AN ABSTRACT OF THE THESIS OF

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Title: A MODEL OF FALL CHINOOK SALMON (ONCORHYNCHUS TSHAWYTSCHA) LIFE HISTORY

Abstract approved: ______________________

William J. Liss

The research involved development of two ecological simulation models to explain the complex dimensionality of chinook salmon (Oncorhynchus tshawytscha) life history structure (represented by the age composition of the spawning stock) and management difficulties entailed in the complexity.

Since different sizes of chinook salmon are thought to adapt differently to heterogeneous habitats, age composition of the spawning stock is determined by characteristics of the habitats of the substocks. Numerical properties of substocks result from the incorporation of individual spawners in different age classes and each substock performs differently because their age compositions are distinctive.

A stock or population consists of substocks whose age compositions are concordant with their habitats. The productive capacity of a population will result from the

incorporation of substocks. If habitat structures of streams are different, the age and size compositions and productive capacity of the populations may differ.

Selective harvesting affects spawners in different ways, so that age compositions must be deformed differently by fishing pressure. Once the age composition deviates from the natural age composition, the productivity of the population will decrease.

Population dynamics are strongly correlated with substock structure which is determined by habitat structure in a stream system. Hierarchical population structure make fisheries management difficult and requires not only quantitative but also qualitative analysis on the populations in relation to habitat classification.

A Model of Fall Chinook Salmon (*Oncorhynchus tshawytscha*) Life History

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I. GENERAL INTRODUCTION

In fisheries management, a great deal of effort has been directed toward quantitative modeling to provide optimal yield of commercial fisheries products. The models usually apply equilibrium explanations to biological phenomena. For instance, if there is no environmental variation, maximum sustainable yield is the point at which the slope of a line tangent to a stock-recruitment curve becomes unity (Ricker 1954, Beverton and Holt 1957). However, since environmental conditions continuously change, it is almost impossible to stabilize escapement. Furthermore, there is little clear information on how environmental variation influences the production of populations and the use of a single fixed equilibrium yield curve may be misleading (Liss 1977).

There is evidence that populations are composed of many phenotypically different life history types that are adapted to different habitats (Beacham and Murray 1987, Holtby and Healey 1986). They differ in their capacity to perform in nature and their sensitivity to selective forces including human harvesting. When the environment fluctuates so that selective forces on different life history types are changing, population life history structure may continually change. In turn, the adaptive capacity of the population can be altered (Hirai 1987). Den Boer (1968) and Andrewarth and Birch (1984) discuss the concept of spreading of risk which emphasizes the importance of maintaining life history diversity. According to this idea, if environmental conditions for a population are heterogeneous and unpredictable in time and space, an increase in capacity to respond to changes in environments through increased life history diversity is necessary for populations to adapt to such unstable circumstances. The main ecological objective is not how the population could maximize its numerical performance, but how it could persist for a long time in changing environments. Thus, as the environment changes, life history types increasing in abundance will tend to counterbalance decreasing ones so that population abundance will be relatively stable. But, if life history diversity is reduced, both variation in abundance and the probability of stock extinction increase.

Larkin (1977) argued that a stock consists of many uniquely adapted local substocks that have different degrees of vulnerability to fishing. In mixed stocks fisheries, if harvesting rate is increased on the basis of MSY estimated for highly productive substocks, less productive substocks will become extinct. As a result, the stock may lose its productive and adaptive capacity. Larkin warned that fishery management should be based on quantitative analysis but with qualitative effects in mind. It is not easy to use the MSY concept when there is much biological and environmental uncertainty.

Other fishery biologists have presented empirical evidence of possible deterioration of population adaptive capacity due to harvesting (Murphy 1968, Schaffer and Elson 1975, Ricker 1981, Hankin and McKelvey 1985). Ricker (1981) has argued that commercial fisheries selectively harvest faster growing and later maturing fish and that this has resulted in reduction in age at maturity and average body size of Canadian Pacific salmon stocks. Murphy (1968) suggested that intensive harvest of California sardines significantly reduced average life span and number of reproductions per lifetime, stripping away the mechanism the population had evolved to persist in an unpredictable environment.

This research will involve development of a model of chinook salmon (<u>Onchorhynchus</u> <u>tshawytscha</u>) to aid in understanding life history and evolutionary adaptation of populations and response to harvest. The adaptive capacity of a population is entailed in and determined by the incorporation of life history types composing the stock. Performance of each life history type can be delimited by the interrelation of life history events including mating, productions of eggs, and survival. Capacity will be variable since life history events are alterable in relation to changes in habitat organization and management including harvesting and other human influence. First, the model will be used to examine the interrelation of life history events in determining life history organization of chinook salmon stocks. Second, stock-recruitment relationships and response to harvest in constant and changing environments will be investigated.

THEORETICAL FRAMEWORK

Classical life history theories state that organisms must face and solve particular ecological problems with their life history tactics, which can be defined as a set of co-adapted traits shaped by natural selection (Stearns 1976). Natural selection will push a population toward a combination of traits which represents an optimal life history type in order to maximize survival and reproduction. As a result, variation will be removed by directional selection forces and random genetic drift. But evolution of life histories is strongly influenced by patterns of spatial and temporal variation of environments. Nothing guarantees that a population will attain the optimal type. A more fit life history type will not always completely replace the less fit types.

The morphological, physiological and behavioral characters of organisms determine their age-specific fecundity and mortality schedules. Those characters are genetically influenced by a combination of many traits (pleiotrophy). The traits selected for or against will depend upon spatial and temporal patterns of variation in the environment. Thus the life history types composing a population will vary in both space and time. The evolutionary capacity to respond to changing environmental states must depend on the amount of genetic variation. That is, although natural selection may temporarily bring out local optima, there would be no global optimal life history.

An organismic perspective illuminates hierarchical aspects of biological organization (Warren et al. 1979). The adaptive capacity of a species is entailed in its organization which involves the incorporation of continuously evolving populations or stocks (Figure 1A). Species evolve in different ways in different environments.

A population or stock can be thought of as a system of continuously developing life history types (Figure 1B). The life history types composing the stock differ in the kinds of habitats to which they are adapted. They perform in different ways in response of different environments (Figure 1C). The realized capacity of a population or stock is entailed in its life history organization which involves the incorporation of interrelated and interpenetrating life history types. Stock evolution entails changes in realized capacity or life history organization. A population with a given potential capacity will evolve in different ways in different evolutionary environments (Figure 1-B).

A population can be subdivided into local subpopulations or substocks comprising different life history types. Among them, gene flow is restricted by behavioral, geographic and physiological barriers (Holtby and Healey 1986). Such restricted gene flow leads to

Figure 1. Potential adaptive capacities and developmental states of species, populations or stocks, and individual life history types in different environments.

A. Species evolve along different trajectories in different evolutionary/developmental environments (D.E). At each developmental state, the state-specific realized capacity (circle drawn by solid line) of the species is determined by incorporation of state-specific realized capacities of the populations (shaded circles) composing the species. Potential capacity and environment determine the course of species evolution.

B. Stock or local populations have the capacity to evolve in concordance with their environments through changes in realized capacity (circle drawn by solid line). The realized capacity is determined by state-specific realized capacities of the life history types (shaded circles). Course of evolution of stocks is determined by potential capacity and environment.

C. The life history capacity of individual organisms allows for the development of different life history patterns in different developmental environments (D.E). Realized life history capacity (shaded circle) will vary depending on potential capacity and environment.

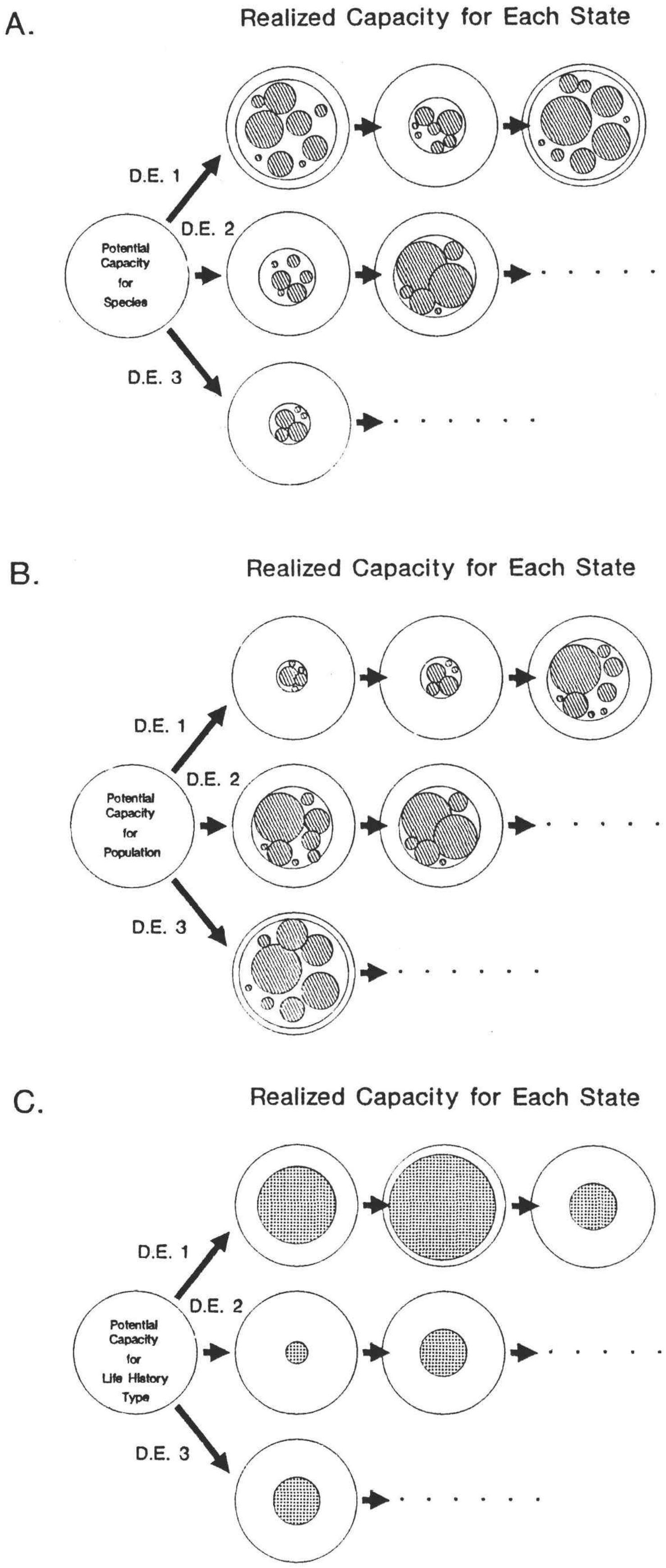

A.
Realized Capacity for Each State
D.E. 1
D.E. 2
D.E. 3
Potential Capacity for Species
B.
Realized Capacity for Each State
D.E. 1
D.E. 2
D.E. 3
Potential Capacity for Population
C.
Realized Capacity for Each State
D.E. 1
D.E. 2
D.E. 3
Potential Capacity for Life History Type

Figure 1.

differentiation of the local subpopulations due to genetic drift and the operation of different natural selection forces. Consequently, within the habitat of the population, different "life history" habitats would be selected by different life history types. The habitat of the population develops or changes as a result of changes in habitats of life history types. Population life history organization tends toward concordance with changes in habitat organization (Figure 2 A and B). Changes in life history organization involve appearance and persistence of some life history types and disappearance of others. The persistence of a life history type depends upon both the availability of its habitat in space and time and the organizaton of the population. Following such changing population organization, the realized capacity and numerical performance of the population would also change. Here, not only the degree of organization as measured by the abundance of existing life history types, but also the evolutionary flexibility of life history organization to respond to changing environments should be considered as the realized capacity of a population at a given point in evolutionary time (AC-I in Figure 3A).

When management becomes involved, a population would need to establish concordance with a new evolutionary force. The intensity and the direction of organizational force of

Figure 2. Schematic representation of the relationship between habitat availability and colonization by life history types. The distribution of life history types within a population is strongly dependent on patterns of habitat availability in evolutionary time and space. Some locations have the potential for becoming habitats(broken circles), while others are already available(solid circles) and life history types have colonized. Panels in A shows the relationship between habitat availability and colonization of life history types through time. Panels in B show life history structure in terms of five life history types(1,2,3,4 and 5) involved in habitat organization. The solid arrows indicates the actual contribution to changes in abundance of life history type j in habitat j from type i in habitat i. Different shading of circles indicates different degrees of colonization in evolutionary time.

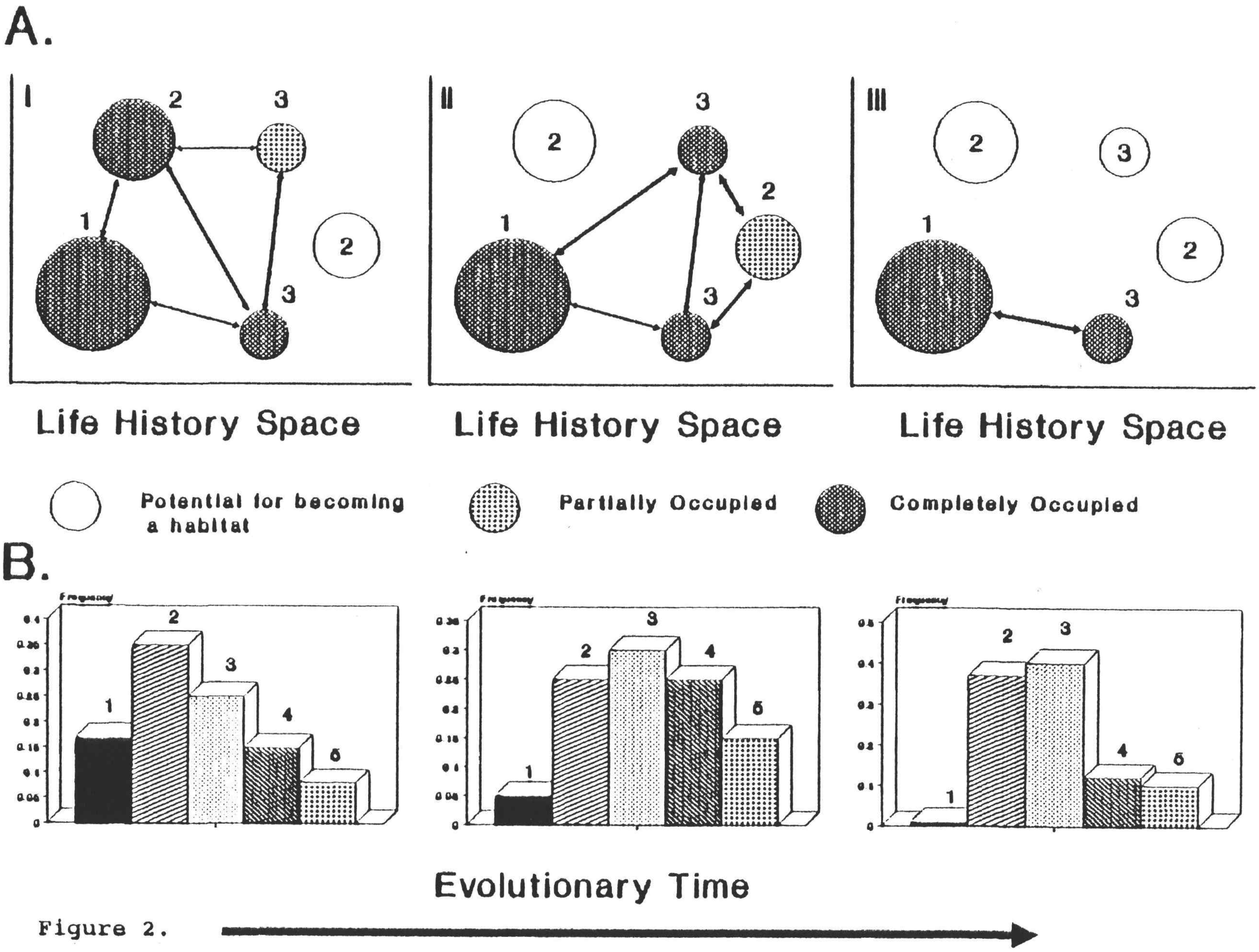
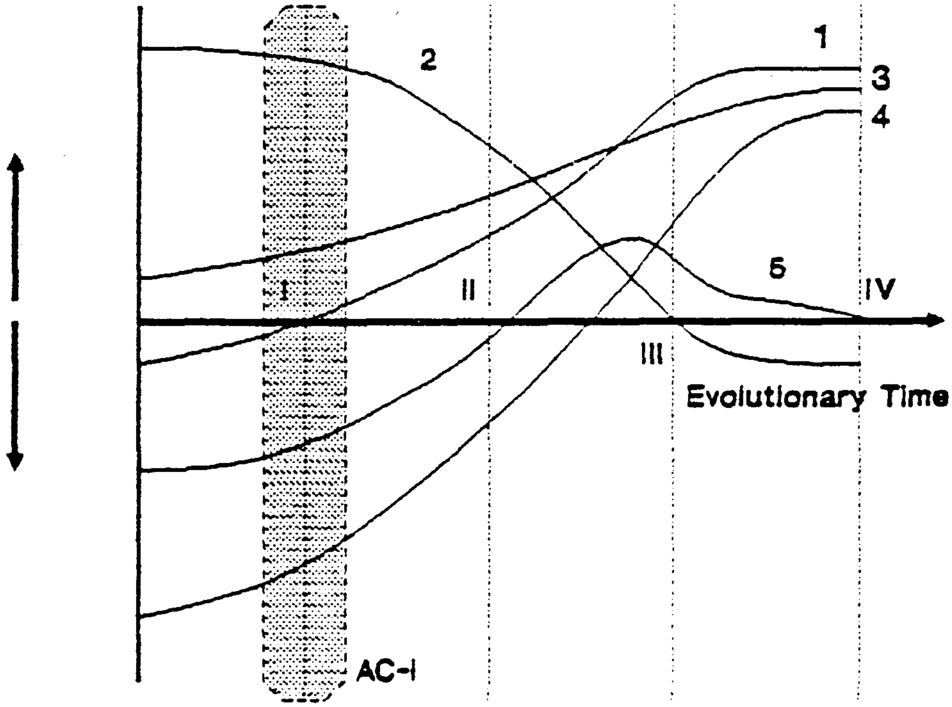
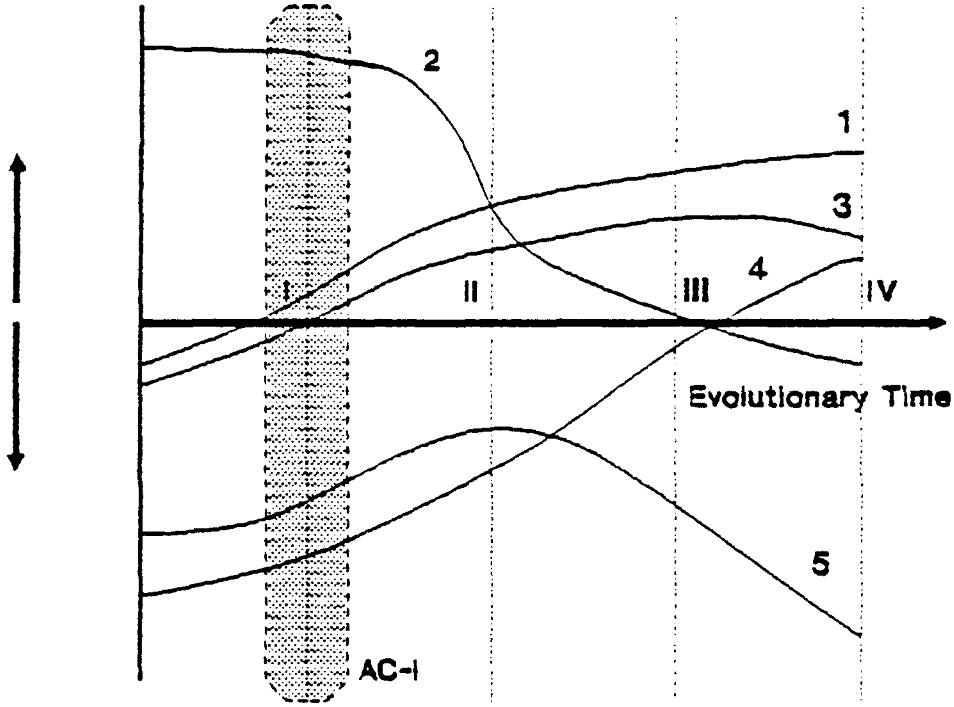

A.
I
II
III
1
2
3
Life History Space
Life History Space
Life History Space
Potential for becoming a habitat
Partially Occupied
Completely Occupied
B.
Frequency
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
1
2
3
4
5
Frequency
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
1
2
3
4
5
Frequency
0.5
0.4
0.3
0.2
0.1
0
1
2
3
4
5
Evolutionary Time

Figure 2.

Figure 3. Changes in life history organization of a population. The x-axis indicates evolutionary time. The y-axis above the center line is the degree of expression of life history types 1-5 (actual abundance) in the populations and below the line the possibility of reappearance of a type that has disappeared from the population. AC-I (shaded area) is the realized adaptive capacity of the population at time I. Some life history types completely occupy their habitat such as life history type 2 at evolutionary time I in A, but other do not (type 3 in I,II). Also, some life history types are not yet expressed in the population (types 4 and 5 at time I in A). They can possibly appear, that is, be organized out of the gene pool, if their habitat appears and persists. The degree or possibility of reappearance or reorganization and the rate of organization for such life history types are closely related to population life history organization and habitat capacity. The trends without any harvesting (A) and with harvesting on some life history types [such as type 3 and 4 in (B)] are different.



A Without management



B With management

Figure 3.

each life history type would be altered differently by harvesting pressure, habitat deterioration and so on (Figure 3B). As a result, abundance of existing life history types and possibility of reappearance of the eliminated types would be decreased. In turn, life history structure would have lost its plasticity (AC-I in Figure 3B) and the capacity of a population would have been reduced.

MODEL DEVELOPMENT

An ecological computer simulation model of fall chinook salmon was developed. The model is written in c-language because of the freedom it allows in defining any kind of user-function in addition to its own library. This allows us to deal with each component of the life history as a specific independent function. The fall chinook salmon (Onchorhynchus tshawytscha) is represented in the model because it exhibits spatial and temporal variation in its life history and a rich base of information on life history and management is available.

Fall chinook salmon deposit eggs in the gravel of streams in late fall to the end of winter. The fry emerge the following spring. Most of these juveniles migrate to the estuary after 3-4 months of freshwater rearing (ocean-type fall chinook). After a period of residency in the estuary as smolts, they enter the sea during their first year. Females mature in the third to sixth year of life and return to the river of origin to spawn and die.

The model of chinook life history is composed of three mechanisms (Figure 4): a mating mechanism (block A) which deals with spawning of males and females and deposition of eggs, a stock-recruitment relationship that determines survival from eggs to smolts in freshwater (block B), and an

Figure 4. Diagramatic representation of the model of the life history of chinook salmon. Each path way represents a connection between life history events and each node represents numbers present at the end of the ith year (i = 1,2,3,4, and 5). Block A indicates the mechanism for mating and total production of eggs. When the spawning stock returns to their original stream to spawn, they mate with each other on the basis of the probability determined by the age composition and the mating regime (see text). As a result, individuals in different age classes 3, 4, 5 and 6 produce different number of eggs b_3, b_4, b_5, and b_6, respectively. $N_0 = \Sigma\ S_i * b_i$ is the total number of eggs laid by the spawning stock, where S_i is the number of females aged i. The progeny reproduced by females in a particular age class will mature at different ages, depending on the age of the male. Since egg-to-smolt survival rates vary with the age of the female that produced the eggs, the number of smolts is separately estimated in block B by means of the Ricker stock-recruitment equation with density dependent mortality, which is a function of the initial number of eggs laid by the entire spawning stock. Density independent mortality in freshwater for progeny reproduced by females aged i is m_i. At the end of the first year, node 1, smolts migrate to the ocean (block C) where they face natural mortality and fishing mortality every year. Survivors mature at age, 3, 4, 5, or 6, depending on the maturation probability estimated in block A, and return to their home stream. OM_1, OM_2, ... OM_5 are the instantaneous natural mortality rates in the ocean. F is the instantaneous fishing mortality, so that $\exp\{-(OM_i+F)\}$ is the proportion of fish surviving at the end of the ith year.

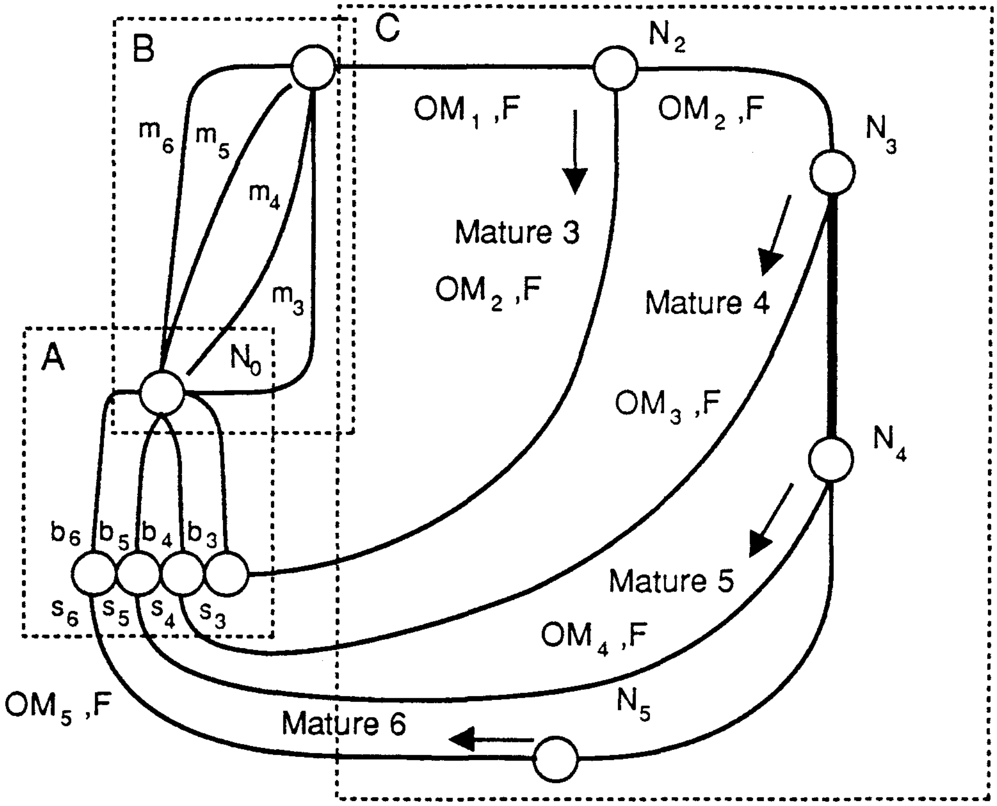

B
C
A
N2
N3
N4
N5
N0
m6
m5
m4
m3
OM1 ,F
OM2 ,F
Mature 3
OM2 ,F
Mature 4
OM3 ,F
Mature 5
OM4 ,F
OM5 ,F
Mature 6
b6
b5
b4
b3
s6
s5
s4
s3

Figure 4.

ocean stage that deals with natural and harvest mortality from the smolt stage until fish return at a later age (age 3-6) to spawn (block C). This section provides a general overview of the structure of the model. Specific parameter values will be given in following sections.

Mating Mechanism (Block A)

The spawning stock of fall chinook salmon in any year is composed of individuals from different cohorts. Spawners aged 6 were born six years ago and spawners age 3 in the same spawning stock were born three years ago. The mathematical mechanism for mating and egg deposition is shown in Figure 5 for age 3 females mating with males aged 3, 4, 5, or 6. Definition of model parameters used in Block A are given in Table 1.

The total number of spawning females aged i is S_i. The number of females aged i that mate with males aged j is S_iP_{ij} where P_{ij} is the proportion of females aged i mating with males aged j. In the model two general mating schemes are examined: assortative and random. In random mating, each female has an equal probability of mating with each male aged j. In assortative mating, females aged i tend to mate preferentially with males of the same age. Details of the mating schemes are presented in later sections.

Figure 5. Mathematical mechanism for reproduction. The total number of returning adult females aged 3 is S_3. The proportion P_{3j} of these females mate with male aged j (j=3, 4, 5, 6) so that a total of S_3P_{3j} females will mate with males aged j. For each mating, 3xj, the total number of eggs produced is $S_3P_{3j}b_3$. The progeny from those eggs will mature at age k (k=3, 4, 5, 6), depending on the maturation probability, $m_{3j,k}$ (see text). Therefore, the total number of eggs produced by females aged 3 mating with males aged j that will potentially mature at age k is $S_3P_{3j}b_3m_{3j,k}$. The total number of eggs produced by females aged 3 and maturing at age k under all possible combinations of matings with males of different ages is $S_3b_3\Sigma P_{3j}*m_{3j,k}$.

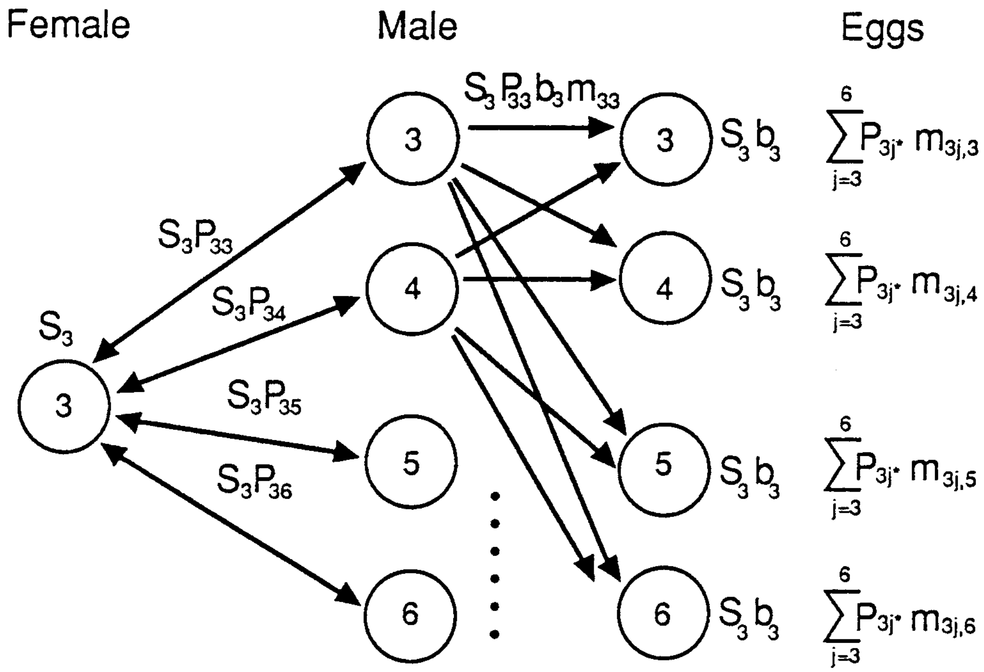

Female
Male
Eggs
$S_3P_{33}b_3m_{33}$
S_3P_{33}
S_3P_{34}
S_3P_{35}
S_3P_{36}
S_3
3
3
4
5
6
3
4
5
6
S_3b_3
S_3b_3
S_3b_3
S_3b_3
$\sum_{j=3}^{6} P_{3j} \cdot m_{3j,3}$
$\sum_{j=3}^{6} P_{3j} \cdot m_{3j,4}$
$\sum_{j=3}^{6} P_{3j} \cdot m_{3j,5}$
$\sum_{j=3}^{6} P_{3j} \cdot m_{3j,6}$

Figure 5.

Table 1. Definition of model parameters in Figure 4, block A. See text for equations.

Parameter	Definition
$\bar{A}_{ij}$	Expected mean age at maturity of offspring from the cross of females aged i with males aged j.
$\bar{P}$	Mean age of returning adults in the spawning population.
R_{ij}	Difference between mean age at maturity of offspring of parents aged i and j and the mean age at maturity of the entire parental generation.
D_{ij}	Deviation of the mean age of the population and the mid-parent value of parents aged i and j.
$\bar{V}_{ij}$	Mid-parent value of parents aged i and j.
I^2	Heritability of age at maturity.
S_i	Total number of returning adult females aged i.
P_{ij}	Proportion of returning adult females aged i which will mate with males aged j.
b_i	Fecundity of female aged i.
$m_{ij,k}$	Probability of progeny maturing at age k from a mating of individuals aged i and j.
E_{ik}	Total number of eggs reproduced by females aged i that will potentially mature at all k under every possible combination of matings with males aged j in a given spawning stock.
E_k	Total number of eggs reproduced by a given spawning stock and maturing at age k.

If the environment fluctuates, the developmental environments of the cohorts composing the spawning stock will differ. Thus, the age composition of the spawning stock will be variable from year to year. As the age composition changes, the probability of individuals aged i mating with those aged j, P_{ij}, must also change even though the mating scheme (assortative or random) remains fixed. Matrices illustrating mating probabilities under two different age compositions are given in Tables 2A and 3A.

Age at maturity in chinook salmon is at least partially genetically determined, that is, the age at maturity of offspring is influenced by the age at maturity of parents. But we are not able to directly observe changes in gene frequencies. In the simplest form of selection, changes in frequency of a particular gene are manifested as changes in mean value of the meristic character related to the gene in the population. The average effect of the parents' genes determines the mean genotypic value of their progeny (Falconer 1981). In the case of chinook salmon, the genotypic value is associated with age at maturity. The mating of females aged i with males aged j produce a group of progeny whose individuals will return to spawn at different ages (ages 3-6). The expected mean age at maturity of the progeny from a cross of fish aged i with

Table 2A. Probability of females aged i mating with males aged j under the given age composition. Mating is assortative.

Age Composition

Age 3	**Age 4**	**Age 5**	**Age 6**
100(0.141)	**230(0.324)**	**240(0.338)**	**140(0.197)**

i\j	**Age 3**	**Age 4**	**Age 5**	**Age 6**
Age 3	0.729	0.112	0.117	0.041
Age 4	0.049	0.687	0.195	0.068
Age 5	0.049	0.187	0.695	0.068
Age 6	0.029	0.112	0.117	0.741

Table 2B. Probability of offspring from females aged i maturing at age k.

i\k	**Age 3**	**Age 4**	**Age 5**	**Age 6**
Age 3	0.271	0.375	0.269	0.086
Age 4	0.191	0.354	0.321	0.134
Age 5	0.134	0.321	0.354	0.191
Age 6	0.086	0.269	0.375	0.271

Table 3A. Probability of females aged i mating with males aged j under the given age composition. Mating is assortative.

Age Composition

Age 3	**Age 4**	**Age 5**	**Age 6**
250(0.336)	**275(0.369)**	**170(0.228)**	**50(0.067)**

i\j	**Age 3**	**Age 4**	**Age 5**	**Age 6**
Age 3	0.772	0.132	0.082	0.014
Age 4	0.120	0.720	0.136	0.024
Age 5	0.120	0.220	0.636	0.024
Age 6	0.072	0.132	0.082	0.714

Table 3B. Probability of offspring from females aged i maturing at age k.

i\k	**Age 3**	**Age 4**	**Age 5**	**Age 6**
Age 3	0.398	0.368	0.191	0.043
Age 4	0.302	0.378	0.248	0.072
Age 5	0.230	0.367	0.296	0.108
Age 6	0.155	0.333	0.342	0.170

those aged j is given by;

$$A_{ij} = \bar{P} + \bar{R}_{ij} \quad \text{----} \ (1)$$

$$R_{ij} = D_{ij} * h^2 \quad \text{----} \ (1)'$$

$$D_{ij} = \bar{V}_{ij} - \bar{P} \quad \text{----} \ (1)''$$

Now, for a particular value of heritability of age at maturity, h^2, the frequency distribution of age at maturity of progeny from a female aged i mating with male aged j can be represented approximately as a normal distribution with mean, A_{ij}, calculated by the above equation with a segregation variance of unity. The probability of progeny maturing at age k (k=3,4,5 and 6) from a mating of individuals age i and j, $m_{ij,k}$, can be easily estimated from the table of area under the standard normal curve. It follows, then, that the total number of eggs that will potentially mature at age k produced by a mating of females aged i and males aged j is $S_i P_{ij} b_i m_{ij,k}$.

Changes in age composition of the spawning stock will change probabilities of maturation at age k. Probabilities of maturation at age k, $m_{ij,k}$, for two age compositions are shown in Tables 2B and 3B. The total number of eggs reproduced by females aged i that will potentially mature at all k (k=3,4,5 and 6) under every possible combination of matings with males aged j (j = 3,4,5 and 6) in a given spawning stock is :

$$E_{ik}(t+1) = S_i(t)*b_i \sum_{j=3}^{6} P_{ij} * m_{ij,k} \qquad \text{--------} \ (2)$$

where t is generation length. The total number of eggs reproduced by a given spawning stock and potentially maturing at age k is:

$$E_k(t+1) = \sum_{i=3}^{6} E_{ik} \qquad \text{--------} \ (2)'$$

$$N_0 = \sum_{k=3}^{6} \sum_{i=3}^{6} E_{ik} = \sum_{k=3}^{6} E_k \qquad \text{---------} \ (2)''$$

where N_0 is the total number of eggs reproduced by a given spawning stock.

Multiple-Age Stock Recruitment Relationship (Block B)

Ricker(1971) argues that competition for limited resources should be more severe in streams than in the ocean. Thus compensatory mortality may be confined to early life history stages. That is to say, since recruitment to the spawning stock of the next generation is explicitly limited by the carrying capacity of the stream, the number of recruits to the fishable stock is determined mainly in the first year of life during freshwater and estuarine rearing. This is the basis for the development of the well known Ricker's stock-recruitment model. In the model, the relationship between stock and recruits is described by humped curves with high recruitment tending to occur at lower spawning stock levels and lower recruitment at higher spawning stocks. The assumption is that all individual spawners are phenotypically identical (Ricker 1954). However, the spawning stock of each generation is composed of different phenotypes or life history types defined in terms of differences in age at maturity, mortality in both freshwater and ocean, fecundity and so on. Different phenotypes may also utilize different places within the stream as spawning and rearing habitat. Eggs and emerged fry in different habitats encounter different magnitudes of environmental effects, so that survival rates may differ among phenotypes. The stock-recruitment relationship should be based on the total number of eggs laid by females in different age classes instead of just total number of spawners.

The development of the model for juvenile survival is fairly straightforward. Definitions of parameters are given in Table 4. It is assumed that density-dependent mortality

Table 4. Definition of model parameters in Figure 4, block B. See text for equations.

Parameter	**Definition**
M_i	The total egg-to-smolt mortality rate for offspring produced by females aged i.
m_i	Density independent egg-to-smolt mortality rate for offspring produced by females aged i.
k	Coefficient of density dependence.
$N_{0,i}$	Total number of eggs laid by spawners in age class i.
S_i	Total number of spawners aged i.
S	ΣS_i
b_i	Average fecundity for spawners aged i.
SR_i	Total number of smolts from spawners aged i surviving at the end of the first year.
$\bar{b}$	Expected fecundity per adult in a multiple age spawning stock.
p_i	Proportion of adult females aged i in the given spawning stock.
$\bar{\alpha}$	A measure of stock productivity or mean fitness of females.

can be accounted for explicitly as a function of the initialnumber of eggs laid by the spawners. If the total mortality rate of eggs produced by females aged i, M_i, is made of a density-independent factor, m_i and a density-dependent factor kN_0, the mortality of eggs produced by females aged i increases linearly with increases in total number of eggs laid by the spawning stock, N_0. The equation is as follows (Cushing 1981, Larkin 1973) :

$$M_i = m_i + kN_0 \qquad \text{--------} \ (3)$$
$$dN_i \ / \ dt = -M_iN_i \qquad \text{--------} \ (4)$$

Since the model always estimates only the number of females, the assumption is that the proportion of males in age class i is same as that of females. Thus, from equation (4), the number of female smolts at the end of the first year is:

$$SR_i = 1/2 * N_{0,i} \exp(-M_i) \qquad \text{--------} \ (5)$$
$$N_{0,i} = S_i*b_i \qquad \text{--------} \ (5)'$$
$$N_0 = \sum_{i=3}^{6} N_{0,i} = \sum_{i=3}^{6} S_i*b_i \qquad \text{--------} \ (5)''$$

If $-M_i$ is replaced with $(-m_i - k \sum_{i=3}^{6} S_i*b_i)$ in equation (5), then

$$SR_i = 1/2 * N_{0,i} \exp(-m_i - k \sum_{i=3}^{6} S_i*b_i) \qquad \text{--------} \ (6)$$

$$SR_i = 1/2 * S_i*b_i \exp(-m_i) * \exp(-k \sum_{i=3}^{6} S_i*b_i) \ - \ (6)'$$

$$SR_i = 1/2 * S_i*b_i \exp(-m_i) * \exp(-k*S*\bar{b}) \text{ ----- } (6)''$$

Therefore, the total number of female smolts produced by a given multiple age spawning stock is :

$$N_1 = 1/2 * S \sum_{i=3}^{6} \{[p_i*b_i \exp(-m_i)]*\exp(k*S*\bar{b})\} \text{ -- } (7)$$

$$N_1 = 1/2 * S \bar{\alpha} \exp\{(-k*\bar{b})*S\} \text{ -- } (7)'$$

$$\bar{\alpha} = \sum_{i=3}^{6} [p_i * b_i \exp(-m_i)] \text{ -- } (7)''$$

Although equation (7)' is identical with the original equation in the Ricker model, $\bar{\alpha}$ and $\bar{\beta}$ ($\bar{\beta}$= k*b) values vary with age composition of the spawning stock. Normally in stock-recruitment models, $\bar{\alpha}$ is assumed to be constant. This is an important distinction between this model and the standard interpretation of the Ricker model and will be considered further in a later section.

Ocean Life History Stages (Block C)

Smolts surviving at the end of the first year migrate to the ocean. They mature at a certain age depending in part on the age of their parents. The genetic procedure in block A estimates the possible total number of progeny produced by a given spawning stock and maturing at age k., $E_k(t+1)$. This number will be reduced by mortality in freshwater (block B) and in the ocean. Suppose that individuals are vulnerable to fishing beginning in their third year. Assume that the only causes of annual mortality in the ocean are fishing and natural mortality. Then the numerical representation of the actual total number of female adult returning at age k, $S_k(t+1)$, under constant annual harvest is:

$$n_k(t+1) = \sum_{1=3}^{6} 1/2 * E_{ik} \exp(-m_i) * \exp(-k*S*b\overline{)} \quad \text{----(8)}$$

$$S_k(t+1) = n_k(t+1) * \exp(-\sum_{r=2}^{k} OM_{r-1}) * \exp\{-F(k-2)\} \quad \text{----(8)'}$$

where the parameter OM_1, OM_2, ... OM_{k-1} are the instantaneous natural mortality rates for different ocean years. The parameter F is the instantaneous fishing mortality.

II. THE LIFE HISTORY PARAMETERS OF CHINOOK SALMON (ONCORHYNCHUS TSHAWYTSCHA)

INTRODUCTION

Life history variation within natural population is thought to be an adaptation to spatially and temporally heterogeneous environments (den Boer 1968, Levins 1968, Andrewarth and Birch 1984). Chinook salmon (*Oncorhynchus tshawytscha*) show considerable life history variation both within and between stream systems (Healey and Heard 1984).

The life history types composing a population are related to the distribution of habitats in space and time. Holtby and Healey (1986) observed that spawning sites selected by female coho salmon are correlated with body size. Large females are likely to select and occupy sites prone to high water flow that usually contain clean gravel and are most suitable for spawning and incubation despite frequent disturbance by scour. Small females seem to prefer sites with lower water flow even though such sites may be poorer for spawning and incubation.

Hankin (1985) and Healey and Heard (1984, 1985) suggested the possible advantages and disadvantages of large and small chinook salmon in different kinds of habitats. Since large chinook have a superior capacity for digging redds, they can select the best sites for spawning, those characterized by high water flow, large gravels, and high percolation rate (Beacham et al. 1989). They dig deeper redds and produce more and larger eggs. More deeply buried eggs tend to be protected from scour during flood years and larger eggs are thought to result in improved survival to smolting. However, in habitats characterized by low water flow, small gravels and low percolation rate, eggs buried too deeply may fail to get adequate oxygen for incubation. Smaller individuals, which can dig only shallow redds and lay smaller eggs, tend to select sites of lower flow where there is less risk of redds being disrupted by high turbulence. In Atlantic salmon large body size is thought to be an adaptation to spawning migration in long, turbulent rivers (Schaeffer and Elson, 1975). In summary, large size, which may be an adaptation for spawning in areas of continual or periodic high flows, is acheived by delaying maturity and spending more time feeding and growing in the ocean. Large size and later maturity are associated with higher fecundity, larger eggs, and possibly greater survival of eggs to smolts.

Salmon, then, may adapt to different kinds of habitats with variation in phenotypic characters. Every stream system is biologically and physically heterogeneous and unpredictable in time and space. Chinook salmon seem to use such heterogeneous and unstable habitats efficiently with a wide range of body sizes and ages at maturity, involving different phenotypical qualities of eggs and different capabilities of nesting at various spawning sites. Therefore, it is assumed that life history organization, here represented by the age composition of spawning stock, should be consistent with the habitat structure.

Exploitation can change life history organization and affect stock productivity (Hirai 1987). In particular later maturing salmon are highly vulnerable to fishing because of their larger size and longer length of ocean life. The abundance of older larger fish in many Pacific chinook salmon stocks is thought to have declined (Ricker 1981, Hankin and McKelvey, 1985). Harvesting then can result in reduction in average age and size of the spawning stock and loss of age diversity.

The main purpose of this section is to examine the possible interrelationships of freshwater and ocean survival, mating regime (assortative or random) and inheritance of age at maturity in determining age composition at maturity. Life history organization is determined by the interrelationship of these parameters. For example, natural selection operating through differences in fertility among adults in different age classes and differences in age at maturity among their progeny may cause changes in age composition of the spawning stock in the next generation. In turn, inheritable characteristics associated with age at maturity may be altered and the probability that individuals aged i will mate with those aged j may also be changed. As a result, the distribution of age at maturity for progeny may shift between generations. This will occur continually.

A better understanding of the determinants of life history organization may lead management to more carefully consider habitat organization in river basins and harvesting strategies. If the order of magnitude of adaptation is clearly dissimilar among different age class in certain habitats, the population may be very sensitive to disruption of life history structure.

THE MODEL

The model shown in Figure 4, comprising a mating mechanism, a multiple-age stock-recruitment relationship of smolts, and ocean life history stages, was used to examine the interrelation of life history parameters. As mentioned above, the age composition of a spawning stock results from the interactive influence of age-specific mortality in both freshwater and the ocean, mating regime and the inheritance of age at maturity. These life history parameters are variable. Thus, life history composition as reflected in the proportion of spawning females aged six, was examined under different levels of freshwater and ocean survival, different values of heritability, and different mating regimes.

There are few independent estimates of life history parameters of chinook salmon. Age at maturity, age-specific mortality schedules in both fresh and salt water, and so on are highly uncertain and difficult to estimate.

Attempts have been made to estimate life history parameters by several researchers. Downey and Nicholas (1985) estimated egg to smolt survival rate of fall chinook in Elk River, Oregon. They estimated the potential number of eggs deposited in the basin on the basis of average fecundity and number of observed females. The summer following spawning, from mid-June through mid-September, the number of juvenile chinook present in the estuary was determined by the Peterson mark and recapture method. They concluded that egg-to-smolt survival rate and smolt-to-adult survival in Elk River were 0.05% and 3.3%, respectively. Other authors suggested that annual natural mortality rate of chinook in the ocean appears to range from 20% to 35% (Cleaver 1969, Ricker 1976). In comparing ocean mortality rates for all Pacific salmon, Healey and Heard (1984) suggested that the possible range of mortality was between 16.5% and 27%.

There have been few attempts to estimate age-specific maturity schedules because they are influenced by variable inheritable characteristics of age composition of the spawning stock and uncertainty of the contribution made by males in determining age at maturity (Larkin and Hourston 1964). Larkin and Hourston (1964) assumed in their simulation model of sockeye salmon that the proportion of the progeny maturing at a particular age could be estimated from the proportion of eggs laid by adults at that age to the total number of eggs produced by the population. Hankin (1986) recursively calculated age and sex-specific maturation probabilities from the observed age composition of exploited chinook stocks which he assumed were at equilibrium.

Chinook salmon show significant variation in fecundity within and between populations (Healey and Heard 1984). Within a population there tends to be a positive relationship between female body size and fecundity. To avoid complexity, fecundity values used in the model are 3500, 4600, 5300 and 5800 for females aged 3,4,5 and 6, respectively, estimated on the basis of data of the relationship of average fork length at age to egg production in the Sixes river (Hankin and Nicholas 1988). Since it is assumed that the carrying capacity of the habitat to which the population is adapted does not have a direct effect on age composition, the coefficient of density dependent mortality, k, is fixed. The test runs were executed for 100 years with various combination of egg-smolt mortality, smolt-adult mortality, mating regime, and inheritance of age at maturity.

MORTALITY

Egg-Smolt Mortality in Freshwater

The survival rate of offspring from phenotypically different parents may be different in different habitats. An index of freshwater survival, index A, was developed that compares freshwater survival of offspring from age 6 females with those from age 3 females, assuming no compensatory mortality. Specifically the index is the ratio of the number of offspring that survive to smolts from age 6 fish to the number that survive to smolts from age 3 fish, under the assumption that the sum of smolt production per individual spawner over all age classes is fixed at 100. Smolt production is assumed to be geometrically related to age. For example, if index A equals 20 the number of smolts produced by an aged 6 female and surviving to the end of the first year is 20 times as large as that from an aged 3 female. The actual values of smolt production are 64.3, 23.69, 8.73 and 3.23 (=100) for fish aged 6,5,4 and 3, respectively, so that the rate of increase with age in the smolt production is 2.71. The index has also another meaning. It indicates the extent to which older, larger spawners are favored in a particular habitat over smaller, younger spawners. The larger the index, the more favorable the habitat for large fish and the substock would be relatively late maturing.

Smolt-Adult Mortality in Ocean Water

Estimates of ocean natural mortality are difficult to obtain. Many kinds of errors may be involved in the estimation, including random sampling error caused by small sample size, variability associated with changes in environmental states and so on (Ricker 1976). Nevertheless, mortality during early ocean life, in general, is thought to be high because of predation on small salmon. Mortality may well decline with age (Parker 1968). However, as in the case of egg-smolt mortality, the degree of difference of mortality between early and late ocean life is unknown. The model divides the five years of ocean life into three different stages, the early ocean life stage for the first two years, the mid-ocean life stage for the third year, and the late ocean life stage for the last two years. Survival rates are assigned to each stage in the model.

To define an index of degree of difference of survival between early (younger maturing) and late (older maturing) ocean stages, termed index B, the survival rate of the mid-ocean life stage is fixed at 80% and the difference in survival rate between early and late stages is estimated.

Therefore, if the value of index B is 10, the survival rates for the three stages are 75%, 80% and 85%, respectively.

Mating Regime

Large chinook salmon appears to exhibit strong territoriality by excluding small individuals from their spawning sites. A large female may not mate with a small male if a large male is present (Hansonard and Smith 1967). The tendency will be enhanced as large individuals become more abundant, so-called density dependent selective breeding. The model provides three different mating regimes to examine selectivity in mating in relation to other life history events.

For simplicity, selectivity indices s_3, s_4, s_5, and s_6 are defined for age 3,4,5 and 6 spawners, respectively. The indices give the proportion of females in each age class that will mate with males of their own types. The remaining females in the age class mate at random. For instance, suppose that the spawning stock comprises the proportion P_i $(i=3,4,5,6)$ for each age class, and half of the number of individuals are female. Then, $P_i s_i$ $(i=3,4,5,6)$ individuals will mate with individuals of their own types. Among the remaining individuals, the probability that age i females mate with age j males is $\{(1-s_i)P_i / (1-\Sigma P_i s_i)\}*\{(1-s_j)P_j / (1-\Sigma P_i s_i)\}$.

Three sets of indices, {0.5, 0.6, 0.7, 0.8}, {0.5, 0.5, 0.5, 0.5} and {0, 0, 0, 0} are defined in the model. The first set, assortative mating 1, represents a strong tendency for larger, older to mate with their own type. The second set, assortative mating 2, is moderately selective with 50 percent of females aged i mating with males aged i. The last set is random mating. Effects of different mating regimes on the age composition of the spawning stock are tested with a fixed inheritance coefficient of age at maturity of 0.25.

Intergenerational Life History Inheritance Coefficient

It is known that age at maturity of chinook salmon is an inherited trait (Ricker 1972). However, there is no way to get exact measurements of heritability because response to selection is highly influenced by environmental conditions and other characters positively or negatively correlated with age at maturity. Thus, the intergenerational life history inheritance coefficient, which is analogous to heritability but abstractly defines intergenerational inheritable characteristics of age at maturity, was used.

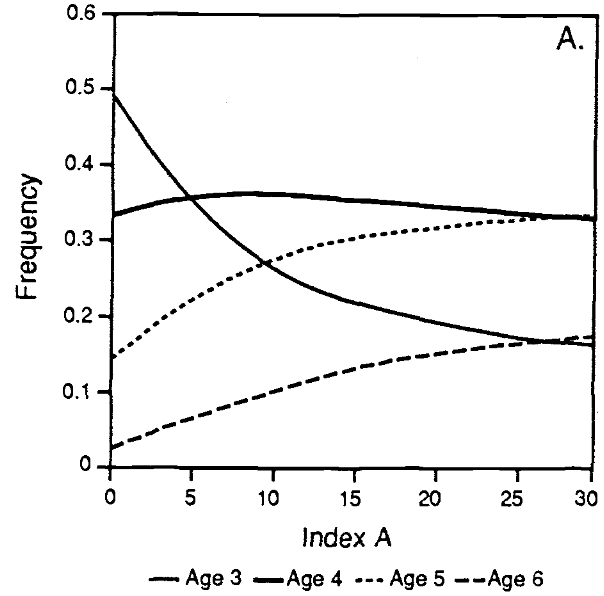
In experimental crosses of fish from the 1974 brood year at Elk River Hatchery, age at return of females from crosses of age 3 x 3 and age 5 x 5 were 3.58 and 4.31 years, respectively. The estimated heritability was 0.37 for females (unpublished ODFW data). This estimate of heritability was somewhat higher than that of 0.25-0.3 suggested by Ricker (1981). Therefore, on the basis of this information, the model tests inheritance coefficients of 0.2, 0.25, and 0.3 under each mating regime, in order to examine the sensitivity of age composition to changes in inheritance coefficient.

RESULTS AND ANALYTIC INTERPRETATION

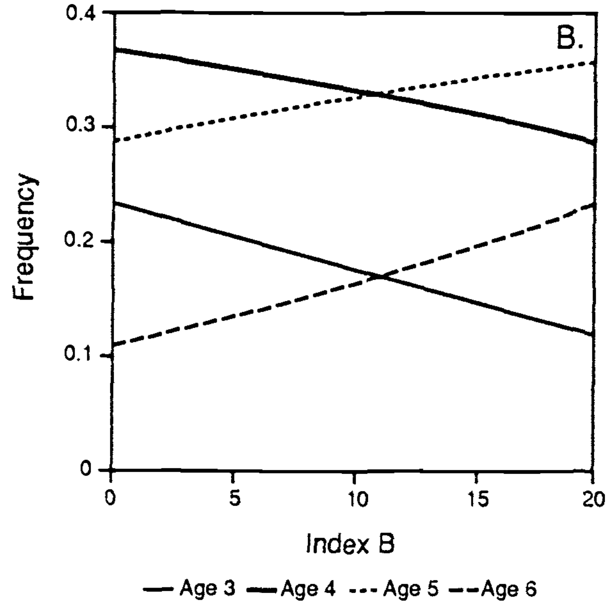
Freshwater and Ocean Survival

In general for fixed levels of index B (relative ocean survival), inheritance coefficient, and mating regime increases in index A (relative freshwater survival) shift the age composition of the spawning stock (Figure 6a). At high values of index A, survival to smolts of offspring from larger, later-maturing females is much greater than survival of offspring from smaller, earlier maturing fish. Consequently older maturing fish make up a greater proportion of the spawning stock at high levels of index A than at low levels. At low values of the index the age composition is strongly skewed toward smaller, earlier maturing fish. Freshwater habitats strongly favoring large fish will have high index A values while those in which large fish have only a slight adaptive advantage over smaller fish will tend to have low values of index A. Changes in index B also shift age composition (Figure 6b) with higher values of this index tending to result in greater proportions of later maturing females in the spawning stock.

Figure 6. Stable age composition in habitats characterized by different values of index A and B. At a high value of the index A, late-maturing, large fish are favored in the freshwater habitat. The age composition of spawning stock is normally distributed with the mean age 4.5 under size-specific assortative mating regime 1. Early-maturing, small fish are more favored at low values of index A and the age composition is skewed toward younger ages. Similarly, the age composition is altered by relative differences in ocean survival between large and small fish (index B).



I.C. 0.2 & Index B 10



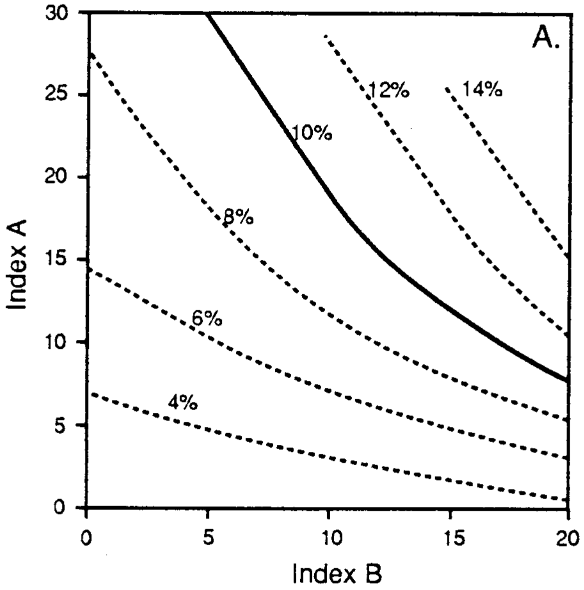
I.C. 0.25 and Index A 25

Figure 6.

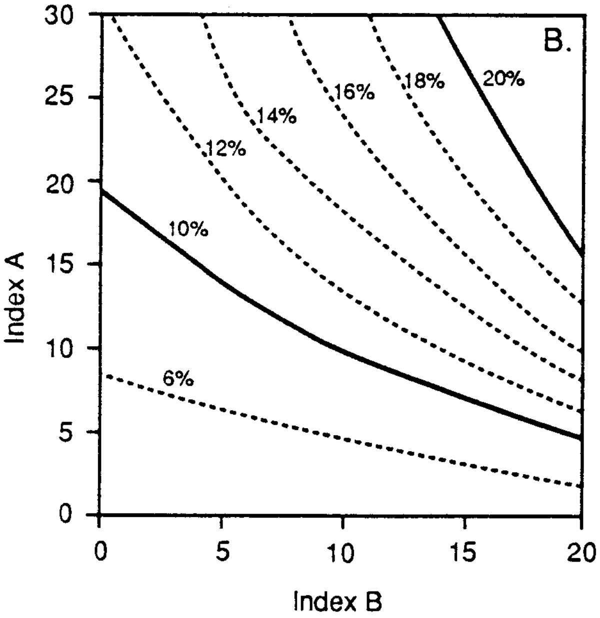
The proportions of spawning females in age class 6 at different levels of inheritance coefficient are shown as convex contour lines in Figure 7. The proportions increase at an increasing rate along the x-axis and at a decreasing rate along the y-axis. For example, suppose index A which shows the difference in production of smolts between small, early maturing fish and large, late maturing fish in freshwater is fixed at 10, and index B, the indicator of degree of difference of survival between early and late ocean life stage varies from 0 to 20 (Figure 7). The proportion of individuals aged 6 in the spawning stock increases exponentially with an increase in index B (Figure 8a). The rate of increase is greater when index A is large than when it is small. On the other hand, if index B is fixed, the frequencies always increase logarithmically (Figure 8b). The rate of increase becomes larger for higher values of index B.

These results imply that when a freshwater habitat of a substock is characterized by large value of index A, which means that progeny of large fish are strongly favored in that habitat, the age composition of the spawning stock is highly sensitive to changes in ocean survival and relatively insensitive to moderate changes in freshwater conditions. By contrast, a substock spawning in a habitat where small fish and large fish are nearly equally well adapted (low

Figure 7. Convex contour lines which indicate proportions of age 6 females in the spawning stock under assortative mating regime 1 with three different values of heritability of age at maturity (A, B, C). The ordinate is the index of freshwater survival which is the proportion of offspring of age 6 spawners surviving to smolts relative to that of age 3 spawners. The abscissa is the difference in ocean survival between the early ocean life stage and the late ocean life stage. Value of inheritance coefficient (I.C) that results in 10 percent of the spawning stock being composed of age 6 fish are shown in D.

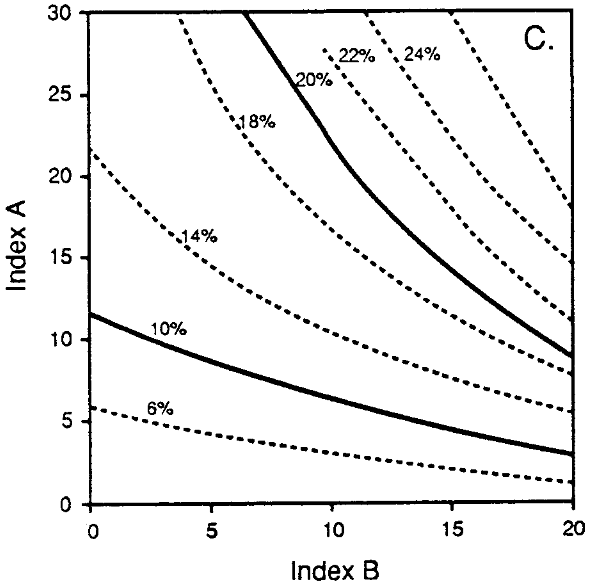


I.C. 0.2 & Assortative Mating 1



I.C. 0.25 & Assortative Mating 1

Figure 7.



I.C. 0.3 & Assortative Mating 1

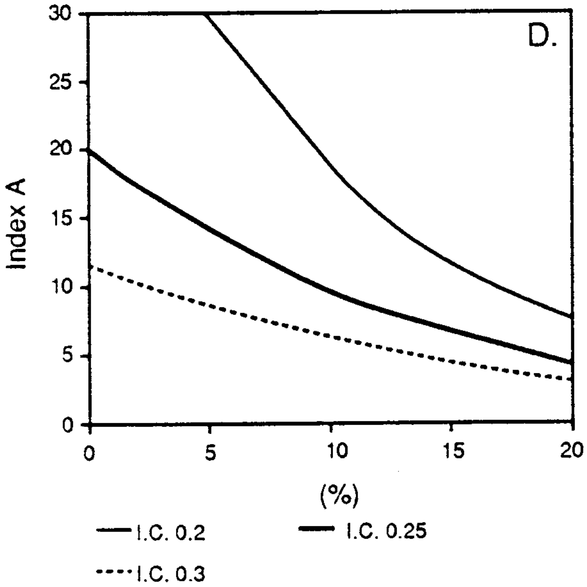


Figure 7 continued.

Figure 8. Changes in proportion of age 6 fish in the spawning stock with increases in index A or B.

A. When index A is fixed (at 0, 10, 20, or 30) and index B is variable, the proportion of age 6 fish increases exponentially.

B. When index B is fixed (at 0, 10 or 20) and index A is variable, the proportion of age 6 fish is a logarithmic function.

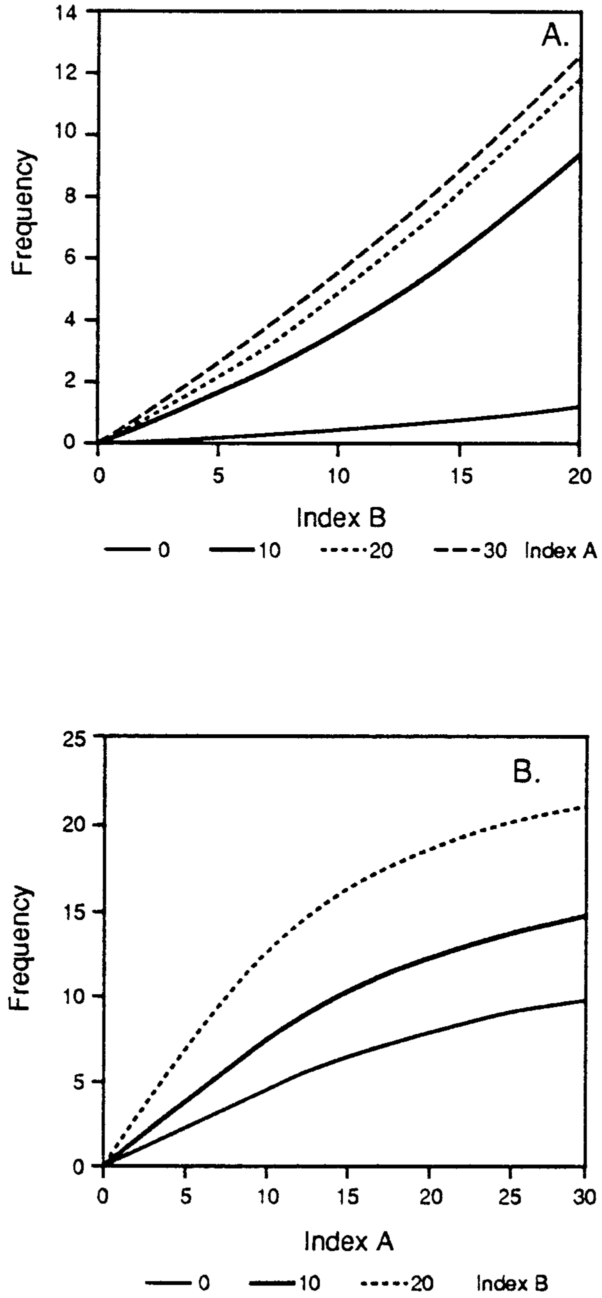

A.
Frequency
14
12
10
8
6
4
2
0
0
5
10
15
20
Index B
0
10
20
30
Index A
B.
Frequency
25
20
15
10
5
0
0
5
10
15
20
25
30
Index A
0
10
20
Index B

Figure 8.

value of the index A), the age composition of spawners is quite variable with changing conditions in freshwater but relatively unresponsive to changes in the ocean environment.

The same generalizations apply to a stock whose habitat changes through time. When the physical quality of a habitat is degraded for large fish so that the difference in freshwater survival of offspring of large spawners and small spawners becomes small(for example, a reduction in stream flows), the frequency of age class 6 declines more severely in the substock having a lower value of the index A (dominated by early maturing fish) than in a substock having a high value of the index A (dominated by late-maturing fish) (Figure 8b). Thus, the age composition may be drastically shifted to early maturing, smaller fish. But, if the survival rate in the late ocean life stage (index B) decreases so that the rate is similar to or smaller than that for early ocean life (eg. due to exploitation), the substock comprised of a relatively large proportion of late maturing fish will show a sharp decline in the frequency of age class 6 in the substock (Figure 8b).

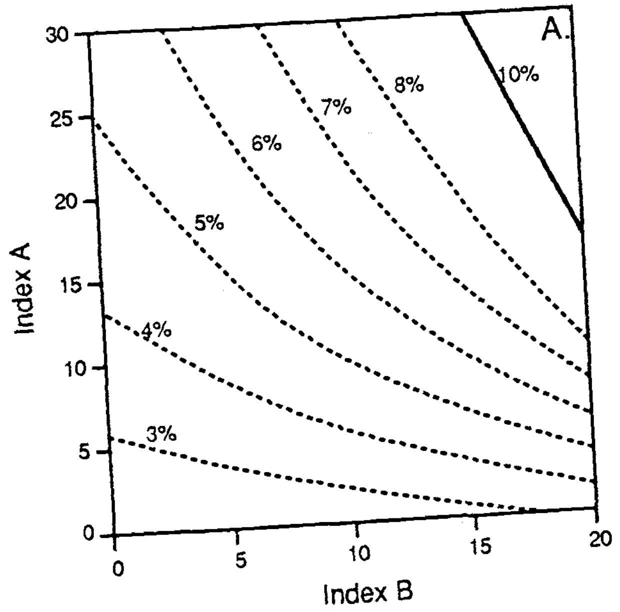
Mating Regime and Heritability

The force affecting both age composition of a stock and the mean age of the spawning stock of the next generation is an outcome of compounded effects of four interacting factors: inheritance coefficient, the strength of mate selection, and variation in number and freshwater survival of offspring of females of different ages.

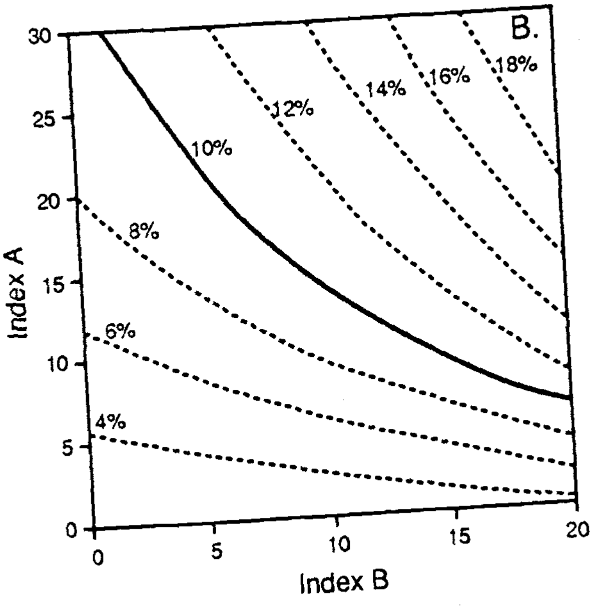
In general, since inheritance coefficient is analogous to heritability, the inheritance coefficient tells us how much of the deviation of the parental phenotype from the population mean is transmitted to the offspring (Falconer 1981, Roughgarden 1979). In addition to inheritance coefficient of age at maturity, both direction and speed of evolutionary changes in age composition of a spawning stock depend on the strength of selection (assumed in the model to be equivalent to an average phenotypic value of age at maturity of the parents) in relation to the mating regime and natural selection in both freshwater and the ocean. Thus, the potential mean age at maturity of offspring at birth (excluding mortality of the offspring) from a certain mating (e.g. 5x6) equals the mean of the population to which the parents belong plus the deviation from the population mean inherited from that specific mating (see equations (1), (1)' and (1)"). However, the production of offspring differs among female parents due to age-specific differences in fecundity and variation of egg-to-smolt survival rates. Further, inheritance of age at maturity results in offspring spending different lengths of time in the ocean, depending on the age at maturity of their parents. As a result, the age composition of offspring produced under a given mating regime is further modified by length of the time spent in the ocean.

The mechanism discussed above is complex, but it is quite clear that there is trade-off between natural environmental effects and genetic effects on the age composition of the spawning stock. The effect of mating regime and inheritance coefficient is shown in Figures 7 and 9. In general, the higher the inheritance coefficient of age at maturity (Figure 7d) and the more strongly mating is age selective (Figure 9), the higher the proportion of age 6 spawners in the stock. When inheritance coefficient is increased, the population requires less intense natural selection for older fish (indices A and B are lower) in order to maintain the same level of abundance of late maturing, large fish. Therefore, the contour lines for any given percentage of age 6 fish in the spawning stock are shifted downward. (Figure 7d). Similarly, if the mating regimes vary from random mating to strong positive assortative mating, the contour lines for any given percentage are shifted downward (Figure 9c). Segregation of late maturing large spawners through through strong size-specific assortative mating may relax the requirement of natural selection favoring those fish in order to maintain

Figure 9. Convex contour lines which indicate the proportion of age class 6 females in the spawning stock under different mating regimes. A in random mating and B is assortative mating regime 2. Contour lines in C show ten percent of age 6 fish in spawning stock for random mating, assortative mating 1, and assortative mating 2.



I.C. 0.25 & Random Mating



I.C. 0.25 & Assortative Mating 2

Figure 9.

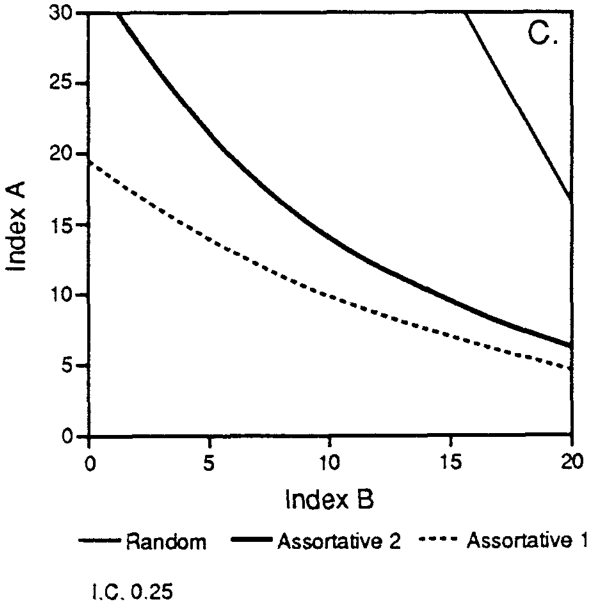


Figure 9 continued.

the same level of abundance in the age composition. If the population does not have relatively high inheritance coefficient of age at maturity or strong age- or size-specific assortative mating, natural selection must favor older larger fish in both the ocean and freshwater environments (indices A and B must be large) to maintain a significant proportion of late maturing fish in the stock. On the other hand, if the inheritance coefficient of age at maturity is high enough and age- or size-specific assorative mating tend to be strong for the population, the spawning stock will be diverse in age composition. Without high relative survival, relatively high inheritance coefficient, and strong assortative mating, the population will be unable to maintain late maturing, large fish in the spawning stock. These results imply that life history structure of a population (here, equivalent to age composition of the spawning stock) is determined by the interaction of natural factors and genetic factors. The effects on a spawning stock presented are summarized below:

1. Since a substock spawning in a habitat where large fish are strongly favored is very sensitive to changes in the ocean conditions, the age composition of the spawning stock might be unstable with environmental fluctuation in the ocean (e.g. harvesting).

2. A substock spawning in a habitat where small fish are favored is more responsive to changes in freshwater than those in the ocean. Therefore, the age composition might be affected most by changing environmental states in freshwater (e.g. habitat degradation).
3. High inheritance coefficient of age at maturity and strong age- or size- specific assortative mating regime have the same effect on the age composition of the spawning stock as natural selection strongly favoring late-maturing large fish.
4. If inheritance coefficient of age at maturity is not high, strong natural selection favoring late-maturing fish in freshwater is necessary to maintain age diversity of spawning stock.
5. Effect of natural selection for late-maturing large fish in freshwater is amplified by an increase in intensity of natural selection in ocean.

DISCUSSION

Bell (1980) argued that the optimum age of maturity in females is the age at which the rate of increase in potential fecundity with age is equal to or greater than the probability of mortality. Natural selection favors females which mature at the optimal age. However, there is variation in age at maturity in the chinook salmon. An increase in age-specific fecundity does not always seem counterbalance an increase in annual mortality. Therefore Healey and Heard (1984) pointed out that this theory is probably not very applicable to salmon. Delay of maturity and increases in fecundity do not necessarily offset increases in mortality.

From a different point of view, the life history structure of a stock (represented by age composition) may result from the development of different life history types that are adapted to different habitats. Life history structure is influenced by mating regime, natural selection, imigration, etc. Changes in life history structure in one generation will affect genetic structure in next generation, which again leads to further changes in life history structure (Lewontin 1974). This process continues as life history structure evolves.

Although the model developed here did not deal with genotypic value associated with age at maturity and age composition of the spawning stock, it is similar in concept to Lewontin's theory and provides an alternative to Bell's theory in explaining life history of chinook salmon. Suppose that heritability of age at maturity is 0.3 and the mating regime is strongly positively assortative in terms of size. Relative difference in number of smolts produced between late maturing, large spawners and early maturing, small ones would need to be thirty-fold (index A) in favor of large fish in order to maintain more than 18% of age class 6 in the spawning stock. This implies that late maturing large fish would never constitute an extremely large proportion of the population, but rather that diversity in age at maturity would be maintained. There are likely several reasons for this. First, some iteroparious species spawn several times during their lifetime and, in a changing environment where chances of successful reproduction in any one year are low, multiple reproduction increases the chance of successfully producing offspring (Murphy 1967, 1968). In the case of semelparous chinook salmon, the environment of the spawning habitats in freshwater is heterogeneous and unpredictable. If all fish from a particular parent returned to spawn at the same time, spawning success may be jeopardized if the environment was unfavorable at that time. Thus, chinook salmon may spread the risk of environmentally induced spawning failure by having offspring which return to spawn in different years, effectively acheiving the advantages of iteroparity.

Second, within the mechanism of the model, since inheritance coefficient is analogous to heritability, inheritance coefficient tells us how much of the genotypic deviation of the parents from the population mean are transmitted to their offspring. Moreover, as with heritability, inheritance coefficient is influenced by changing environmental conditions and nonadditive genetic variance. It is strongly correlated with total variance V: $I^2 = V_A / (V_A + V)$ where V_A is additive genetic variance and I^2 is inheritance coefficient . A large V will lead to reduction of inheritance coefficient and cause the genotype to have greatly overlapping phenotype distribution, so that strong phenotype selection does not always result in strong genotype selection (Falconer 1981, Crow and Kimura 1970). The distribution is assumed to produce two different kinds of effects on the capacity of the population. First, since the capacity of the population to respond to natural selection is a function of the amount of phenotypic variance which results from additive genetic variance (Fisher 1958), the avoidance of strong genotype selection causes the stock to maintain genetic variance and to increase the adaptive range of their offspring. The other effect is opposite.

Low inheritance coefficient causes a high proportion of unfavorable genotypes so that the life history organization of a stock cannot be particularly concordant with the habitat to which the stock must adapt due to a large genetic load. Although nonadditive genetic variance may counteract the problem, it does not seems to be enough to offset the negative effect on the life history organization of a stock. Chinook salmon may solve this problem by the means of strong assortative mating since the mating regime may accelerate the process of selection for favorable life history types.

Third, suppose that in addition to high fecundity of late maturing, large fish, the survival rate of their offspring is very high. The large smolt production of late maturing large fish will contribute not only to its life history type (fish maturing at age 6) but also to the other three types (fish maturing at ages 3, 4, and 5). A certain proportion of smolts will mature early and have the advantage of a smaller mortality risk in the ocean owing to shorter ocean life. This counteracting force may play a role as negative selection against large fish (the right tail of phenotypic distribution of the spawning stock) whereas the high survival rate of large fish works as positive selection. The age composition of the spawning stock results from a balance of these forces.

The model illustrated the complex adaptive mechanism resulting from the incorporation of different kinds of life history events. However, for simplicity, the model has dealt with one adaptive trait which is age at maturity, although age at maturity is an indicator of a complete life history which implies large size, high fecundity, larger eggs, higher egg to smolt survival and lower ocean survival. However, since meristic characters of individuals in a population are genetically correlated, selection for one character may mean selection for or against another character correlated with it (Lande 1982, Falconer 1981). Furthermore, although the model has used unit segregation variance, the value may change, depending upon the degree of epistasis (Falconer 1981). Further development of the model requires research on genetic correlations with changing environments.

III. RELATION OF LIFE HISTORY ORGANIZATION OF FALL CHINOOK SALMON (ONCORHYNCUS TSCHWAYTSHAW) TO HABITAT AND FISHING

INTRODUCTION

Natural environments are seldom homogeneous but most often are heterogeneous mosaics of more or less isolated habitat patches. Stream systems inhabited by chinook salmon can be classified into different kinds of habitats having different physical and biological characteristics (Frissell et al. 1986). Different classes of habitats may differ in their favorability for life history types of individual spawners. Therefore, spawners may counteract habitat heterogeneity with life history diversity.

Large body size in chinook is an apparent advantage for successful construction of nests in habitats having high flows and large gravels such as mainstems of streams and streams subjected to frequent flood events (Hankin and McKelvey 1985). Older maturing, larger spawners tend to lay larger eggs (Hankin and Mckelvey 1985) which is associated with higher survival rate of offspring in freshwater (Ricker 1981). Moreover, since migration to upstream spawning areas in long rivers requires large amounts of energy, delayed maturity to increase growth at sea is thought to have adaptive significance (Schaffer 1979, Schaffer and Elson 1975). However, Healey and Heard (1984) pointed out that large body size may not be always advantageous. The apparent advantage of large size may be reduced in some habitats. For instance, deeper nests constructed by large spawners may not receive adequate oxygen at low water flow sites. Therefore, females of all sizes may be nearly equally fit. A wide range of female sizes in the spawning stock may be necessary for the population to adapt to heterogeneous habitats (Holtby and Healey 1986).

In the previous section I illustrated possible effects of differences in survival in freshwater habitats between late maturing, large fish and early maturing, small fish on size diversity associated with age at maturity under different mating regimes and heritability of age at maturity. Quite large differences in survival in freshwater between large and small fish would be required to maintain a reasonable proportion of large fish in the spawning stock.

If a substock consists of individual spawners having different capacities to adapt to the habitat, and survival and reproduction are quite dissimilar among the life history types, age composition and abundance may change considerably in response to fishing. If stocks consist of different substocks each adapted to their own habitats in particular ways, different stocks may be influenced differently by management activities. This section will examine the following: 1) the relation of age composition of stocks and substocks to the organization of their habitat, and 2) the response of stocks and substocks to harvest.

THE MODEL

A hypothetical watershed consisting of two stream systems, A and B, was established to examine the possible influence of fishing effort on age composition and productivity of a spawning stock (Figure 10). Each stream system was divided into three different habitats. The habitats were characterized by differences in index A, the index denoting relative survival advantage of progeny of large spawners over small spawners and by differences in carrying capacity, denoted by the sizes of the circles and differentiated by the value of the coefficient of density-dependence, k. In each habitat, a multiple age spawning stock is governed by the basic mechanisms of the chinook life history model (Figure 4) with one modification. The first year of freshwater life was divided into two parts. During the first half of the year, density-dependent mortality was explicitly a function of the initial number of eggs laid by the spawners in each habitat. For the remainder of the year, it was assumed that fry produced in the different spawning habitats aggregate in common rearing areas (mainstems, estuaries). Density-dependent mortality during this time period is an explicit function of the initial number of fry surviving at that time.

Habitat 1 is assumed to strongly favor late maturing,

Figure 10. Hypothetical watershed for chinook salmon. Two stream systems, A and B, are composed of three different kinds of habitats, 1,2 and 3. The ratios of the sizes of habitats are 10:3.5:1 in stream A and 1:2.5:4 in stream B for habitat 1, habitat 2, and habitat 3, respectively. Habitat 1 strongly favors late maturing, large fish, while early maturing, small fish are well adapted to habitat 3. Habitat 2 is intermediate between 1 and 3. The age composition of the stock in each stream is shown in A and B and the age composition of substocks in each habitat is shown in C, D, and E.

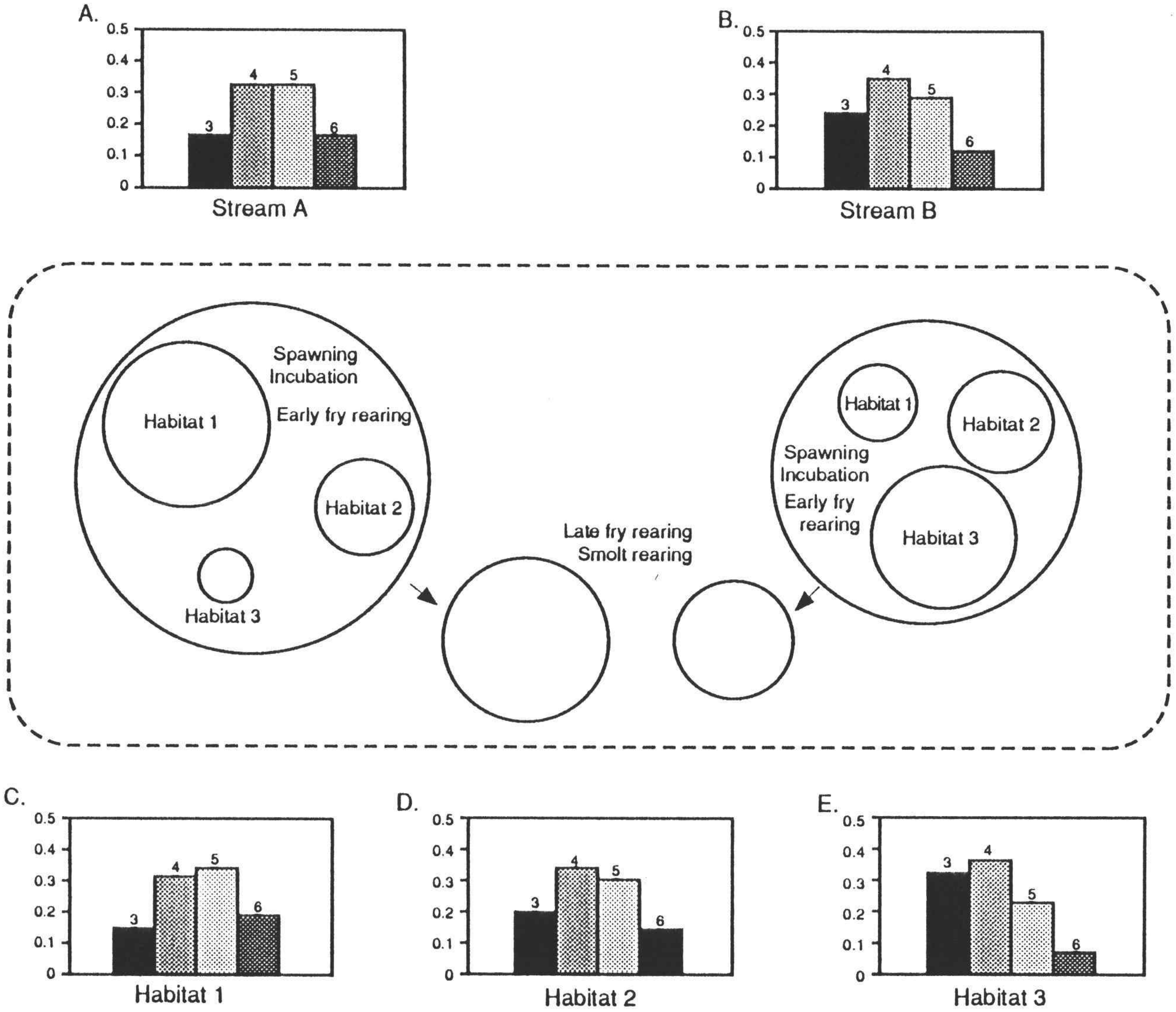

A.
0.5
0.4
0.3
0.2
0.1
0
3
4
5
6
Stream A
B.
0.5
0.4
0.3
0.2
0.1
0
3
4
5
6
Stream B
Spawning
Incubation
Early fry rearing
Habitat 1
Habitat 2
Habitat 3
Late fry rearing
Smolt rearing
Habitat 1
Habitat 2
Spawning
Incubation
Early fry
rearing
Habitat 3
C.
0.5
0.4
0.3
0.2
0.1
0
3
4
5
6
Habitat 1
D.
0.5
0.4
0.3
0.2
0.1
0
3
4
5
6
Habitat 2
E.
0.5
0.4
0.3
0.2
0.1
0
3
4
5
6
Habitat 3

Figure 10.

large spawners because of high flows, large gravel, etc. It is equivalent to the situation in which index A has a value of 30. Hence, the age composition of an unexploited spawning stock tends to be skewed somewhat toward older fish (Figure 10C). In habitat 3, there is much less survival advantage for older maturing fish and index A has a value of 5. Early maturing spawners are dominant in this habitat (Figure 10E). Habitat 2 is intermediate between habitats 1 and 3, having a value of index A of 15. The age composition is somewhat skewed to early maturing spawners (Figure 10D).

Habitat structure of the two stream systems is different. Stream A is assumed to have approximately a ten times larger proportion of habitat 1 than habitat 3. This could be thought of as a long river with a large proportion of mainstem area with high water flow. Therefore, physical strength is required to reach spawning habitats far upstream and to construct nests at sites with large gravels disturbed by turbulence. Stream B is of almost opposite character to stream A. It is mainly composed of habitat 3, which is four times larger than habitat 1 in the stream. Since habitat 3 could be characterized by shallow tributaries with small gravels and low water flow, late maturing fish may have restricted access. Even if they are successful in constructing redds in this habitat, their eggs, deposited in deep redds, may suffer high mortality because of oxygen deprivation during incubation (Healey and Heard 1985).

Age composition of the stock clearly reflects characters of habitat distribution in each stream system. The stock in stream A maintains a relatively high proportion of late maturing, large fish (Figure 10A), while in stream B, the age composition is somewhat skewed toward early maturing, small fish (Figure 10B).

PRODUCTION PARAMETER

The production parameter can be defined as the potential number of offspring returning to spawn in the next generation per individual spawner in the present generation. Here, potential number means recruitment per spawner without any compensatory mortality but with density-independent natural mortality in both freshwater and the ocean. It seems to be equivalent to the alpha parameter in Ricker's stock-recruitment relationship. However, instead of the parameter being fixed as is usually the case in stock-recruitment equations, the production parameter in the multiple age spawning stock model is variable and will be shown to depend on age composition.

The age composition of the spawning substock in a given habitat is consistent with the magnitude of differences in fitness of individual spawners in different age classes in that habitat. Depending on the magnitude of fitness, the stock expresses its performance as recruitment per spawner in different ways. As long as the spawning stock consists of individual spawners in different age classes, the production parameter of a specific substock is a structural parameter. That is, substocks are viewed as systems that consist of individual spawners in different age classes. The production parameter of substock j, α_j, is entailed in its organization which involves incorporation of spawners in different age classes because $\alpha_j = \sum_{i=3}^{6} [p_i * b_i * \exp(-m_i)]$. Where P_i is the proportion of adult females aged i in the spawning stock, b_i is the average fecudnity of spawners aged i, and m_i is density-independent egg-smolt mortality of offpsring produced by femalesx aged i (Table 4). The production parameter, α_j, may vary with changes in the age composition of spawning stock.

Stocks or populations are viewed as systems that consist of substocks adapting to different habitats in different ways (eg. with different age compositions). The production parameter of a stock is entailed in its organization which involves incorporation of substocks. Therefore, the stock production parameter α may be altered by changes in both habitat structure and age composition of spawning substocks because $\alpha = \Sigma\ \alpha_j l_j$ where l_j is proportion of habitat j in a stream.

EFFECTS OF FISHING ON AGE COMPOSITION, PRODUCTION PARAMETER, AND STOCK-RECRUITMENT RELATIONSHIPS

Let us assume that all individuals have an equal probability of being caught at fixed proportion H, annually. That is, the longer they stay in ocean the higher the total fishing mortality. Therefore, fishing pressure may have a greater effect on abundance of late maturing than early maturing fish because late maturing fish spend a longer time at sea (Hankin 1987). In all habitats and in both stream systems A and B, with increases in fishing effort, late maturing spawners are eliminated from the spawning stock and the age composition becomes skewed toward earlier maturing fish (Figure 11 and 12). Age 3 spawners tend to increase and then decline as H increases. There are several factors which stimulate this increase in abundance of early maturing spawners. First, severe compensatory mortality on early maturing fish may be released because of reduction of abundance of late maturing fish. Second, the probability of production of offspring that will mature early will be increased because of changes in size-specific assortative mating and decreases in mean age of the spawning stock (implying loss of genes associated with late maturation). As a result, the age composition of spawning stock will be skewed toward early maturing fish and the production

Figure 11. Changes in age composition of spawning substocks in habitats 1, 2, and 3 in stream A with increases in harvesting rate. Solid, bold, dotted and broken lines indicate changes in age classes 3, 4, 5 and 6 respectively.

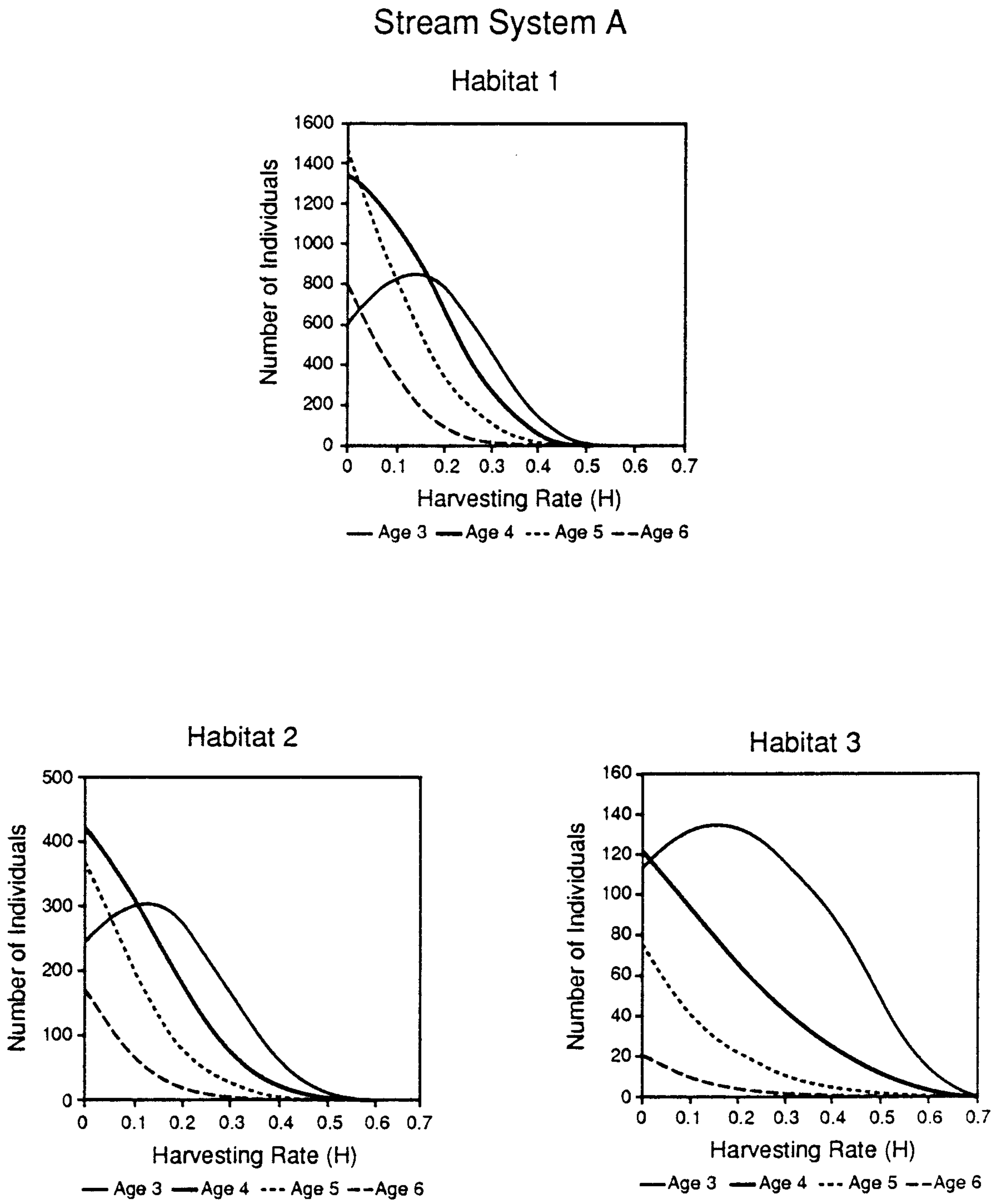

Stream System A
Habitat 1
Number of Individuals
1600
1400
1200
1000
800
600
400
200
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Harvesting Rate (H)
Age 3
Age 4
Age 5
Age 6
Habitat 2
Number of Individuals
500
400
300
200
100
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Harvesting Rate (H)
Age 3
Age 4
Age 5
Age 6
Habitat 3
Number of Individuals
160
140
120
100
80
60
40
20
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Harvesting Rate (H)
Age 3
Age 4
Age 5
Age 6

Figure 11.

Figure 12. Changes in composition of the spawning stocks in streams A and B with increases in harvesting rate. Solid, bold, dotted and broken lines indicate changes in number of individuals in age classes 3, 4, 5 and 6, respectively.

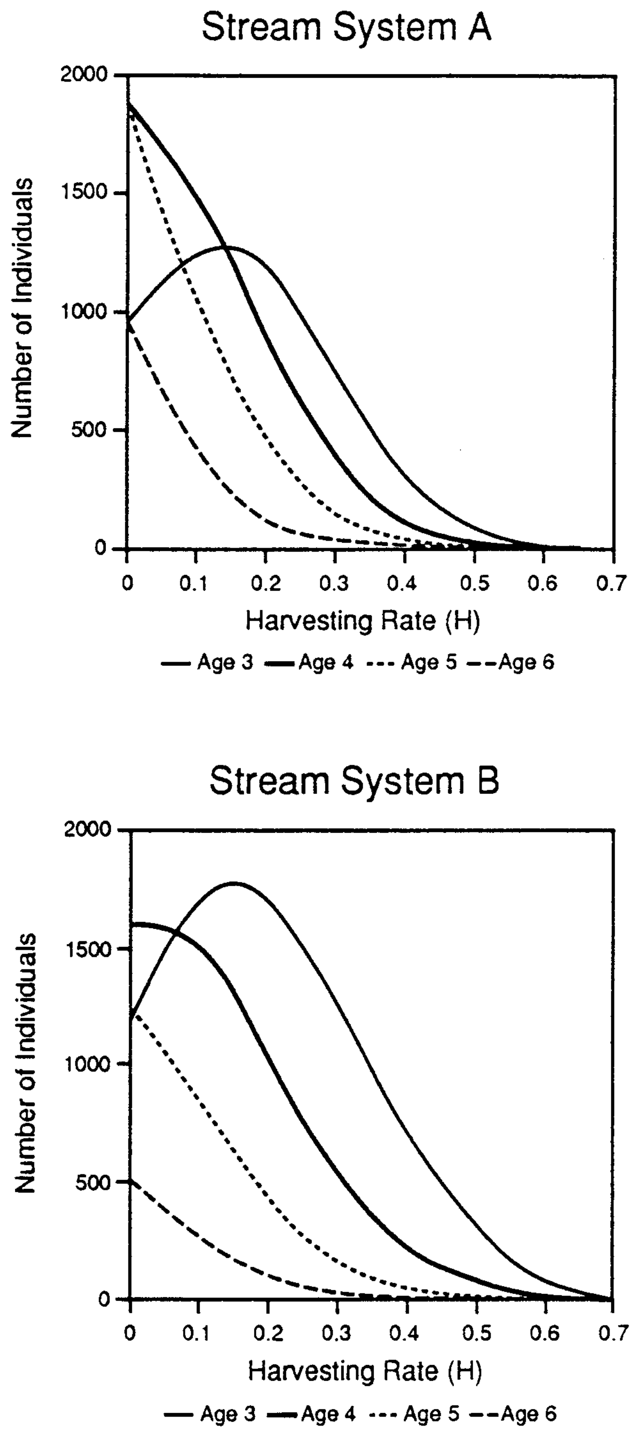

Stream System A
Number of Individuals
2000
1500
1000
500
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Harvesting Rate (H)
Age 3
Age 4
Age 5
Age 6
Stream System B
Number of Individuals
2000
1500
1000
500
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Harvesting Rate (H)
Age 3
Age 4
Age 5
Age 6

Figure 12.

parameter will be reduced (Figure 13). The stock-recruitment curve is reduced in magnitude and flattened (Figures 14 and 15). These trends are very obvious for the substock in habitat 1 where late maturing, large fish are strongly favored (Figures 13A and 14A). In this habitat, the production parameter of the substock is mainly supported by late maturing, large fish. The production parameter of the substock in habitat 3, to which small fish are relatively well adapted, is less sensitive to an increase in fishing effort (Figures 13A and 14B). Thus, the sensitivity of substocks to fishing effort is influenced by the age compositon of the spawning stock which is related to characteristics of the habitat.

Not only the production parameter but also the replacement level (the intersection of the recruitment curve and the replacement line) may be reduced by increased harvest (Figures 14 and 15). The replacement level can be represented by the equation, $\ln(\alpha)/kb$. Since the numerator is a logarithmic function, the reduction is accelerated with a decrease in α. But the average fecundity, b, in the denominator is relatively insensitive to deformation of age composition. Thus replacement level is mainly dependent on the production parameter α. That is, when the parameter is reduced, the replacement level is also decreased.

Figure 13. Effect of harvesting rate on the production parameter of substocks in habitats 1, 2, and 3 and stocks in streams A and B.

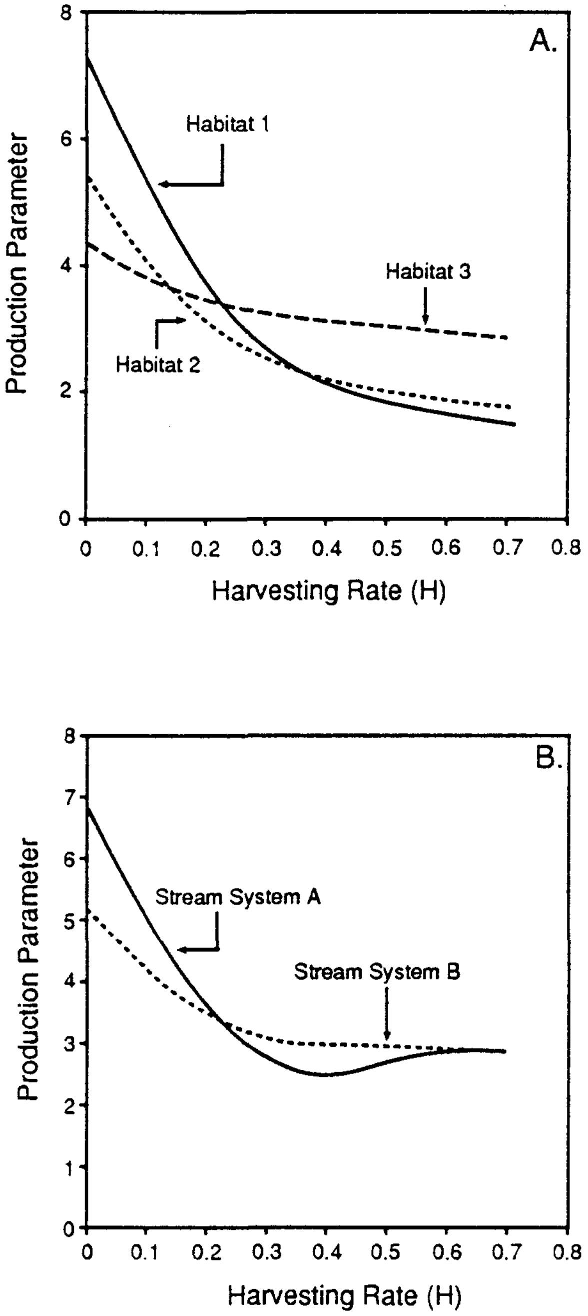

A.
Habitat 1
Habitat 2
Habitat 3
Production Parameter
Harvesting Rate (H)
0
2
4
6
8
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
B.
Stream System A
Stream System B
Production Parameter
Harvesting Rate (H)
0
1
2
3
4
5
6
7
8
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8

Figure 13.

Figure 14. Effect of harvest on the stock-recruitment relationships of multiple age spawning substocks in habitats 1 and 3, stream A. Three levels of harvesting (H = 0.0, 0.2, and 0.4) and the associated production parameters (P.P.) are shown.

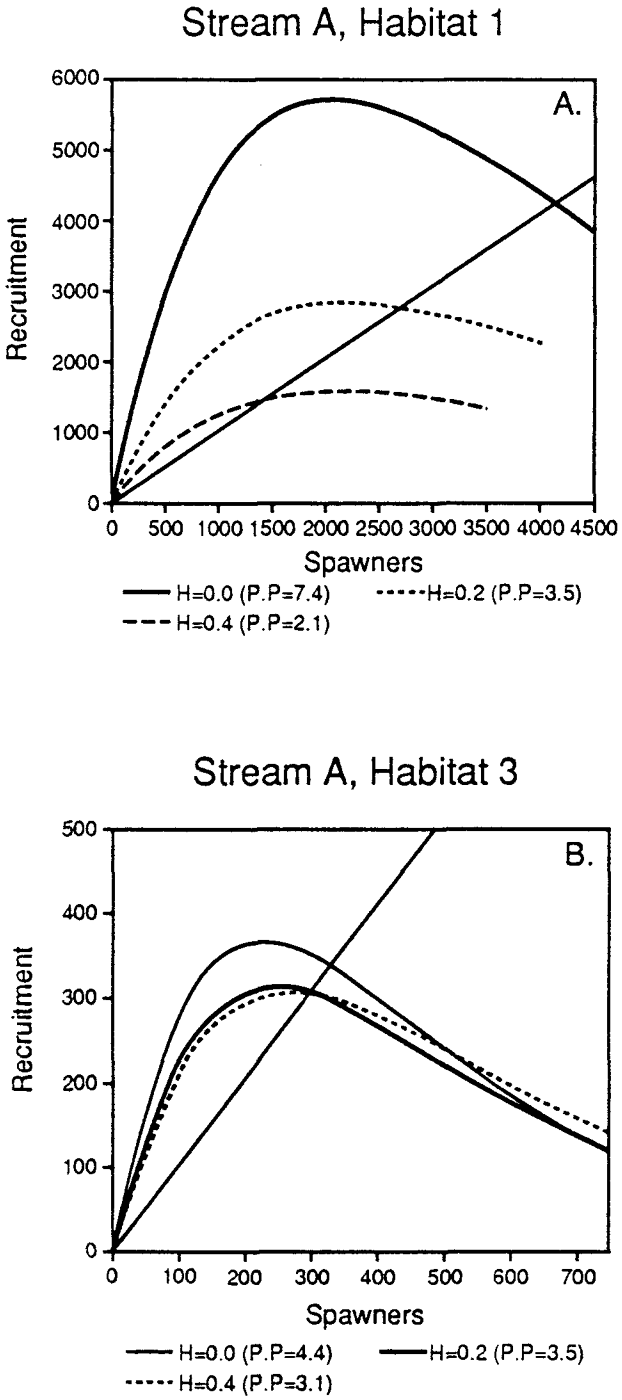

Stream A, Habitat 1
A.
Recruitment
6000
5000
4000
3000
2000
1000
0
0
500
1000
1500
2000
2500
3000
3500
4000
4500
Spawners
H=0.0 (P.P=7.4)
H=0.2 (P.P=3.5)
H=0.4 (P.P=2.1)
Stream A, Habitat 3
B.
Recruitment
500
400
300
200
100
0
0
100
200
300
400
500
600
700
Spawners
H=0.0 (P.P=4.4)
H=0.2 (P.P=3.5)
H=0.4 (P.P=3.1)

Figure 14.

Figure 15. Effects of harvest on the stock-recruitment relationships of multiple age spawning stocks in streams A and B. Three levels of harvesting (H = 0.0, 0.2, and 0.4) and the associated production parameters (P.P.) are shown.

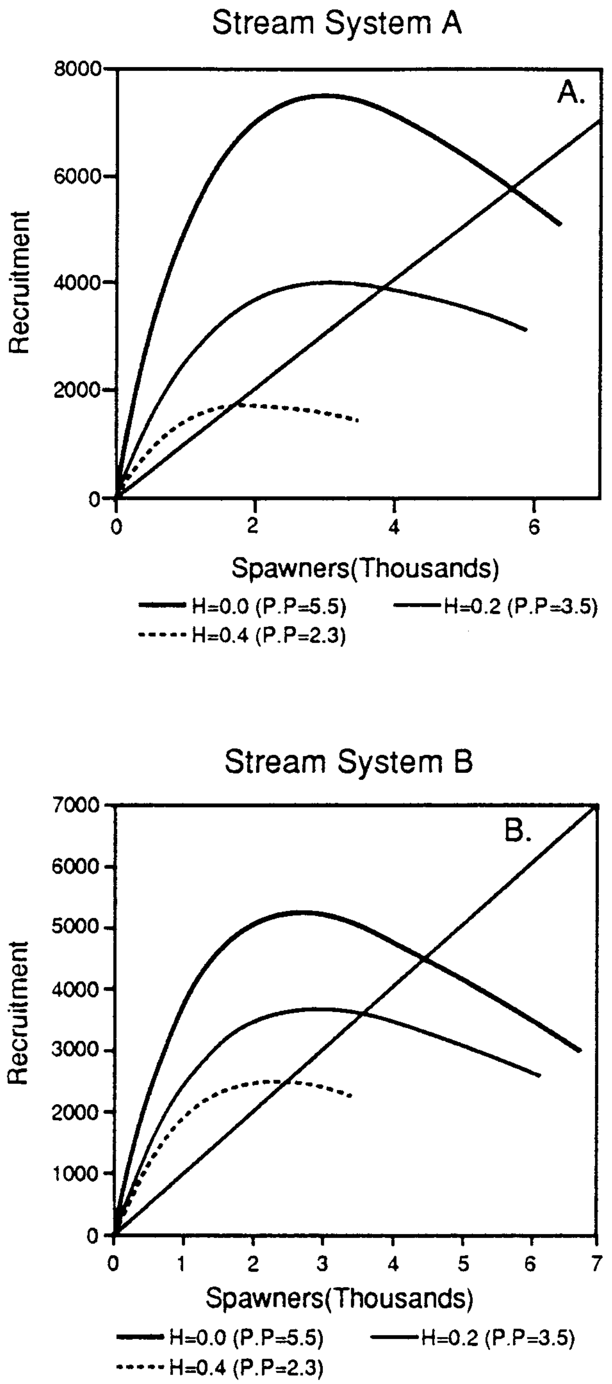

Stream System A
A.
8000
6000
4000
2000
0
Recruitment
0
2
4
6
Spawners(Thousands)
H=0.0 (P.P=5.5)
H=0.2 (P.P=3.5)
H=0.4 (P.P=2.3)
Stream System B
B.
7000
6000
5000
4000
3000
2000
1000
0
Recruitment
0
1
2
3
4
5
6
7
Spawners(Thousands)
H=0.0 (P.P=5.5)
H=0.2 (P.P=3.5)
H=0.4 (P.P=2.3)

Figure 15.

This can be explained biologically. The habitat space of a substock is not homogeneous but a heterogeneous mosaic of microhabitats (Frissell et al. 1986). Suppose that large fish are strongly favored in the habitat. Although there must be a large proportion of available spawning sites for late maturing, large fish, early maturing, small fish can probably still find sites in which they are able to successfully spawn. However, once late maturing fish are eliminated due to fishing, spawning sites suitable only for large fish may not be effectively utilized. Habitat that is not efficiently utilized is analogous to reduction of habitat capacity, which may lead to decreases in replacement level of the substock. The magnitude of the reduction is larger in habitat 1 than in habitat 3 (Figure 14).

In the case of a stock, the magnitude of reduction of the production parameter and replacement level will be influenced by habitat distribution in the stream system. For instance, if a stream system is comprised of a large proportion of habitat 1 where late-maturing large fish are well adapted, such as the stream A, the stock will be quite responsive and vulnerable to increases in fishing effort (Figures 12A, 13B, and 15A). On the other hand, if habitat 3, where early maturing fish are favored, occupies a relatively large proportion of the stream system, such as in stream B, reduction of the production parameter and magnitude of the recruitment curve is not as great (Figures 12B, 13B, and 15B).

STOCK ABUNDANCE AND YIELD

For a constant fishing rate (H), a single age stock will reach an equilibrium stock level (S^*) with sustained yield (Y^*) if natural mortality, habitat capacity, other physical and biological factors are unchanged (Ricker 1975). Similarly, a multiple age spawning stock will form an approximate equilibrium age composition at a given fishing rate. Now, let us assume that equilibrium stock size and sustained yield can be obtained from a given age composition as follows (Ricker 1975, Hilborn 1985):

$$S^* = S_r + S_r / \ln(\alpha) * \ln(1-H) = [\ln(\alpha) + \ln(1-H)]/ \beta \text{ -(10)}$$

$$Y^* = H * S^* \alpha \exp(-\beta * S^*) \text{ ----(10)'}$$

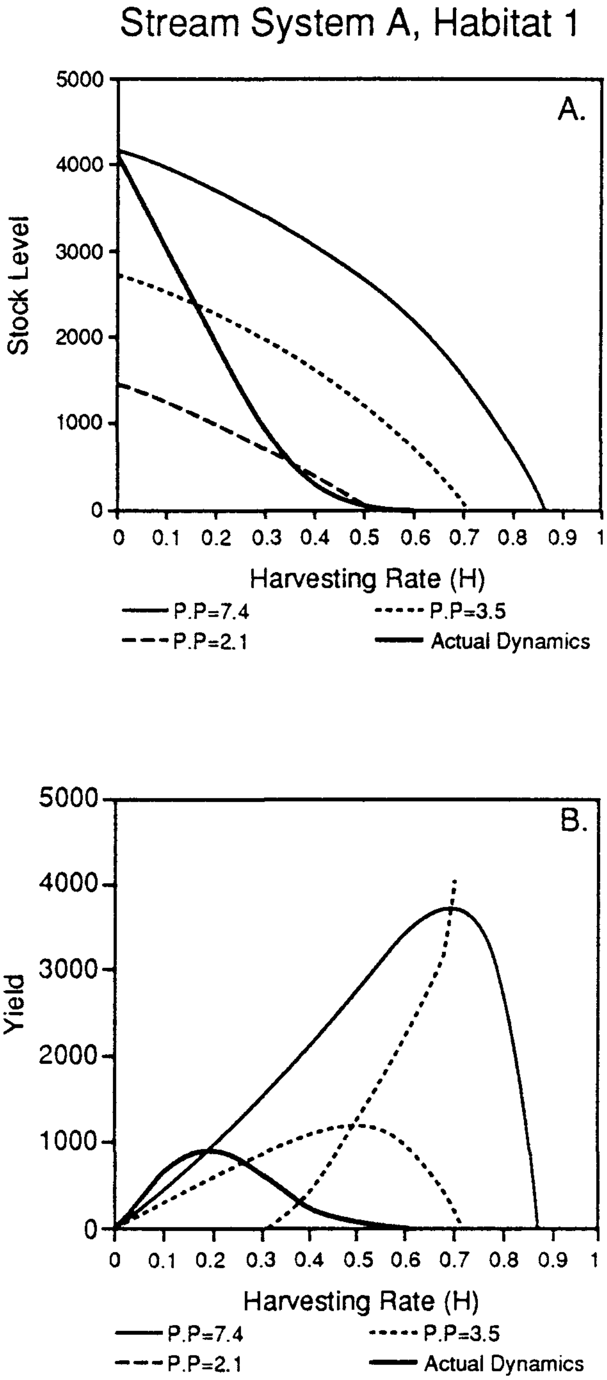
where α is the production parameter, S_r is the replacement level and β is $\ln(\alpha)/S_r$.

As shown in the previous section, age composition will be altered by increased fishing effort with corresponding changes in the production parameter and replacement level. Thus each change in H will cause a corresponding change in the magnitude of the stock-recruitment relationship (Figures 14 and 15). Moreover, age composition of the spawning stock in each stream is unique. It is concordant with its habitat. Thus, an increase in fishing effort may have different effects on the age composition and the stock-recruitment curves of different stocks.

Figures 16 and 17 shows clear differences in the response of the substocks in habitat 1 and habitat 3 toward increases in fishing effort. The solid, dotted and broken lines indicate expected equilibrium distribution of stock size and sustained yield generated with a fixed production parameter and replacement level. Normally the production parameter is assumed to remain constant with changing fishing effort. In this case effort merely shifts the equilibrium point along a single stock-recruitment curve and a single yield curive. This implicitly assumes a constant age composition (or that changing age composition has no effect on α and S_r).

Since late maturing, large fish are more vulnerable to fishing than early maturing, small fish because of the longer duration of ocean life and larger size, fishing pressure seems to have an effect similar to directional selection favoring early maturing fish. Thus, the age composition of the spawning stock is deformed by fishing. The magnitude of deformation is much larger in a substock which has a large proportion of late maturing, large fish than the substock mainly composed of small fish (Figures 11 and 12). When the age composition is deformed, the production parameter and replacement level are reduced

Figure 16. Equilibrium stock abundance and sustained yield for a substock in habitat 1. Solid, dotted and broken lines indicate expected equilibrium distribution of stock size and sustained yield estimated on the basis of the production parameter (P.P.) and replacement level produced by the model under fixed harvesting rates H = 0.0 (P.P. = 7.4), 0.2 (P.P. = 3.5) and 0.4 (P.P. = 2.1), respectively. Bold lines indicate the actual dynamics of stock size and yield as a consequence of changes in age composition, production parameter, and replacement level with increasing fishing effort.



Stream System A, Habitat 1

Figure 16.

Figure 17. Equilibrium stock abundance and sustained yield for a substock in habitat 3. Solid, dotted and broken lines indicate expected equilibrium distribution of stock size and sustained yield estimated on the basis of the production parameter (P.P.) and replacement level produced by the model under fixed harvesting rates H = 0.0 (P.P. = 4.4), 0.2 (P.P.=3.6) and 0.4 (P.P. = 3.1), respectively. Bold lines indicate the actual dynamics of stock size and yield as a consequence of changes in age composition, production parameter, and replacement level with increasing fishing effort.

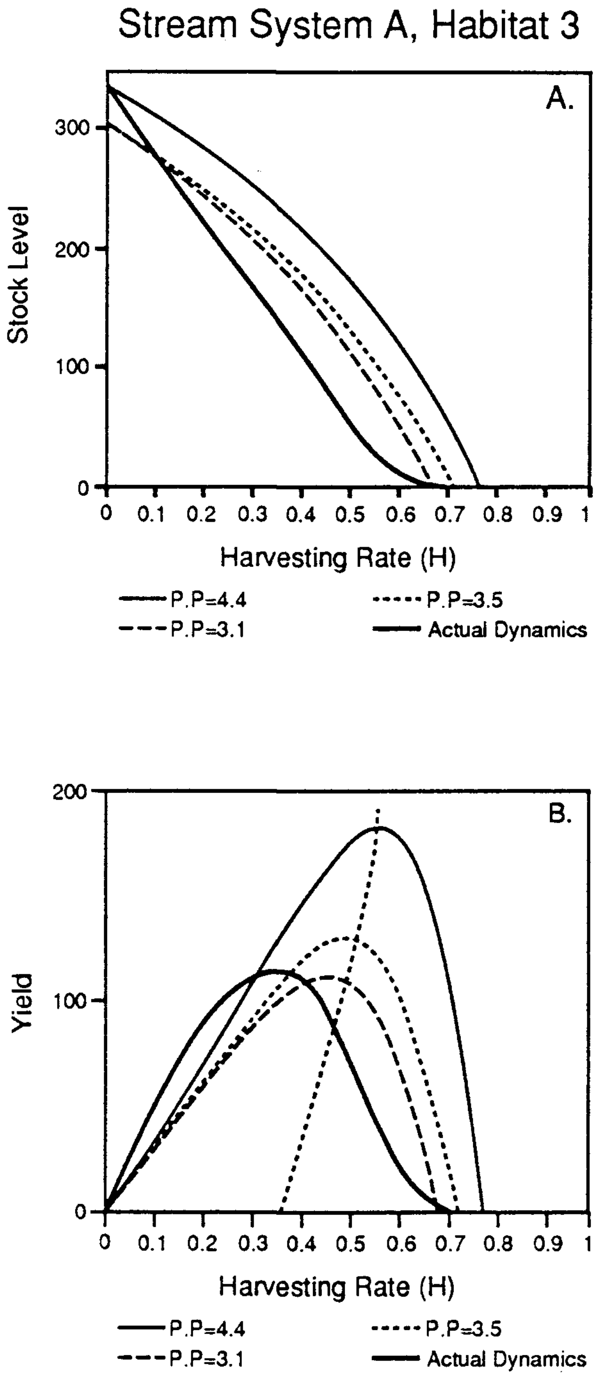

Stream System A, Habitat 3
A.
Stock Level
300
200
100
0
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Harvesting Rate (H)
P.P=4.4
P.P=3.5
P.P=3.1
Actual Dynamics
B.
Yield
200
100
0
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Harvesting Rate (H)
P.P=4.4
P.P=3.5
P.P=3.1
Actual Dynamics

Figure 17.

(Figure 13). The bold lines in Figures 16 and 17 indicate the actual dynamics of substock size and yield, with increasing fishing pressure that results in changes in age composition and reduction of the production parameter and replacement level S_r. There is a larger discrepancy between actual equilibrium stock size and sustained yield and the expected ones in habitat 1 than habitat 3. The level of MSY decreases with increases in fishing effort and reduction in production parameter. The magnitude of reduction of level of MSY is larger in habitat 1 than in habitat 3. This reflects differences in sensitivity of age composition of the substock in different habitats.

The dynamics of stocks are similar to that of substocks, but more complex. The actual output depends on organization which involves the incorporation of substocks. Although the stock in stream A which consists of a large proportion of habitat 1 is strongly influenced by the substock in that habitat, the tendency of decreasing stock size, yield and level of MSY may be buffered by other stock that are less sensitive to fishing such as substocks in habitat 3 (Figure 18). On the other hand, the stock in stream system B, whose age composition is mainly influenced by the substock in habitat 3, will be also be affected by substocks that are sensitive to fishing pressure such as the substock in habitat 1 (Figure 19). Thus, the sensitivity of

Figure 18. Equilibrium stock abundance and sustained yield for a stock in stream system A. Solid, dotted and broken lines indicate expected equilibrium distribution of stock size and sustained yield estimated on the basis of the production parameter (P.P.) and replacement level produced by the model under fixed harvesting rates H = 0.0 (P.P. = 6.6), 0.2 (P.P. = 3.5) and 0.4 (P.P. = 2.3), respectively. Bold lines indicate the actual dynamics of stock size and yield as a consequence of changes in age composition, production parameter, and replacement level with increasing fishing effort.

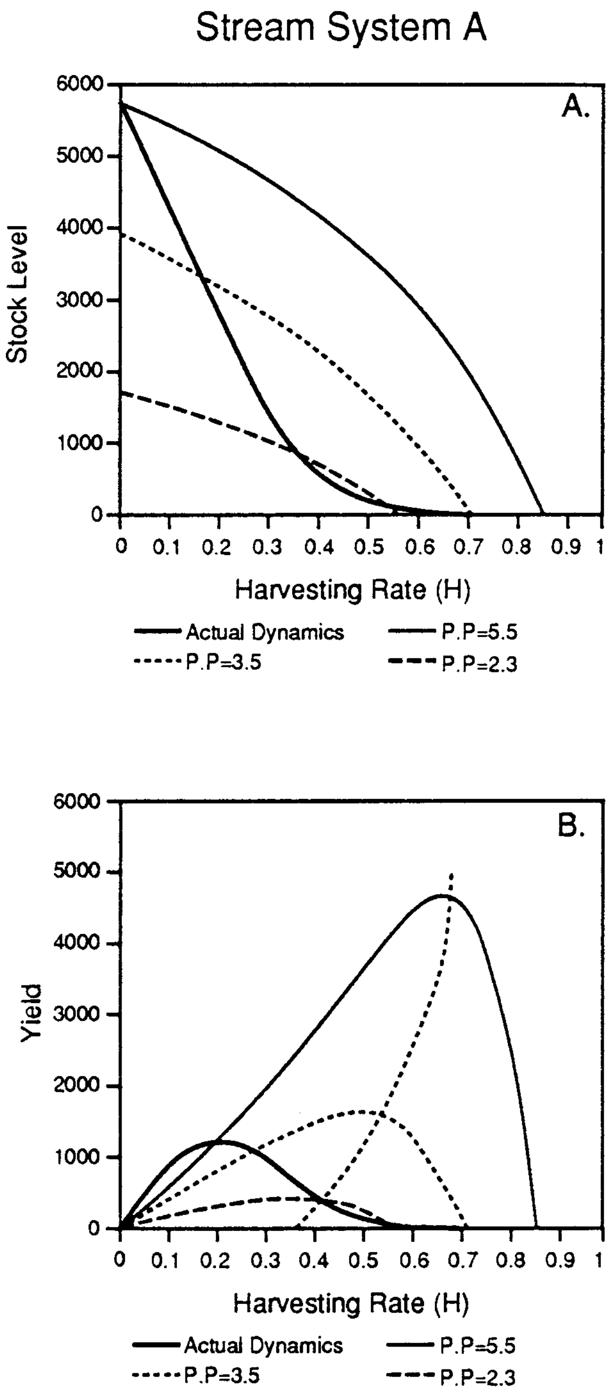

Stream System A

Figure 18.

Figure 19. Equilibrium stock abundance and sustained yield for a stock in stream system B. Solid, dotted and broken lines indicate expected equilibrium distribution of stock size and sustained yield estimated on the basis of the production parameter (P.P.) and replacement level produced by the model under fixed harvesting rates H = 0.0 (P.P. = 5.5), 0.2 (P.P. = 3.4) and 0.4 (P.P. = 2.9), respectively. Bold lines indicate the actual dynamics of stock size and yield as a consequence of changes in age composition, production parameter, and replacement level with increasing fishing effort.

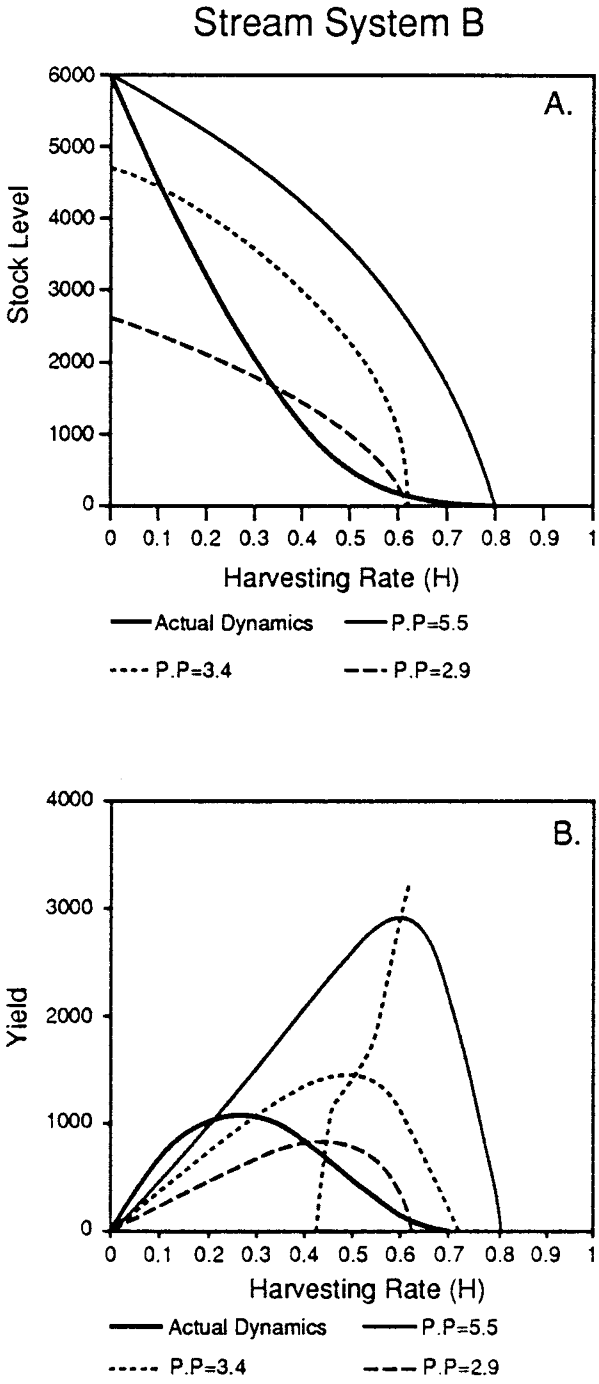

Stream System B
A.
Stock Level
6000
5000
4000
3000
2000
1000
0
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Harvesting Rate (H)
Actual Dynamics
P.P=5.5
P.P=3.4
P.P=2.9
B.
Yield
4000
3000
2000
1000
0
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Harvesting Rate (H)
Actual Dynamics
P.P=5.5
P.P=3.4
P.P=2.9

Figure 19.

the stock to fishing pressure will be amplified.

CHANGING ENVIRONMENTS

Environmental states in each habitat were assumed to change among three different conditions, A(average), D(dry) and W(wet). Changes in these conditions affect the habitat-specific age composition of substocks differently. For instance, since egg-to-fry survival rate is negatively correlated with scour depth caused by peak discharges (Healey and Heard 1984), the survival rate of offspring of small spawners would be quite low relative to large spawners in habitat 1 in a wet year due to destruction of shallow nests by high turbulence. However, relative survival rate of small fish may be improved during periods of low flow in a dry year, while deeply buried eggs of large spawners may begin to suffer from oxygen deprivation because of the reduction of percolation rate. Therefore, in a dry year, the magnitude of difference in the survival rate of offspring of small and large female spawners may be reduced. The model uses index A to indicate how relative survival in each freshwater habitat will be modified by changing environments (Table 5). Yearly environmental fluctuations in each habitat were randomly generated by the computer. Simulations were run for 100 years.

The standard fishing method defined in the model is selective fishing. Annual fishing mortality is fixed and

Table 5. Environment matrix. Values of index A in average (A), dry (D), and wet (W) years in each habitat.

	A	**D**	**W**
Habitat 1	30	20	40
Habitat 2	15	5	25
Habitat 3	5	Even	15

consequently later maturing spawners suffer higher total fishing mortality over their lifetime than younger maturing fish. Another fishing method, called nonselective fishing, was developed to test the effect of age class diversity on the response of the spawning stock in changing environments. In nonselective fishing, a fixed proportion of each age class in a given cohort is caught per lifetime of the cohort. The annual fishing rate on early maturing fish is increased and that on late maturing fish is decreased. Thus total fishing mortality of large spawners is equal to that of smaller spawners. Selectivity caused by differences in length of ocean life among age classes vanishes and age diversity is maintained.

Results of simulation runs with changing environments for stream system A are summarized in Table 6. Trends are similar for stream B. The numbers in parentheses are variance/mean which is an index of magnitude of fluctuation of stock and yield. Under selective fishing, the production parameter decreases with increases in harvest rate in all habitats because of deformation of age composition due to reduction and elimination of large fish. However, substocks under nonselective fishing maintained almost the same or a better value of the parameter. Stock level and yield were higher under nonselective than selective fishing except for the substock in habitat 3. Early maturing, small spawners

Table 6. Average stock size, yield and production parameter (P.P.) of each substock in stream system A. Number in parenthesis is variance/mean.

Stream System A
Habitat 1

		Harvest Rate							
		0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7
Stock	Selective Fishing	4182	3198	2147	1114	318	41	2	0
		(0.2)	(0.2)	(0.2)	(0.2)	(0.5)	(1.1)	(1.9)	
	Nonselective Fishing	4182	3622	2981	2268	1502	737	144	4
		(0.2)	(0.2)	(0.2)	(0.2)	(0.2)	(0.3)	(0.4)	
Yield	Selective Fishing	0	808	1097	893	322	45	3	0
			(0.3)	(0.4)	(0.3)	(0.6)	(1.2)	(2.0)	
	Nonselective Fishing	0	1092	2216	3246	3856	3404	1170	47
			(0.2)	(0.2)	(0.3)	(0.3)	(0.4)	(0.6)	
P.P	Selective Fishing	7.5	5.5	4.0	2.9	2.2	1.8	1.6	
	Nonselective Fishing	7.5	7.5	7.6	7.7	8.0	8.5	9.3	10.2

Habitat 2

		Harvest Rate							
		0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7
Stock	Selective Fishing	1192	883	579	308	113	24	2	0
		(0.2)	(0.2)	(0.2)	(0.3)	(0.6)	(1.1)	(1.6)	
	Noselective Fishing	1192	991	771	538	301	94	9	0
		(0.2)	(0.2)	(0.2)	(0.2)	(0.2)	(0.3)	(0.7)	
Yield	Selective Fishing	0	199	256	212	99	25	3	0
			(0.3)	(0.3)	(0.3)	(0.5)	(1.0)	(1.8)	
	Nonselective Fishing	0	297	573	769	768	417	60	2
			(0.2)	(0.3)	(0.3)	(0.4)	(0.5)	(0.8)	
P.P	Selective Fishing	7.5	4.0	3.1	2.5	2.2	2.0	1.8	
	Nonselective Fishing	7.5	7.5	7.6	7.7	8.0	8.5	9.3	

Table 6 continued.

Habitat 3

		Harvest Rate							
		0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7
Stock	Selective Fishing	323	262	209	160	112	61	17	1
		(0.2)	(0.2)	(0.3)	(0.4)	(0.5)	(0.6)	(0.9)	
	Nonselective Fishing	323	259	189	114	45	6	0	0
		(0.2)	(0.2)	(0.2)	(0.2)	(0.2)	(0.6)		
Yield	Selective Fishing	0	50	80	102	104	78	28	2
			(0.3)	(0.4)	(0.4)	(0.5)	(0.6)	(0.9)	
	Nonselective Fishing	0	77	138	160	108	26	2	0
			(0.2)	(0.3)	(0.3)	(0.3)	(0.6)		
P.P.	Selective Fishing	4.2	3.6	3.3	3.1	3.0	2.9		
	Nonselective Fishing	4.2	4.2	4.3	4.4	4.6	5.1	5.6	0

are usually dominant in habitat 3. As a result of increased annual fishing rate on those fish under the nonselective fishing method, all age classes in the spawning stock are evenly depressed. Although the stock level is lower under nonselective than under selective fishing, the production parameter is maintained at a higher level and yield is also high. The magnitude of fluctation of stock and yield increases with increased fishing effort. The increases are greatest under selective fishing.

POPULATION RECOVERY FROM HARVESTING

It is hypothesized that adaptive capacity of a stock in fluctuating environments is more closely related to the production parameter than to abundance. The production parameter is optimized when age composition is concordant with its habitat organization. If a substock maintains a diverse age composition, it may recover more easily after the cessation of fishing.

Figures 20 and 21 show stock recovery in stream system A after nonselective (H=0.6) and selective (H=0.5) fishing, which occurred from the 30th to the 70th year, were terminated. At termination of harvesting, although the abundance of the stock under nonselective fishing (H=0.6) was approximately one third that of the stock under selective fishing (H=0.5), age diversity and the production parameter (Figure 21B) of the nonselectively fished stock was higher than that of the selectively fished stock. The selectively harvested stock is strongly skewed toward earlier maturing fish (Figure 20A). The nonselectively harvested stock recovers more rapidly than the selectively harvested one (Figure 21A), even though abundance at the intiation of recovery was lower. During the first 15 years, the selectively harvested stock first recovers age diversity (Figure 20A) and then increases more rapidly in abundance.

Figure 20. Recovery of each age class in the spawning stock after selective (A) and nonselective (B) fishing. From year 30 to year 70 the nonselectively fished stock was harvested at H = 0.6 and the selectively fished stock at H = 0.5. Age composition upon termination of fishing is given in each panel. The solid, bold, dotted and broken lines indicate abundance of age classes 3, 4, 5, and 6, respectively.

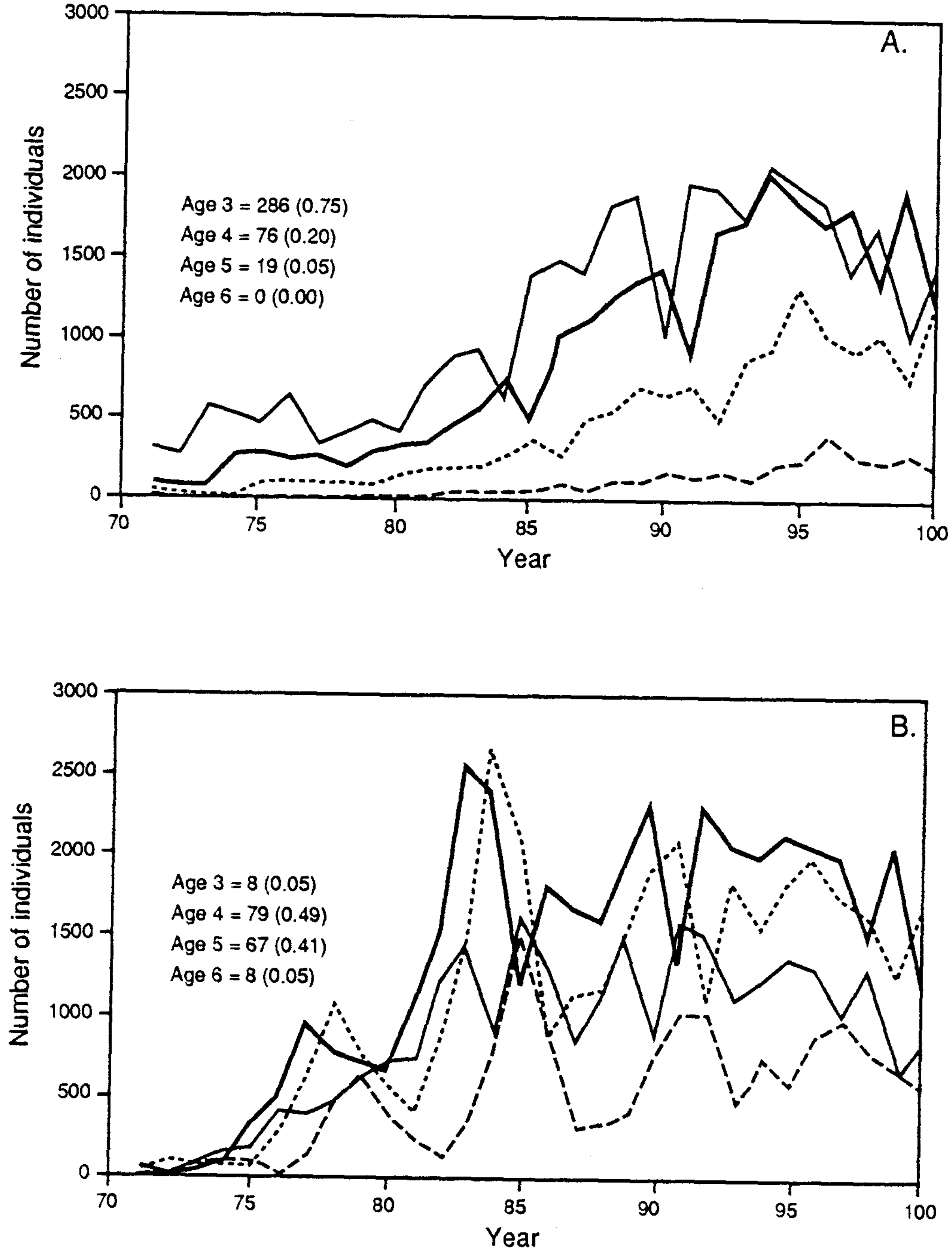

A.
Number of individuals
3000
2500
2000
1500
1000
500
0
Year
70
75
80
85
90
95
100
Age 3 = 286 (0.75)
Age 4 = 76 (0.20)
Age 5 = 19 (0.05)
Age 6 = 0 (0.00)
B.
Number of individuals
3000
2500
2000
1500
1000
500
0
Year
70
75
80
85
90
95
100
Age 3 = 8 (0.05)
Age 4 = 79 (0.49)
Age 5 = 67 (0.41)
Age 6 = 8 (0.05)

Figure 20.

Figure 21. Trends in population abundance (A) and production parameter (B) in stream A after termination of fishing in year 70. The solid line indicates the nonselectively fished stock while the bold line indicates the selectively harvested population.

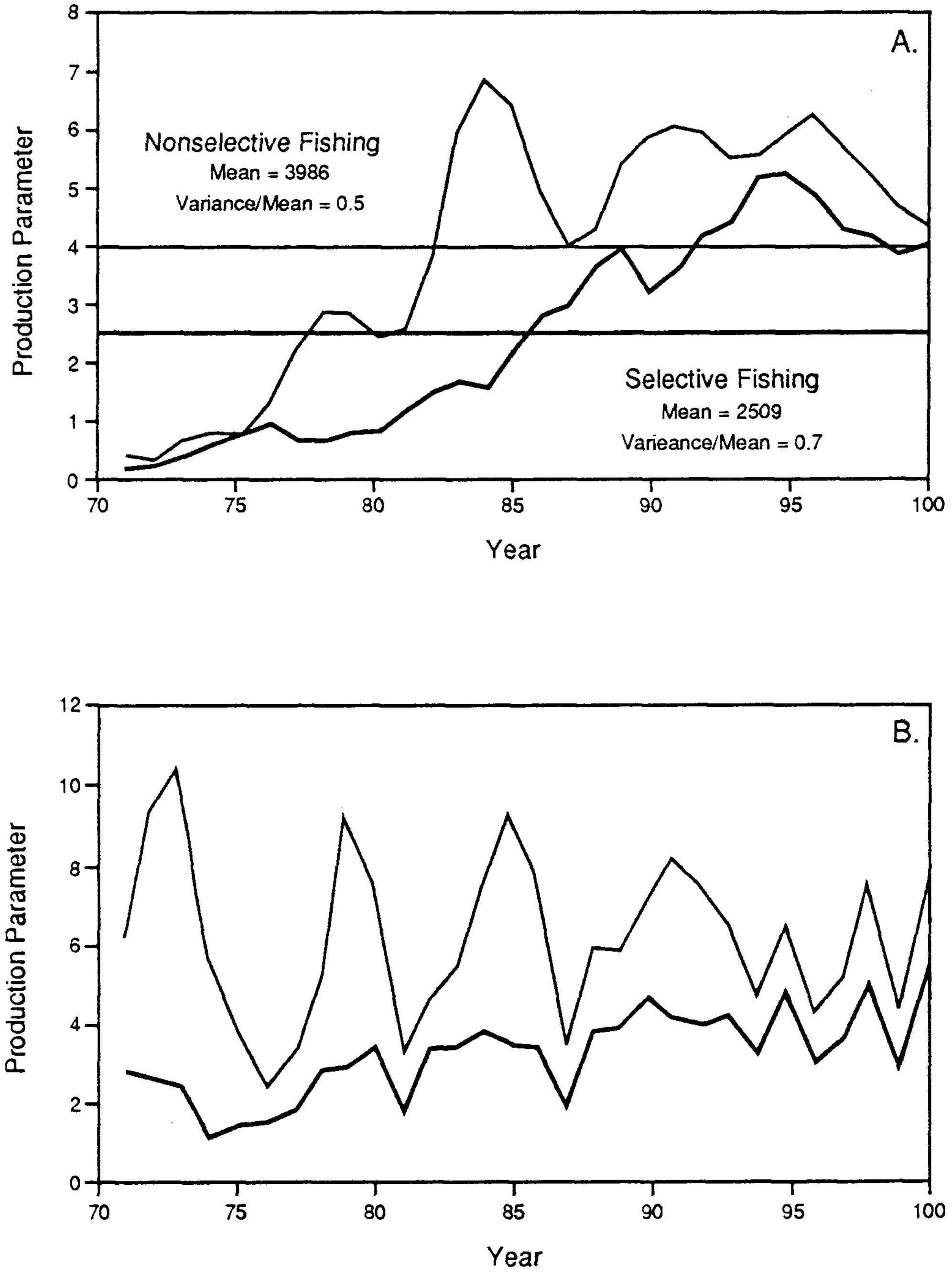

A.
Nonselective Fishing
Mean = 3986
Variance/Mean = 0.5
Selective Fishing
Mean = 2509
Varieance/Mean = 0.7
Production Parameter
0
1
2
3
4
5
6
7
8
Year
70
75
80
85
90
95
100
B.
Production Parameter
0
2
4
6
8
10
12
Year
70
75
80
85
90
95
100

Figure 21.

DISCUSSION

Adaptive Significance of Age At Maturity and Effect of Fishing

Unlike a single age stock-recruitment relationship, a multiple age chinook salmon stock model is a complex system which consists of individual spawners from different age classes. Those individuals are adapted to different habitats in different ways, which provides selective advantages for the population under heterogeneous circumstances (Healey and Heard 1984, Hankin and McKelvey 1985, Holtby and Healey 1986, Healey 1986). The capacity of a multiple age stock is determined through incorporation of the life histories of individual spawners. The age composition of the spawning stock is transformed by fishing pressure and the capacity of the population may change. As a result, some of the characteristics of the population which have adaptive significance may be lost.

Eberhardt (1977) described differences between two stock-recruitment curves, Ricker's humped curve (1954) and Beverton and Holt's model (1956). These two curves were originally derived from different theoretical concepts. The Ricker curve is applicable when density dependence is operative during the early stages of life. Population size can increase rapidly at low abundance and overshoot the asymptote. On the other hand, the Beverton and Holt curve imposes a carrying capacity in the similar fashion as the logistic equation and the population will grow at moderate rates up to the limitation. Hence, Ricker's humped curve represents a classical r-selected species in unstable environments. That is, since future reproductive success is uncertain under fluctuating environments, the stock that is capable of rapid growth with high r-value under favorable conditions is at an advantage (Stearn 1977). Thus the degree of the hump in the curve may have adaptive significance.

It is widely recognized that the Ricker curve is well suited to Pacific salmon and the alpha parameter determines the degree of humpedness of the curve. Similarly, the production parameter used in the multiple age model also influences the humpedness of the stock-recruitment curve. However, the value of the production parameter will decrease as the age composition is deformed by fishing pressure (Figure 13). In turn, the stock-recruitment curve will be flattened (Figures 14 and 15). Thus the stock cannot respond as quickly to favorable conditions (Figure 21).

The stream systems of chinook salmon usually are composed of patches of spawning and rearing habitats. The habitats consist of a heterogeneous mosaic of microhabitats. These habitats have different physical and hydrological characteristics which may affect fish of different sizes in different ways. Fish of different sizes may utilize different kinds of habitats to spawn (Healey and Heard 1984, Hankin and McKelvey 1985, Holtby and Healey 1986, Healey 1986) so that variation in size associated with variation in age at maturity enables the population to utilize the whole habitat efficiently. Therefore, the adaptive capacity of a population is related to the degree of temporal and spatial diversity in the population. Greater diversity confers superior capacity to maximize and stabilize performance (production parameter) in spatially and temporally heterogeneous environments.

Two types of fishing methods, trolling and gillnetting, are highly selective for size of chinook salmon (Ricker 1981, Healey 1986). The fishery is also age selective because later maturing fish spend a longer time in the ocean and are more vulnerable to harvest (Hankin and Healey 1986). Thus, age diversity can be reduced in exploited populations (Figures 11 and 12) and consequently some parts of the habitat may not be fully utilized.

The inefficient utilization of habitat is analogous to decreases in the capacity of the habitat so that the replacement level of the substock may be reduced (Figures 14 and 15).

Murphy (1967) demonstrated the significance of multiple reproductions per lifetime for iteroparious species such as sardines. He argued that if organisms live in fluctuating environments, there is a high probability of environmentally induced reproductive failure. Thus, the organisms offset high probability of reproductive failure in any year with repeated reproduction over several years. These kinds of populations have a diversity of age classes. However, harvesting pressure on older age classes may cause reduction of age diversity so that the population may lose this adaptive mechanism. The work of den Boer (1968) and Andrewarth and Birch (1984) illustrated the necessity of temporal and spatial life history diversity (here equivalent to different age classes) for a population to persist in a fluctuating environment. In their theory of "spreading of risk", maintenance of a diversity of life history types tends to buffer the influence of environmental changes and stabilize the abundance of the population. Thus, if diversity is reduced, abundance fluctuates considerably due to the inability of the population to counterbalance unfavorable environmental effects on some life history types with the favorable effects on others. As shown in Table 6, increased fishing rate reduced age diversity and increased variation of stock abundance and yield. Variability was greater under selective fishing than under nonselective harvest.

Chinook salmon are semelparous and so cannot repeatedly reproduce. Their spawning habitats are relatively unstable and unpredictable. Offspring of a female spawner will mature and return to the stream of origin at different ages (from the second to the fifth year of ocean life). In this way the chinook may achieve some of the benefits of iteroparity. The age composition of the spawning stock always consists of individual spawners from different cohorts. The age composition reflects conditions in the developmental environments experienced by each year class in the spawning stock. Therefore, even though a spawning stock would confront an unfavorable environment for successful reproduction in a particular year, the disadvantageous effect on a cohort will be spread over four years and will be counteracted by other year classes whose developmental environments have been more favorable. The flexibility to reform a diverse age composition in a spawning stock may play an important role in stabilizing productivity of chinook salmon populations in spatially and temporally heterogeneous environments (Table 6). The population can be viewed as a system capable of reforming its life history structure (age composition) for adaptation. Selective fishing may strip away this flexibility so that the population will not be able to buffer environmental changes.

Moreover, since the probability that early maturing small fish will be produced becomes much greater in selectively exploited stocks due to the disappearance of late maturing, large fish, the speed of degradation of these qualitative characteristics for adaptation to changing environments may be high.

Management Implication

The basic concept of maximum sustainable yield in a surplus production model tells us that if we will harvest surplus production of a species at the maximum point, the resource will be utilized forever (Schaefer 1954). If stocks can be assumed to be at equilibrium in salmon fisheries, a similar concept could be applied to the stock-recruitment relationship to determine optimal harvest rate (Ricker 1975). However, environmental states are hardly constant. Age composition of substocks and, in turn, substock structure of populations are significantly influenced by natural events and human activities. The equilibrium stock-recruitment model does not allow the incorporation of changes in life histories associated with changes in system composition.

Most fisheries are size or age selective. The size associated with age at maturity seems to be an adaptive trait in habitats in which there is a relatively high proportion of large fish (e.g. habitat 1, Figure 10). Thus, size selective fisheries may have a large impact on the age composition of spawning substocks in such habitats but less impact on substocks in habitats where small fish are dominant (e.g. habitat 3). As a result, the productivity (determined by the production parameter in the model) will be reduced in the first instance and will be only slightly affected in the second instance (Figure 13).

At the stock level, the degree of effect of fishing pressure will be determined by the substock structure of the population which is associated with the habitat structure in the stream. For instance, a population in a stream mainly composed of habitats that favor late maturing, large fish is more vulunerable than the population in a stream with habitats favoring early maturing, small fish.

In general, although the optimal harvest rate depends on the productivity (Moussalli and Hilborn 1986, Hankin and Healey 1986), the production parameter or alpha parameter representing productivity would substantially vary in time and space. Once the production parameter decreases, the yield curve may be reduced in magnitude. Consequently, the optimal harvest rate will be lower than the rate expected from a constant production parameter (Figures 16, 17, 18, and 19). There is a strong correlation between the degree of the reduction of the production parameter and the age composition of the stock. Therefore, the optimal harvest rate always needs to be re-estimated as the production parameter changes. The best policy will involve some feedback relationship (Walters 1988) among harvest rate, stock structure, age composition and a re-estimated production parameter. The following may be necessary to implement :

1. Habitat classification for each substock in relation to hydrology, physical and biological (especially impact of other species) characteristics. Habitat classification for a stream system should be extended to the adjacent system.
   a. Regularly monitoring local patterns of stream flow in relation to stream bed scour.
   b. Monitoring escapement of spawners returning to a specific habitat and rapid re-estimation of the age composition.
2. Estimating age composition of each substock and comparing it with the present one to diagnose the productivity of the substock.

IV. CONCLUSION

Two ecological simulation models have been presented in the research to examine chinook salmon life history organization to demonstrate difficulties in properly managing chinook salmon stocks. The difficulties relate to:

1. Since freshwater spawning habitats are characterized by variation of physical, hydrological and biological factors, stocks require individual spawners with different capabilities of adapting to the habitats.

2. Habitat-specific substocks are uniquely composed of individual spawners. Substock capacity is determined by the incorporation of life history events and parameters. Therefore, changes in the life history events and parameters will lead to changes in structure of the substock and in turn changes in capacity. The vulnerability to exploitation will differ between substocks.

3. There is variation of habitat structure among stream systems so that stocks composed of the habitat-specific substocks must be different. Their capacity is entailed in their organization

which involves the interrelation of the habitat-specific substocks.

4. Since habitat-specific substocks are differentially vulnerable to exploitation, stock composition may be transformed differently by exploitation and the capacity will change in different ways. Hence, the vulunerability of stocks must differ.

5. Chinook salmon fisheries are mixed stock fisheries due to their extensive migratory characteristics. This makes it difficult to use the fixed escapement strategy or the fixed harvesting rate strategy that has been advocated by some fisheries biologists.

Models are communicative and illustrative and they are useful heuristic tool for studying biological complexity. Quantitative models in fisheries population biology and management have been well developed and have been successful in characterizing parts of problems. However, the utility of models sometimes can be overstated and management may be misled by their simplicity. Models are unable to reflect all the complexity of natural systems, so that their utility must be limited to a particular domain. Utility of a particular model strongly depends on the specific purpose for which it was built. Although models have increased our understanding of the dynamics of exploited chinook salmon stocks and might be useful in fisheries management, models still have the limitation of explicitly coupling the dynamics of the exploited stock to unexpected interrelation between environmental and biological factors (eg. genetic mechanism with respect to changing environment). Further research is necessary to articulate population interactions within a community with reference to habitat classification and stock identification.

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