FRAMEWORK FOR ESTIMATING SALMON SURVIVAL AS A FUNCTION OF HABITAT CONDITION

Michael L. Cuenco, Ph.D.
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March 18, 1996, Revised August 19, 1997

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Technical Report 96-4

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Columbia River Inter-Tribal Fish Commission
729 NE Oregon St., Suite 200
Portland, Oregon 97232
(503) 238-0667

ACKNOWLEDGEMENTS

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INTRODUCTION

Proposed land use actions (timber harvest, road construction, livestock grazing, irrigation water withdrawals, mining, etc.) that may adversely affect Snake River salmon species listed under the Endangered Species Act (ESA) are submitted to the National Marine Fisheries Service (NMFS) annually by the Forest Service, Bureau of Land Management, and other federal agencies for review under Section 7 of ESA whereas non-federal entities eventually may submit proposed actions under Section 10 of ESA. NMFS needs a means to provide timely and consistent evaluation of these proposed land use actions to insure that they are not likely to jeopardize the continued existence of any endangered or threatened species or result in the destruction or adverse modification of critical habitat of such species.

The focus of a jeopardy determination is the probability of long-term survival as affected by the proposed action in the context of present and future management actions. Without the context of the full set of factors, the concept of jeopardy for one isolated proposed action has no meaning. It does not make sense to attempt to make a jeopardy decision on an isolated proposed action without taking into account other factors that could change and that could be deliberately managed. Thus, land use actions should not be evaluated in isolation from other management factors (e.g., hydropower operations) that could affect the listed species.

The problem of evaluating the effects of land use actions on salmon survival is difficult because of the complexity of salmon biology and freshwater ecology. Most land use actions do not affect salmon survival directly. Land use actions affect habitat variables, which in turn affect salmon survival. Thus, the problem can be partitioned into: 1) effects of habitat variables on salmon survival, and 2) effects of land use actions on habitat variables. The effects of land use actions on habitat variables are covered in a separate report (Rhodes 1995). This present report deals with the effects of habitat variables on salmon survival.

GOAL AND OBJECTIVES

The goal of this project is to develop a framework for estimating salmon survival as a function of habitat condition. The framework can serve as a starting point for developing quantitative models that predict salmon survival as a function of one or more habitat variables. The specific objectives of this project are:

1) Organize available information on habitat-fish relations applicable to Snake River salmon through a review of published and unpublished literature and consultations with resource scientists and managers.

2) Evaluate, either qualitatively or quantitatively, the potential use of these relations as single factor predictors for survival of listed salmon species.

3) Evaluate, either qualitatively or quantitatively, the potential for predicting survival of listed salmon species as a function of the interaction of multiple habitat variables.

4) Develop a mathematical model that employs habitat/survival relationships and knowledge of current habitat condition of a stream system within the Snake River Basin to examine the effects of population size and productivity on the rate of recovery/decline of a wild/natural stock faced with current versus improved habitat conditions.

MODELING APPROACH

There are no clear-cut procedures for developing quantitative models (Cuenco 1989). The approach taken is dictated by the intended use of the model, the reality to be described, the competing demands for generality, precision and reality, the state of the science, and the training and preference of the modeler (Levins 1966). Steps in modeling tend to be exploratory and iterative with continual modifications of previous steps. The following steps outline an initial approach for providing a framework for estimating salmon survival as a function of habitat condition.

A. Level of resolution

Models are not intended to be exact copies of the real world but are simplifications that reveal key processes necessary for understanding and prediction (Cuenco 1982). As part of the modeling process, it is important to choose an appropriate level of resolution (Starfield and Bleloch 1986). The resolution of a model tells us which aspects of the subject being modeled are distinguishable or clear and which are hidden, ignored, submerged or blurred. Whenever we observe the world around us, we do so selectively; we pay attention to some features and ignore others. There are two aspects to the concept of resolution (Starfield and Bleloch 1986): scope or which components we include in our model and which we leave out, and detail or how much emphasis we ascribe to the components we include.

The scope of a model depends primarily on the questions we want to ask of the model. Only those variables that influence the answers sought are included. The proper information about only a relatively small number of well chosen variables is often sufficient basis for effective models because key variables often account for most of the phenomena to be explained (Odum 1971; Ackoff 1978; Hall and Day 1977).

We define the scope of the model to include the time the pre-spawning adults enter the Snake River tributaries to the time the juveniles (smolts) exit the same Snake River tributaries. Portions of the Snake River affected by mainstem dams are deliberately excluded. During this period, salmonids live through several stages during which several biological and environmental factors act to define subsequent smolt yield. Biological factors include spawner abundance, predation, intra-specific and inter-specific competitions (Seelbach 1987). Environmental factors include fluctuating climatic factors such as precipitation and temperature and human-induced perturbations. The scope is restricted to the freshwater habitat used by prespawning and spawning adults, incubating embryos, preemergent alevins, and postemergent juveniles. Thus, the overall input is the number of prespawning adults entering a specific Snake River tributary to spawn and the overall output is the number of juveniles leaving the same Snake River tributary as a function of key habitat variables. Smolt yield can be quite variable from year to year; the maximum smolt yield is often three to ten times the minimum yield (Seelbach 1987). The model will focus on data specifically applicable to Snake River spring/summer chinook.

As part of determining an appropriate level of resolution, the problem will be partitioned into a series of key life stages and biological processes by analyzing what the salmon needs from its environment and how the natural habitat meets those needs. The series of life history stages will be the basis for developing a series of linked life history models based on the postulated mechanisms relating habitat condition to salmon survival. The relevant life stages are those during the time when the listed species are present in the specific Snake River tributary. This period includes the following life stages and their respective biological activities:

1. Pre-spawning and spawning adults. Ability of salmon adults to enter the spawning streams, to find suitable holding habitat until time to spawn, and to survive and spawn successfully (egg deposition) in freshwater riverine habitat. Spring/summer chinook migrate to the Snake River tributaries in spring and summer and, spawn in autumn.

2. Incubating eggs and alevins. Pre-emergent phase in intra-gravel (redd) environment. Ability of the eggs to develop and hatch successfully; ability of alevins to develop and emerge from the gravel successfully. Spring/summer chinook eggs and alevins incubate in fall and winter; eggs hatch in winter; alevins emerge in spring.

3. Feeding, overwintering, and outmigrating juveniles. Post-emergent phase in stream rearing environment. Ability of the juveniles to escape predators, feed, grow and develop in the riverine environment. The juvenile component includes, a) feeding and growing during spring, summer and autumn, b) hiding and overwintering during late autumn, winter, and early spring, and c) juvenile outmigration in the spring from the Snake River tributary.

B. Define output variables

The primary output variable we are interested in modeling is survival rate by key life stages. Fish have specific environmental requirements in order to perform vital life functions and survive. For an individual fish, survival is measured as either 0, dead or 1, alive. For a group or population of fish, survival is measured as the proportion of the number of live fish to the total number of fish, alive or dead, e.g., 0.83 survival rate. Any measure of survival must be referred to some interval of time either expressed or implied.

The key life stages were identified by evaluating the distinct salmon life stages, the relative magnitudes and durations of mortalities by life stage, and the discreteness in environments. The place and time of occurrence of the major mortality components and whether or not the components are affected by fish population density, human-induced, and/or natural factors were also determined. The units and range (min, max) of these variables observed from laboratory or field studies should be defined. The following survival rates by key life stages are used in this model:

1. S_{adult} is the survival rate of pre-spawning adults from the time they enter a specific Snake River tributary to the time they complete spawning.

2. S_{fry} is the survival rate of pre-emergent eggs and alevins from egg deposition to emergence of fry from the redd. This is a period when eggs and alevins are incubating in the redd.

3. S_{sparr} is the survival rate from the time fry emerge from the redd to the time parr goes into winter hiding in the fall. This is a period when the juveniles are actively feeding and growing.

4. S_{wparr} is the survival rate from the time parr goes into winter hiding in the fall to the time they emerge from hiding in the spring. This is a period when juveniles are relatively inactive as far as feeding and growing. Some juveniles of spring/summer chinook do not go into winter hiding but outmigrate from the tributary in the fall. The genetic and environmental determinants of this behavior is poorly understood.

5. S_{smolt} is the survival rate from the time parr emerge from winter hiding in the spring to the time they outmigrate from the Snake River tributary as smolts. This period coincides partly with the period of parr to smolt transformation.

Based on survival rates and a given number of prespawning adults migrating to the spawning grounds (ADULTS), we can compute the abundance or numerical production of the following life stages:

SPAWNERS is the number of live spawners that deposited eggs.

EGGS is the number of eggs fertilized and deposited.

FRY is the number of live fry that emerged from the redd.

SPARR is the number of parr that survived the summer rearing period and are ready to go into winter hiding.

WPARR is the number of parr that survived over the winter hiding period.

SMOLTS is the number of smolts that migrated out of the Snake River tributary.

The relations between the number of spawners, eggs deposited in redds, fry that emerge from the redds, and outmigrating smolts take on a variety of forms depending on the species, life history, stream and incubation conditions (Bjornn and Reiser 1991). The number of eggs deposited may increase with the number of spawners as long as the amount of suitable spawning area is not limiting, but level off when suitable habitat becomes in short supply. Usually the number of fry emerging is directly related to the number of eggs deposited; if these two quantities are plotted against each other, differences in slope between areas probably reflect differing qualities of the incubation environment. Finally the number of outmigrating juveniles is directly related to the number of emerged fry but level off when suitable rearing or overwintering environments become limiting. Differences in slope reflect differing qualities of the summer rearing and winter environments.

The abundances of various life stages are limited by the carrying capacities of the habitat for those particular life stages. The carrying capacity is a function of when and how the different life stages of the fish population use specific freshwater habitats and the quantity and quality of available habitat to support the biological needs of those life stages. Carrying capacity by life stage can be expressed in abundance or biomass per unit habitat (stream length, area, volume, or flow). The following carrying capacities are used in this paper:

1. K_{adult} is the holding or resting habitat capacity in terms of pre-spawning adults. This may be a function of water volume (no two fish can occupy the same space at the same time), water or bottom surface (fish want to stay close to stream or pool bottom where velocity is minimal to conserve energy), behavioral (what degree of crowding is tolerated), dissolved oxygen concentration (fish need to meet their respiration demand for oxygen), and temperature (fish can tolerate more crowding at colder temperatures because their respiration needs are less). Of course there are also low and high limits to suitable temperatures, and a lower limit to suitable oxygen level.

2. K_{redd} is the spawning/incubating habitat capacity in terms of redds, eggs, spawners, or alevins. This may be a function of redd size, inter-redd space, and area with suitable gravel, water velocity, water depth and hydraulic conditions (transition areas with accelerating flows, downwelling currents).

3. K_{sparr} is the summer rearing habitat capacity in terms of parr. This may be a function of summer low flows and percent embeddedness which limit water surface area and pool volume available for the fish, and food supply.

4. K_{wparr} is the winter rearing habitat capacity in terms of parr. This may be a function of volume of interstitial space for smaller juveniles and large woody debris for larger juveniles, water temperatures above freezing and winter low flows which will limit physical space.

C. Identify "key" habitat (input) variables

The fourth step is to identify and define the "key" habitat variables that account for most of the response in salmon survival. The goal is to discover by means of observation, analysis and experiment which factors are "operationally significant" and to determine how these factors bring about their effects on the individual and population (Odum 1971). Defining the habitat variables consists of where, when, and how the variables are measured. As much as possible this should indicate the actual environmental conditions experienced by the salmon. Thus, in addition to developing or using a standard procedure, it would be useful to have some knowledge of the spatial variability (places actually occupied vs. adjacent areas) and temporal variability (diel, seasonal during time life stage is present, and interannual within relevant season) of these variables. Specifically the domain (min, max) of these variables observed from laboratory and field studies should also be documented and would provide limits to the applicability of models developed from these variables (Cuenco 1989).

The following considerations were used to help identify the key habitat variables:

1. Data are available and applicable to Snake River salmon and their habitats.

2. The habitat variable is affected by land use activities and resulting changes are measurable.

3. The variability in the habitat variable under natural conditions or the conditions of interest has a major effect on salmon survival, i.e., goes outside the optimum or tolerance limits of the salmon for that variable. Factors which have small effects or which have large effects but only in rare cases will be omitted. Thus, it will be necessary to define the domain or levels of interest for each habitat variable, i.e., natural range of undisturbed environment and range of disturbed environment. For example, diel incubation temperatures in salmon redds during winter vary by less than 1 or 2°C in undisturbed environment. However, in disturbed environment they may vary by 2-5°C.

4. Assess the relative risk that the optimum levels of each habitat variable, that is essential for maximum survival of a specific life stage, will not be met. Estimate the deviation from optimum levels and the effect on salmon survival. Select those habitat variables that are likely to have a major effect on salmon survival.

5. The procedure for measuring the habitat variable provides the necessary degree of accuracy and precision relative to the natural variability of the habitat variable.

6. The procedure for measuring the habitat variable is easy to do and is cost-effective compared to other procedures.

7. Collecting data on the habitat variable has little or no effect on the stream biota.

Some habitat variables can be classified as control factors which operate at all levels (within lethal limits) of the factor concerned (Fry 1971). For example, temperature sets the pace for all metabolic processes in poikilotherms. Other variables are classified as limiting factors and become operational at a particular level characterized by dependent and independent stages (Fry 1971). Thus, beyond the critical value any change in a factor will have no added effect on the variable of interest. Limiting factors restrict the supply of needed metabolites (oxygen, food) or the removal of waste metabolites (carbon dioxide, nitrogenous waste).

D. Quantify effects of the habitat variables

To quantify the effect of a habitat variable on salmon survival, we need data that allows us to separate the effects of other variables that can potentially affect salmon survival. These data are traditionally obtained from laboratory and field experiments that provide the necessary controls to avoid ambiguous explanations. It is important to take note of the domain (min, max) of input variable and the resulting range (min, max) of output variable because they set limits to the applicability of the relation to other cases. The relation of the habitat variable to salmon survival is quantified by a mathematical equation or graph (increasing or decreasing, linear or exponential, saturation, etc.). Suitable data are required to estimate parameters of the equations. In many cases, the effect of one variable depends on the levels of other variables. In such cases, multi-factor experiments are required to determine the effects of interactions between two or more variables. Such experiments are usually only possible under highly controlled laboratory conditions. In some cases, it may be only possible to estimate relative survival rates instead of absolute survival rates. Single factor predictors are feasible if under the conditions of interest the habitat factor generally accounts for a major part of the change in survival compared to other factors affecting survival.

ADULT SPAWNING MIGRATION

Adult salmon must reach their spawning grounds at the proper time and with sufficient energy reserves to complete their maturation and spawn successfully (Bjornn and Reiser 1991). Spring/summer chinook salmon usually have some flexibility in their migration schedule to accommodate delays caused by naturally occurring low flows, high turbidities, unsuitable temperatures, or physical barriers. When upstream migration is not delayed, some stocks that migrate long distances arrive in the spawning areas 1 to 3 months before they spawn. At this time and during migration, the salmon needs suitable holding or resting habitat to conserve energy. Human-induced migration changes can cause large delays which prevent the fish from reaching the spawning grounds at the proper time to spawn successfully.

SPAWNERS

From a given number of prespawning upstream migrant ADULTS, the number of spawners reaching the spawning grounds to actually spawn is:

$$SPAWNERS = ADULTS * S_{adult}$$

where: SPAWNERS is the number of spawners surviving to the spawning ground to actually spawn; ADULTS is the given number of upstream migrant adults measured at some point in a Snake River tributary; S_{adult} is the proportion of ADULTS surviving to the spawning ground to actually spawn.

ADULT MIGRANT SURVIVAL

During their upstream migration to the spawning grounds, the proportion of ADULTS, S_{adult} that survive to become actual SPAWNERS depends on a number of habitat variables.

Barriers

Irrigation diversion structures (permanent concrete dams, temporary rock berms, culverts) placed in the stream can cause adult migration blocks or delays (Delarm

1991). A number of unscreened diversions that affect spring/summer chinook salmon still exist in the Snake River Basin. On some streams, water users divert the entire stream during low flow periods, thus temporarily eliminating stream habitat (Delarm 1991). Waterfalls and debris jams can delay or prevent upstream migration (Chapman 1962b). The ability of salmon to pass over barriers depend on swimming velocity, horizontal and vertical distances to be jumped, and the angle to the top of the barrier (Powers and Orsborn 1985). Maximum jumping heights of salmon based on darting speeds ranged from 0.8 m for brown trout to 3 m for steelhead (Reiser and Peacock 1985). In laboratory studies, Stuart (1962) determined that leaping conditions are ideal when the ratio of height of falls to depth of pool below the falls is 1:1.25.

Passable and impassable barriers can be determined by using the models developed by Stuart (1962), Powers and Orsborn (1985), and Reiser and Peacock (1985).

Stream temperature

Unsuitable temperatures can lead to disease outbreaks in migrating and spawning fish, delayed migration, and accelerated or retarded maturation. Spring, summer, and fall chinook are able to migrate within the temperature ranges 3.3-13.3, 13.9-20.0, and 10.6-19.4°C, respectively (Bell 1984).

It is common for water temperatures in the Columbia River to exceed the upper migration limit of 21°C during August (Shew et al. 1985; Meyer 1989) and for temperatures in the Snake to be even higher (>24°C) (Sylvester 1958; Collins 1963; Thompson 1974). The 1990 water temperatures in Lower Granite Reservoir peaked on approximately August 13 at 25°C and gradually declined to about 21°C by September 16. The fall chinook migration period commences approximately at the same time that the peak temperatures are reached. At Ice Harbor Reservoir during 1990, water temperatures were 23°C on August 15 but they had declined to only 22°C by September 16.

Laboratory tests confirm that temperatures above 21°C equal or exceed incipient lethal temperatures for Columbia River steelhead and chinook stocks migrating during the summer season. For example, Becker (1973) identified the thermal tolerance of chinook jacks to be 21-22°C based on a 168 hr TLM test. Coutant (1970) identified the incipient lethal temperature for chinook jacks as 21-22°C.

Laboratory tests are typically conducted at a constant temperature. Temperatures in a stream or river generally fluctuate on a diel basis. It is often assumed by optimistic biologists that survival is high if temperature excursions into incipient lethal zones are brief. However, studies of adult salmon subject to fluctuating temperatures illustrate the increased mortality risk with increasing temperatures. A study by Fish (1944)(as cited by Parker and Krenkel 1969) revealed that adult sockeye

survival was 51% when adults were subjected to fluctuating temperatures of 9.4-23.3°C ($\bar{x}$=16°C) but were 96% at 11.1-15.6°C ($\bar{x}$=11.9°C). Chinook survival under the same two temperature regimes were 36% after 56 days holding and 75% after 58-61 days holding, respectively.

In a laboratory experiment conducted by EPA, adult sockeye salmon at 10°C lost an average of 7.5% of their body weight over the test period and still had visible fat reserves (Bouck et al. 1976). At 16.5°C, typical of the Columbia River in early July, adult sockeye salmon lost an average of 12% of their body weight and visible fat reserves were essentially depleted. Females with their developing eggs lost more body weight that the males at both temperatures. Testes were more than 25% smaller at 16.5°C than at 10°C. Adverse gonadal development was evident among adult females, which produced smaller and lighter eggs at the higher temperature.

Andrew and Geen (1960) (as cited by Raleigh et al. 1986) report that temperatures in excess of 12.8°C produce increasing pre-spawning mortalities in sockeye adults. The maximum spawning temperature range recommended by Bell (1986)(as cited by Bjornn and Reiser 1991) for spring, summer, and fall chinook is somewhat narrower (5.6-13.9°C) than the full range under which they have been observed. EPA and NMFS (1971) recommend maximum temperatures of 12.8°C. Bell (1984, p. 95) gives a narrower range (5.6-10.6°C) as the preferred spawning zone.

Most salmon spawn in autumn when seasonal temperatures are decreasing from about 13°C to 5°C (Chambers 1956, as cited by Raleigh et al. 1986). It appears that the critical temperature threshold of approximately 12.5°C and a declining temperature regime is one that is associated with ability to complete the spawning act, maximum long-term viability of eggs and alevins, and good and improving resistance to death by disease in adults and eggs. Although prespawning mortality attributed to bioenergetic stress may be a significant factor in overall adult mortality for adults up to spawning time, it is uncertain at present how to separate disease and bioenergetic stress effects.

Subsequent egg mortality or delayed inhibition of alevin development can occur when ripe females or newly deposited eggs in gravel are exposed to temperatures above approximately 12.5°C. Consequently, for protection of eggs and facilitating the act of spawning under a wide range of conditions, a spawning temperature range of 5.6-12.8°C appears to be most appropriate.

It is a difficult modeling challenge to determine how to apply the information available regarding temperature effects on adults during the spawning period. Given the available studies it appears that temperatures greater than 12.8°C can be assumed to begin inhibiting the spawning act. At temperatures greater than approximately 16°C we can assume that spawning will not occur. If spawning time for each individual reaching the spawning grounds in the early portion of the spawning period is delayed by 3 or more days, survival to the egg deposition stage should begin to decrease. If the

delay is greater than 24 days for these same fish, survival to egg deposition should be zero. For those adults that normally arrive at spawning grounds late in the spawning period, a further delay for reasons of water temperature elevation may have even shorter potential survivals times, assuming they naturally have expended most energy reserves by the time they arrive. Survival of eggs for adults exposed to temperatures of 16°C just prior to spawning can be assumed to be 50% if eggs are exposed to water temperature of 16°C during incubation. At 18°C egg survival will be assumed to be 0% and at 2-12°C survival will be taken to be optimal (approx. 95%).

Delayed Migration. Delays in upstream migration because natal streams were too warm have been observed for sockeye salmon (21.0°C, Major and Mighell 1966), chinook salmon (Hallock et al. 1970), and steelhead (Monan et al. 1975). Hatch et al. (1993) reported that as water temperature reached 22.8°C in the Okanogan River, sockeye passage upstream to Lake Osoyoos terminated. During the migratory period, sockeye did not migrate from the Columbia River staging area upstream on the Okanogan River until temperatures dipped below 22.8°C. Even though Hatch et al. (1993) observed initiation of migration below 22.8°C, it appears likely that the optimal migration temperature is about 14.4°C, the temperature at which the sockeye cruising speed is maximum (see Bell 1984).

Spring chinook in the Grande Ronde River have a migration peak at Bonneville Dam on approximately April 15 and a spawning peak near September 5. Migration up the Grande Ronde River occurs in May. If temperatures in Snake River reservoirs exceed 21°C in May, it is likely that a critical window of opportunity to migrate up the mainstem Grande Ronde would disappear. Summer chinook bound for the South Fork Salmon River have a migration peak at Bonneville Dam on June 15 and spawning peak on September 1. Passage through the Snake River reservoirs occurs during July. This stock in the Snake River may be especially subject to thermal blockages. Fall chinook historically entered the Snake River from late August through November with a peak in September. Currently, the run extends to mid-December. Peak spawning at the Lyons Ferry hatchery occurs in late November. Of 3241 adults returning to the hatchery in 1987, pre-spawning mortality was 32% at the hatchery alone. Because of the large volume of warm water retained in Snake River reservoirs, elevated temperatures can be prolonged thermal barriers to fall chinook. Fall chinook in the Columbia River in late August ready to enter the Snake River could have to delay their upstream migration by 4 weeks until suitable temperatures exist for passage. Even then, high temperatures can lead to metabolic stress or disease.

Delays caused by an unfavorable migrating environment may contribute to reproductive failure. Adults, which fast during what may be a months-long upstream journey, exhaust virtually all energy reserves prior to spawning and death (Idler and Clemens 1959; Gilhousen 1980). High temperatures can increase the rate at which limited energy is consumed for standard metabolism (Fry 1971). Delays of as little as

3-4 d at migration barriers have been associated with premature mortalities (Andrew and Geen 1960), as has unusual exertion (DeLacy et al. 1956; Paulik 1960).

Migration occurs when temperatures are <21°C and stops when temperatures are ≥21°C. If adults are forced to hold in a coldwater tributary (such as when escaping warm Columbia River temperatures) or in the Columbia itself when blocked by thermal barriers at the Snake River mouth, water temperatures in holding water may be suitable, in which case migration delay may be the sole negative factor. This factor may not cause early mortality but the effect may be the same to the population if the delay results in inability to reach spawning grounds at the appropriate time.

Migration delay that is long enough to cause adults to arrive on spawning grounds after the start of the normal spawning period can be expected to cause some pre-spawning mortality because a small portion of the spawning population spawns at the outset of the spawning period and dies soon thereafter. Effect of migration delay may be more severe if an inability to find mates in holding areas prior to a final spawning migration inhibits successful spawning.

If a migration delay causes adults to hold under adverse water temperatures, direct thermal effects on the population must be considered. The same effects must be considered for adults migrating through warmwater reaches or adults that have reached headwater holding areas which are above suitable temperatures.

Disease. Temperatures below 15.6°C reduce the probability of infectious warmwater diseases in adult chinook (EPA and NMFS 1971; Snyder and Blahm 1968, as cited by Armour 1990; Burrows 1960, as cited by Parker and Krenkel 1969). Temperatures of 20°C were reported to result in 100% mortality of chinook during columnaris outbreaks (Ordal and Pacha 1963). These authors found that strains of low virulence initiated infection at water temperatures ≥20°C but highly virulent strains were infective with temperatures as low as 12.8°C. They consider temperature-induced columnaris as a major factor responsible for declines of Columbia River chinook. Fujihara and Nakatani (as cited in EPA and NMFS 1971) report that columnaris is associated with temperatures above 12.8°C. They suggest that it is extended periods of warm water conditions rather than simply peak temperatures that especially increase incidence of the disease. Columnaris in sockeye becomes increasingly active above 15.6°C (Colgrove and Wood 1966, as cited by Parker and Krenkel 1969) and has been implicated in high sockeye mortalities in the Columbia River (Fish 1948, as cited by Parker and Krenkel 1969). Bouck et al. (1970)(as cited by EPA and NMFS 1971) did not observe sockeye mortalities from columnaris at 16.7°C but did note frequent lesions and death at 20°C.

Adult infection with columnaris in warm mainstem reaches has implications for survival of juveniles because adults often carry virulent strains into tributaries and infect juveniles (Ordal and Pacha 1963). The spread of columnaris organisms among adult

salmon occurs freely in fish ladders with high populations of coarse fishes and low water flows (Fujihara and Nakatani, MS 43, cited in EPA and NMFS 1971).

Other common salmon diseases are aggravated by increased temperatures during summer flows. Temperatures >13.3°C increase the incidence of furunculosis. For adult sockeye on Fraser River spawning grounds, mortality of females ranged from 5-86% from gill bacterial infections at temperatures of 22°C (International Pacific Salmon Fisheries Commission 1962, as cited by Parker and Krenkel 1969). Temperatures >18.3°C favor the protozoan causing ichthyophthiriosis (ich). The growth of the fungus *Saprolegnia parasitica* is enhanced at higher temperatures. The threshold temperature for initiating infection by *Ceratomyxa shasta* is about 10°C (Fryer and Pilcher 1974). Once the infection develops, death is hastened by increased temperature and infected adult fish may die before they can spawn. In contrast, kidney disease and IHN (Sacramento River Chinook Disease) are more virulent at 7.2 - 10°C (CWRD 1988).

If adults are infected with disease organisms, the survival rate of a population depends upon the inherent resistance of the population, the thermal regime, and the virulence of the disease. In addition to this, survival rate depends upon the infection rate. Antibody levels in Columbia River fish show that the peak yearly infection rate with columnaris is 70-80% of adults. Occurrence of the disease is associated with temperatures above 12.8°C. Incidence of columnaris is higher in the Snake and the Columbia for some distance below the mouth of the Snake than in the remainder of the Columbia (Fujihara and Hungate, MS 42, cited in EPA and NMFS 1971, p. 37).

Fryer and Pilcher (1974) and Fryer et al. (1976) provide a wealth of information regarding survival of salmonids exposed to a variety of infectious diseases and held at temperatures between 3.9 to 23.3°C. Fryer and Pilcher (1974) studied *Chondrococcus columnaris* infection in rainbow trout, coho, and spring chinook salmon; *Aeromonas salmonicida* infection in coho and spring chinook; and *Aeromonas liquefaciens* infection in steelhead trout. In all cases survival rates were low at 17.8-20.6°C, moderate at 12.2-15°C, and very high at 3.9-9.4°C. Progress of the infections was accelerated at higher temperatures and was progressively inhibited as temperature levels decreased.

Coho infected with *Ceratomyxa shasta* exhibited low survival at 20.6°C, high survival at 9.4-12.2°C, and very high survival at 3.9-9.4°C. For rainbow trout infected with *Ceratomyxa shasta*, survival was high at 3.9°C but was low at all other temperatures. The disease progressed most rapidly at higher temperatures, and became progressively slower as temperature decreased. That is, when fish were infected, life expectancy was extended as temperatures decreased. The mean life expectancy was 42 days after exposure to *C. shasta* in the Willamette River for 72 hr at a mean water temperature of 15.2°C followed by holding in a tank at 15°C. At 22°C the mean life expectancy is reduced to 16 days. This has implications for survival to spawning. Contraction of diseases during migration through warm water reaches may

not result in pre-spawning mortality, provided the bulk of the migration and holding period is spent in cold water. However, spring or summer chinook, which hold for extended periods may succumb to disease prior to spawning if inadequate holding water temperature is available.

Fryer and Pilcher (1974) believe that their experiments on survival of steelhead and coho after exposure to *C. shasta* for 72 hr reflect minimum estimates of survival under field conditions because these species under natural conditions are exposed for longer periods to infectious organisms. They indicated that *Aeromonas liquefaciens* and *Chondrococcus columnaris* were common in the river. Because of the prevalence of bacterial diseases and the likelihood of multiple sources of mortality by infection, bacterial diseases were suppressed with the antibiotic terramycin.

For the Snake River spring/summer chinook salmon, we assume that only high temperatures can be a problem during upstream adult migration. This biological relation can be modeled by (Figure 1):

$$S_{adult} = 1.0 \qquad\qquad\qquad TP <= TP_{crit}$$
$$S_{adult} = (TP-TP_{zero})/(TP_{crit}-TP_{zero}) \qquad TP_{crit} < TP <= TP_{zero}$$
$$S_{adult} = 0.0 \qquad\qquad\qquad TP_{zero} < TP$$

where: TP is the stream temperature during upstream adult migration; TP_{crit} defines the lower temperature below which S_{adult} is 1.0; and TP_{zero} defines the upper temperature above which S_{adult} is zero. Estimates of these parameter are: $TP_{crit} = 13°C$; $TP_{zero} = 21°C$.

Streamflow

Streamflows must provide suitable water velocities and depths to facilitate upstream migration. Thompson (1972) developed a procedure for estimating minimum flows required for migrating fish based on minimum depth (24 cm for chinook) and maximum velocity (2.44 meters/second for chinook) criteria and measurements in critical stream reaches. Baxter (1961) reported that salmon needed 30-50% of average annual flow for passage through the lower and middle reaches in Scottish rivers and up to 70% for passage through headwater streams.

Stream velocity (V) can be modeled by assuming an optimum range of velocity where adult migrant survival is maximum and beyond which it drops to zero.

$$S_{adult} = 1.0 \qquad\qquad V_{min} <= V <= V_{max}$$
$$S_{adult} = 0.0 \qquad\qquad V < V_{min} \text{ or } V > V_{max}$$

where: S_{adult} is the proportion of ADULTS surviving to the spawning ground to actually spawn; V_{min} is the minimum velocity below which upstream migration is stopped; V_{max} is the maximum velocity above which upstream migration will not occur.

Water depth can be modeled by assuming a minimum depth below which adult migrant is stopped (Figure 2).

S_{adult} = 1.0 $D >= D_{min}$
S_{adult} = 0.0 $D < D_{min}$

where: S_{adult} is the proportion of ADULTS surviving to the spawning ground to actually spawn; D is the stream depth during upstream migration; D_{min} is the minimum depth below which upstream migration is stopped (22 cm).

Stream dissolved oxygen

Low dissolved oxygen levels (DO) can adversely affect swimming performance of and delay migrating salmon. Maximum sustained swimming speeds of juvenile and adult coho salmon at temperatures of 10 - 20°C were reduced when DO dropped below air saturation levels and performance declined sharply below 6.5 - 7.0 mg/l (Davis et al. 1963). Low DO may elicit avoidance reactions (Whitmore et al. 1960; Hallock et al. 1970). Chinook adult migration ceased when DO fell below 4.5 mg/l and did not resume until it exceeded 5 mg/l (Hallock et al. 1970). Minimum DO recommended for spawning fish (at least 80% saturation and not even temporarily less than 5 mg/l) should provide minimum needs of migrating salmon (Bjornn and Reiser 1991).

This factor can be modeled by:

S_{adult} = 1.0 $DO_{crit} <= DO$
S_{adult} = $(DO-DO_{zero})/(DO_{crit}-DO_{zero})$ $DO_{zero} < DO < DO_{crit}$
S_{adult} = 0.0 $DO <= DO_{zero}$

where: DO is the dissolved oxygen concentration of the stream during upstream migration; DO_{crit} = 8.0 mg/l; and DO_{zero} = 4.0 mg/l.

Suspended Sediment

High levels of suspended sediment can delay or stop salmon migration (Cordone and Kelley 1961). Salmon did not move in streams when suspended sediment levels exceeded 4,000 mg/l as a result of a landslide (Bell 1986). Arrival of chinook at spawning grounds can vary by a month or more depending on the suspended sediment levels along the migration route (Bjornn 1978). In 1965 and 1966, upstream migration of salmon in the lower Columbia River was delayed when Secchi disk visibility was less than 0.6 m (Bjornn and Reiser 1991).

Based on the above data the effect of suspended sediment (SS) can be modeled by:

$$S_{adult} = 1.0 \qquad SS < SS_{crit}$$
$$S_{adult} = 0.0 \qquad SS > SS_{crit}$$

where: SS_{crit} is the critical suspended sediment level (4,000 mg/l) above which salmon migration is stopped, preventing the salmon from reaching the spawning ground on time.

ADULT MIGRANT CARRYING CAPACITY

Sufficient habitat carrying capacity is needed for temporary holding, resting and energy conservation for final maturation of pre-spawning adults during their migration to spawning grounds. Large pools are significant habitat units in stream channels that provide cover during prolonged adult holding prior to spawning. For spring chinook, which enter tributaries approximately four months prior to spawning and must occupy these sites during the hot summer months, the availability of deep pools can determine the survival of adults. Other microhabitats, such as overhanging vegetation, undercut banks, accumulations of large woody debris, and pocket pools behind submerged logs and large boulders, provide cover for adult salmon (Giger 1973). However, large pools are very effective in providing protection from disturbance, from predators and also in maintaining a layer of water cooler than the main body of the flow. Holding pools should be considered at a minimum to include primary pools. These are pools of >1 m depth and with a maximum diameter that measure 0.9 x (mean stream width) or greater (Platts et al. 1983) or occupy over 50% of the wetted channel width (Schuett-Hames et al. 1993).

Survey of the stream's carrying capacity should account for stream water temperature. Spring chinook in the Grande Ronde and John Day Rivers depend heavily on large holding pools during summer months. This is especially true in stream reaches that lack shade and are warmed from upstream land uses. In such locations deep pools retain cooler water at their bottoms from groundwater upwelling that provide a micro layer that adults can occupy to aid in regulating metabolism (Torgerson, pers. comm.; McIntosh, pers. comm.). Anderson and Miyajima (1975) as cited by Reeves et al. (1991) and Nielsen et al. (1994) noted that peak water temperature in a pool was 2.2°C cooler than temperature in an adjacent riffle. In stream reaches where peak temperatures are <18°C holding capacity can be calculated based upon area of stream bottom that have at least 1 m^2 area sheltered by large boulders or having significant bank cover and suitable water velocity (0-10 cm/s).

Thus, the number of adult salmon that can be supported in temporary holding habitats during their upstream migration is:

$$K_{adult} = A_{pool} / D_{hold}$$

where: K_{adult} is the number of adult salmon that can be supported in temporary holding habitats during their upstream migration; A_{pool} is the total area of pools in m^2 with suitable temperature (<18°C), water depth (>1 m), velocity (0-10 cm/s), and cover (overhanging banks, large woody debris, boulders); D_{hold} is the average holding density in adults per m^2 of pool which depends on the area occupied by each salmon (size dependent) and inter-fish space (behavior dependent). In the absence of data, we assume a value of 1 adult/m^2).

KEY VARIABLES FOR INTERIM ADULT MIGRANT MODEL

During the migration of pre-spawning adults, the key habitat variables associated with major mortality problems in the Snake River tributaries are the presence of barriers (culverts, small dams), low flows (minimum depths less than 24 cm for chinook), and high temperatures during the migration and holding periods. Dissolved oxygen and suspended sediment are usually not a problem if streamflow is adequate. For the adult migrant carrying capacity, the key habitat variable is the availability of temporary holding or resting pools with suitable temperature (<18°C), water depth (>1 m), velocity (0-10 cm/s), and cover (overhanging banks, large woody debris, boulders).

SPAWNING AND EGG DEPOSITION

After reaching the spawning riffle, the female salmon selects a clean gravel site and constructs a redd in which she lays her eggs. The male salmon immediately fertilizes the eggs, and the female covers them up. The redd is a contiguous area of the gravel stream bottom that has been excavated by a female salmon to deposit a series of nests or egg pockets (Hobbs 1937; Hawke 1978; Chapman 1988). Egg pocket is the very small portion of the redd in which eggs are found. There are usually several egg pockets in a salmon redd. Depth of egg pockets varies with fish size and substrate particle size. Large chinook may dig as deep as 43 cm below the streambed, but average egg pocket depths are 20-30 cm (Hobbs 1937; Hawke 1978; Chapman 1988). Salmon usually select areas composed mostly of gravel and small rubble which can withstand most of the natural stream velocities without the substrate movement damaging the embryos (Platts et al. 1979).

In the process of redd construction the female salmon reduces the amount of fine sediments and organic matter in the egg pockets (McNeil and Ahnell 1964; Ringler 1970; Chapman and McLeod 1987; Everest et al. 1987a). During incubation, redds may become less suitable if suspended inorganic and organic fine sediments are deposited in the redd. Intrusion of fines into the redd increases as particle size in transport decreases (Cooper 1965; Beschta and Jackson 1979). When fine sediments in transport are large enough to bridge the pore spaces, they may only settle into the surface of the redd where they can block other sediments (Hobbs 1937; Beschta and Jackson 1979; Chapman 1988).

Available data from the Snake River Basin consistently indicate that cleaned gravels or gravels in artificial redds show an increase in fine sediment levels during the incubation period (King and Thurow 1991; King et al. 1992; Maret et al. 1993), except where it appears interstitial spaces were already completely filled with fine sediment (King and Thurow 1991). The active cleaning of gravels within redds by spawning salmon probably has a limited effect on the ultimate survival-to-emergence of salmon because it probably cannot offset rapid subsequent sedimentation by fine sediment, especially in streams with fine sediment at the bed surface or in transport during the incubation period.

REDDS

Assuming that a female builds and spawns in one and only one redd, the number of redds built is equal to the number of female spawners which can be estimated as:

REDDS = (P$_{fem}$ * SPAWNERS)

where: SPAWNERS is the number of spawners surviving to the spawning ground to actually spawn; P$_{fem}$ is the proportion of SPAWNERS that are females.

EGGS

The number of fertilized eggs laid per redd or per female spawner depends upon the proportion of the average fecundity that is actually deposited, fertilized, and covered by gravel. Chinook fecundity varies within and between populations with approximately 50% of the variation explained by female size (Healey and Heard 1984, as cited by Healey 1991).

Some of the eggs that a female salmon carries are retained or not laid. Healey (1991) reported that egg retention was 0.5-12% for chinook from a number of studies but can be as high as 25% when fish are harassed, subjected to disease, or die prematurely. Some of the eggs laid are not fertilized. The fertilization rate, reported by Healey (1991) from studies by Briggs (1953) and Vronskiy (1972), ranged from 92% to 99%. Some of the eggs laid are swept out of the nests during egg deposition. Estimates for chinook ranged from 12% to 90% and appear to depend on the water velocity over the redd (Healey 1991).

The number of fertilized eggs that are successfully deposited is:

EGGS = REDDS * F$_{egg}$ * (1-R$_{et}$) * (1-L$_{ost}$) * F$_{ert}$

where: EGGS is the number of fertilized eggs that are successfully laid in the redd; REDDS is the number of redds built; F$_{egg}$ is the average fecundity of female SPAWNERS in eggs per female (a function of age and size); R$_{et}$ is the egg retention rate; L$_{ost}$ is the proportion of eggs laid that is lost or washed away by water current; F$_{ert}$ is the proportion of eggs that is successfully laid and covered in the gravel that is fertilized.

REDD CARRYING CAPACITY

The carrying capacity or the maximum number of salmon redds that can be supported in a stream is a function of the area required for each redd (a function of fish size), and inter-redd space (a function of fish behavior), and the area with suitable spawning gravel and water conditions, i.e., stream temperature, stream depth, stream velocity, and hydraulic gradient (Reiser and Ramey 1984, 1987; IEC Beak 1984; Reiser 1986). Thus, carrying capacity (K_{redd}) can vary from stream to stream and from year to year.

$$K_{redd} = A_{suit} / (A_{redd} + I_{space})$$

where:

A_{redd} is the average redd size (species specific and proportional to fish size).
I_{space} is the average inter-redd space (species specific and behavior dependent).
A_{suit} is the total stream area with suitable gravel size (1.3 - 10 cm in diameter), water depth (20 - 150 cm), water velocity (20 - 100 cm per second), and hydraulic gradient (riffle areas with downwelling currents) (Bell 1973).

Redd Size and Inter-Redd Space

Large fish make large redds; tolerance of nearby fish varies by density and species; and poor quality spawning areas may force females to make several redds. Anadromous salmon redds range in size from 0.6 m^2 for pink salmon to 10 m^2 for chinook salmon (Burner 1951; Bjornn and Reiser 1991). Burner (1951) measured 850 redds of spring chinook, summer chinook, fall chinook, coho, chum, and sockeye salmon in the Columbia River basin and found an inter-redd space approximately three times the redd size (2.8 - 5.1 m^2).

Suitable Stream Area

The suitable stream area is based on suitable gravel size, water depth, water velocity, and hydraulic gradient.

Substrate. Large fish can use larger gravel sizes than smaller fish. Bell (1986) reported that substrate for anadromous salmon should range from 1.3 - 10.2 cm in diameter which is in general agreement with substrate sizes found in natural redds (Orcutt et al. 1968; Dill and Northcote 1970; Hooper 1973; Hunter 1973; Smith 1973; Reiser and Wesche 1977). Salmon have been observed spawning in areas with substrate particles larger than 30 cm but most often in areas where the majority of the particles were smaller 15 cm (Shepherd et al. 1986b). The particle size composition of redds or spawning areas has been characterized by the proportion within specified size

ranges (Tappel and Bjornn 1983), the geometric mean particle diameter (Shirazi and Seim 1981), and the Fredle index (Lotspeich and Everest 1981).

Streamflow, depth, and velocity. Streamflow regulates the amount of spawning area available by regulating the area covered by water and the velocities and depths over the gravel beds (Hooper 1973). Relations between flow and amount of suitable spawning area have been assessed or predicted by methods based primarily on measurements of water depths and velocities in areas with suitable substrate (Collings 1972, 1974; Thompson 1972). Water depths measured at anadromous salmon redd sites ranged from a minimum of 15-35 cm depending on species and water velocities ranged from 3-152 cm/s, but most were 20-100 cm/s (Thompson 1972; Reiser and White 1981a; Smith 1973; Collings 1974). Measurements of depth and velocity were usually taken at the upstream edge of the redd because that point most closely approximated conditions before the redd was constructed and reflected depths and velocities selected by the fish. Two locations in the water column have been used for making estimates of preferred velocities: 0.6 X depth from water surface, and nose velocity which approximates location of the fish close to the streambed.

Hydraulics. In streams, part of the water flows above the streambed and part flows under the streambed and in the banks (Pollard 1955). The surface water is continually aerated whereas the intra-gravel water is not and dissolved oxygen can be low; the surface water flows much faster than the intra-gravel water which just seeps through the gravel streambed. Salmon eggs incubating in a stream gravel require oxygen which must be supplied by a continuous flow of oxygenated water (Wickett 1954). The supply of oxygen to a redd depends on its concentration in the intragravel water and on the rate at which this water flows through the gravel (Pollard 1955). Salmon prefer to spawn in the transitional areas between pools and riffles (Hazzard 1932; Hobbs 1937; Briggs 1953; Stuart 1953) associated with downwelling currents and are relatively free of silt and debris (Stuart 1953; Wicket 1954; Pollard 1955; Vaux 1962, 1968; Brannon 1965; Coble 1961; Philipps and Campbell 1962; Silver et al. 1963; Shumway et al. 1964; Cooper 1965).

Stream temperature. Bell (1986) summarized recommended temperatures for spawning of salmon: chinook, 5.6-13.9°C; coho, 4.4-9.4°C; sockeye, 10.6-12.2°C; steelhead, 3.9-9.4°C. In British Columbia, most of the sockeye salmon spawned in water of 8-13°C, chinook salmon in water of 10-17°C, and coho in water of 5-6°C. Observed spawning of chinook in a wide variety of locations is reported for a composite temperature range of 2.2-18.9°C (Mattson 1948; Burner 1951; Raleigh et al. 1986; Crawford et al. 1976; Olson and Foster 1955; Snyder et al. 1966, as cited by Parker and Krenkel 1969). Inhibition of spawning has been reported to occur at temperatures of 15.6°C (Combs and Burrows 1957).

KEY VARIABLES FOR INTERIM REDD CARRYING CAPACITY MODEL

During the spawning period (selection of spawning site, construction of redds, egg deposition), the key habitat variable which affects the salmon redd carrying capacity is the total stream area with suitable incubation conditions for egg and alevins: gravel size (1.3 - 10 cm in diameter), water depth (20 - 150 cm), water velocity (20 - 100 cm per second), and hydraulic gradient (riffle areas with downwelling currents or substantial intragravel water flow).

EGG AND ALEVIN INCUBATION

When the female salmon selects a spawning site, it is also selecting the initial incubation environment which it modifies in the process of redd construction. Successful egg incubation and emergence of fry depend on intragravel water flow, water temperature, and particle size composition (Bjornn and Reiser 1991). During incubation, sufficient intragravel water must circulate through the egg pocket to supply oxgyen and carry away waste products from embryos. Because the oxygen supply is dependent on the subsurface movement of water in a stream, apparent velocity and permeability of the spawning gravels have been related to incubation success. Streambed particles in the redd at the end of spawning, and organic and inorganic particles that settle into the redd and surrounding substrate during incubation affect the rate of water exchange between the redd and the stream, the amount of oxygen available to the embryos, the concentration of embryo wastes, and the movement of alevins especially when they are ready to emerge from the redd. Organic matter decomposition and embryo respiration consume oxygen; if oxygen is consumed faster than intragravel water flow can replace it, intragravel dissolved oxygen may be reduced to lethal levels.

EMERGED FRY

The number of emerged fry can be computed as:

$$FRY = EGGS * S_{fry}$$

where: EGGS is the number of eggs deposited; S_{fry} is the survival rate from eggs to emerged fry which is a function of key habitat variables.

Measuring Egg to Emergent Fry Survival Rate

Egg to emergent fry survival rate is measured as the ratio of two quantities:

$$S_{fry} = FRY / EGGS$$

where: EGGS is the number of eggs deposited; and FRY is the number of emergent fry. Values of S_{fry} from field and laboratory studies may not be strictly comparable with each other because of different methods used to estimate S_{fry} (Burton et al. 1990; Young et al. 1991).

1. Different initial life stages may be used, e.g., newly fertilized egg, eyed egg, newly hatched alevins.

2. Different field methods are used to determine the number of eggs deposited in an area of the natural stream:

   a. Observing the number and size of spawning females in the spawning area and estimating average fecundity per female based on female size-fecundity relation (McNeil et al. 1964).

   b. Excavating natural redds and counting the number of live and dead eggs. This assumes that dead eggs do not decompose between time of egg deposition and excavation although some do depending on the duration between deposition and excavation and other conditions (Harris 1973).

   c. Number of eggs are counted and artificially planted in the stream (Maret et al. 1993).

   d. When estimating the number of eggs deposited in a single natural redd, it is assumed that the eggs from a single female were deposited in one natural redd.

3. Laboratory methods generally enumerate all the eggs deposited and incubated in artificial redds in the laboratory.

4. Different final life stages may be used, e.g., eyed egg, newly hatched alevin, after yolk is absorbed, newly emerged alevins or fry, several days or several weeks old fry.

5. Different field methods may be used to determine the number of emerged alevins or fry:

   a. Redd capping of a natural redd and counting the number of emerged fry trapped.

   b. Fry trapping downstream from natural redds; total number of emerged fry estimated from fry efficiency and actual number of fry trapped.

   c. Counting the number of live and dead fry within a redd trap (Phillips and Koski 1969).

6. Laboratory methods generally enumerate all emerged fry.

EGG TO EMERGENT FRY SURVIVAL RATE

During the intragravel phase of egg and alevin incubation (3 - 6 months depending on temperature and species), the following biological requirements are essential for maximum survival, normal egg and alevin development, and emergence of fry from the redd: suitable intragravel temperature, streamflow, intragravel water flow (apparent velocity) to supply dissolved oxygen and carry away metabolic wastes, fine sediment does not impede intragravel water flow and gravel size composition provides cover from light and predators.

Streamflow

Suitable streamflow (velocity 30-90 cm/s, water depth 20 -50 cm or deeper) is needed to prevent dewatering of the redd, minimize sediment deposition on or in the redd, and prevent embryos and alevins from being washed out of the redd by floods and from physical shock (slow enough in combination with redd stability despite natural fluctuations in streamflow).

Substrate size composition

Suitable substrate size composition (gravel and small rubble, 2-10 cm, Dill and Northcote 1970) is needed to provide interstitial space (pore size, **porosity**) for eggs and movement and emergence of alevins (Dill and Northcote 1970); porosity is the ratio of pore space to total volume of the redd, and to cover eggs and alevins from **predation** by fish, birds, invertebrates, or mammals (deep enough, egg pocket ave. 20-30 cm below streambed), and to provide **darkness** during incubation of embryos and alevins. Light especially the ultraviolet component is inhibitory to development and could be fatal (Smith 1957; Brannon 1965; Piper et al. 1982). Riparian vegetation and trees contribute to providing subdued light over the redds. Fish embryos subjected to bright artificial light before the formation of eye pigments will suffer high mortality at all stages of development (Piper et al. 1982). Affected eggs exhibit retarded development and accelerated hatch and if they do hatch, the fingerlings often have reduced growth and severe liver damage. Eggs exposed to artificial light after formation of eye pigments are less susceptible to light but still exhibit increased mortality and reduced growth.

Percent Fine Sediment

Small fine sediment (<0.83 mm) can decrease gravel permeability and consequently restrict intra-gravel water flow or water exchange from stream to egg pocket (measured as apparent velocity) which supplies oxygen and removes metabolic wastes (e.g., carbon dioxide) from embryos and alevins. Permeability is the ability of particles in the redd to transmit water per unit of time.

Large fine sediment (0.83 mm - 4.71 mm, Platts et al. 1983; 2-6 mm, Platts et al. 1979) can also restrict the emergence of alevins from redd. If we take out fines, will the natural variability in gravel permeability significantly affect supply of oxygen and S_{fry}? There was no difference in alevin survival to emergence between large gravel (3.2-6.3 cm) and small gravel (1.9-3.2 cm) although alevin movement was more extensive and area used per alevin was greater in the larger gravel (Dill and Northcote 1970). Intragravel dissolved oxygen is inversely proportional to % fines (<6.3 mm, Burton et al. 1991; <2 mm, Maret et al. 1993; <6.35 mm, King and Thurow 1991).

Most studies have indicated that S_{fry} is reduced significantly as the amount of fine sediment in spawning gravel is increased under laboratory conditions (chinook, McCuddin 1977; chinook, Tappel and Bjornn 1983; kokanee, cutthroat trout, rainbow trout, Irving and Bjornn 1984; rainbow trout, NCASI 1984; Atlantic salmon, Peterson and Metcalfe 1981; rainbow trout, MacCrimmon and Gots 1986; Iwamoto et al. 1978; USFS 1983; Everest et al. 1987; Hicks et al. 1991; Scully and Petrosky 1991; Rich et al. 1992) and field conditions (coho, Koski 1966, Cederholm 1981; Maret et al. 1993). The reduction in S_{fry} with increased fine sediment has been ascribed primarily to reduced flow of oxygenated water to the incubating eggs (Cooper 1965; Chapman and McLeod 1987; Maret et al. 1993) or entrapment of the emerging alevins within channel substrate (Koski 1966; Dill and Northcote 1970; Phillips et al. 1975; Burton et al. 1990). This biological relation can be expressed mathematically by (Figure 3):

S_{fry} = 1.0 $\qquad\qquad\qquad\qquad$ FS <= FS_{crit}
S_{fry} = (FS-FS_{zero})/(FS_{crit}-FS_{zero}) $\qquad$ FS_{crit} < FS <= FS_{zero}
S_{fry} = 0.0 $\qquad\qquad\qquad\qquad$ FS_{zero} < FS

where: FS is the percent fine sediment; FS_{crit} is the value of FS below which S_{fry} is one; FS_{zero} is the value of FS above which S_{fry} is zero.

Incubation Temperature

Lacking a means of maintaining an independent body temperature, the aquatic poikilotherm is entirely subject to the variations of environmental temperature (Brett 1956). Temperature sets lethal limits to aquatic life; it conditions the animal through acclimation to meet levels of temperature that would otherwise be intolerable; it governs the rate of development; it sets the limits of metabolic rate within which the animal is free to perform; and it acts as a directive factor resulting in the congregation of fish

within given thermal ranges or movements to new environmental conditions (Brett 1956).

Physiological processes are affected by body temperature which in poikilotherms is close to ambient environmental temperature (Brett 1952). Temperature governs the state of molecular activation or rate of all biochemical reactions. Temperature above or below critical values may result in denaturation of enzymes and death (Campbell 1977). The higher the temperature within the acceptable range, the faster the rate of development and the shorter the incubation period and time to emergence. Time to 50% hatch for Pacific salmon ranges from 115 to 150 days at 4°C and from 35 to 60 days at 12°C; coho require the least time and sockeye the most (Alderdice and Velsen 1978; Tang et al. 1987; Velsen 1987; Beacham and Murray 1990). Steelhead and rainbow trout require about 85 days at 4°C and 26 days at 12°C to reach 50% hatch.

Incubation temperatures, regulate timing of juvenile emergence from the redd and may be related to the time of spawning (Heggberget 1988). For fall spawners, newly spawned embryos must reach a critical stage of development before the water becomes too cold (Brannon 1965). Survival of eggs after exposure to cold temperatures depends upon the stage of development. If incubation temperature is reduced from 8°C to 2°C in early stages of egg development, survival rate is less than at later stages. Embryo sensitivity to a temperature reduction of this magnitude is great in stages before completion of epiboly (Beacham and Murray 1987). Emergence of fry usually occurs the following spring when environmental conditions are suitable (Sheridan 1962a; Miller and Brannon 1982; Godin 1982; Burger et al. 1985; Heggberget 1988; Murray and McPhail 1988).

The basic response of S_{fry} to constant incubation temperatures can be expressed mathematically by (chinook salmon, Seymour 1956; chinook, Eddy 1972; chinook, sockeye, coho, chum, pink, Murray and McPhail 1988; coho, Tang et al. 1987; chinook, Heming 1982; chinook, sockeye, Combs 1965; Combs and Burrows 1957) (Figure 4):

$$S_{fry} = 0.0 \qquad\qquad\qquad TP <= TP_{zero1}$$
$$S_{fry} = (TP-TP_{zero1})/(TP_{crit1}-TP_{zero1}) \qquad TP_{zero1} < TP <= TP_{crit1}$$
$$S_{fry} = 1.0 \qquad\qquad\qquad TP_{crit1} < TP <= TP_{crit2}$$
$$S_{fry} = (TP-TP_{zero2})/(TP_{crit2}-TP_{zero2}) \qquad TP_{crit2} < TP <= TP_{zero2}$$
$$S_{fry} = 0.0 \qquad\qquad\qquad TP_{zero2} < TP$$

where: TP_{crit1} and TP_{crit2} are parameters defining optimum temperature values where S_{fry} is 1.0 (6 - 12°C); TP_{zero1} (1 - 2°C) and TP_{zero2} (15 - 16°C) are parameters defining lower and higher temperature values beyond which S_{fry} is zero.

Emergence Time. Egg/alevin incubation during the period from fertilization to fry emergence is a period of generally cold water temperatures. Cumulative loss of riparian cover caused by timber harvest, road building, and grazing can shift the

temperature regime of a stream in the interior Columbia River basin so that maximum summer temperatures are higher and minimum wintertime temperatures are lower. Alteration to the winter thermal regime has the potential to result in a decrease in accumulation of thermal units during the incubation period. Eggs have a wide window of temperature tolerance (conservatively, 2 to 12°C) that confers high survival . However, small decreases in average daily temperature can result in large cumulative changes in degree-days experienced. The accumulation of thermal units necessary for proper hatching and emergence are very well described mathematically (Alderdice and Velsen 1978, Crisp 1981, Beacham and Murray 1990).

Beacham and Murray (1990) examined available data for mean time to hatching and to emergence for five species of Pacific salmon. One of these models (their model 4), of the form ln$D$=ln$a$ + $b$ln(T-c), was relatively simple and accurate. Model parameters include: D, the observed hatching or emergence time after fertilization; T, observed mean temperature (°C); and the coefficients a, b, and c. For chinook, coho, and sockeye the equations used to predict emergence time are:

Chinook   ln$D$=10.404 + (-2.043)ln(T-[-7.575]) r^2=0.970

Coho   ln$D$= 7.018 + (-1.069)ln(T-[-2.062]) r^2=0.979

Sockeye   ln$D$= 7.647 + (-1.134)ln(T-[-3.514]) r^2=0.969

Coho require fewer days from fertilization to emergence than either chinook or sockeye at any temperature between 2 and 16°C, but the magnitude of the difference between these species is greatest at temperatures below 8°C. As few as 50 days are required for chinook and coho emergence at a constant temperature of 16°C while low temperatures of 2°C lengthen time to emergence to 325 days for chinook and 250 days for coho (Figure 12). Taking the difference between the number of days to emergence at temperature T°C from the days at (T+1)°C, allows one to plot the effect of 1°C changes in temperature from a base temperature. For the three salmon species, the effect of a 1°C warming of stream water is most dramatic at low base temperatures. For example, when the base temperature is 2°C, warming the water by 1°C results in a shortening of time to emergence by 60 days for chinook (Figure 13). A more normal initial mean winter temperature might be 5°C. If this mean temperature is increased by 1°C it would result in a 27-day decrease in incubation time. By increasing mean temperature by another 1°C, incubation to emergence would require 22 days less time. If water temperatures are declining from 7 to 5°C, a lengthening of the incubation period by 49 days would occur. It is easy to see how relatively minor changes in thermal regime at these low temperatures can result in significant ecological impacts to emergence timing.

Beacham and Murray (1990) noted that compensation in rate of development under various temperature regimes is typical of Pacific salmon. That is, more thermal units are required for completion of development from egg to emergence when

incubation occurs at high temperatures than at low temperatures. This mechanism moderates development rate at high temperatures and tends to stabilize emergence dates under annual temperature variations. This biological effect is responsible for the shape of the temperature-development rate curve under constant temperatures.

Alderdice and Velsen (1978) reported for *Oncorhynchus tshawytscha* that egg development rate at a constant 6-7°C was less (i.e., more days are required for emergence) than at ambient temperatures having the same mean but varying from a high initial incubation temperature to lower temperatures later in incubation. However, by assuming that incubation occurs at daily temperatures of 5 ± 3°C, that this diel variation obeys a sine wave function, and that egg development responds instantaneously to temperature change, one can apply the temperature-development time predictors of Beacham and Murray (1990) to calculate development time under fluctuating and constant temperature incubation. This procedure results in calculation of development times of 187 and 205 days of incubation to emergence under constant 5°C vs. fluctuating 5 ± 3°C for the entire period. Diel winter water temperature fluctuations may not be as great as ± 3°C, so the difference in predicted development times between a constant and fluctuating regime may not be significant.

Apparent Velocity

During incubation, sufficient water must circulate through the egg pocket to supply oxygen and carry away metabolic waste products from embryos. Because the oxygen supply is dependent on the subsurface movement of water in a stream, apparent velocity and permeability of the spawning gravels have been related to spawning success. Apparent velocity is the average rate of seepage expressed as the volume of water flowing per unit time through a unit area of redd (solids plus voids) perpendicular to the direction of flow (Pollard 1955). It is estimated as the product of gravel permeability and hydraulic gradient (Pollard 1955; Vaux 1962). Permeability is the capacity of the gravel to transmit water (Coble 1961). True or pore velocity is the actual velocity of flow through the interstitial spaces and differs from pore to pore (Pollard 1955).

Some studies have found that S_{fry} is directly proportional to apparent velocity (eyed sockeye eggs, Cooper 1965; preemergent rainbow trout embryos, Sowden and Power 1985); or to permeability (pink and chum salmon fry, Wickett 1958; green egg to emergence of chinook and steelhead, McCuddin 1977; coho embryos in natural redds, Tagart 1984). Laboratory and field studies involving intragravel flow show that S_{fry} if a function of IGDO which is a function of apparent velocity which in turn is a function of gravel permeability (Wickett 1954; Pollard 1955; Terhune 1958; Coble 1961; Vaux 1962; Cooper 1965; Silver et al. 1963; Shumway et al. 1964; Brannon 1965; Taggart 1976; Reiser and White 1981). Permeability is inversely related to % fines (<0.833 mm, McNeil and Ahnell 1964; <0.85 mm, Tagart 1984). This biological relation can be expressed mathematically by (Figure 5):

$$S_{fry} = 0.0 \qquad\qquad\qquad AP <= AP_{zero}$$
$$S_{fry} = (AP-AP_{zero})/(AP_{crit}-AP_{zero}) \qquad AP_{zero} < AP <= AP_{crit}$$
$$S_{fry} = 1.0 \qquad\qquad\qquad AP_{crit} < AP$$

where: AP is the apparent velocity (cm/hr) in the gravel; AP_{zero} is the value of AP below which S_{fry} is zero; AP_{crit} is the value of AP above which S_{fry} is maximum (1.0).

Incubation Dissolved Oxygen Concentration

During incubation, sufficient water must circulate through the egg pocket to supply oxygen and carry away metabolic waste products from embryos and alevins. Under natural conditions oxygen lack is a much more likely limiting factor than carbon dioxide excess particularly since it is only under anaerobic conditions that free carbon dioxide can ordinarily reach high levels (Fry 1971). An adequate supply of oxygen depends on the supply of oxygen relative to the oxygen demand of the embryos and alevins. Oxygen supply is a function of interchange between stream and intragravel water or intragravel waterflow (apparent velocity) and stream dissolved oxygen concentration. Stream dissolved oxygen is usually at saturation.

Oxygen demand is a function of temperature and stage of development which is critical just before and during hatching (the alevin's respiratory system is more efficient than the embryo which is limited by the egg capsule, Fry 1971, Donaldson 1955). Oxygen demand starts out low for newly fertilized embryos and increases to hatching and for alevins (Krogh 1941; Fry 1957; Smith 1957; Davis 1975). Oxygen requirement is basically a function of temperature which sets respiration rate for poikilotherms. In the developing egg, embryo development exerts a high oxygen demand (Smith 1957). To satisfy this demand fully, a high ambient dissolved oxygen concentration is often required. The most critical time for developing eggs as far as oxygen lack is concerned comes just prior to hatching (Lindroth 1942 cited by Fry 1957). Before hatching there is a slight excretion of ammonia only (Smith 1957) while other nitrogenous materials are retained in the egg. The level of protein catabolism is high before, during and after hatching but then settles down to a fairly steady low level which is maintained throughout the yolk-sac stage. Organic matter in the egg pocket can decompose and also consume intragravel oxygen.

The effect of incubation dissolved oxygen concentration on the survival of eggs and alevins, S_{fry} has been studied under laboratory conditions (chum, Alderdice et al. 1958; steelhead and chinook, Silver et al. 1963; steelhead and coho, Shumway et al. 1964; sockeye, Brannon 1965; coho, Mason 1969) and under field conditions (chum, Wicket 1954; steelhead, Coble 1961; steelhead and coho newly fertilized egg to 3 weeks post hatch, Phillips and Campbell 1962; pink and chum, McNeil 1969, Wells and McNeil 1970; chum, Koski 1981; rainbow trout, Sowden and Power 1985; chinook, King and Thurow 1991; brown trout, Maret et al. 1993). Although artificial redds may not have the exact morphology of natural redds, IGDO concentrations, temperatures, and

fine sediments in artificial redds were not significantly different from those of nearby natural redds (Burton et al. 1990; King and Thurow 1991, Maret et al. 1993) (Figure 6).

$$S_{fry} = 0.0 \qquad\qquad\qquad\qquad\qquad\qquad IGDO <= IGDO_{zero}$$
$$S_{fry} = (IGDO-IGDO_{zero})/(IGDO_{crit}-IGDO_{zero}) \quad IGDO_{zero} < IGDO <= IGDO_{crit}$$
$$S_{fry} = 1.0 \qquad\qquad\qquad\qquad\qquad\qquad IGDO_{crit} < IGDO$$

where: $IGDO_{zero}$ (3 mg/l) is value of IGDO below which S_{fry} is zero; and $IGDO_{crit}$ (8 mg/l) is the value of IGDO above which S_{fry} is 1.0.

KEY VARIABLES FOR INTERIM INCUBATION MODEL

During the incubation of eggs and alevins, the key habitat variables associated with major mortality problems in the Snake River that are affected by land use actions are high percent intragravel fine sediment and unsuitable incubation temperatures. The lowest and highest temperatures during incubation should be measured. Measure percent surface fine sediment, which is easier to measure and is correlated to percent intragravel fine sediment (see Monitoring Report, Rhodes et al. 1994), and is non-destructive.

SUMMER REARING OF PARR

After emergence in the spring, the salmon fry feed and grow into parr after the first few weeks of stream life (Everest and Chapman 1972). Newly emerged fry use shallow water areas with low velocity close to the stream margin after they emerge from the redd (Lister and Genoe 1970; Everest and Chapman 1972; Chapman and McLeod 1987). Salmon parr defend a territory in the stream and grow while eating aquatic and terrestrial insects drifting downstream. They begin using deeper and faster water for feeding (Everest and Chapman 1972; Lister and Genoe 1970; Campbell and Neuner 1985). They associate with velocity shear lines and occupy habitat much like that used by adults.

Most salmonids which remain in streams are strongly territorial and this provides a mechanism limiting numerical production since it determines, through the size of the territories, the maximum numerical density which even suitable stream beds can support (Allen 1969). As fish grow larger, the size of their territory increases and its physical characteristics change. Fish which are in excess of the number of available territories or which, due to growth, can no longer find territory with suitable characteristics, are displaced from the area and thus cease to contribute to production. Both the average area of stream bed per fish and the area of the territory increase roughly in proportion to the weight of the fish, and do not differ significantly for different species of salmonids at the same size. The relation for area of stream bed per fish corresponds to an average density of about 1.7 g/sq. m. (15 lbs/acre) and, in many streams studied by biologists, tends to be about 1/15th of the density found in the actual territories (Allen 1969).

For abundant populations, newly emerged fry usually experience a large mortality in the stream as they adjust their population size to the stream's carrying capacity (McFadden 1969). The mortality rates are usually density-dependent and self-regulatory in nature, thus in a year of low fry emergence there is proportionally lower mortality (Crow et al. 1976). The greatest mortality occurs in the spring and summer and usually about 80% of each year's emergent fry die by September (Chapman 1965). The greatest portion of the mortality is caused by density-dependent competition for space; other causes such as predation account for only a minor portion of the total mortality (Au 1972; McNeil 1962a).

Growth is a function of temperature and food abundance and goes through a seasonal variation. The growth rate is high in spring and early summer but in later summer, during the period of maximum temperatures, the feeding rate is reduced and growth stops and remains negligible through the winter. Then in the spring, after the streamflow increases, the temperature rises, and the abundance of insects available to fish increases, the fish enter a period of heavy feeding and rapid growth until they migrate to the ocean (Cordone and Kelley 1961; Shapovalov and Taft 1954).

PARR SUMMER ABUNDANCE

For most salmonids that spend an extended period in streams, the abundance of older fish (summer parr, winter parr, smolts) generally increases as the abundance of emergent fry increases until an upper limit (carrying capacity) is reached (Bjornn 1978).

$$SPARR = FRY * S_{sparr}$$

where: SPARR is the number of parr surviving through the summer; FRY is the number of emerged fry; S_{sparr} is the survival rate from FRY to SPARR as a function of key habitat variables.

PARR SUMMER SURVIVAL

Stream Temperature

Temperature influences the metabolism, behavior, and survival of fish (Mihursky and Kennedy 1967). Growth is reduced at both low temperatures and high temperatures. Diel summer temperatures can fluctuate more than 15°C in small streams with flows less than 1 cubic meter per second and little or no shade (Meehan 1970; Bjornn 1978). Temperatures can increase 6°C in 1 km within a stream (1.4 cubic meter per second flow) in central Idaho (Bjornn et al. 1968).

The upper incipient lethal temperature (UILT) is a function of acclimation temperature. For chinook juveniles acclimated to 20°C, the upper incipient lethal temperature is 24.0°C (Armour 1992). This is the temperature at which 50% mortality is observed within a 24-h period. If acclimation temperature is increased to 24°C, the constant exposure temperature required to produce 50% mortality is 26.4°C. This temperature is the upper incipient lethal temperature for fish acclimated to 24°C. This is also the highest acclimation temperature for which UILT continues to increase. Consequently, 26.4°C is the ultimate upper incipient lethal temperature (the highest temperature at which tolerance does not continue to increase with increasing acclimation temperature). Above this temperature, mortality increases rapidly.

If maximum temperatures are contained within the 15.6°C upper boundary for purposes of ensuring proper chinook growth, the acclimation temperature could be

considered to be approximately 15.6°C, which then has a UILT of 24.8°C. Using the formula of Coutant (1972b) (see Armour 1992) to estimate that temperature that would result in 100% survival with an acclimation temperature of 15°C, one calculates that juveniles exposed to 22, 23, 24, and 25°C can tolerate these temperatures for 62.2, 18.1, 5.3 and 1.5 hours, respectively.

The temperature zone in which juvenile growth is positive encompasses 4.5-19.1°C (see Armour 1992). However, at these extremes, growth reaches zero. Above this boundary growth becomes negative as feeding ceases and respiration rate increases rapidly. Below this critical limit juveniles cease feeding and seek cover. Metabolic inhibition can occur below 4.5°C (Elliott 1981). Because the growth optimum falls within 10.0-15.6°C and because diseases become a significant mortality risk beyond this upper optimum growth level, it is necessary to restrict increases in maximum temperature beyond 15.6°C.

This biological relation of S_{sparr} to high summer temperatures (TP) can be expressed mathematically by (Figure 7):

$$S_{sparr} = 1.0 \qquad\qquad\qquad\qquad TP <= TP_{crit2}$$
$$S_{sparr} = (TP-TP_{zero2})/(TP_{crit2}-TP_{zero2}) \qquad TP_{crit2} < TP <= TP_{zero2}$$
$$S_{sparr} = 0.0 \qquad\qquad\qquad\qquad TP_{zero2} < TP$$

where: TP_{crit2} (14.0°C) defines critical temperature below which S_{sparr} is one; TP_{zero2} (17.0 - 18.0°C) is the higher temperature beyond which S_{sparr} is zero.

Food Availability

Under unlimited food availability, the optimal growth zone for spring chinook is between 10.0-15.6°C and the zone of positive growth between 4.5-19.1°C (McCullough and Rhodes 1993). If food becomes limiting, the positive growth zone can shrink dramatically (i.e., the maximum temperature at which growth is still positive declines) and the optimum growth zone will shift to lower temperatures to compensate for elevated respiration/growth ratios (Elliott 1981). Elliott found for brown trout that the temperature at which growth is zero drops from 19 to 8°C when food rations are reduced from maximum to 12.5% of maximum. Food Abundance is related to substrate composition, the amount of riffles, and the amount of riparian vegetation.

The effect of food abundance (FD) during summer rearing on S_{sparr} can be expressed mathematically by (Figure 8):

$$S_{sparr} = 0.0 \qquad\qquad\qquad\qquad FD <= FD_{zero}$$
$$S_{sparr} = (FD-FD_{zero})/(FD_{crit}-FD_{zero}) \qquad FD_{zero} < FD <= FD_{crit}$$
$$S_{sparr} = 1.0 \qquad\qquad\qquad\qquad FD_{crit} < FD$$

where: FD_{crit} is the critical value of FD above which S_{sparr} is one (maximum) and represents the level which meets or exceed the appetite of the fish. FD_{zero} is value of FD below which S_{sparr} is zero, and represents the food abundance level where S_{sparr} is zero is the level which just provides for the maintenance ration of the fish.

PARR SUMMER CARRYING CAPACITY

The carrying capacity is defined as the greatest weight or numbers of fish that a stream can naturally support during the period of least available habitat (Burns 1971). For abundant populations, carrying capacity is often exceeded during fry emergence and many young fry may die from lack of food, premature migration, or from living in unsuitable habitats. Thus, perturbations of the stream environment do not affect the fish population immediately after fry emergence since, this is normally a period of high mortality and the perturbation just changes the cause of death, not the total amount of mortality. Once the population has reached the carrying capacity, however, any change in the stream environment would alter the population size (Allee 1974; Brown 1972). Also if the number of emerging fry is reduced, the abundance of fry remains fairly constant because of increased survivorship of the fry through density-dependent mortality (McFadden 1969). The stable levels of the fry population are achieved through territoriality and antagonistic behavior (Au 1972).

It is the size of the territory that determines the carrying capacity of the stream (Crow et al. 1976). Once all the available habitat is covered by territories all excess fish are displaced. If the territory size is increased, the carrying capacity is reduced. The territory must be able to supply food and shelter for the fish. Territory size is a function of the species involved, the size of the fish, water velocity, shelter, gravel composition of the streambed, the temperature, and the availability of drift food, and it is independent of the density of the fish. There is however a minimum size of the territory. The most important determinant of territorial size is food availability. As the abundance of food increases, the aggression decreases and the territorial size decreases. Thus, the fish population responds to increased food availability by increasing the number of fish rather than the average size (Allen 1969; Burns 1971; Chapman 1966; Iverson 1972; McFadden 1969). If the insect density increases after the population size has been set, however, there is no increase in the population size.

Large wood debris (LWD), in conjunction with sediments, has marked effects on salmon stream habitats (Bisson et al. 1987; Sedell and Swanson 1984; Sedell et al. 1985). Removal of LWD reduces the stream area in pools and increases that in riffles (Sullivan et al. 1986). Stream sections cleaned of LWD had lower densities of coho salmon and dolly varden compared to uncleaned sections (Dolloff 1986). Dolloff (1986) attributed the decline in density to reduced visual isolation in summer and loss of winter cover.

Abundance of juvenile salmonids in rearing and overwintering habitats appears loosely and negatively correlated with percent embeddedness (Chapman and McLeod

1987). Embeddedness appears promising as a tool for evaluation of effects of sedimentation on the rearing phases of salmonids (Klamt 1976; Kelley and Dettman 1980; Burns 1984). Embeddedness is generically defined as the amount of fine sediment that is deposited in the interstices between larger stream substrate particles (Burns 1984; Burns and Edwards 1985). Using data from Bjornn et al. (1977), Stowell et al. (1983) regressed summer carrying capacity of age 0 chinook to % embeddedness using the following equation:

$$K_{sparr} = B0+B1*EMBED+B2*EMBED^2$$

where: K_{sparr} is the summer carrying capacity in numbers of fish/m^2 of runs; EMBED is the % embeddedness of the runs; B0, B1 and B2 are regression coefficients. The correlation coefficient was 0.87 with 12 data points.

KEY VARIABLES FOR INTERIM SUMMER REARING MODEL

During the parr summer rearing period, the key habitat variables associated with major mortality problems that are affected by land use actions in the Snake River are high summer temperatures. The quantity of pools and % embeddedness are key habitat variables affecting parr carrying capacity during summer.

OVERWINTERING OF PARR

During winter, salmonid nursery streams are characterized by low winter temperatures accompanied by snow, ice, or severe freshets (Bustard and Narver 1975). As water temperatures decrease to 4°-8°C in the late fall, parr become less active and seek deeper (>45 cm), slower (<15 cm/sec) water where they overwinter in suitable cover or move downstream (Everest and Chapman 1972; Edmundson et al. 1968; Chapman and Bjornn 1969). As water temperatures drop below 5°C, the behavior of juvenile salmonids changes markedly (Hartman 1963; Chapman and Bjornn 1969; Bustard and Narver 1975; Rimmer et al. 1983; Everest et al. 1984; Cunjak 1986; Heifetz et al. 1986). The fish become essentially inactive and take up hiding positions in log cover, rock cover, and in the bottom of deep pools.

Bjornn (1971) found that late fall downstream movement of juvenile steelhead and chinook in the Lemhi River did not occur if adequate overwinter habitat in the form of class 1 and 2 pools and relatively silt free substrate, was locally available. Silt deposits greater than 5% to 30% in gravel-rubble areas tend to impair and eventually prevent the use of the gravel-rubble substrate for escape and winter cover by juvenile chinook. Subyearling trout emigrated from Big Springs Creek which contained no rubble substrate but remained in the Lemhi River which did. In both field and laboratory tests, more fish remained in troughs or stream sections with large rubble substrate than in troughs or sections with gravel substrate. Trout and salmon in Idaho enter the substrate when stream temperatures declined to 4 to 6°C. In the study streams, behavior of salmonids changed from active feeding and territory occupation (or hierarchies) in the summer to "hiding or hibernation" in the winter. Few fish left the study streams during summer but with the onset of fall, requirements of the fish apparently changed and an environment which fish found suitable in the summer became less suitable and they began to leave. Fish emigrated before abundance of drift insects declined in winter. Emigration occurred in spite of the relatively stable flows in both streams. Chinook migrated primarily as subyearlings (70-120 mm) in the fall-winter after their first summer.

The hiding behavior during winter has obvious adaptive value (Bustard and Narver 1975). A fish spending winter in near freezing temperature has a lowered metabolism, reduced food requirements, and less energy available for activity (Reimers 1957). The hiding response is probably a means of avoiding predation during a period

of low, clear water and reduced swimming ability; and reduces downstream displacement during freshets.

Bustard and Narver (1975) listed three major factors contributing to overwinter losses of juvenile chinook, coho, and steelhead in the Morice River: 1) stranding and freezing, 2) low dissolved oxygen, and 3) predation. All three factors were correlated with too low winter flows. An annual base flow >50% of the average annual daily flow is considered excellent for salmonid production, 25-50% is considered fair to good, and <25% is considered poor (adapted from Binns and Eiserman 1979; Wesche 1980).

PARR WINTER ABUNDANCE

The abundance of parr after overwintering can be computed as:

$$WPARR = SPARR * S_{wparr}$$

where: WPARR is the number of parr surviving through the winter; SPARR is the number of parr surviving through the summer; S_{wparr} is the survival rate from SPARR to WPARR as a function of key habitat variables.

PARR WINTER SURVIVAL

The harsh conditions of winter make salmonid survival highly variable and generally a significant production bottleneck (Nickelson et al. 1992a,b; Heifetz et al. 1986; Mason 1976, see Dolloff 1987), even when all other habitat condition factors are optimum. Recent work by Kiefer and Forster (1991), and Chapman et al. (1990) in natal tributaries of the Salmon and Clearwater Rivers has documented an overwinter survival range (parr-to-smolt) of 5 to 31% for juvenile chinook. Heifetz et al. (1986) reviewing several studies on overwinter survival summarized that 6 to 73% of juvenile salmonids present in late summer survive through the winter period. Martin et al. (1984) determined that winter survival of juvenile coho ranged from 17 to 38% in Mount St. Helens streams unaffected by the volcanic eruption and were 0 to 18% in affected streams. Effects of the eruption included loss of channel stability, high suspended sediment, low LWD, and high bed sedimentation. Tripp and Poulin (in press) (as cited by Hicks et al. 1991) reported that overwinter survival of coho salmon was 1.8% in logged streams affected by debris torrents and was 24.5% in logged streams unaffected by torrents. Torrents eliminated LWD from stream reaches and reduced overwintering pool habitat by 75%. Smolt output from unlogged streams that were also unaffected by debris torrents was estimated to be approximately 6 times greater than in logged, untorrented streams.

Key factors responsible for overwinter survival and rearing densities include (1) structure of the stream channel and channel structural elements, (2) water quality (temperature, turbidity, suspended or bedload sediment), and (3) discharge. Physical condition factors which create refuge areas are highly related to overwinter survival.

These are principally the presence of cobble in rearing areas that have low embeddedness; abundant LWD associated with pools and slow-water marginal or side-channel habitats; overhanging banks that may have tree roots extending into the water.

Pools can be found in streams that are devoid of LWD and these may be associated with channel constrictions followed by widening, inflection points in channel bends, tributary entry to a mainstem, and changes in bedrock at geologic contacts. However, pool frequency and quality is positively correlated with occurrence of LWD volume (Tshaplinski and Hartman 1983, Murphy et al. 1984, Heifetz et al. 1986). Murphy et al. (1984) found that coho salmon parr density during winter increased from approximately 0.15 to $0.35/m^2$ as LWD volumes increased from 0.05 to 0.12 m^3/m^2, representing a continuum from clearcut to buffer strip blowdown conditions. Parr that overwinter in stream reaches with more LWD were assumed to produce more smolts than clearcut reaches (Murphy et al. 1986, as cited by Hicks et al. 1991).

Clearcutting of riparian areas or floodplains adjoining a given stream reach or upstream of the stream reach can decrease the volume, average length, and effectiveness of LWD in the reach in creating pools suitable as overwinter habitats (Johnson et al. 1986, Hartman et al. 1987, Hogan 1987, Thedinga et al. 1989, Ralph et al. 1994). Johnson et al. (1986) found that up to 91% of fish emigrated before winter from stream reaches lacking cover due to riparian logging. Age 3+ steelhead were never found in clearcut reaches; 1+ and 2+ age steelhead densities increased dramatically in buffered and old-growth reaches because of the emigration from clearcut reaches.

Water quality can affect the ability of juveniles to inhabit overwinter stream reaches. For example, if riparian vegetation cover is removed from streamsides, the ability of the stream to exchange heat with the atmosphere in cold, inland regions of the Columbia River basin increases. This effect increases if loss of riparian vegetation leads to increased channel width, thereby decreased effectiveness of remaining riparian cover. The decrease in minimum daily water temperatures in winter tends to decrease to higher likelihood of winter icing (Platts 1984, 1991) and subsequent periods of ice scour during periods of breakup. Icing and ice flows can kill juveniles overwintering in interstitial spaces in streambed substrate by physical dislodgement or impact (Platts 1984). In streams subject to ice damage, deep mainstem pools or deep quiescent backwater areas would likely be the most benign environments for overwintering. Availability of stable, unembedded rubble or cobble habitat can also provide security in streams subject to ice flows and high magnitude flows (Bjornn 1971).

Temperature-related overwinter mortality in salmonid parr populations include hypothermia, physical damage from anchor and frazil ice, inadequate lipid reserves and subsequent starvation, and predation (cited in Seelbach 1987; Brett and Alderdice 1958; Reimers 1963; Hartman 1965; Chapman and Bjornn 1969; DeVries 1971; Bustard and Narver 1975; Mason 1976; Everest et al. 1984). Temperatures affect the behavior of fish during winter in ways that contribute to exposure of fish to mortality

factors such as predation, floods, and bioenergetic stress. Chapman and Bjornn (1969)(as cited by Bjornn and Reiser 1991) reported that steelhead and chinook were active in the water column at temperatures above 6°C but were completely hidden in the substrate when temperatures were less than 4°C. Coho were found to feed at temperatures as low as 2.5°C (McMahon and Hartman 1989).

Winter water temperature is highly correlated with air temperature, although this is mediated by management of riparian cover. Seelbach (1987) found that the overwinter survival of juvenile steelhead in Little Manistee River, Michigan was negatively correlated with an index of winter severity (the number of days with minimum air temperatures of -12°C or less during January and February in Cadillac, Michigan. Although there were only three data points, the relation was linear.

% Survival	Index of winter severity
13	42
64	27
90	20

High levels of suspended or bedload sediment can result in increased embeddedness, which reduces interstitial crevice habitat. This habitat is essential for fish at low water temperatures. Elimination of large crevice habitat can reduce the overall capability of a stream to provide overwinter rearing for 1+ or 2+ age juveniles (i.e., those juveniles requiring larger crevices), thereby depressing smolt output. Chapman and Witty (1993) believed that low fish survival was attributable to streambed sedimentation. USFS (1983) developed a curvilinear regression of 0+ age chinook on percentage embeddedness. This relationship encompassed a 0+ age juvenile density of approximately 2.5 individuals/m^2 at 0% embeddedness, 0.4 individuals/m^2 at 50% embeddedness, to near 0 individuals/m^2 at 100% embeddedness. Although Chapman and McLeod (1987) dispute the suitability of the laboratory experiments used to determine this relationship between winter rearing density and embeddedness, they express that there is unquestionably a functional relationship between embeddedness and winter rearing capacity that is greatest at 0% embeddedness and declines to a minimum at 100% embeddedness. These authors suggest that the best available information suggests that overwinter survival decreases with each increment of increase in embeddedness. They suggest that the fate of autumn downstream migrants needs to be determined so that survival of the entire overwintering population can be assessed.

Bjornn (1971) found that the emigration of steelhead and spring chinook from two Idaho streams before winter was primarily influenced by the lack of unembedded cobble substrate. When interstitial spaces were filled by fine sediment, these fish migrated downstream until locating unembedded substrate in which to overwinter. By experimentally adding cobble to the same upstream reaches, Bjornn was able to induce 1+ steelhead to overwinter in place. Hillman et al. (1987) similarly noted up to an 80% emigration of spring chinook from the Red River, Idaho when water temperatures

reached 4-8°C, apparently due to high cobble embeddedness. By adding cobbles under banks and in mid-channel areas, these same reaches were found to have overwinter densities that were 19 times greater than under conditions of high embeddedness. Rate of survival of those fish emigrating in autumn is a subject needing considerable research (Chapman and McLeod 1987). Early emigrants are commonly assumed to represent lost production (i.e., to experience high mortality), although it is also thought that this trait might be a life history characteristic with adaptive value. The generally poorer condition of downstream habitat, though, makes it less certain that this behavior would result in good survival.

Wintertime discharge in most tributaries is not affected by irrigation, so abnormally low baseflows caused by management are typically not of concern unless flow is decreased to refill reservoirs, but peak flows of heightened magnitude resulting from altered snowmelt runoff stemming from patterns of timber harvest can result in lowered survival. High winter or early spring flows can affect juvenile fish that are overwintering or those that just emerged from the gravel and are seeking first feeding. Stocked coho fry in old-growth and clearcut watersheds migrated downstream during periods in which streamflow change of greater than 3%/day occurred, but if change was more rapid they tended to seek shelter (Bilby and Bisson 1987). Coho typically seek shelter when winter water temperatures are low and discharge is high (Taylor 1988). The availability of complex cover was sufficient to prevent emigration of coho from Carnation Creek, British Columbia during periods of winter freshets.

Temperature and flows interact to affect the timing and success of first feeding. Delays in initial feeding because of inappropriate temperature, food availability, or flows can lead to reduced survival (Heming et al. 1982). Jensen et al. (1989) determined the time required for 50% of the populations of three salmonid species to achieve first feeding at temperatures below 8°C. Salmon avoided feeding when water temperatures were less than 8°C and during spring peakflows. Successful strategies were to initiate first feeding either before spring peakflows or after them. First feeding chinook fry do not develop normally at temperatures exceeding 12.8°C (Burrows 1954). It appears reasonable that chinook might have a temperature zone between approximately 8 and 12.8°C in which first feeding must occur. Flows that occur during the period producing these desirable water temperatures must then be appropriate so that fry can exist in the water column. Success depends partially upon the winter water temperature regime governing time of emergence. Emergence timing can be advanced in coastal streams (Scrivener and Andersen 1984) and can be retarded in interior streams, such as in the Snake River basin (Platts 1984), as a result of riparian canopy removal.

In regions where winter temperatures are moderate, overwinter mortality is usually related to the severity of winter flooding (Hartman 1965; Chapman and Bjornn 1969; Seegrist and Gard 1972; Bustard and Narver 1975; Holtby and Hartman 1982). In colder regions, cold temperatures and low flows have been related to overwinter mortality (cited in Seelbach 1987; Needham et al. 1945; Cunjak 1986).

PARR WINTER CARRYING CAPACITY

Parr winter carrying capacity is considered in this model to be a function of pool availability and embeddedness of pool substrate. Pool availability is highly correlated with presence of LWD. Pools and embeddedness do not vary greatly seasonally or from year to year, so they are taken as indices of carrying capacity. Winter survival, then, is related to factors such as temperature, flow, and turbidity, which vary more rapidly. Nonetheless, clear separation of survival and capacity factors is difficult. As mentioned, debris flows can occur catastrophically, rapidly changing the availability of LWD and pools, causing direct fish mortality by flood displacement, resetting capacity and leading to elimination of fish numbers exceeding capacity.

In some streams, the availability of overwinter habitat may be the critical factor limiting smolt production (Chapman 1966; Bustard and Narver 1975; Mason 1976). Everest et al. (1984) found that steelhead concentrated in winter refuge areas and that these were limited to approximately 10% of the total stream area. Winter flow levels define the wetted area, and thus the potential overwinter area of streams. Juvenile salmon occupy different habitats in the winter than in the summer and log jams and rubble provide important winter cover (Bustard and Narver 1975; Hartman 1965; Everest 1969).

The role of LWD in creating large, deep pool habitats, is a key factor in providing high quality winter habitat. In southwestern British Columbia, Tschaplinski and Hartman (1983) reported that the midwinter numbers of juvenile coho salmon in each study reach were linearly correlated with LWD volume (R^2=0.89); coho juveniles were eliminated from clearcut stream sections without stable LWD when late fall/early winter freshets occurred. Murphy et al., (1984) found a similar relationship in Alaskan streams. Dolloff (1987) found that winter production of coho was lowest in areas with low pool volumes and where LWD was ineffective in creating habitat structure. Heifetz et al. (1986) cite several Alaskan studies emphasizing the importance of maintaining high quality overwintering habitat created by LWD for salmonids that spend one or more years in freshwater. Multiple year freshwater rearing periods are common for salmon in the Snake River Basin.

Based on laboratory and field studies, Chapman and McLeod (1987) inferred that minimum embeddedness or maximum crevice availability should provide the greatest overwintering capacity although they felt that no threshold value can be set for embeddedness as it affects overwintering. In laboratory stream studies, Bjornn et al. (1977) evaluated different levels of embeddedness on carrying capacity. Juvenile salmonids were placed in the laboratory streams in excess of estimated carrying capacity. Winter carrying capacity of pools for age 0 chinook, age 0 steelhead, age 0, 1 and 2 cutthroat trout was related to percent embeddedness by using regression equation of the following form (Bjornn et al. 1977; Stowell et al. 1983).

K_{wparr} = A*exp(-B*EMBED)

where: K_{wparr} is the winter carrying capacity in numbers of fish/m^2 of pools; EMBED is the % embeddedness of the pools; A and B are regression coefficients.

KEY VARIABLES FOR INTERIM WINTER HIDING MODEL

During the winter rearing and hiding phase, the key habitat variables associated with major mortality problems that are influenced by land use actions in the Snake River are low winter temperatures in conjunction with low winter flows (Figure 9). Measure winter water temperature during periods of low winter flows. Peak flows during winter or early spring causing flooding can be a major mortality factor. The quantity of pools and % embeddedness are key habitat variables that affect carrying capacity during the winter phase.

OUTMIGRATION OF SMOLTS

After overwintering, Snake River spring and summer chinook parr begin to develop into smolts as they outmigrate in the spring and are observed at Lower Granite Dam in April through June (Matthews and Waples 1991). The number of smolts produced by a stream is limited by the stream's summer productivity (Phillips 1971) and overwintering capacity. In streams that reach carrying capacity, smolt yield tends to be fairly constant, with the variation in eggs laid and fry emergence moderated by density-dependent fry mortality (Au 1972). Depending of the stream and species, however, the smolt production may be highly variable.

OUTMIGRANT SMOLT ABUNDANCE

The number of smolts that outmigrate out of a Snake River tributary can be computed as:

$$SMOLTS = WPARR * S_{smolt}$$

where: SMOLTS is the number of smolts outmigrating from the Snake River; WPARR is the number of parr that survive over the winter to outmigrate; S_{smolt} is the survival rate from WPARR to SMOLTS as a function of key habitat variables during outmigration.

SMOLT OUTMIGRATION SURVIVAL

Little is known about the causes of mortality of smolts outmigrating from the Snake River system before they reach Lower Granite dam. Survival of wild chinook salmon from the Salmon River traps near Riggins and Whitebird to Ice Harbor Dam ranged from 85% - 95% for 1966-1968 before construction of Lower Monumental, Little Goose, and Lower Granite dams (Chapman and Witty 1993). After completion of Lower Monumental and Little Goose dams, survival in the early 1970s averaged 33% (Raymond 1979). Fifty to 60% of 18 - 23 million chinook and steelhead hatchery smolts released in 1990-1992 did not reach Lower Granite Dam (Chapman and Witty 1993).

Stream temperature

Suitable water temperature is needed to allow and maintain smoltification (Zaugg et al. 1972) during juvenile migration out of the system. Parr-smolt transformation may not occur or persist above 12°C. Steelhead need to be exposed to cooler temperatures of 6-10°C for 1-2 months prior to migration in order to allow parr-smolt transformation. Using this information, we can relate smolt mortality to the stream temperatures during outmigration (Figure 10).

$$S_{smolt} = 1.0 \qquad\qquad\qquad TP <= TP_{crit}$$
$$S_{smolt} = (TP-TP_{crit})/(TP_{crit}-TP_{zero}) \quad TP_{crit} < TP < TP_{zero}$$
$$S_{smolt} = 0.0 \qquad\qquad\qquad TP_{zero} <= TP$$

where: S_{smolt} is the smolt survival rate during outmigration; TP is the stream temperature during outmigration; TP_{crit} (8.0°C) is the critical temperature below which S_{smolt} is one; TP_{zero} (12.0°C) is the temperature above which S_{smolt} is zero.

KEY VARIABLES FOR INTERIM SMOLT OUTMIGRATION MODEL

Although mortality during the smolt outmigration period from the Snake River can be high, little is known of the factors that cause high mortalities. In the interim, we will use high temperatures during the smolt outmigration phase because it is related to parr-smolt transformation.

DISCUSSION

MODEL LIMITATIONS

Creation of a model of the impact of habitat conditions on fish survival that could be applied at a watershed scale is complicated by (1) cumulative effects in space and time for any individual habitat parameter (e.g., fine sediment increase), and (2) cumulative effects (additive effects and interactions of variables, leading to synergisms, multiplicative effects, compensatory mechanisms) of combinations of two or more parameters. Because there are numerous variables controlling survival at all life stages and many of the mechanisms for variable interaction are not well understood, it is not possible to accurately predict cumulative mortality from all combined sources over the course of freshwater development of any fish species. Even though in some instances there may be compensating mechanisms that resist alteration in fish carrying capacity or survival when certain habitat conditions are affected by management (e.g., availability of deep pools, overhanging banks, large woody debris, and unembedded cobble substrates may all provide juvenile overwintering habitat and a reduction in one may be compensated by an increase in another), for management purposes it would be risky to assume that deliberate alterations to natural conditions will not have adverse consequences.

In some cases, certain parameters have not been intensively examined in the field; also, some of these parameters have not received geographically widespread analysis or the mechanisms for variation are not understood (e.g., percentage egg retention), making their application one of introducing a constant survival coefficient or a coefficient based on limited sampling.

This model is also not appropriate for attempting to apportion blame for fish mortality among various watershed-wide alterations in habitat conditions (i.e., mortality due to temperature vs. sediment vs. other factors). The cumulative effects involved imply that all sources of habitat damage contribute to overall mortality. Current limitations in land use models and spatial/temporal variability in natural processes and anthropogenic actions, lag times in impact and recovery, likewise, make it difficult to use these models to apportion blame among land use actions in creating existing habitat conditions.

NEED FOR QUANTITATIVE DATA

Much of ecology began as a purely descriptive activity. It consisted primarily of making qualitative observations and then devising plausible explanations for the observations. Because alternative explanations of the observed phenomena frequently are available, the process by which the conclusions have been reached is known as "weak inference" (Platt 1964). It is not that the conclusions are necessarily wrong; the problem is that there is little assurance that they are right. The biological significance, if indeed there is any, of the results from purely observational studies, remains obscure (Hairston 1989). Although these observations are necessary for the identification of ecological problems and the construction of hypotheses, they should not be claimed to justify conclusions until the hypotheses have been put to scientifically satisfactory tests.

The process of formulating clear hypotheses and devising acceptable experiments, called "strong inference," was clearly described and vigorously promoted three decades ago (Platt 1964). Experiments are conducted for the purpose of answering specific questions about nature. These questions ordinarily are stated as hypotheses, which are statements about how someone thinks nature works. In other words, they contain implied predictions, and confirmation of those predictions is the most powerful means available to demonstrate the accuracy of our understanding of the world around us.

In general, many of the data available in fish-habitat relations were not the result of strong inference. A relatively few laboratory experiments, where the levels of the habitat variables and other conditions were controlled, provide some data to help quantify the cause and effect relations of habitat variables at least under experimental conditions. In contrast, most field data were derived from observational studies which lack proper controls (Hurlbert 1984; Hairston 1989). In these studies, the effects of habitat variables are usually confounded and the habitat variables themselves are loosely defined because their natural and man-influenced variability in space and time were not taken into account.

An important aspect of a model is the translation of verbally stated mechanisms into a mathematical form. Mathematics provides models with a clear and precise language for describing, examining, and manipulating ecological systems. This present work represents our attempt to provide a framework to quantify the cause and effect relations between habitat variables and fish survival.

COMBINED EFFECTS OF HABITAT VARIABLES

Virtually all of the data available lends itself only to developing single-factor models. Thus, the previous relations developed between key habitat variables and salmon survival are single factor models. They only look at the effect of each habitat variable and ignore the effects of the other variables. This is an important step to help us understand how habitat conditions affect salmon survival. However, in reality,

salmon survival is a function of the combined effects of all relevant habitat variables affecting salmon survival. Thus, ultimately, it is necessary to elucidate the interactions or combined effects of habitat variables on salmon survival. It is the interactions between variables and not the action of any single variable that determines salmon survival. Thus, the role, relevance, and importance of a variable can only be assessed properly in relation to the whole system of which it is a part (Cuenco 1982). It is in this area that data are usually absent and models fail to simulate known interactions. This would require a deeper understanding of the mechanisms that determine salmon survival and is an important subject for future research. Limiting factors (e.g., food, oxygen) can be combined by using the minimum function (Cuenco 1989). Cumulative factors (e.g., invertebrate drift, benthic invertebrates) can be combined simply by adding them together. Compensatory factors can be combined by computing their average effect. Control factors (e.g., body weight, water temperature) can be combined by multiplying their effects. This process of combining the factors is continued until all the components of the model have been included.

As an example of a mechanistic multi-factor model, we can look at the mechanism which determines IGDO in the salmon redd, i.e., the supply and consumption of dissolved oxygen. The consumption of oxygen in the redd consists of the respiration of the eggs or alevins and the aerobic decomposition of organic matter within the redd. Organic matter decomposition is a function of temperature and the carbon to nitrogen ratio of the organic matter.

Organic matter decomposition = f(temperature, C:N ratio)

The salmon egg or alevin respiration is a function of temperature and stage of development.

Salmon respiration = f(temperature, stage of development)

The supply of oxygen to a redd depends on the dissolved oxygen concentration of the stream water just before it enters the gravel and the rate at which this water flows through the gravel (Pollard 1955).

$DO_{supply} = V_{app} * DO_{sb}$

where: DO_{supply} is the rate of oxygen supply in grams per hour per square cm of redd; DO_{sb} is the concentration of dissolved oxygen in mg/l of the stream water just before it seeps into the gravel. Measure near the stream bottom just upstream of the redd. V_{app} is the apparent velocity in cm/hr of the ground water.

The apparent velocity is a function of the gravel permeability and the hydraulic gradient.

$V_{app} = K * S$

where: V_{app} is the apparent velocity in cm per hour; K is the gravel permeability in cm per hour; S is the hydraulic gradient.

The gravel permeability is a function of the % fine sediment within the gravel which acts to restrict intragravel flow.

K = 1/FS

where: K is the gravel permeability in cm per hour; FS is the % fine sediment in the gravel.

NATURAL HABITAT VARIABILITY

The preliminary models developed in this project were based primarily on fixed levels of the habitat variables under controlled laboratory conditions. Laboratory experimentation gives the most convincing results, because all the variables are under the control of the investigator. One of the variables is manipulated in a systematic way in order to answer a specific question while holding other variables constant. Laboratory experiments should, in principle, be repeatable - a hallmark of a convincing scientific test. However, an unsettling question with laboratory experiments is their applicability in nature.

Under field conditions, it is not possible to exercise control over most variables. Usually, the variable of interest is manipulated in a predetermined way, and the remaining variables fluctuate independent of the experiment. Occasionally, more than one variable can be manipulated, but the number is severely limited. The questions asked in field experiments tend to be less precise than those asked in the laboratory. It is assumed that the naturally varying factors affect all experimental treatments equally, or at least randomly. The assumption introduces an element of uncertainty into the interpretation of the outcome and reduces the assurance of being able to repeat the result. In reality, streams are highly complex and dynamic in nature. They are not well enough understood to be treated as wholly deterministic. Diel, seasonal, and annual variations in habitat variables characterize the system. Fluctuations in water temperature, dissolved oxygen, and pH are basically sinusoidal whereas other factors are more difficult to characterize. The large array of substrates make one kind of challenge and the huge variations in rates of flow constitute irregular disturbances that may easily destroy replicates and controls in the best planned experiment.

Experiments carried out in the field provide the assurance that results are applicable in the real world from which was derived the hypotheses that were tested (Hairston 1989). The price to be paid for the realism is that normally rather simple experimental designs must be followed, because the variability of most factors requires a number of replicates and for motile animals the size of experimental units must be large enough to ensure a relatively small proportion of emigration and immigration.

Experiments that are designed to detect several ecological phenomena and their interactions require low variances among replicates and control by the experimenter over the sources of such variance. That nearly always means that the experiments must be carried out in the laboratory. The disadvantages of laboratory experiments involve the simple environments that must be used and the limited kinds of species that can be carried through completion of the experiment. Both of these features greatly reduce the realism of the study.

Thus, developing our ability to predict salmon survival under natural stream conditions would require a combination and integration of laboratory and field experiments. There is a need to link laboratory results under fixed levels with field results under fluctuating levels in such a way that survival could be inferred. The problem is basically one of characterizing fluctuating levels to their equivalent constant levels resulting in the same survival rate. This would open up the majority of survival experiments, which were and are conducted in the laboratory, for application in the field. Experiments in this critical area are essentially non-existent.

The following provide a brief overview of what we know about natural habitat variability. Most of the information apply during winter incubation of eggs and alevins.

Intragravel Temperature

Seasonal variability. The incubation period in the natural redd begins sometime in the fall during a period of decreasing temperatures and reaches the lowest temperatures in the winter. During the latter part of incubation, the alevins are exposed to increasing temperatures in the spring before they emerge from the redd. This seasonal temperature fluctuation is minimal varying by 1 - 3°C from November through March (Hall and Lantz 1969; Shepherd et al. 1986; Beschta et al. 1987). Chinook incubation times at ambient water temperatures were determined (Alderdice and Velsen 1972).

Diel variability. Diel temperatures in the natural redd during the incubation season are also minimal, varying by 1 - 2°C (Hall and Lantz 1969; Shepherd et al. 1986; Beschta et al. 1987). Thus, overall, fairly constant temperatures occur during the natural incubation period in salmon redds in undisturbed habitats. This is fortunate because laboratory studies using constant temperatures will more easily apply to natural temperature conditions. However, deforestation and other land disturbing activities can greatly increase both seasonal and diel temperature fluctuations during the natural incubation period resulting in higher high temperatures and lower low temperatures (Hall and Lantz 1969).

Intragravel Dissolved Oxygen

Spatial variability. Intragravel dissolved oxygen is generally lower in the gravel compared to the dissolved oxygen in the stream (Maret et al. 1993).

Seasonal variability. Significantly greater seasonal fluctuation occurs in logged watersheds (Hall and Lantz 1969).

Diel variability. Intragravel dissolved oxygen ranges from 1-3 mg/l during incubation in unlogged streams ranges from 1-2 mg/l during incubation in unlogged streams (Hall and Lantz 1969). Significantly greater diel fluctuation occurs in logged watersheds (Hall and Lantz 1969).

Percent Fine Sediment

Spatial variability. Fine sediment should be measured at egg pockets since there is substantial stratification in stream gravels above or below the level of egg deposition (Chapman 1988). Also, because the salmon cleans the gravel in the egg pocket, there could be substantial difference in fine sediment between the egg pocket and elsewhere in the redd (Chapman 1988).

Seasonal variability. If prediction of S_{fry} is desired, all samples should be collected from redds just prior to onset of emergence due to seasonal variation in % fine sediment (Adams and Beschta 1980). Because of sediment intrusion, the % fine sediment in the redd is expected to increase as incubation proceeds.

Diel variability. Little or no diel variability is observed in the level of fine sediment.

Apparent Velocity

Except for a few field studies of intragravel water (Pollard 1955; Coble 1961; Phillips and Campbell 1962), we do not know much about the spatial and temporal variability in apparent velocity.

FLUCTUATING REARING TEMPERATURES

Effects of temperature on summer-rearing fish under natural conditions must be assessed by accounting for cyclic temperature fluctuations and the exposure time to critical maximum temperatures. Temperature effects on coldwater fish species can be described in terms of effects on growth, distribution, and survival. For purposes of modeling fish survival in terms of principal environmental (habitat) conditions, studies on survival under various constant temperature exposure tests might appear to be most relevant. However, the difficulty of fully representing field conditions in laboratory experiments and the ability of fish in the field to behaviorally regulate their body temperature by seeking cooler waters under high ambient temperature conditions make it necessary to evaluate evidence for temperature effects on other aspects of the juvenile summer rearing period.

Effects on Growth

Hokanson et al. (1977) studied growth and survival of rainbow trout, *Oncorhynchus mykiss*, juveniles reared on maximum rations at fluctuating temperatures with a mean of T°C ± 3.8°C vs. that at constant temperatures. The physiological optimum (PO) temperature of rainbow trout is 16-18°C. These authors noted that specific growth rate at mean temperatures less than PO is lower for a given mean temperature under constant (T°C) vs. fluctuating temperature regime (T°C ± 3.8°C). In this temperature zone, a constant temperature of T+1.5°C provided comparable specific growth rate to juveniles reared at T°C ± 3.8°C. However, specific growth rate at mean temperatures greater than PO was higher under a given mean temperature at constant vs. fluctuating temperature regime.

Hokanson et al. (1977) found that rainbow trout specific growth rate at a fluctuating temperature of 22 ± 3.8°C was zero. Population production involves a balance between mean individual growth and mortality rate of the population. Hokanson et al. (1977) determined that a rainbow trout population would exhibit zero increase over a 40-d period (maintenance) at a constant temperature of 23°C and a fluctuating temperature with a mean of 21°C ± 3.8°C because growth balances mortality. With this laboratory information on constant and fluctuating temperatures and corroborating field information, Hokanson et al. (1977) recommend a mean weekly temperature of 17 ± 2°C for rainbow trout so that maximum yield is not reduced more than 27% when trout are subjected to normal fluctuating temperature regimes.

There appears to be considerable controversy regarding the effect of fluctuating temperatures vs. constant temperatures on juvenile growth rate. Thomas et al. (1986) measured growth of juvenile coho for 40-d periods under constant 11°C temperature vs. diel temperature cycles of 10-13, 9-15, 8-17, and 6.5-20°C, all of which averaged 11°C. They found that the growth rates of 0+ age fish at any of the food rations were not significantly different among temperature regimes, although the growth at 4 and 8% ration (i.e., 8% of body weight/day) was better than at 1%.

We have identified an optimal growth zone for spring chinook between 10.0-15.6°C and the zone of positive growth between 4.5-19.1°C under unlimiting food availability. If food becomes limiting, the positive growth zone can shrink dramatically (i.e., the maximum temperature at which growth is still positive declines) and the optimum growth zone will shift to lower temperatures to compensate for elevated respiration/growth ratios (Elliott 1981, p. 231). Elliott found for brown trout that the temperature at which growth is zero drops from 19 to 8°C when food rations are reduced from maximum to 12.5% of maximum.

If we assume that food availability is unlimited in a spring chinook-bearing stream so that 19°C would represent the temperature at which growth declines to zero, analysis of the suitability of a stream reach in terms of long-term growth potential would

consist of assessing what percentage of the time growth is zero or negative. If temperature cycles from 18-23°C for a one-week period according to a sine wave pattern, the mean temperature is 20.5°C and the 70% of the day is spent at temperatures above 19°C. If the diel fluctuation was from 16 to 23°C with a mean temperature of 19.5°C, 55% of the day would be spent at temperatures above 19°C. Maximum temperatures are frequently achieved by 4pm. It is very likely that temperatures that could allow for positive growth would occur essentially during darkness when feeding is minimal. If feeding is suppressed at high temperatures, growth may be negative even during darkness when temperature descends to temperatures below 19°C. Darkness could be a period of some growth without concurrent feeding provided that gut filling can occur during daylight hours. More studies of net daily growth would be useful under fluctuating temperature regimes extending above 19°C to assess effects of photoperiod in combination with temperature cycles.

Effects on distribution

Juvenile chinook salmon and steelhead were found to have high densities and normal growth in an Idaho stream that fluctuated from a minimum of approximately 8-12°C to 24°C (Bjornn 1978, as cited by Bjornn and Reiser 1991). For several larger Idaho stream reaches having temperatures fluctuating from minima of 15-16°C to maxima of 24-26°C, most juvenile salmon and trout migrated upstream or into cooler tributaries (Mabbott 1982, as cited by Bjornn and Reiser 1991).

Hahn (1977) (as cited by Bjornn and Reiser 1991) found that fish density in laboratory streams held at a constant temperature of 8.5°C was double that of channels at 13.5°C, which was, in turn, double that for a channel at 18.5°C. When a fluctuating temperature regime (8-19°C) was provided, twice as many fish remained in the channel than were found at a constant 18.5°C.

Dimick and Merryfield (1945) state that no salmonids were observed in reaches of the Willamette River where water temperatures exceeded 22.8°C. Li et al. (1992) found that steelhead biomass declined steadily from 18g/m^2 to 0g/m^2 as maximum temperatures increased from 16 to 28°C. In a study of spring chinook distribution in the John Day River, Oregon, a 2-week period prior to sampling in which mean maximum water temperatures were ≥19.4°C resulted in total absence of juveniles on the Middle Fork. On the North Fork, no juveniles were found in reaches where temperatures exceeded 22.8°C. Theurer et al. (1985) estimated that spring chinook production on the Tucannon River, Washington would be zero for all stream reaches having average maximum daily July water temperature greater than 23.9°C. Based on actual field observations of Bugert et al. (1992) on the Tucannon River, no juvenile spring chinook were observed in the July-August, 1990 period in the lower 25 miles of the river. Although water temperature data are not available for 1990, August water temperature

data indicate that daily maxima as high as 27.2°C were observed. The mean daily temperature for the month was 22.2°C and the mean maximum temperature was 25°C.

Data on salmonid distribution relative to temperature gradients in stream systems are useful for inferring integrated effects of natural temperature regimes. There are, however, some difficulties in interpreting such data. Distribution of rearing juvenile salmonids in relation to temperature regimes can be a reflection of a variety of interacting factors. For example, it appears that water temperatures having a maximum of 23°C constitute the upper limit to distribution of a wide array of salmonid species, including chinook. It may be that juveniles rearing in downstream reaches during the summer are unable to escape high diel temperature peaks by taking refuge in coldwater seeps or pockets in deep pools. These fish that cannot escape high temperatures may acquire a lethal temperature dose. If no instream physical migration barriers exist (e.g., falls, high gradient reaches), juveniles may be able to migrate upstream as seasonal mean temperatures increase. Using the temperature-fish biomass regression developed by Li et al. (1992) for the John Day River as a basic concept, one might assume that fish densities may increase from, for example, a reach that attained a maximum of 23°C in an upstream direction to a reach that attained 12°C as a maximum. A temperature of 11.7°C has been identified as the spring chinook final temperature preferendum (Hokanson and Beiningen, unpub. report, as cited in Armour 1991) or the temperature zone that they would finally select regardless of acclimation history (Armour 1990). Or possibly spring chinook biomass might reach a maximum in reaches having a maximum temperature of 14.8°C, the growth optimum (Brett et al. 1982, as cited by Armour 1991). Low biomass or densities in the temperature range 18-23°C, for example, might be caused by a variety of factors. In this zone, food might be limiting because the invertebrate food base shifts to less accessible food items (see Li et al. 1994). Lower biomass or density can also be caused simply by a preference for temperatures nearer to 11.7°C, which occur upstream. Increases in disease in downstream reaches caused by temperatures greater than 15°C might cause higher mortality in these stream zones and cumulative thermal stress could lead to direct mortality. Overall habitat degradation, which normally increases in a downstream direction, could accentuate the effect of temperature because sedimented substrate has less food producing capacity, leading to increased metabolic stress (Elliott 1981). In addition, increasingly severe competition from warmwater tolerant species such as redside shiner (see Reeves et al. 1991) could cause upstream displacement of salmonids. Variation in strength of such competition might be the cause of the variation in downstream distribution of chinook juveniles in the North Fork vs. Middle Fork John Day River found by Lindsay et al. (1986).

Given the potential range of factors linked to temperature regimes that are probably all partially responsible for the decline in biomass and abundance of chinook with increasing temperature, it is not clear how to quantify survival at temperatures less than 23°C. However, the fact that a maximum temperature of 23°C under natural fluctuating temperature regimes is sufficiently high to cause ecological elimination of juvenile chinook from stream reaches implies that one need not require calculation of

survival from exposure to temperatures in the range 23-29°C to justify altering land management to reduce temperatures far below 23°C. If escapement is far below carrying capacity, increased temperatures downstream might not cause density dependent mortality provided that juveniles have the ability to migrate upstream to avoid both diel temperature peaks and increasing seasonal temperatures. In the case of very low escapement, crowding of juveniles into upstream coldwater reaches may not cause densities to exceed carrying capacity. On the other hand, it seems unlikely that all fish can migrate to zones with temperatures conveying high survival. For sake of modeling simplicity, we will apply known temperature-disease relationships for all temperatures above 15°C, assume zero chinook density at temperatures above 23°C, zero individual growth rate above 19°C, and we will estimate cumulative thermal loads for exposures to temperature greater than 23°C.

Effects on survival

Temperature tolerance of fish is evaluated either as an incipient lethal temperature by acclimating the fish to one temperature and then subjecting them instantaneously to another temperature (e.g., see Fry et al. (1946), Hart (1952), and Brett (1952)) or by evaluating the critical thermal maximum (CTM)(see Becker and Genoway 1979), whereby fish acclimated to one temperature are subjected to uniform rates of temperature change until loss of equilibrium occurs. CTM is calculated as the arithmetic mean of the temperatures at which individual test fish lose equilibrium (LE) or die (D) given a prescribed rate of heating from an acclimation temperature that allows deep body temperature to track environmental temperature without significant time lag. Becker and Genoway (1979) recommend the use of a temperature increase rate of 18°C/h. They subjected coho (*O. kisutch*) to acclimation temperature of 15°C for 2 weeks and then a rate of heating of 18°C/h. The LE-temperature was 28.70°C and the D-temperature was 29.72°C. This is greater than the value of 26.0°C incipient lethal temperature (ILT) recorded by Brett (1952) for this species with 20°C acclimation. However, the ILT method assesses the temperature needed to produce 50% mortality in 1000 min (Bjornn and Reiser 1991). The CTM method is the arithmetic mean of the temperature at LE or D.

Although Becker and Genoway (1979) recommend use of a temperature increase rate of 18°C/h, other heating rates have been used by other researchers. The mean D-temperature expressed for a 15°C acclimation temperature varies with rate of temperature increase. Becker and Genoway (1979) found that by lowering the heating rate to 1°C/h (about half the rate that occurred during the diel cycle in the Thomas et al. (1986) experiment), the D-temperature was 27.6°C; at a high heating rate (60°C/h) the D-temperature increased to 31.1°C. The mean time to death at heating rates of 18 and 60°C/h were 0.82 h and 0.27 h, respectively.

The CTM method for assessing thermal tolerance tests exposure to increasing temperatures. The alternate means for determining tolerance is by use of the incipient

lethal temperature (ILT) method whereby acclimated fish are immediately transferred to test temperatures to determine median survival rates after 24 h exposure or median time to death. When applying the coefficients (*a* and *b*) derived from the ILT method by Brett (1952), as summarized by Armour (1990), to spring chinook acclimated at 15°C and subjected to exposure in 29.72°C water (i.e., the coho D-temperature for 15°C acclimation and heating rate of 18°C/h), one calculates a median survival time of 0.05 h using the formula (no.8) in Armour (1990). Although test fish are different among the ILT and CTM experiments, it appears that survival time is reduced the faster that heating occurs.

Becker and Genoway (1979) note that Fry (1967) and Hutchinson (1976) considered the ILT method more physiologically meaningful than the CTM method. However, the CTM method provides more rapid analysis and requires fewer test organisms. Because death results from the combination of water temperature and exposure time of fish to the temperature, a high rate of heating results in death occurring at a higher temperature than when the heating rate is lower. That is, at a rapid heating rate, a fixed exposure time of, for example, 5 minutes elapses at a point where water temperature reaches a high level; at a lower heating rate, temperature is not as high after the fixed time period. Because of this relationship between temperature and exposure, the CTM D-temperature may not accurately reflect ecological responses in the field. Rates of heating similar to those occurring in the field can be simulated in CTM tests, such as the maximum rate of increase of 2.25°C/h used by Thomas et al. (1986).

The CTM test evaluates the response to the continuing rate of increase more than it does to a prolonged exposure. The ILT method assesses response to a prolonged exposure after transfer from acclimation temperature to test temperature. During the transfer, fish are subjected to a rapid temperature increase, and then a test of their survival to exposure. The ILT method provides data on survival time under constant temperature exposures. Because temperatures in the field fluctuate daily from minimum to maximum, roughly according to a sine wave pattern, fish under these conditions are exposed to increasing temperatures and decreasing temperatures, cumulative exposure to temperatures in the incipient lethal range, and repeated exposures from day to day. Because of the complex nature of the exposure in the field, aspects of both the CTM and ILT methods are relevant to predicting effect on fish in the field. The CTM test provides data on effect of rate of temperature increase; the ILT method provides data on temperature-exposure relationships. Potential effects that are overlooked in these simplistic laboratory tests involve identifying the effective acclimation temperature for fish subjected to a fluctuating regime; the effect of a fixed rate of temperature increase up to a maximum temperature within the incipient lethal range, and the effect of repeated exposure to this fluctuating regime.

Based on laboratory studies on juvenile coho, blackside dace, and sculpin, DeHart (1975) showed that predicted times to 100% mortality from fractions of lethal

doses, calculated from constant temperature ILT studies, accumulated over a 2-day period of cyclic temperature fluctuation are very similar to observed mortality rates. Assuming that this response to cumulative thermal load may hold true for 2- or 3-day periods for chinook, one can take the warmest 2- or 3-day period, apply the a and b coefficients for the temperature-dose relationship developed by Blahm and McConnell (1970)(as cited by Coutant 1972b) from their tests on Columbia River spring chinook acclimated at 20°C for computing time to 10, 50, and 90% population mortality. Their *a* and *b* coefficients for 50% survival are 21.3981 and -0.7253, respectively, very similar to values provided by Armour (1990). Armour (1990) provides an equation from Coutant (1972b) describing the expected survival time for 50% of a population at various exposure levels given acclimation temperature. This equation is of the form log (minutes survival) = *a* + *b*(exposure temperature, °C). Using coefficients from Blahm and McConnell one can calculate times to 10, 50, and 90% mortality of 24.9, 30.7, and 39.0 h at 25°C, respectively. From these data one might assume that 39.0 h represents very nearly the time required for 100% mortality. Times to 90% mortality at 24, 25, 26, and 27°C are 196.6, 39.0, 7.74, and 1.5 h, respectively (Fig. 15). Assuming that temperature cycles between minimum and maximum conform to a sine wave pattern, the exposure times of fish experiencing temperatures above 23°C can be calculated for each 1°C increment and converted to percentage of a lethal dose. If one can estimate from constant temperature laboratory experiments that a lethal dose can be accumulated in a 2- or 3-day period in a fluctuating temperature regime, one can hypothesize that this is sufficient to eliminate fish from the reach.

Integration of the thermal load during a temperature cycle in the field using the techniques described above involves application of tests at constant temperature of population survival. The time to death at various temperatures above 23°C given above were derived from constant temperature experiments after acclimation to 20°C. Under fluctuating temperature regime it is uncertain what temperature constitutes the effective acclimation temperature when assessing the effects of high temperatures. Cutthroat trout juveniles rearing in fluctuating temperature environments can achieve acclimation equivalent to that at 0.75 x (max.-min.) above the daily minimum temperature (Golden and Schreck 1978), although Heath (1963)(as cited by Elliott 1981) reported that cutthroat trout (*Salmo clarki*) appeared to acclimate to the maximum temperature rather than mean for temperatures cycled between 10 and 20°C. If field temperatures are fluctuating between 18 and 27°C for several days, for example, it appears likely that the effective acclimation temperature would be greater than 20°C. However, even if this acclimation temperature is 24°C, one can expect no more than a 1.5°C increase in the ILT (i.e., the UILT is 26.4°C for spring chinook when the acclimation temperature is 24°C).

Thermal stress can act in a cumulative manner between the feeding limit (temperature at which feeding ceases, which is slightly beyond the chinook growth limit of 19.1°C) and the UILT (Elliott 1981). Within this zone the combined effects of limiting stresses such as food limitation, low oxygen concentration, high turbidity, and competition for space plus loading stress of temperature result in mortalities (Elliott

1981, p. 233)(see Fig. 4 for brown trout, Elliott 1981). In addition, the more that temperatures exceed 15°C, the higher the risk of disease mortalities and the greater the loading stress. This zone is the so-called tolerance zone, identified by Elliott as the area of the exposure/acclimation temperature graph (Fig. 4) bounded by the UILT for 7-day exposure.

Hokanson et al. (1977) reported that, at a fluctuating temperature of 22 $\pm$ 3.8°C, mortality rate of juvenile rainbow trout was 42.8%/day during the first 7 days. For experiments within the optimum range, average specific mortality was 0.36%/day. Formulas are available for calculating long-term temperature exposure indices such as Maximum Weekly Average Temperature (MWAT) for protection of fish populations. Hokanson et al. (1977) advise caution in application of short-term exposure experiments to calculations of acceptable long-term exposures. Given a physiological optimum of 16-18°C and an upper incipient lethal temperature of 25.6°C (at 16°C acclimation), one would calculate an MWAT of 19°C and a maximum temperature (applying the 2°C safety factor of Coutant 1972a) of 24°C for short-term exposure. So that population production (i.e., accounting for growth and mortality) is not reduced by more than 27% from maximum, they recommend a mean weekly temperature of 17 $\pm$ 2°C for rainbow trout to allow no more than a 27% reduction from maximum yield in fluctuating temperature regimes.

Thomas et al. (1986) studied the effects of fluctuating temperature regimes on juvenile (0+ and 2+ age) coho salmon survival after acclimation to either a constant 11°C or fluctuating 10-13°C regime. A sequence of fluctuating regimes were created in the experiments by progressively increasing maximum temperatures by 2°C and lowering minimum temperatures by 1°C every 2 days. For fish acclimated to a constant temperature regime of 11°C and transferred to the fluctuating series, survival was 50% for both age groups under a 4-24°C regime. When these age groups were acclimated to the 10-13°C regime and transferred to the fluctuating series, 50% of 0+ age fish died when the regime reached a 3-28°C cycle; for 2+ age fish 50% died when the regime reached 4-28°C. Survival was 100% under a 5-23°C regime and was 0% under a 2-29°C regime. In these experiments approximately 95% of the fish that died did so within 24 h of reaching the maximum temperature. However, the manner in which these experiments were conducted subjected fish to a thermal regime that was nearly as high as the one resulting in mortalities during the previous 2-day period. That is, if 95% died within 24 h of exposure to a 4-28°C regime, they had previously been exposed to a 5-26°C regime for 2 days, a 6-24°C regime prior to that, etc. It has been documented that juvenile mortality can result from accumulation of a full lethal temperature dose by cumulative exposure over a 2-day period under fluctuating temperature regimes (DeHart 1974).

In experiments as conducted by Thomas et al. (1986), juvenile salmon were subjected to diel temperature regimes fluctuating to a maximum of 2-29°C. Under these conditions the temperature increased by 27°C over a 12-h period. This is an

increase of 2.25°C/h. It is often assumed that increased amplitude of temperature fluctuation that accompanies canopy removal along streams can have undesirable biological effects. Based on short-term studies in which juvenile chinook are subjected to rapid temperature increases or thermal shock of up to 20°C, few negative effects have been documented (Becker 1973). However, long-term effects may be important. Studies such as that of Thomas et al. (1986) suggest that it is the cumulative exposure to incipient lethal temperatures rather than the rate of temperature increase that is most important.

Effect on Production

Cyclic temperature fluctuations in a stream system occur within each stream reach on a seasonal and a diel basis. Maximum daily and maximum mean monthly temperatures are reached generally during July and August. Mean and maximum daily temperatures also increase progressively in a downstream direction on a river continuum (Vannote et al. 1980). For any given reach, maximum daily temperatures achieved have the potential to become elevated when upstream riparian canopy cover is removed from the stream or when the channel width becomes greater from a process of streambank destabilization and/or streambed aggradation, allowing more solar radiation to reach the stream. The magnitude of the effect is correlated with mean stream depth or wetted channel volume in upstream reaches. The spatial distribution of interactive stream reaches, connected in series according to an overall downstream thermal gradient, creates a complex environmental template upon which fish production is determined. Estimating average (and annual variation in) late spring, summer, and fall fish production potential on a watershed basis from a temperature regime standpoint would involve a variety of steps: assessment of the average thermal regime for all reaches based upon water temperature records; the probability of daily temperature maxima exceeding critical levels under average and extreme conditions based upon correlation of maximum air temperatures with water temperatures and inferring frequency of water temperature maxima from air temperature frequency distributions; probability of exceeding temperatures greater than 20°C and 23°C (in 1°C increments) and daily duration of exposure to temperatures in this range; assessment of potential of juvenile salmonids to migrate up or downstream to seek their temperature preferences; determination of the upstream swimming rate from various locations on the mainstem in relation to rate of temperature increase (daily cycle; weekly trend in maximum temperatures) into incipient lethal zones; distribution and size of thermal refuges within the mainstem; estimation of the carrying capacity for the entire rearing period in terms of thermal criteria.

The carrying capacity of a stream for a salmonid species during the rearing period is a function of the thermal regime in the series of reaches down the river continuum, the availability of thermal refuges (that offer local departures from the continuum), and habitat organization. Habitat organization involves concepts of the quantity/quality of channel units (riffles, pools) and their spatial arrangement. Spatial

relationships among channel units and their component microhabitat units involve length of riffles (benthic insect production units) in relation to length and volume of pools; availability of low velocity marginal areas in riffle channel units; distribution of velocity refuges that provide rearing microhabitats in riffles; gradient, thermal regime, and position in the river continuum of channel units used as rearing areas. Although some of the concepts of habitat organization at the stream system, reach, and channel unit scales have become incorporated into current hierarchical frameworks for stream systems (Frissell et al. 1986, McCullough 1988) many of these theoretical concepts remain as untested hypotheses. However, despite the heuristic appeal of the theoretical concepts, it remains to future field research to evaluate how well this framework, as a whole, or how, in particular, mathematical indices to spatial organization of habitat units within hierarchical levels serve as a tool for predicting fish production potential or mean annual production given a certain level of escapement.

Production of a species on a watershed basis is limited by the current watershed fish carrying capacity (a subset of the long-term carrying capacity, which is a product of the stable features of the watershed (geology, soils, potential natural vegetation) and its environment (regional characteristics, long-term climatic characteristics). Field analysis of fish carrying capacity could involve allowing a known spawning escapement into a watershed each year, carefully monitoring all relevant environmental parameters for key reaches during the rearing period, and monitoring the distribution of fish use in the watershed. By increasing spawning escapement from year to year, the greatest number of juveniles that can be supported could be identified. However, there is variation from year to year in key climatic factors, leading to annual, seasonal, and daily variation in solar radiation and water discharge that could influence production even if the entire stream system or watershed could remain identical from year to year. But there are continual natural developmental changes in a stream system and management related alterations that shift the annual potential for production within the overall limits of the particular watershed. Because it is not possible to predict future climatic events it is not possible to predict annual realized production potential and a maximum rearing density observed in one year may not reflect the potential for the next year.

Production during the spring-summer-fall rearing period can be subject to chance short-term catastrophic events (flood, fire, sedimentation, drought, high air temperature and solar radiation, long duration of high water temperature) that can act as key factors limiting annual production. These factors have low probabilities of occurrence but can occur jointly or in temporal or spatial patterns within a watershed that, in relation to key life history stages, may have varying and unpredictable effects on total fish production. Field determination of a long-term average production capacity would require long-term monitoring of juvenile production given seeding to excess. If a long-term average carrying capacity were determined, annual carrying capacity would then be higher or lower, depending upon the timing and magnitude and intensity of climatic events. Other sources of annual variation exist that may appear to have a random behavior, such as

annual intensity of competition or predation by other species or adult escapement, which can lead to production less than at capacity.

Production is a product of the growth, survival, and initial number of individuals in the population. The initial number results from egg deposition and survival to emergence. Survival from emergence to the fall juvenile rearing stage is a function of rearing capacity in relation to spawning capacity, and in particular to hydrologic events, competition and predation, and thermal regimes. Data on density of a salmonid species before and after a peak flow or drought of a certain magnitude can define percentage survival. Ability to survive a storm is a function of availability of velocity refuges (undercut banks, stream margins or floodplains, boulder shadows, LWD, deep pools, debris jams, riparian root masses along banks). For this reason, it is not enough to correlate peak flow height to survival; rather, the habitat organization of the stream helps determine the capability to buffer losses to population density. Competition among species for a common food supply limits the density or production of a single species. For this reason, it is not possible to study production of one species in isolation without knowing the composition of the rest of the fish community. Competition for space can result in the carrying capacity being reduced from a potential to a realized capacity. For example, the redside shiner-steelhead competition studied by Reeves et al. (1987) resulted in an effective reduction in steelhead carrying capacity, mediated by the current thermal status of the stream. Although many of the factors affecting production of a salmonid species on a watershed basis are poorly known and difficult to model or monitor, the effects of temperature modifications are more amenable to modeling and often temperature is responsible for establishing the pre-conditions for predation stress.

By application solely of temperature criteria, Theurer et al. (1985) were able to estimate the improvement in useable rearing area and the potential increase in spring chinook production achievable from restoration of riparian vegetation and channel morphological structure on the Tucannon River, Washington. They assumed that no chinook production would occur in the mainstem Tucannon River downstream of the point where mean daily temperature for July exceeded 20°C and the mean maximum July water temperature exceeded 23.9°C. Under current conditions the critical temperatures are reached at a point 40 km above the mouth during July, on average. By restoring riparian vegetation and channel structure (decreasing stream width) rearing potential was estimated to increase from 170,000 to 430,000 juvenile chinook by shifting the point where the critical temperature is achieved to the river mouth, thereby opening 40 km of stream to rearing.

As habitat conditions deteriorate and the coldwater plume providing suitable rearing temperatures extends less and less far downstream from the river headwaters, summer rearing salmonid juveniles must migrate upstream to seek suitable temperatures. If migration barriers exist on the mainstem such as falls or high velocity chutes, the ability of these fish to continue to escape incipient lethal temperatures may not exist. Habitat above these barriers to upstream migration of juvenile chinook may

actually be useful for juvenile rearing provided that adults are able to spawn in or upstream of these reaches, thereby seeding these rearing areas with juveniles that may rear in place (i.e., not migrate downstream to reaches below barriers preventing return migration upstream) throughout the summer and fall. Access of adults to spawning areas may be controlled by late spring to autumn discharge (consequently, water depth) during immigration. This may set an upper limit on spawning capacity. Summer baseflow discharge (consequently, wetted area and depth) may also set an upper limit to rearing capacity. Rearing capacity of a stream system is also constrained by the longitudinal profile of the mainstem and its tributaries. Rearing of salmonids generally is restricted to reaches with effective gradient of <4, 5, and 6% for chinook, steelhead, and cutthroat trout, respectively. With potential rearing area defined by the combination of wetted area having suitable depth and gradient, rearing density depends upon availability of food and density of competitors.

CONCLUSIONS

This present work lays an initial framework for identifying key habitat variables and quantifying their effects on salmon survival by specific life stages and identifies areas where knowledge is lacking. Modeling can be an important tool for organizing and synthesizing masses of information into a consistent and meaningful whole. The preliminary models developed in this paper provide an initial approach to developing predictive models and point out the issues involved in developing such models. High priority should be placed on developing a research program that integrates modeling, laboratory experiments, and field experiments.

Streambed fine sediment (surface fine sediment and embeddedness), and water temperature are key habitat variables that determine salmon survival and are highly anthropogenically influenced in the Snake River Basin. The literature base describing effects of fine sediment and water temperature are extensive. Increased fine sediment is a major factor affecting salmon survival in the egg/alevin incubation stage and in the juvenile overwinter rearing life stage. Increased water temperature is also a major factor affecting salmon survival in all freshwater life history stages. We recommend, in the interim, that management focus on these two factors as primary indicators of habitat condition in the Snake River Basin (Rhodes et al. 1994).

The potential for significant biological effects arising from fine sediment and temperature increases can be large under most conventional forest and range management scenarios in the Snake River basin, making application of even this limited portion of the model framework that is currently highly developed a useful tool for estimating minimum level of mortality attributable to habitat condition. By using this modeling routine and with support of sediment and temperature modeling applied at a watershed level, the potential for improvement in carrying capacity (or usable habitat) and survival can be estimated as the difference in carrying capacity/survival under existing conditions and conditions restored to standards.

It is known that most populations of ESA-listed species of salmon in the Snake River basin are steadily declining in numbers. This is a reflection that the numbers of adults in one generation are less than those in the previous generation. Although there are numerous causes for this condition, it is well known that degraded habitat

conditions result in both a reduction in carrying capacity of tributary stream systems and a reduction in survival.

Because many of the factors reducing survival are not always well studied or easily documented, mortality estimates based on sediment and temperature effects will always be less than total habitat-related mortality. Given the uncertainties and gaps in accurately modeling all mortality sources throughout freshwater development, it is not reasonable to use this model in its present form as a tool for attempting to gauge how much habitat degradation can be permitted yet not reduce survival by more than a fixed percentage. Likewise, it is risky to attempt to use land use models (e.g., sediment or temperature models) in an attempt to maximize land disturbance and yet attempt to achieve a habitat target. The combination of setting standards below what is biologically optimum and also using a land management model or BMPs that are assumed to be efficient in achieving a fixed habitat target or a rate of habitat improvement needed to produce a fish production ratio just above 1.0 (i.e., a minimum level habitat improvement that could stabilize a small fish population) is even more risky.

However, even apart from modeling, increases in fine sediment and summer temperature or maintenance of degraded conditions will lead to extirpation, or in the language of ESA, jeopardy. While fine sediment and summer temperature are key variables, any degradation of other key variables, e.g., large wood debris, should be treated as contributing to extirpation.

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FIGURES
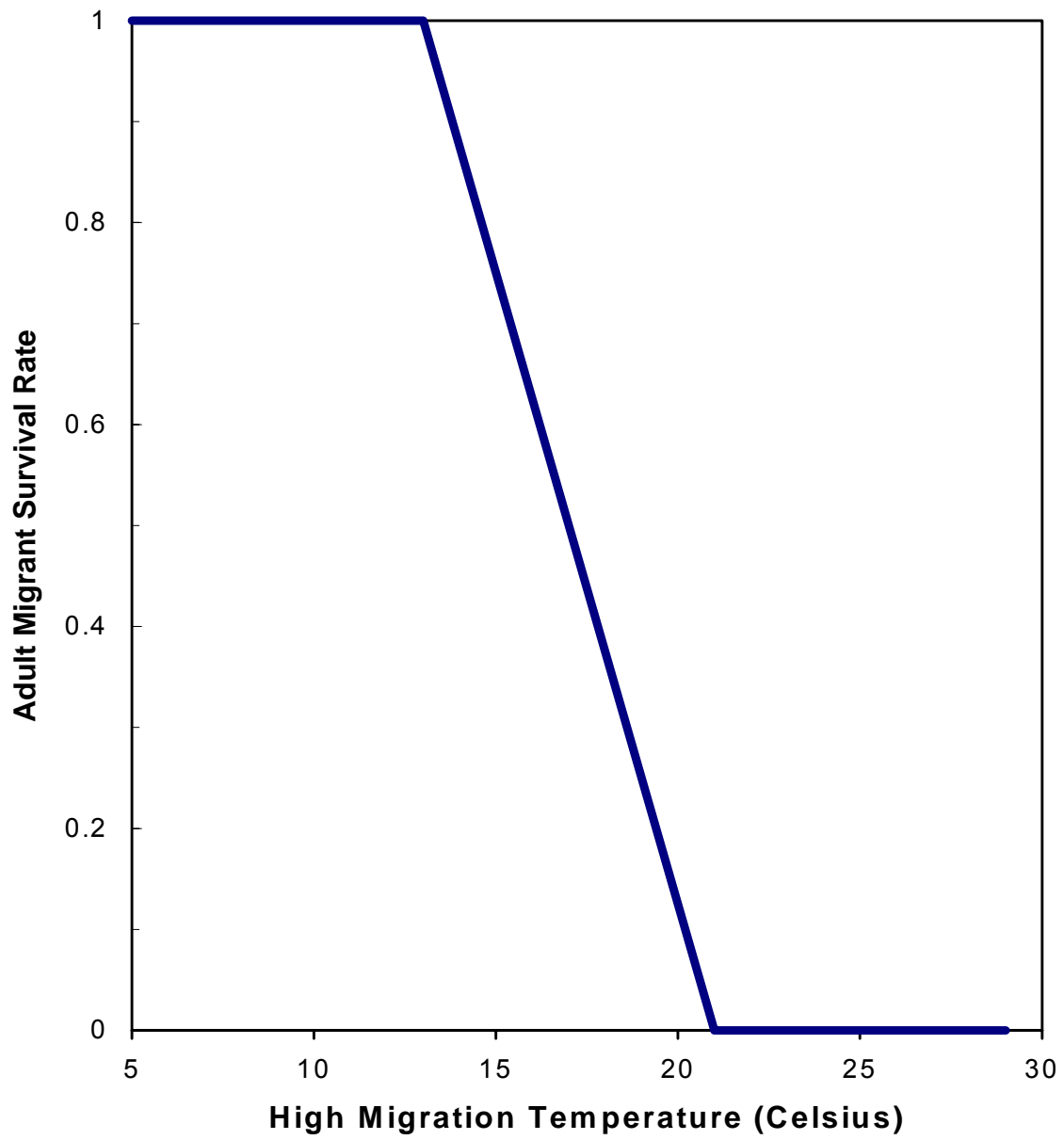
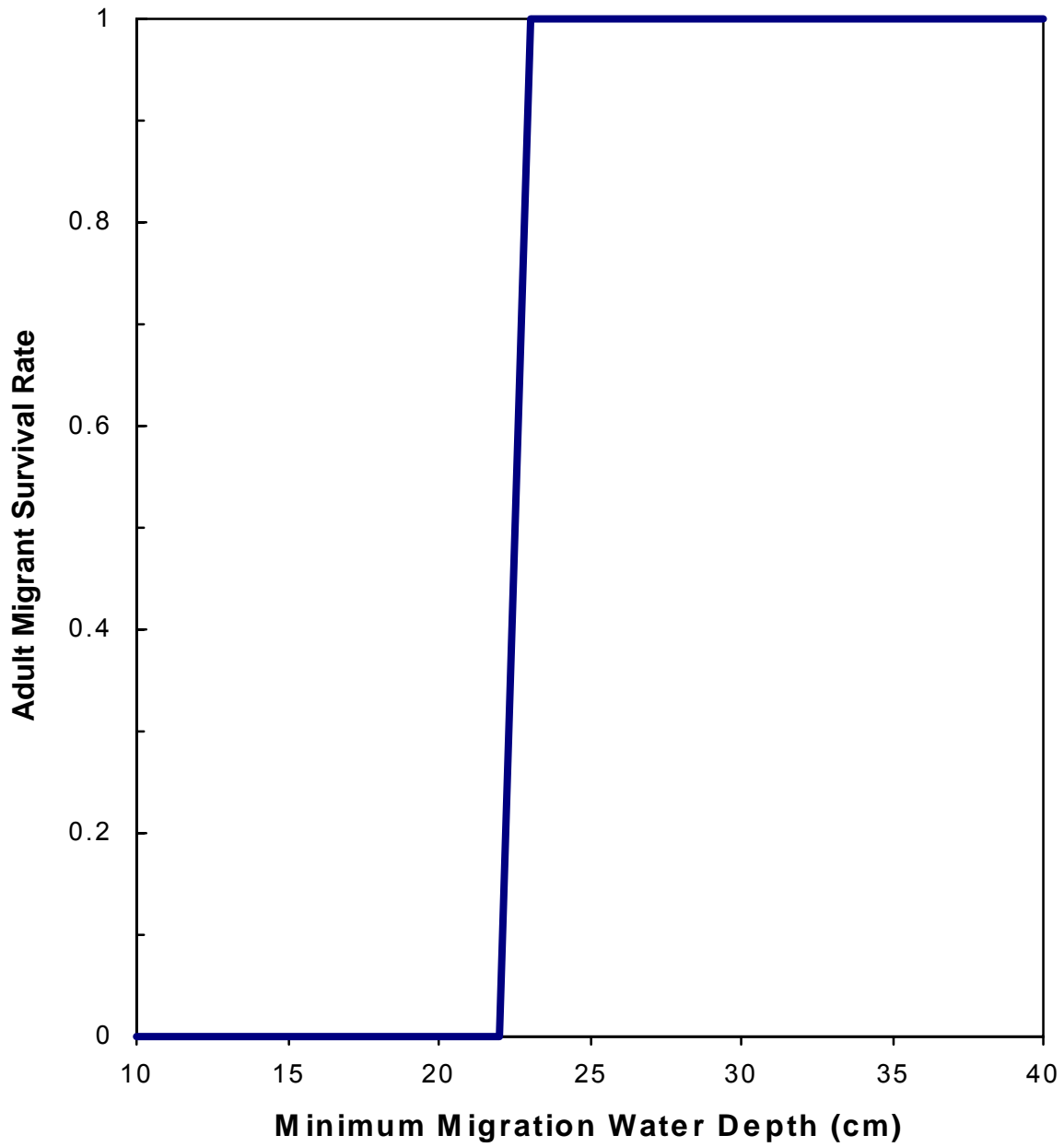Figure 1. Effect of high migration temperatures on survival rate of pre-spawning adults.

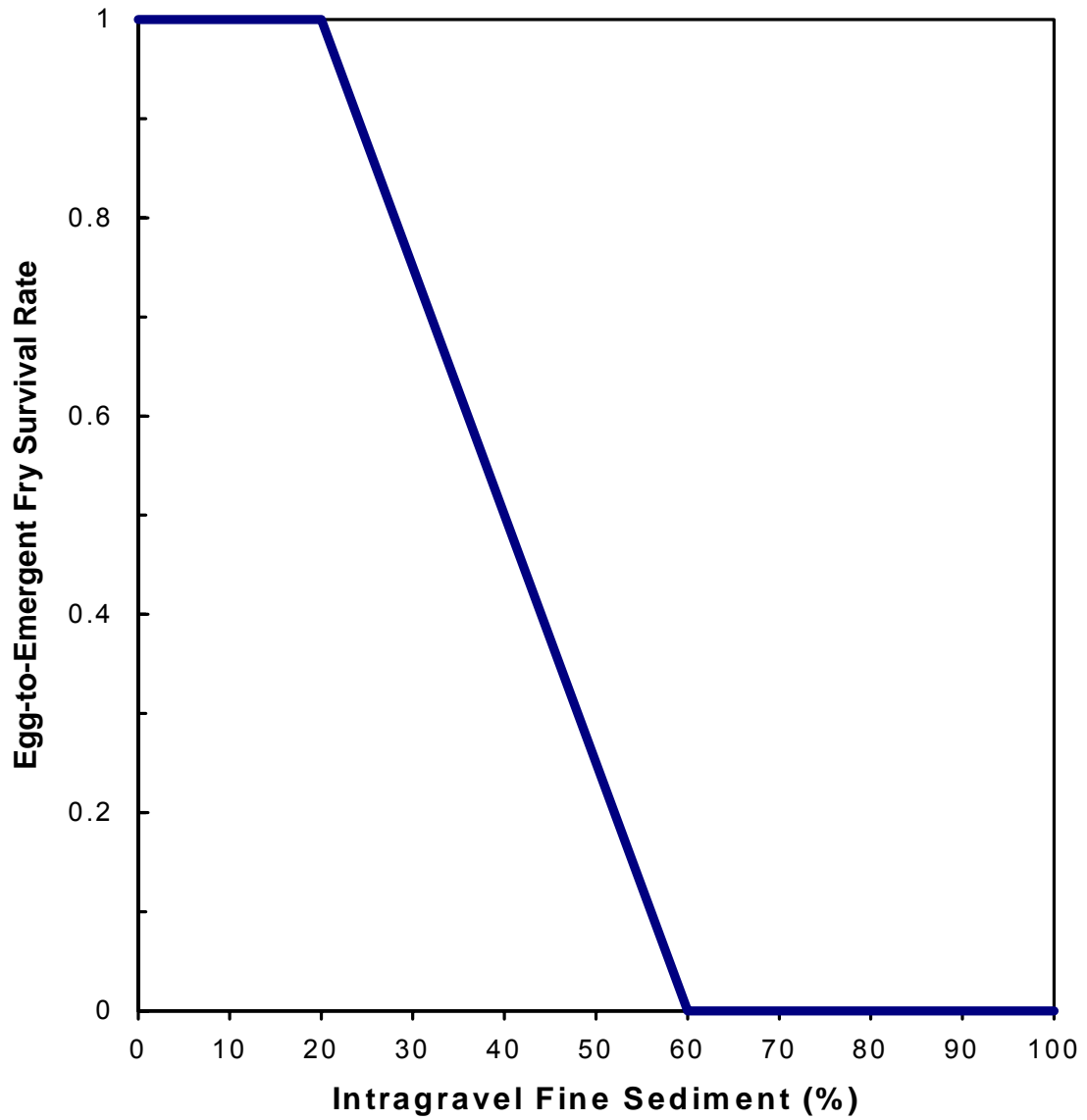Figure 2. Effect of minimum water depth on survival rate of adult migrants.

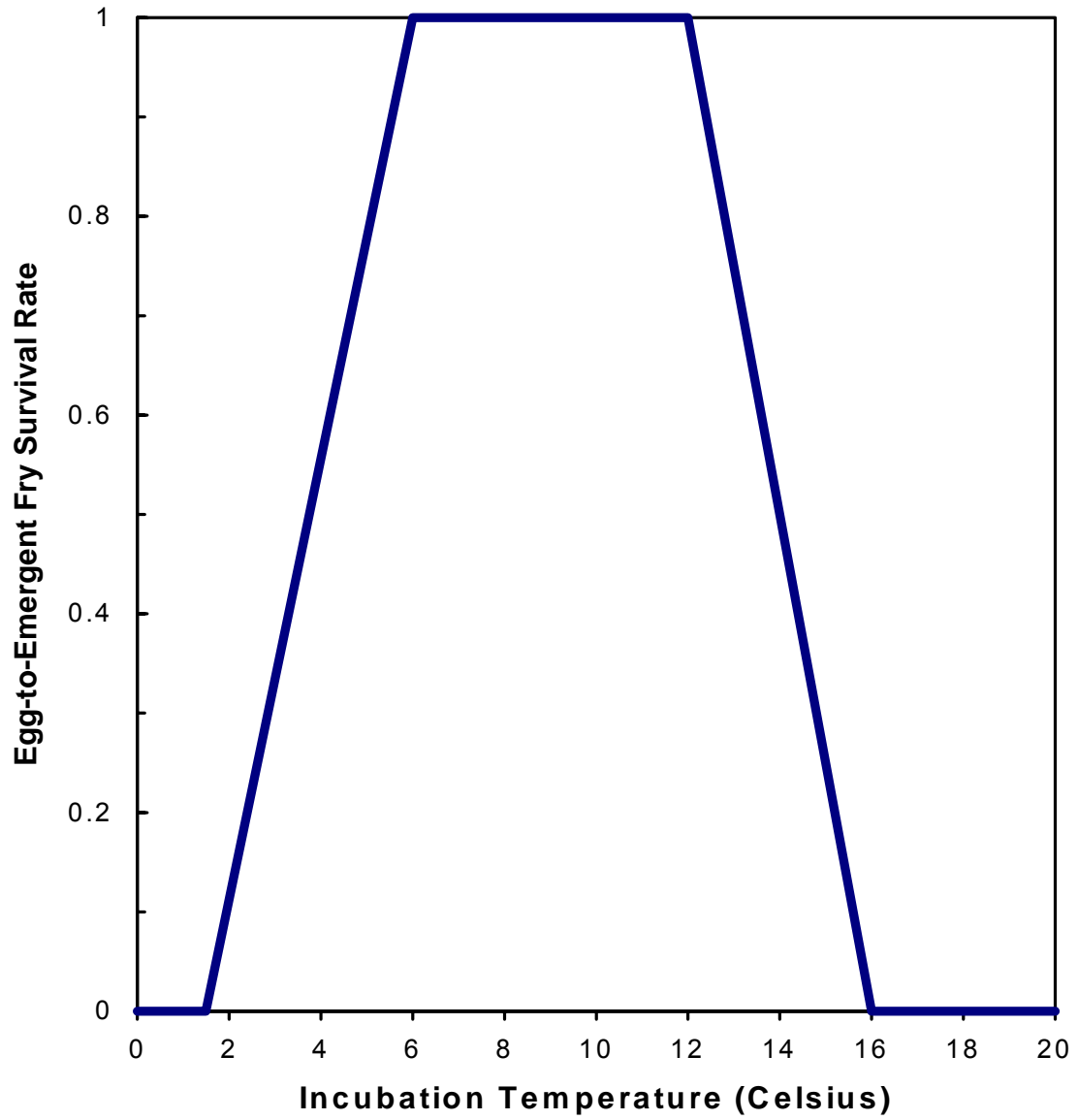Figure 3. Effect of intragravel fine sediment content on survival rate of eggs and alevins.

Figure 4. Effect of incubation temperature on survival rate of eggs and alevins.
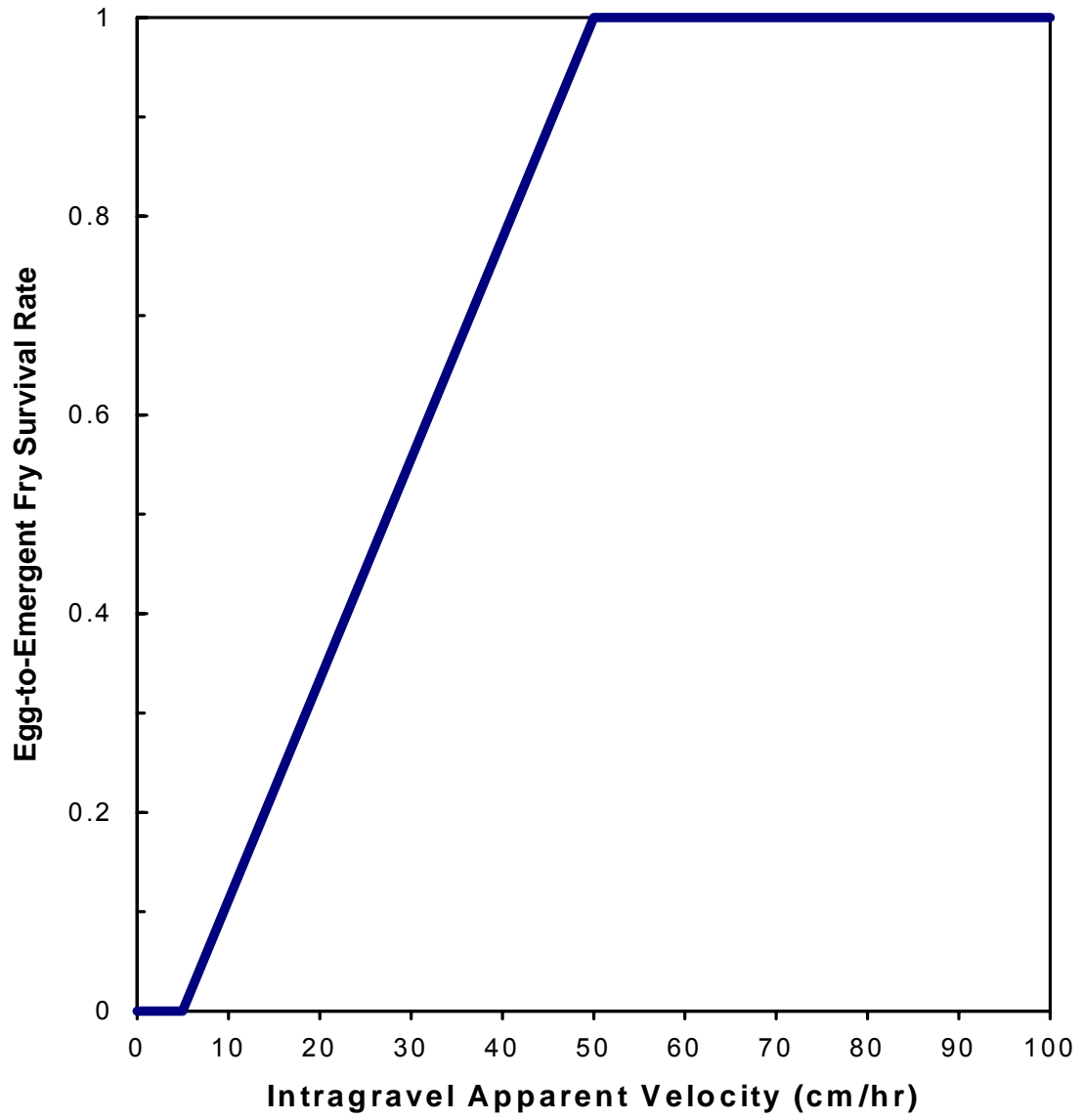
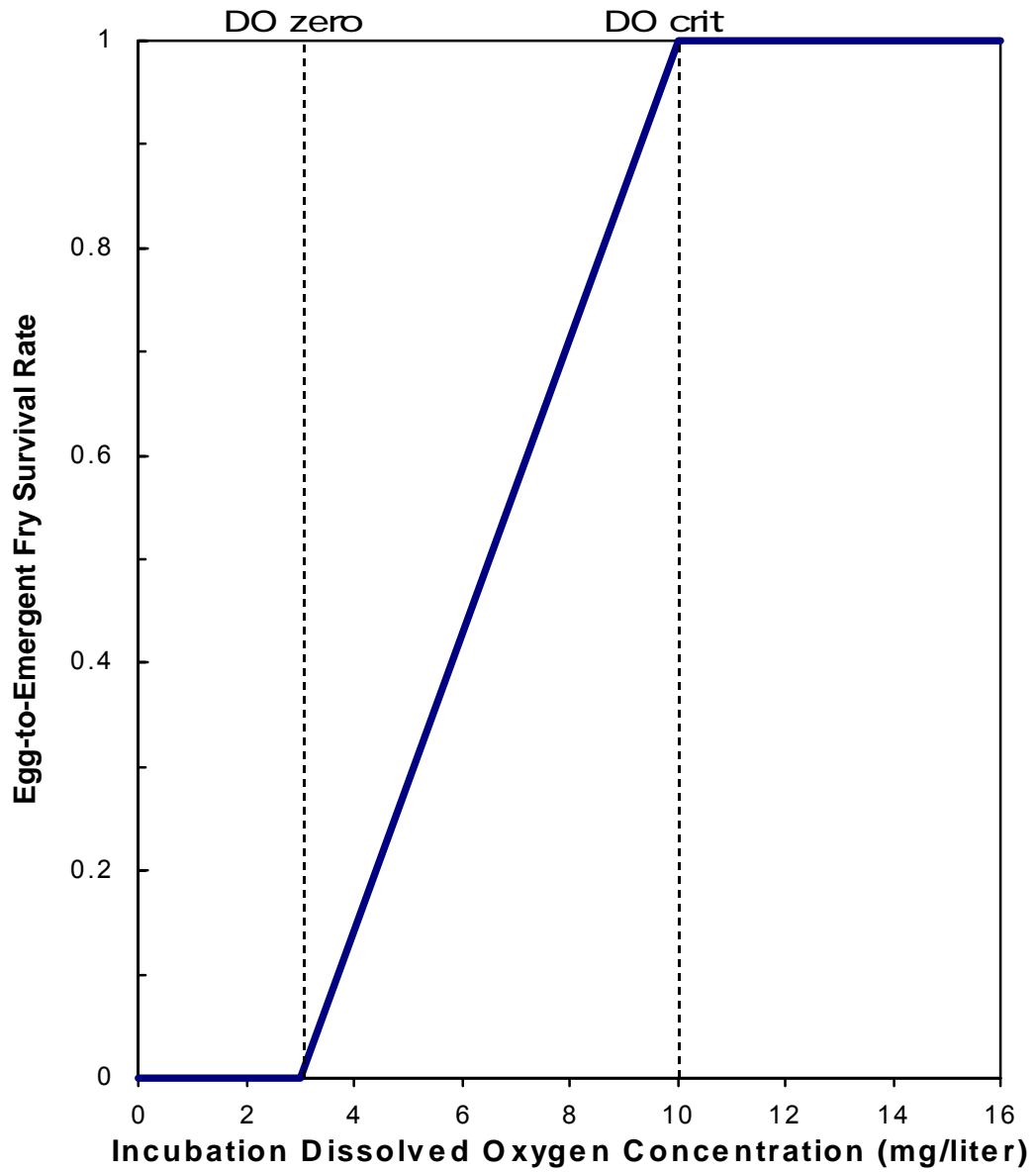Figure 5. Effect of apparent velocity on survival of eggs and alevins.

Figure 6. Effect of high summer temperatures on survival rate of parr.
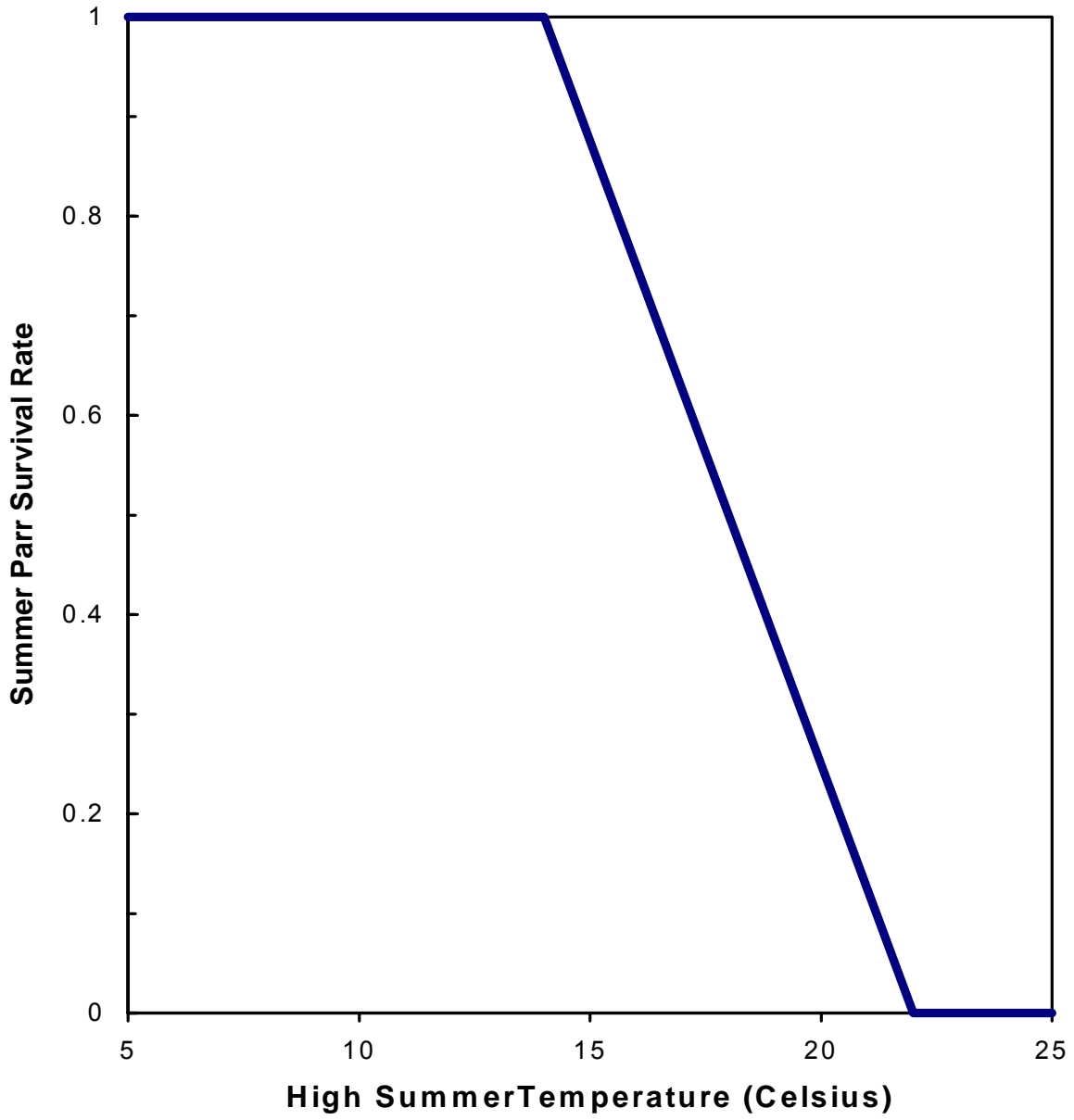
Figure 7. Effect of high summer temperatures on survival rate of parr.
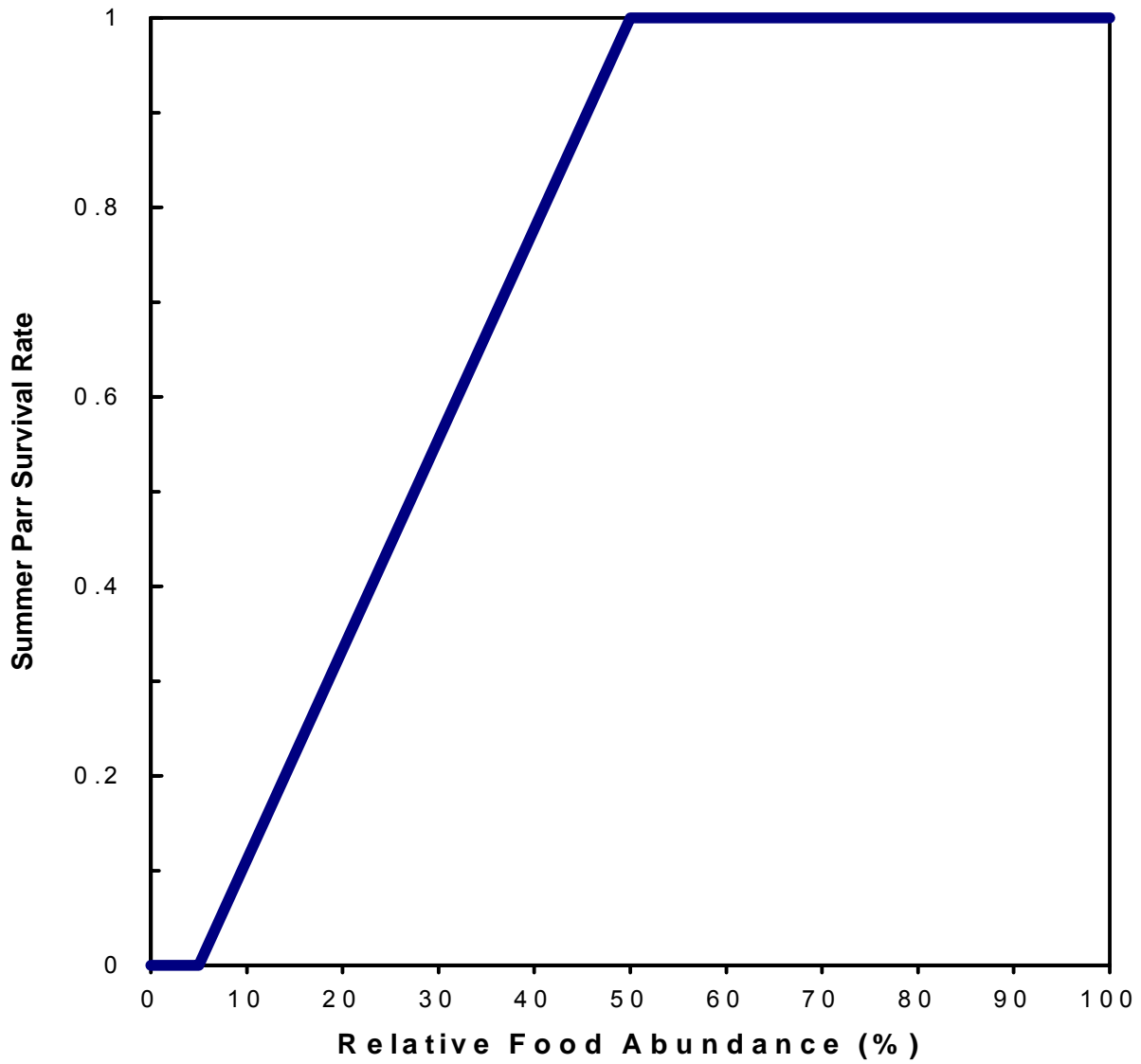
Figure 8. Effect of relative food abundance on survival rate of summer parr.
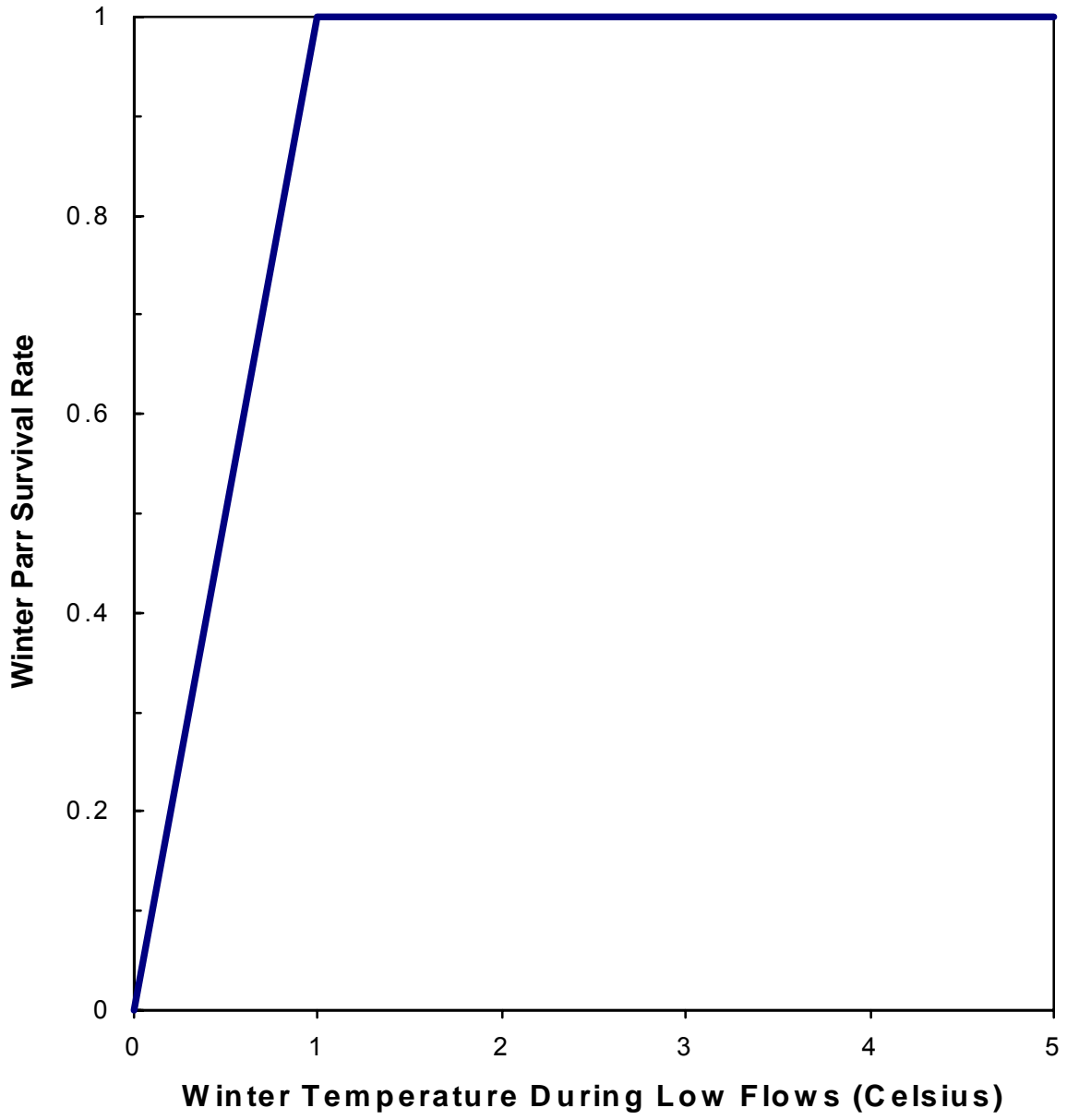
Figure 9. Effect of high migration temperatures on survival rate of smolts.
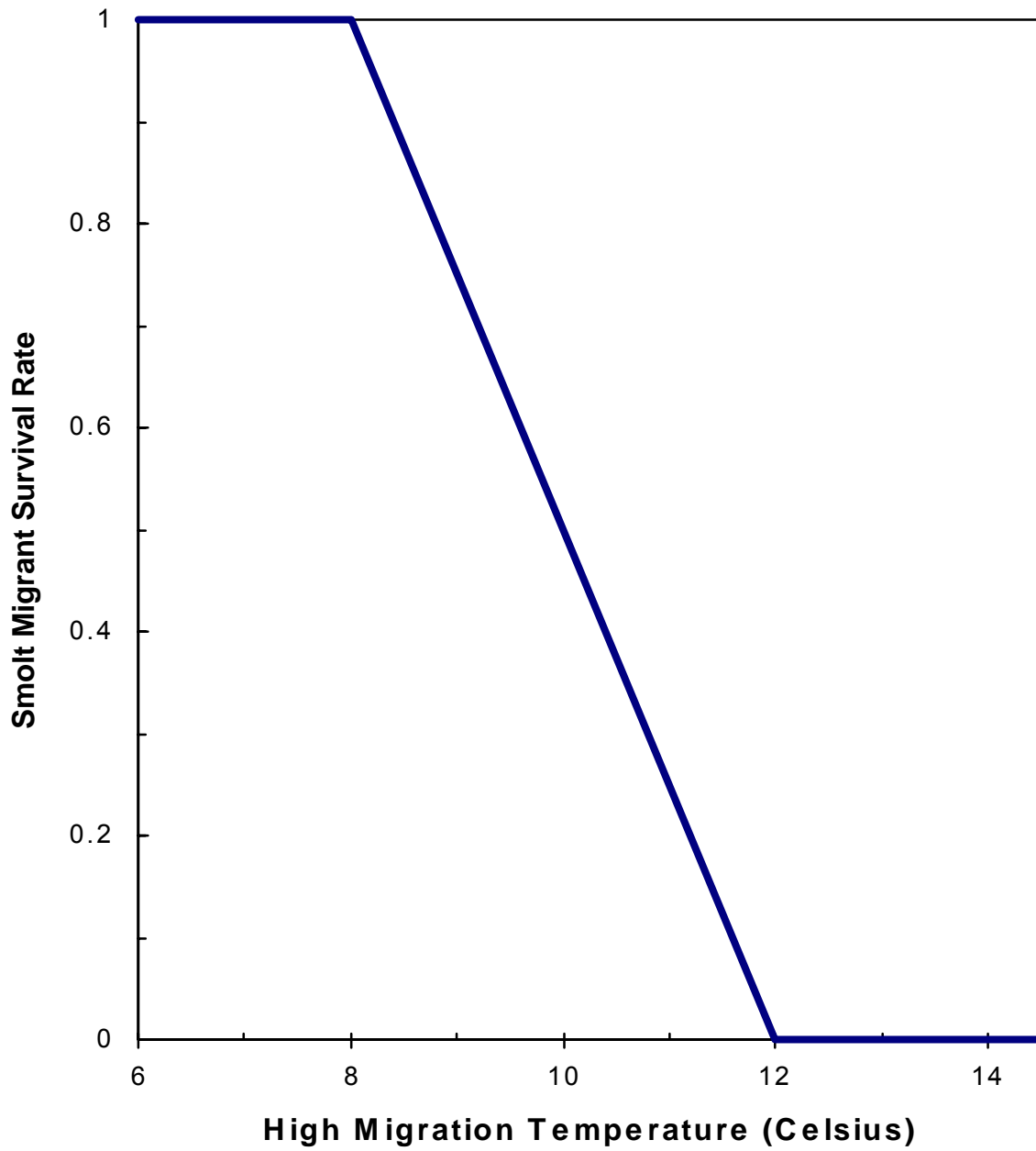
Figure 10. Effect of high migration temperatures on survival rate of smolts.
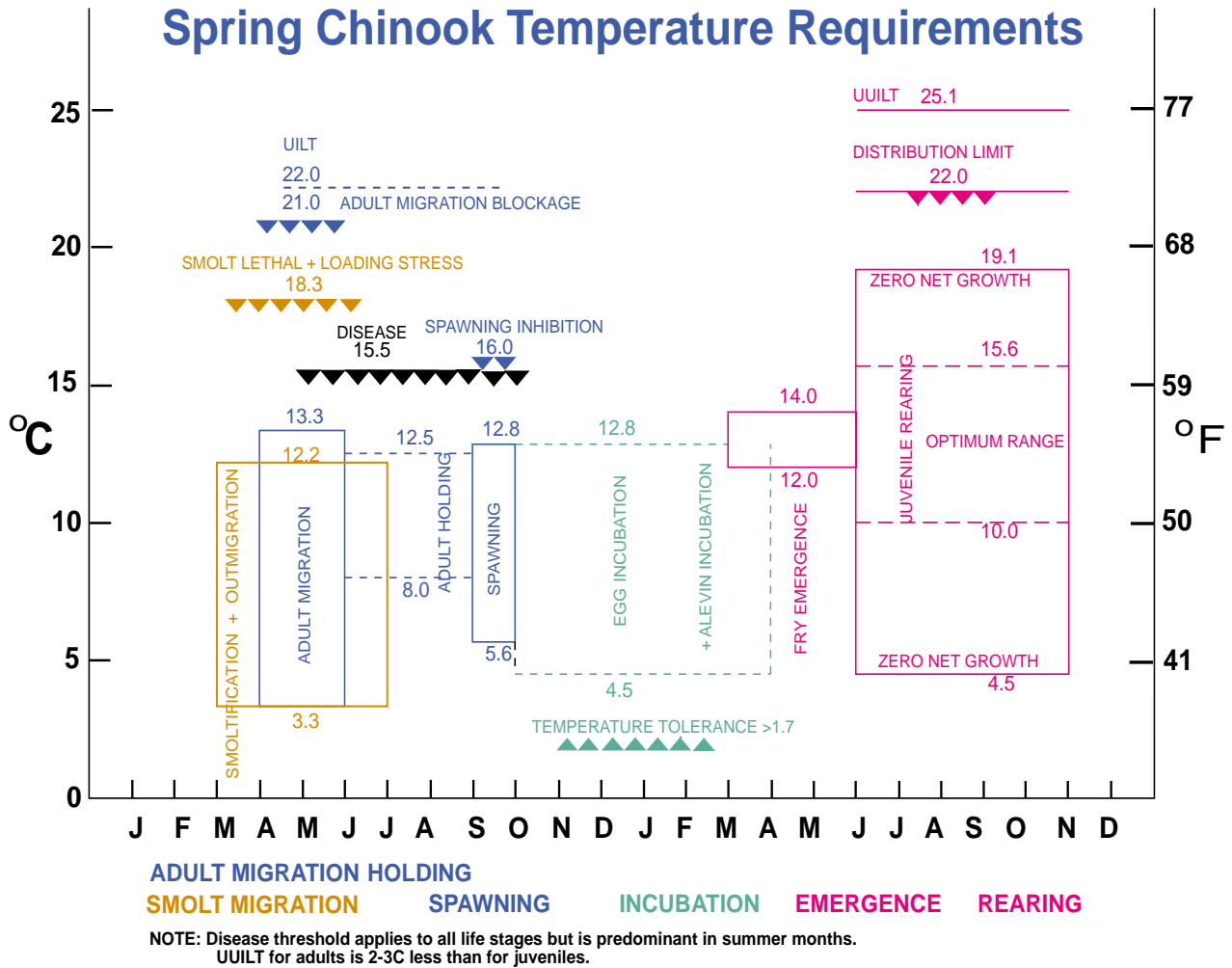
Figure 11. Spring chinook water temperature requirements by lifestage. Although water temperatures in diagram are instantaneous, duration of exposure influences the biologic response of salmon.
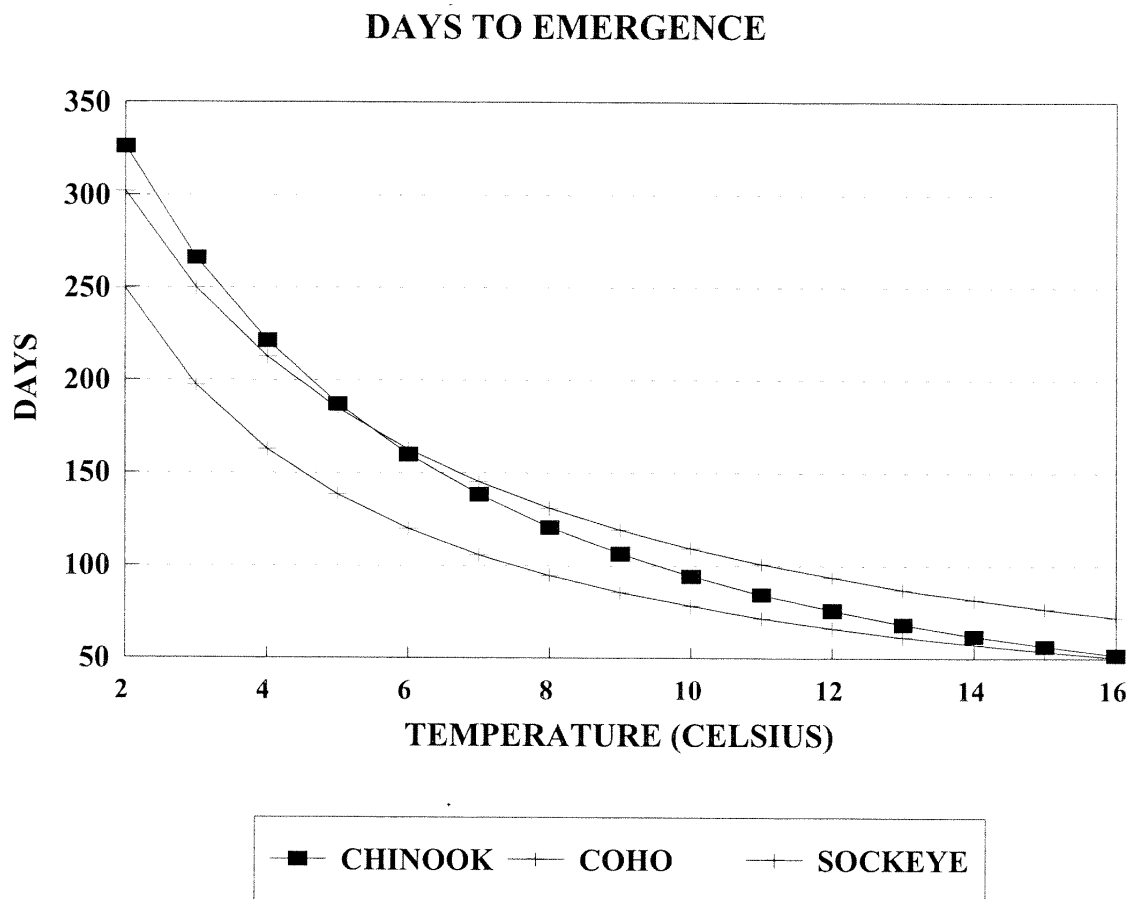
DAYS TO EMERGENCE

Figure 12. Days from fertilization to emergence for chinook, coho, and sockeye salmon calculated from formulas of Beacham and Murray (1990).

REDUCED NO. DAYS TO EMERGENCE
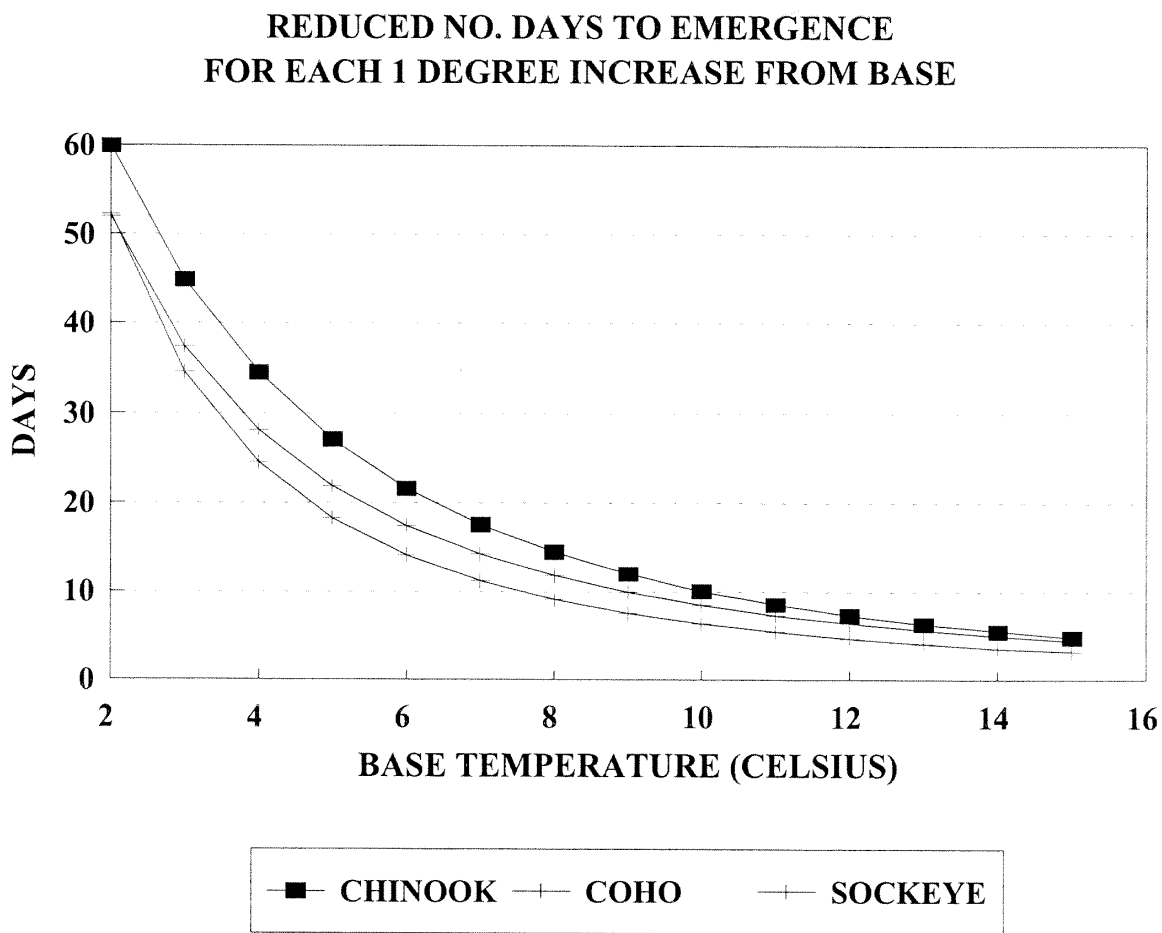## FOR EACH 1 DEGREE INCREASE FROM BASE

Figure 13. Reduction in number of days to emergence for each 1°C increase from a base temperature of 2°C, calculated for chinook, coho, and sockeye from data plotted in Figure 12.