existing functional relationships more comprehensive with time.

A second assumption of management concern is that environmental conditions in past (i.e., reference) and present breeding seasons are sufficiently similar to warrant equating W to W' in expression (1). When environmental conditions fluctuate around a mean value, this assumption may be tolerable. However, expression (1) will need modification if the historical record shows a unidirectional change in the value of important physical parameters (e.g., water temperature). It may be possible to add coefficients to correct the values of population variables on either side of equality (1), but only if enough is known about the impact of the physical parameters on these variables. Thus, the selection of reference breeding seasons will be greatly complicated under the conditions of unidirectional environmental trends (refer to discussion by Kapuscinski and Lannan 1984a).

Management must recognize also the lack of density dependent behavior in the existing functional relationships for the model. This may not be a serious limitation if, eventually, the functional relationships are incorporated into a population dynamics model that exhibits density dependence (e.g., the Ricker stock-recruit function for Pacific salmon). Additionally, it may be possible to include interaction terms for age specific mean fitnesses or variances of fitness (e.g., covariance terms) into the existing functional relationships. This will require some estimation from empirical evidence for such age specific interactions.

Research Questions

The exercise of developing an example of functional relationships for the conceptual model (equation 1) has led to the identification of research questions whose study would improve our ability to understand the genetic implications of fisheries management. They must be addressed for each species of interest (owing to different life history patterns) and they include:

1. How does age at reproduction affect the probability distribution of fitness, particularly the mean and variance ($kbar_x$, $s^2_{k,x}$)?
2. What is the magnitude of the difference among ages for $kbar_x$ and $s^2_{k,x}$ values?
3. Do age-specific probability distributions of fitness change significantly when the total number of parents (N_{t-1}), the age distribution (N_x for each x) or the range of ages change?
4. If density dependence (within or among ages) exists, how does it alter the probability distribution of fitness?
5. Are bimodal or multi-modal probability distributions of fitness (Kapuscinski and Lannan 1984b) better than unimodal ones for appropriate incorporation of life history patterns into the conceptual model (equation 1)?
6. Must $s^2_{k,x}$ be estimated directly (from k_x or $kbar_x$) or can reliable indirect estimates be developed, for example, from fecundity and survival data?
7. What are typical immigration rates and how variable are they with time for a given life history pattern?
8. If immigration rates are relatively high (Kapuscinski and Lannan 1984b), do they warrant correction via the estimation of the coefficient of relationship between immigrants and the recipient stock?

SUMMARY

The results presented in the preceding chapters are summarized below:

1. A conceptual model and examples of functional relationships for maintaining the reproductive fitness of exploited stocks were developed.
2. The model is: an extension of the stock concept; general in that it can accomodate the life history pattern of any species; a phenotypic model requiring values for population variables capable of being estimated or already routinely monitored in fisheries management (values for classical genetic properties of the stock, e.g., percentage homozygosity are not required.)
3. The fitness of a stock is modelled as a random variable described by a probability distribution (W) with a characteristic mean ($\overline{W}$) and variance (V_w).
4. Because the long-term survival of a stock is more dependent on the value of V_w than simply on the value of $\overline{W}$, the genetic objective of conservative fisheries management is: maintaining the probability distribution of fitness to allow the stock to perpetuate in a dynamic environment.
5. The conceptual model is expressed as $W = W'$ and the functional relationships are applied to the model via $N_{e(v)} = N'_{e(v)}$ where the prime notation distinguishes

the breeding seasons under management from the reference breeding seasons.

6. An equation for the variance effective number, $N_{e(v)}$, was developed which expresses $N_{e(v)}$ as a function of population size in successive breeding seasons, age structure, the variance of successful gametes (an estimate of V_w) and immigration.
7. In its final form, $N_{e(v)}$ provides an index of genetic risk and it is not meant to replace the $N_{e(v)}$ found in the literature of quantitative and population genetics.
8. Genetic risk is defined as the probability of a reduction in the adaptibility of a stock to its habitat due to a reduction in genetic variation.
9. Application of $N_{e(v)} = N'_{e(v)}$ to stock management can be achieved by rearranging terms to solve for any one population variable, assuming that estimates for other variables are available; for example, the output can be the escapement required at breeding seasons t + n to maintain the above equality.
10. The values of $N_{e(v)}$ and V_k (an estimate of V_w) are most sensitive to changes in the values for population size in successive breeding seasons ($N_{t-1,n}$ $N_{x+n,t+n}$), suggesting that management of stock escapement levels (or conversely exploitation rates) provides the most powerful means of achieving the genetic objective. This is especially true when the variance is a direct function of

the mean of the probability distribution of fitness.

11. The descending order of importance for the response of $N_{e(v)}$ and V_k to other input variables is: (1) the probability distribution of age specific fitness; (2) age structure (including range of ages, age distribution and age specific differences in the mean and variance of fitness); (3) immigration rate.
12. The responses of $N_{e(v)}$ and V_k to simultaneous changes in two or more inputs cannot be generalized owing to interactions among the input variables.
13. The functional relationships behave quite differently with asymmetrical probability distributions of fitness (characterized by a high frequency of small individual fitness) than with symmetrical or nearly symmetrical probability distributions (characterized by a low or even zero frequency of small individual fitness).
14. The minimum data requirements for developing a rational management plan for a given stock are: estimates of the type of probability distribution of k_x, age composition (N_x for each x), age specific differences in kbar$_x$ and $s^2_{k,x}$, and population size (N_{t-1} and $\Sigma_n N_{x+n}$).
15. Application of the conceptual model and the functional relationships to the management of Pacific salmon stocks was illustrated; a Poisson probability distribution of fitness was assumed.

16. Accomodation for the different life histories of the various species was demonstrated by considering fictitious chum salmon (with age structure) and pink salmon (without age structure) stocks.

17. The chum and pink stocks behave identically in response to changes in input variables only when kbar (an estimate of $\bar{W}$) in the pink stock is equal to kbar weighted for all ages ($kbar_2$, $kbar_3$, $kbar_4$, $kbar_5$) in the chum stock; this requires that $kbar_2$ for pink salmon is greater than $kbar_2$ for chum salmon.

18. A loss of reproductive ages in the chum stock leads to an increase in the escapement (N_{t-1}) required to maintain a constant value of $N_{e(v)}$.

19. An increase in migration (M) counteracts the reduction in V_k caused by the loss of reproductive ages in the chum stock; the escapement required to maintain a constant value of $N_{e(v)}$ decreases as M increases in either stock.

20. The escapement required to maintain a constant value of $N_{e(v)}$ is greater for a declining than for an increasing stock.

21. Although there is an inherent danger in applying any simplistic equations to stock management, the conceptual model and the illustrative functional relationships are likely to err in favor of conservatism if they are found to be in error.

22. The conceptual model and the functional relationships provide a rational approach to considering the genetic implications of fisheries exploitation and management.

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APPENDIX

APPENDIX A: PROBABILITY DISTRIBUTIONS OF K

The derivations of the variance formulas (Hillier and Lieberman 1974) and the range of tested values for the parameters are described below for each probability distribution. In all cases the range for kbar was 1 - 4, including stocks declining in abundance by fifty percent from t-1 to t (kbar = 1) and stocks doubling in abundance from t-1 to t (kbar = 4).

Poisson Distribution of K_x

$$\text{Expected value} = \lambda \text{ and}$$

$$\text{variance} = \lambda,$$

$$\text{thus variance}_x = \text{mean}_x,$$

$$\sigma^2_{k,x} = \text{kbar}_x .$$

Negative Exponential Distribution of K_x

$$\text{Expected value} = \theta \text{ and}$$

$$\text{variance} = \theta^2 ,$$

$$\text{thus variance}_x = (\text{mean}_x)^2,$$

$$\sigma^2_{k,x} = (\text{kbar}_x)^2.$$

Gamma Distribution of K_x

$$\text{Expected value} = \alpha\beta \text{ and}$$

$$\text{variance} = \alpha\beta^2 ,$$

$$\text{thus variance}_x = (\text{mean}_x)\ \beta ,$$

$$\sigma^2_{k,x} = \text{kbar}_x\ \beta.$$

When β is 1, the variance is identical to the variance for the Poisson distribution. The possible values for β were constrained by the values of α and kbar_x ($\alpha\beta$):

kbar_x ÷	α =	β
1	1	1
2	2	1
2	1	2
3	3	1
3	1	3
4	4	1
4	2	2
4	1	4

Binomial Distribution of K_x

$$\text{Expected value} = np \text{ and}$$

$$\text{variance} = np\,(1-p),$$

$$= np\left(1 - \frac{np}{n}\right),$$

$$\text{thus variance} = \text{mean}_x\left(1 - \frac{\text{mean}_x}{n}\right),$$

$$\sigma^2_{k,x} = \text{kbar}_x\left(1 - \frac{\text{kbar}_x}{n_x}\right).$$

In n trials, the probability of a parent producing a successful gamete (k = 1) is p and the probability of a parent failing to do so (k = 0) is 1 - p. The maximum fecundity for females of age x will determine the maximum number of trials (n_x). Thus a binomial distribution for a stock would describe the probabilities of k = 0 to k = maximum fecundity. Values for n_x corresponding to an average n for the stock and assuming a linear increase in maximum fecundity as age increases were:

	Average n						
Age	2000	200	20	8	6	4	2
2	1143	114	11	5	3	2	1
3	1714	171	17	7	5	3	2
4	2286	229	23	9	7	5	2
5	2857	286	29	11	9	6	3

Normal Distribution of K_x

Expected value = μ and

variance = σ^2,

thus variance_x cannot be estimated from

mean_x, $\sigma^2_{k,x} \neq f(\text{kbar}_x)$.

An infinite number of values are possible for the variance associated with a given mean of a normal distribution. But the biological requirement for only positive values of k ($k \geq 0$) constrained the range of values for $\sigma^2_{k,x}$ as follows:

kbar_x	$\sigma^2_{k,x}$	K_x ($\text{kbar}_x \pm \sigma_{k,x}$)
1	0 - 1	0 - 1
2	0 - 4	0 - 2
3	0 - 9	0 - 3
4	0 - 16	0 - 4

APPENDIX B: PASCAL PROGRAM FOR SENSITIVITY ANALYSIS

```
b
Program EffnumXY;
( computes effective population number, allowing varia-
tion of all inputs in Anne's equation for Ne; fills an array
with x and y (Ne) values that can be interchanged with business
graphics; choice of variables for x.Composed 25-May-84.Modified
26,27-May-84;4-Jun-84 to include exponentially inc. kbarage.)

type table = record
               stock, parents, progeny :array[1..20] of integer;
               kmean, migration, kvar, neffec :array[1..20] of real;
               end;

Var
  T,I,age,first,last,choice,xchoice,kchoice     :integer;
  sumnpar, sumnprog, row, col                        :integer;
  kbar,m,migterm,normalvar,n,beta,sumtemp,Vk   :real;
  numerator,denominator,Ne             :real;
  npar                                :array [1..10] of integer;
  Kbarage, sigmasq, ssq, kage             :array [1..10] of real;
  coord                             :array[1..20, 1..2] of real;
  filename                            :string[30];
  f2,fout                             :text;
  answer                               :char;
  all                                 :table;

Procedure title1;
begin
  writeln (fout);
  writeln (fout);
  write (fout, ' ':10,'Generation of Variance Effect');
  writeln (fout, 'ive Numbers');
  write (fout,'stock':10,'sumnpar':10,'sumnprog':10,'kbar':10,'m':10);
  writeln (fout, 'Vk':10, 'Ne':12);
end;  {general title}

Procedure title2;
begin
  writeln(fout);
  writeln(fout);
  writeln(fout,' ':10,'Age Specific Data of Stock',I:4);
  writeln(fout);
  write(fout,'age':10,'npar':10,'Kbarage':10,'sigmasq':10,'ssq':10);
  writeln(fout);
end;  {age specific title}

Procedure print;
begin
  for I:= 1 to T do
   begin
    write(fout,all.stock[I]:10,all.parents[I]:10,all.progeny[I]:10);
    write(fout,all.kmean[I]:10:2,all.migration[I]:10:2,all.kvar[I]:10:3);
    writeln(fout,all.neffec[I]:12:2);
   end;  {for T loop}
  writeln(fout);
  writeln(fout);
end;  {print data table for Generation of Ne for T stocks}

Procedure print1;
begin
  write (fout,I:10, sumnpar:10, sumnprog:10, kbar:10:2, m:10:2);
  writeln (fout, Vk:10:3, Ne:12:2);
```

```
   writeln(fout);
   writeln(fout);
   writeln(fout);
 end:  {print data table for Generation of Ne for stock I}
       {user must insert call for title1 and print1 after call
       for print2 if a separate printing for each stock I is desired}

 Procedure print2:
 begin
   for age:=first to last do
    begin
     write (fout,age:10,npar[age]:10,kbarage[age]:10:2);
     write (fout,sigmasq[age]:10:2,ssq[age]:10:2);
     writeln (fout);
    end:  {for loop}
 end:  {print age specific data}

 Procedure Estimatekbarage;
 var sumage,sumexpage,nage :integer;
     q,denomsum                  :real;
 begin
  sumage:=0;
  sumexpage:=0:
  nage:=0;
  denomsum:=0;
  for age:= first to last do
      nage:=nage + 1:
  writeln('Options for age specific kbar are:'):
  writeln('1. linear increase as age increases');
  writeln('2. exponential increase as age increases (exp=3)');
  writeln('Enter number of one option');
  readln (Kchoice):
  CASE kchoice OF
    1: begin
        for age:=first to last do
         sumage:=sumage + age;
        for age:= first to last do
         kage[age]:= (age*kbar*nage)/sumage;
       end; {case 1 linear increase}
    2: begin
        for age:=first to last do
         sumexpage:=sumexpage + (age*age*age):
        for age:=first to last do
         kage[age]:= (age*age*age*kbar*nage)/sumexpage:
       end: {case 2 exponential increase}
  end:  {for kchoice}
  for age:=first to last do
   denomsum:=denomsum + (kage[age]*npar[age]);
  q:=(Kbar*sumnpar)/denomsum;  {makes Kbar=sum kbarages weighted by npar}
  for age:=first to last do
   kbarage[age]:=q*kage[age];
 end: {procedure which computes kbarage from kbar weighted for}
      { increased fecundity at older age.}
```

```
Procedure sumnparcalc;
begin
sumnpar:=0;
for age:= first to last do
   begin
      writeln ('enter npar value for age = ,age:4);
      readln (npar[age]);
      sumnpar:=sumnpar+npar[age];
      end; {for loop}
end; {procedure}
      {computes N for all reproducing ages at t-1}

Procedure distribution;
begin
   writeln('Options for probability distrib. of kbar are:');
   writeln('1. Poisson: variance=u ');
   writeln('2. Binomial: u=np, var.=u(1-p) ');
   writeln('3. Exponential: variance=u*u ');
   writeln('4. Gamma: u=alpha*beta, var.=u*beta');
   writeln('5. Normal: variance not related to u');
   writeln('Enter the number of your choice');
   readln (choice);
end; {for procedure}

Procedure choicecalc;
begin
CASE choice OF
   1: sigmasq[age]:=kbarage[age];
   2: begin
         writeln ('Enter value for n in binomial for age',age:10);
         readln (n);
         sigmasq[age]:=(1-(Kbarage[age]/n))*Kbarage[age];
      end;
   3: sigmasq[age]:=Kbarage[age]*kbarage[age];
   4: begin
        writeln ('Enter value for beta in gamma func. for age',age:10);
        readln (beta);
        sigmasq[age]:=Kbarage[age]*beta;
      end;
   5: begin
         writeln ('Enter value for variance in normal func. for age',age:10);
         readln (normalvar);
         sigmasq[age]:=normalvar;
      end;
 end; {for case choice}
end;  {for procedure}

Procedure calcsumtemp;
begin
sumtemp:=0;
for age:= first to last do
   begin
      ssq[age]:=(npar[age]-1)/npar[age]*sigmasq[age];
      sumtemp:=sumtemp+ssq[age]*npar[age];
   end;    {sums variances over ages for numerator of Uk}
end;  {for procedure}
```

```
Procedure fillall;
begin
  all.stock[I]:=I;
  all.parents[I]:=sumnpar;
  all.progeny[I]:=sumnprog;
  all.kmean[I]:=kbar;
  all.migration[I]:=m;
  all.kvar[I]:=Vk;
  all.neffec[I]:=Ne;
end:    {fill Generation of Ne table with data}

Procedure fillcoord;
begin
  writeln ('Options for X axis variable are: ');
  writeln (' 1. sumnpar = no. parents at t-1 ');
  writeln (' 2. kbar ');
  writeln (' 3. m ');
  writeln (' 4. Vk ');
  writeln ('Please enter number of one option');
  readln (xchoice);
  CASE xchoice OF
   1: coord[I,1]:=sumnpar;
   2: coord[I,1]:=kbar;
   3: coord[I,1]:=m;
   4: coord[I,1]:=Vk;
  end;  {case xchoice}
  coord[I,2]:=Ne;
 end;  {for procedure}

Procedure plotfile;
begin
  for row:= 1 to T do
   begin
    for col:= 1 to 2 do
     begin
      write(fout,coord[row,col]:10:4);
      write(f2,coord[row,col]:10:4);
     end; {for col}
    writeln(fout);
    writeln(f2);
   end;  {for row}
 end;  {procedure}

begin  {main}

  rewrite (fout,  'Printer:');
  writeln ('enter  disk:filename.text for storing XY data ');
  writeln('warning:suffix (.text) needed for interchange to B.Graphics ');
  readln (filename);
  rewrite (f2, filename);
  writeln(' Remember, 20=max. no. stocks/generation of Ne table. ');
```

```
  T:=0;
  I:=0;
  repeat  {start of loop for calculations for a stock }
   writeln('Enter I.D. no. for this stock');
   readln (I);
   T:=T + 1; {counter for no. stocks in generation of Ne table}
   title2: {table of age specific data}
   writeln ('first reproductive age class? ');
   readln (first);
   writeln ('last reproductive age class? ');
   readln (last);
   sumnparcalc;
   writeln ('Enter value of sumnprog');
   readln (sumnprog);
   kbar:= (2*sumnprog)/sumnpar;  {computes kbar for whole stock,t-1}
   writeln ('enter value of m');
   readln (m);
   migterm:=(1-m)*(1-m);    {computes migration correction term}
   estimatekbarage;         {computes age specific kbar}
   distribution;  {chooses a probability distrib. for kbar}
   for age:= first to last do
    choicecalc;  {computes sigmasq[age] based on kbar distrib.}
   calcsumtemp:  {computes numerator of Vk equation}
   Vk:=sumtemp/sumnpar;
   numerator:=sumnpar*kbar;
   denominator:=(Vk/kbar)*migterm+1;
   Ne:=numerator/denominator;
   print2;  {age specific data table for stock I}
   fillall; {fill record for Generation of Ne}
   fillcoord; {fill xy array to be used by business graphics}
   writeln ('Do you want calculations for another stock?y/n');
   readln (answer);
  until (answer = 'n') or (answer = 'N');
  {end of repeat loop for stock calculations}
  title1;
  print;   {Generation of Variance Effective Numbers printed}
  plotfile; {xy data are printed and written to filename}
 close (f2,lock);
 close (fout);
end.  {main program}
```